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Marine Animal Forests

The Ecology of Benthic Biodiversity Hotspots

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With 343 Figures and 48 Tables

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Dedicated to

Sergio Rossi*: To my father Fernando, for understanding my devotion on marine biology, and to my mother Placida, for unconditional support*

Lorenzo Bramanti*: In memory of Prof. U. Formentini (zio Ubaldo) who has been an inspiration and a guide*

Andrea Gori*: To my mother Flavia and my father Stefano, for their unconditional love and support*

Covadonga Orejas*: To my parents, Teresa and Enrique, for their love and unconditional support throughout my career, although this support often means accepting physical remoteness and uncertainty*

Marine Animal Forests: Foreword

This volume is a multiauthored compilation of established and recent knowledge on a particular kind of marine epifaunal communities and ecosystems. Having this in mind, readers might be struck by the unusual term “forest” used in this context. Most people connect this term with assemblages of trees on land, with tall trunks and a majestic canopy of branches and leaves as in the case of mahogany trees, oaks, beeches, or sequoias, often with a second canopy of younger trees and bushes underneath. There are also other types of complex architecture of lower tiering in the terrestrial vegetation such as cactus forests, shrubs, savannas, and meadows. They all have in common a three-dimensional structure, their way of energy assimilation, and a function of ecosystem services for other biota.

Transferring this image to the marine realm, one would think first of another type of vegetation: the gigantic kelp forests, which reach similar size, shape, and three-dimensionality and have similar functions for their associated biota. On the faunal side, the largest architecture is performed by scleractinian corals, gorgonians, and sponges. Just as on land, there are many other structures of minor tiering but similar architectural complexity and related functions on the ocean floor, both on the floral and the faunal side. Some of them such as seagrass meadows and mussel banks are fairly well studied, whereas others, particularly in deep or remote regions of the oceans, have remained undetected or have received attention only recently due to the development of new techniques and facilities, often provided by increased international cooperation. For convenience and as a unifying concept, all complex epifaunal shapes and constructions in the sea are assembled under the term “animal forests” in this book, although many coral reefs and gorgonian “forests” resemble shrubland rather than trees, some large scleractinian reefs rather appear like buildings, sponges do not reach tree size and the big ones are not branched, and most of the smaller members of three-dimensional zoobenthic communities are comparable to herbs at best.

“Marine animal forests” (MAF) as understood in this compilation are composed of many epi-zoobenthic taxa and comprise as a common trait their three-dimensional architecture tiering from a few centimeters to tens of meters; if the fossil parts of some coral reefs are included, the height of these structures may even reach hundreds of meters. They occur in all oceans, from the tropics to the poles and from shallow water to the deep sea. Zoobenthic communities with a marked tiering are very old; they date back to the Palaeozoic when stalked crinoids (“sea lilies”) dominated the ocean floors. Irrespective of whether these ecosystems and communities do indeed bear major structural analogies to their terrestrial vegetational counterparts and to three-dimensional plant architecture in the ocean, they definitely reveal analogies in many functions. There are, however, decisive differences in many characters not only between land and sea as well as between animal and plant architects, but also among the various ecosystems and communities presented in this book. For example, as a consequence of very different media (air and water), terrestrial vegetation and MAF differ in energy flow and dispersal opportunities. Tropical reef corals host unicellular primary producers and depend, like kelp and terrestrial vegetation, on sunlight, whereas the Mediterranean coralligenous depends like other MAF systems on the input of allochthonous organic matter.

A wealth of old and recent information on MAF systems has accumulated, which makes a joint presentation and a distinction of common traits and differences worthwhile. In the first chapter, an overview of these findings is presented. The areas from where the information was derived extend over a wide geographical range of seascapes, including tropical shallow-water coral reefs, shallow communities in the Mediterranean and in Mesoamerica, mesophotic coral communities on the continental slope, bathyal cold-water “coral gardens” on Azores seamounts of the Mid-Atlantic Ridge, and other cold-water ecosystems in the deep sea as well as in northern and southern cold-temperate and polar regions. Structuring ecosystem engineers comprise the entire variety of hermatypic and soft corals, notably gorgonians, other cnidarians, sponges, bryozoans, polychaetes, and other taxa which emerge from the seafloor. This elevation signifies improved access to food particles, less siltation and overgrowth, avoidance of shading, improved light conditions, better dispersal of offspring, and (for cnidarians) protection of the fragile polyps. MAF ecosystems are of paramount importance for hydrodynamic and biogeochemical cycles, food webs, and sedimentation levels. Tropical reef corals export nitrogen and organic matter into the surrounding environment and produce and cement carbonate. Many suspension feeders act as carbon sinks, retaining part of the organic matter involved in pelagic-benthic coupling in their long-lived structures. They adapt to changes in seston availability by increased food intake during phytoplankton blooms and consumption of stored food at times of low seston presence. Bivalve filter feeders in shallow waters increase the seston flux due to mixing caused by the exhalant jets from their siphons. There are many more interactions between suspension feeders and their environment presented in this volume, which have to be omitted here for reasons of space.

As a unifying concept, both in the ocean and on land complex structures of key species (“engineers”) usually support high species diversity and density, sometimes also biomass, of associated fauna. These engineers shape their environment, increase habitat heterogeneity, create a multitude of niches and cryptic habitats, and provide food, shelter, and reproductive facilities for an associated mobile fauna. On land, arthropods, birds, reptiles, and mammals are the main users; in the ocean, this fauna consists of a huge variety of invertebrates, many fish, and some other vertebrates.

However, vertical exchange is much more pronounced in the sea: planktonic invertebrates and suprabenthos undergo diel vertical migrations into and out of MAF. Many invertebrates and fish use the “second floor” in these communities as “watchtowers” for improved outlook, greater food availability, and better dispersal of eggs and larvae.

All these properties and services contribute to the ecosystem services provided by MAF to their associated fauna and the entire marine ecosystem. Another important part of these services are those granted to man. Without going into much detail (all these services are mentioned exhaustively in this book) some of the principal human activities using MAF ecosystems include, e.g., fishing (fish, invertebrates, turtles), collecting (precious corals, other corals and seashells, fish and invertebrates for aquaria, species for pharmaceutic and medical use, construction materials), and tourism (diving, sightseeing). They involve occupation and income for many coastal populations and are the basis for many goods, trades, and commercial activities worldwide. Both facets of the ecosystem services provided by MAF represent enormous values, as is stated by one of the authors of this book, although some managers seem to consider only that part which is of direct use to humans.

A second unifying property between terrestrial forest, kelp, and marine animal forest ecosystems is that all of them are exposed to natural perturbations and threatened by human impacts and global climate change (which after all is a human impact as well). Natural disturbances (e.g., hurricanes, floods, occasional warming caused by El Niño) are an innate property of ecosystems, and, as long as they are not frequent or chronic, most ecosystems tend to recover from their effects fairly well. As for forest fires in some terrestrial ecosystems, the medium term effects of some major perturbations on marine ecosystems can even be positive, but continuous disturbance will lead to biodiversity degradation, destruction of complex ecosystem structures, simplification of functions, and loss of ecosystem services. In recent times, anthropogenic impacts have increased enormously: destructive fishing practices, other forms of harmful or exaggerated harvesting, inconsiderate aquaculture, contamination, pollution, eutrophication, oil and gas exploitation, mining, urbanization, and increased use of coastal areas are posing severe threats to many MAF ecosystems. Simultaneously, global warming is proceeding, increasing the sea level, seawater acidity, iceberg scour and the frequency of hurricanes, and worsening the bleaching effects caused by El Niño.

In these days, a compilation of review chapters highlighting the richness and vulnerability of animal structures in the sea is a timely and badly needed venture. This book contains the experience and joint knowledge of a large number of marine scientists who have been involved in one way or another in the exploration, investigation, or conservation of marine epifaunal communities. Their take home message in this volume is: Let us take special care of these ecosystems! Not only to save their commercial services to man, to continue exploiting fish, seafood, and precious corals in the future. There is yet another, innate wealth in these ecosystems: Like terrestrial complex systems, above all tropical rain forests, they are part of nature’s evolutionary and genetic heritage which makes man’s life worthwhile and enjoyable. These ecosystems have taken a very long time to develop from the stalked crinoid assemblages in the Palaeozoic to present times. If we do not take precautions, they might disappear in a few decades, just as some of the kelp forests and coldwater coral reefs which were destroyed by trawling. Probably, not forever – ecosystems tend to recover if they are given sufficient time – but as part of man’s vital environment.

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This book has been one of the main targets of the Sergio Rossi Project ANIMAL FOREST HEALTH (Marie Curie International Outgoing Fellowship Grant Agreement Number 327845). This project inspired the followed line of the manuscript. The main idea was to make a book gathering different views of these complex ecosystems, trying to unify in one idea the benthic ecosytems in which suspension feeders are dominant. Furthermore, this book takes us across latitudes and from coastline to abyssal environments. It shows the ecological significance of megabenthic communities and the vital importance of understanding the complex interconnections between water masses in the oceans of the world. This holistic approach to understanding deep-sea North Atlantic ecosystems is at the heart of the European ATLAS project. ATLAS includes several authors who have contributed to this book. It has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement No 678760. This output reflects only the authors' views, and the European Union cannot be held responsible for any use that may be made of the information contained therein.

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Contents

Volume 1

Volume 2

Volume 3

About the Editors

Sergio Rossi is a research scientist specialized in marine natural resources and biological oceanography. His primary focus is in global change indicators of stress in coastal benthic populations, marine invertebrate distribution, ecology and physiology, benthic-pelagic coupling processes, and marine wildlife conservation. His lines of research are related with marine biodiversity and global change and can be synthesized as: (1) Studying the role of environmental and biological factors of the water column on the distribution, nutritional condition, and survival of benthic organisms to increase the knowledge and tools for coastal management; (2) Studying the physiology and trophic ecology of benthic organisms in warm-temperate, tropical, polar, and upwelling systems; (3) Underwater mapping and distribution of benthic suspension feeders through remote and deep-diving techniques (remotely operated vehicle (ROV)), as a tool for the exploration beyond scuba dive limits (30–40 m); (4) Conservation research on marine biodiversity in marine protected areas and population recovery and resilience, centered mainly on octocorals; and (5) Marine ecosystem services and environmental education, studying aspects of natural ecosystem and resource management, including the vision of the animal forest as carbon sinks and source of biodiversity, but also citizen science using tools or ecological economic and anthropological approaches. During the last 10 years, he has been a senior researcher at the Environmental Science and Technology Institute (ICTA-Universitat Autònoma de Barcelona, Spain). Prior to that, he was at the Institut de Ciències del Mar (ICM-Consejo Superior de Investigaciones Científicas, Spain) for more than 13 years.

Lorenzo Bramanti is a senior researcher at CNRS-LECOB (Observatoire Oceanologique de Banyuls sur mer, France). He obtained his Ph.D. in 2004 at University of Pisa, Italy.

In 2005, he founded a company for environmental consultancy and research (www.seaproject.net), working on marine conservation and public awareness.

In 2007, he worked as postdoctoral researcher on the demography of the Mediterranean red coral (*Corallium rubrum*) at University of Pisa.

In 2009, he moved to ICM-CSIC of Barcelona where he worked, as a Marie Curie postdoctoral fellow, on the ecology and distribution of Mediterranean and on the effects of climate change on their populations, with a focus on gardening techniques for the restoration of *Corallium rubrum*.

In 2012, he obtained a postdoctoral researcher position in the framework of a NSF (National Science Foundation) project at the California State University, Northridge (California, USA), where he worked on the ecophysiology of scleractinian corals at National Museum of Marine Biology and Aquarium (NMMBA) in Taiwan.

In 2013, he joined Université Pierre et Marie Curie (UPMC) at the Observatoire océanologique de Banyuls-sur-Mer (France) as postdoctoral researcher where he worked on population and metapopulation modeling of Mediterranean gorgonians.

In 2014, he obtained a NSF project (Cal State Northridge, California) on the ecology of gorgonians of the US Virgin Islands National Park, and in 2015 he cooperated with Cal State Northridge in the study of climate change effects on the coral reefs of Moorea (French Polynesia).

In 2016, he was hired by CNRS (France) as senior researcher at the Observatoire oceanologique de Banyuls-sur-Mer where he works on the functional ecology of gorgonian canopies both in the Mediterranean Sea and in the Caribbean.

Since 2010, Lorenzo Bramanti works with FAO GFCM (General Fishery Commission for the Mediterranean) in the management and conservation of the Mediterranean red coral and with the UNDP (United Nations Development Program) in the development of marine protected areas in Djibouti (Africa).

The research of Lorenzo Bramanti has always been centered on corals, from individual (ecophysiology, life history traits) to populations (population and metapopulation dynamics modeling) to functional ecology (role of the coral canopies) both on the Mediterranean and the tropics with the main goal to understand the dynamics of the populations and forecast their changes under climate change and human disturbance scenarios.

Andrea Gori The research conducted by Andrea Gori focuses on the study of the ecology and ecophysiology of marine ecosystem engineering species (primarily gorgonians, soft and stony corals) to provide understanding for the sustainable management and conservation of marine ecosystems in shallow and deep areas.

This research is developed following a multidisciplinary approach combining field work and experimental studies. In this sense, his research ranges from the study of taxonomy, spatial distribution patterns of gorgonian and coral abundances, the state of their populations, as well as their energetic state, reproductive and trophic ecology, and ecophysiological processes. By means of the combination of sampling by SCUBA diving and the use of remotely operated vehicles (ROVs) and manned submersibles, benthic species are studied over extensive areas covering their entire spatial distribution, as the best way to achieve a comprehensive understanding of their ecology and the variability of their responses to environmental features and human induced stressors.

Covadonga Orejas is a benthic ecologist, specialized on the study of cold-water corals (CWCs) since more than 20 years. Her main research interests focus on the biology and ecology of benthic communities dominated by those organisms and in general on vulnerable marine ecosystems (VMEs).

She is interested in understanding the spatial distribution patterns of CWCs, linking those with their ecophysiological responses. She carried out most of her research on deep shelf areas in different oceans, from polar to tropical areas, using mostly noninvasive methods and applying her investigations to the conservation of these fragile ecosystems, which are increasingly threatened by multiple anthropogenic activities.

She has developed her research in four different research institutes in Germany and Spain. Since 2009, she is senior researcher of the Spanish Institute of Oceanography (IEO), based in Palma (Mallorca, Spain).

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Animal Forests of the World: An Overview

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Sergio Rossi, Lorenzo Bramanti, Andrea Gori, and
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Abstract

In the marine benthos, megabenthic communities dominated by sessile suspension feeders (such as sponges, corals, and bivalves) form three-dimensional structures which provide architectural complexity and shelter for several species. These communities are, in part, structurally and functionally similar to the terrestrial forests, with the main difference that they are dominated by animals instead of plants. The term "animal forests" has been introduced to describe these communities, highlighting the structural and functional similarities with their terrestrial counterparts trying to gather, in a single concept, all the three-dimensional alive structures dominated by sessile animals. Among the animal forests, tropical coral reefs, due to their high biodiversity, have been defined as the "rainforests of the sea" and have attracted the interest of scientists all over the world. However, during the last decades, many other animal forests have been subjected to the attention of the scientific community; Cold-water coral

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communities, with their key role in ecosystem functioning, fisheries sustainability, and potential carbon sinks in deep benthic ecosystems, are an example of other animal forests that probably cover larger extensions than the tropical shallow coral reefs, but for which the distribution and fully understanding of their functionality are still largely unknown. Similarly, recent technological advances have allowed scientists to explore the mesophotic environment, revealing complex and unknown animal forests in the so-called twilight zone. Gradually, we begin to understand the real extension of these three-dimensional benthic communities and their ecological importance. The animal forests are probably one of the most widely distributed ecosystems on the planet, due to the wide spectra of environments they occupy, from the shallow mussel beds to the tropical and the deepest cold-water coral communities or Antarctic sponge grounds. However, during the last 20 years or so, there has been an increasing evidence of important changes in marine ecosystems due to human-induced disturbances, which are dramatically reducing biodiversity, biomass, and the potential recover of the animal forests all over the world. Many aspects related to the occurrence, distribution, life history, population dynamics, trophic ecology, or physiology of the organisms which structure these communities still need to be understood in order to get an insight into their functional ecology and dynamics. The concept of animal forests imply a holistic approach allowing the pooling of different ecosystems under the same umbrella and possibly lead to a better understanding of their ecological role and the application of effective management and conservation measures.

Keywords

Benthic communities • Filter feeders • Three dimensional architecture • Biodiversity hotspots • Engineering species • Anthropogenic impacts

Contents

1 What Is a Marine Animal Forest?

Forests belong to terrestrial communities and are dominated by trees (Fig. 1a). These ecosystems are complex three-dimensional environments that support high biodiversity, by providing structure, food, and shelter to many other sessile and mobile organisms which establish relationships with both live and dead parts of the trees (see Sasaki and Putz 2009 for updated definitions). These communities may be dominated by a single tree species (e.g., several types of boreal forests) or by several species (e.g., tropical rain forest), depending on the environmental conditions. In marine environments, megabenthic communities dominated by sessile suspension feeders (such as sponges, corals, and bivalves) are capable of generating three-dimensional frameworks with high structural complexity that give shelter to other species. These communities have structural and functional similarities with terrestrial forests, but they are dominated by animals instead of plants. These animal-dominated ecosystems can be described as "animal forests" highlighting the similarities with their terrestrial counterparts (Fig. 1b; Rossi 2013). As terrestrial forests, marine animal forests can also be dominated by a single species (e.g., monospecific mussel beds or sea pen assemblages) or by several species with different morphologies and trophic needs (e.g., tropical coral reefs). Thus, the definition of animal forest includes all the living three-dimensional communities dominated by megabenthic suspension feeders.

The high diversity associated with these animal-dominated communities results from the high heterogeneity in the environmental conditions also induced by these structuring organisms. The term "ecosystem engineer species," coined by Jones et al. (1994) refers to *an organism that directly or indirectly modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials*. Marine ecosystem engineers can modify their surrounding habitat by increasing the structural complexity, changing current flow velocity, with consequent changes of sediment resuspension (Garcia and Duarte 2001), stabilizing the substrate (Eckman et al. 1989), and increasing the local accumulation of suspended particles, enhancing the residence time of food particles inside the canopies they form (Gili and Coma 1998, Guizien and Ghisalberti, ▶ Chap. 18, "Living in the

Fig. 1 Comparison of three-dimensional alive structures: landscape (*above*) and seascape (*below*) structures in tropical areas. (**a**) Coastal forest in Moorea (French Polynesia). (**b**) Underwater gorgonian forest in St. John (US Virgin Islands) (Photo credits: Lorenzo Bramanti)

Canopy of the Animal Forest: Physical and Biogeochemical Aspects", Riisgård and Larsen, ▶ Chap. 28, "Filter-Feeding Zoobenthos and Hydrodynamics"). Complex biogeochemical cycles (nutrient release, particle retention, carbon fixation, etc.) take place in these animal forests, in which the input and output of inorganic and organic matter may have a remarkable impact on the near-bottom seston (e.g., phytoplankton productivity, zooplankton feeding, particle retention, and recycling, Rossi and Gili 2009, Huguet, ▶ Chap. 26, "Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles").

2 Marine Animal Forests Through Depths and Latitudes

Animal forests are distributed worldwide, ranging from tropical (e.g., Jordán-Dahlgren and Reyes-Bonilla, ▶ Chap. 2, "Caribbean Coral Reefs: Past, Present, and Insights into the Future"; Soares et al. this volume) to polar latitudes (e.g., Arntz et al. 1994; Gutt et al., ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" this volume). They are present in warm and temperate waters (e.g., Kleypas et al. 1999; Gori et al., ▶ Chap. 7, "Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea"; Boudouresque et al., ▶ Chap. 13, "Where Seaweed Forests Meet Animal Forests: the Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem") as well as in cold waters (e.g., Montiel and Cárdenas, ▶ Chap. 9, "Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes" this volume; Försterra et al., ▶ Chap. 10, "Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters" this volume; Gutt et al., ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" this volume; Henry and Roberts, ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume; Buhl-Mortensen et al., ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems" this volume; Mortensen and Buhl-Mortensen 2004; Roberts et al. 2009). Marine animal forests also thrive from shallow (e.g., McClanahan and Obura 1997; Oliveira Soares et al., ▶ Chap. 3, "Brazilian Marine Animal Forests: A New World to Discover in the Southwestern Atlantic" this volume; Montiel and Cárdenas, ▶ Chap. 9, "Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes" this volume) or even intertidal (e.g., Milazzo et al., ▶ Chap. 12, "Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean" this volume) to deep-sea zones (e.g., Orejas et al. 2009; Bo et al. 2015; Buhl-Mortensen et al., ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems"). The topography and characteristics of the seafloor and the environmental conditions of the surrounding water masses are usually the main factors boosting the presence of different animal forests. However, historical settlement (i.e., the ecological succession of the community, driven by perturbations or the dominance of one species, Margalef 1998), as well as the capability of different species to resist and recover from perturbations, are also key determinants of the composition and distribution of animal forests (Bramanti and Edmunds 2016).

In warm oligotrophic tropical waters, with strong light penetration, tropical coral reefs dominate. In these ecosystems, light is the main driver of species distribution, due to the symbiotic relationship between microscopic algae (mainly the dinoflagellate *Symbiodinium* spp.) and their hosts, which is an extremely efficient mechanism for the optimization of light harvesting (Enríquez et al. 2005; Schubert et al., ▶ Chap. 31, "Symbiotic Versus Nonsymbiotic Octocorals: Physiological and Ecological Implications" this volume). This is the case for several scleractinians, gorgonians, sponges, and other animals. Tropical coral reefs are among the most productive and diverse ecosystems on earth (Connell 1978), being mostly confined to regions which experience a narrow and stable range of environmental conditions, such as temperature, salinity, light penetration, and nutrients concentration (Kleypas et al. 1999). The three-dimensional hard structure of the reef is mainly built up by scleractinian symbiotic corals (Fig. 2) (Fabricius and De'ath 2008; Jordán-Dahlgren and Reyes-Bonilla, ▶ Chap. 2, "Caribbean Coral Reefs: Past, Present, and Insights into the Future" this volume), but octocorals and sponges are also important components (Fig. 3) (Lenz et al. 2015; Maldonado et al., ▶ Chap. 5, "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns" this volume; Sánchez, ▶ Chap. 4, "Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America" this volume).

Corals do not only dominate in shallow warm oligotrophic waters. Indeed, cold-water coral (CWC) reefs are comparable to their tropical counterpart in terms of structural and functional complexity and are widely distributed in the world oceans, mostly at 200–1500 m depth (Roberts et al. 2006; Roberts 2009; Henry and Roberts, ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume; Buhl-Mortensen et al., ▶ Chap. 32, "Trophic Ecology and

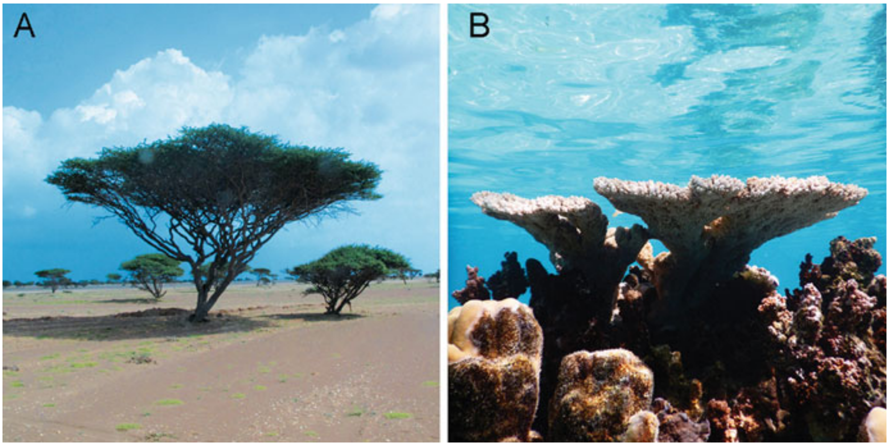

Fig. 2 Three-dimensional morphological convergence. (**A**) *Acacia* sp. in the Afar desert (Djibouti). (**B**) *Acropora* sp. in Moorea (French Polynesia) (Photo credits: Lorenzo Bramanti)

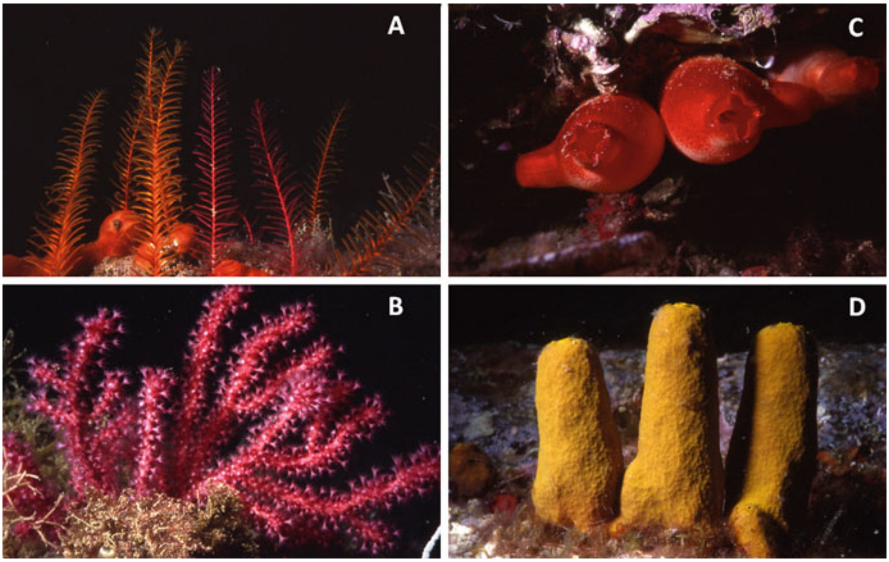

Fig. 3 Different structures and different complexity in some Mediterranean suspension feeders. (**A**) Crinoids (*Antedon mediterraneum*), (**B**) gorgonian (*Paramuricea clavata*), (**C**) ascidians (*Halocynthia papillosa*), and (**D**) sponges (*Aplysina aerophoba*) (Photo credits: Sergio Rossi)

Habitat Provision in Cold-Water Coral Ecosystems" this volume). CWC occurrence seems to be mainly driven by temperature (from ~4 °C to ~14 °C) and hydrodynamic conditions, like the presence of intermediate and deep-water masses that supply food, rather than by depth *per se* (Buhl-Mortensen et al. 2010; Buhl-Mortensen et al., ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems" this volume; Roberts et al. 2006). CWC lacks symbiotic zooxanthellae, and their energy input relies completely on heterotrophic feeding. Although CWC reefs have been discovered in the eighteenth century, it is mostly due to the technological advances of the last decades that knowledge on distribution, biology, and ecology of CWC has been significantly improved. Visual nondestructive methods based on the use of photographic cameras, sledges, remotely operated or autonomous vehicles (ROVs and AUVs, respectively), landers, and manned submersibles enable quantitative observation and sampling of these hidden reefs to be performed (Roberts et al. 2006, 2009), in the topographic features (e.g., sea mounts and submarine canyons) on which they have developed since ancient times (Henry and Roberts, ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume; Orejas and Jiménez, ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume; Wienberg and Titschack, ▶ Chap. 25, "Framework-Forming Scleractinian Cold-Water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective" this volume). Both tropical and CWC (both shallow and deep waters) ecosystems are among the most widely distributed animal forests of the world, with the Australian Great Barrier Reef and the Norwegian CWC reefs being paramount examples.

In temperate seas, gorgonians, sponges, and bryozoans may form dense forests in shallow coastal areas (Linares et al. 2008), as well as on the continental shelf and slope (Boudouresque et al., ▶ Chap. 13, "Where Seaweed Forests Meet Animal Forests: the Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem" this volume; Gori et al., ▶ Chap. 7, "Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea" this volume). The species composition of the forest may depend on the type of substrate and on the productivity of the system (Montiel and Cárdenas, ▶ Chap. 9, "Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes" this volume; Försterra et al., ▶ Chap. 10, "Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters" this volume). In several Mediterranean coastal communities, gorgonians can form monospecific forests that support highly structured and diverse associated fauna (Ballesteros 2006; Gori et al. 2011). In these shallow seasonal habitats, species distribution and life cycles as well as population dynamics and resilience are tightly related to environmental conditions, water column primary productivity and stratification, and by the hydrodynamics (Rossi et al., ▶ Chap. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests" this volume; Viladrich et al. 2016). Conversely, multispecific dense assemblages of gorgonians occur on the rocky areas of the continental shelf edge (Cau et al. 2015; Grinyò et al. 2016; Gori et al., ▶ Chap. 7, "Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea" this volume) as well as on the top of seamounts (Bo et al. 2011), under more stable environmental conditions (Bo et al. 2011; Cau et al. 2015; Grinyò et al. 2016).

At polar latitudes, for instance in the Antarctica, benthic suspension feeders, such as sponges, gorgonians, and bryozoans, dominate benthic communities in several zones. Indeed, despite the extreme environmental conditions of Antarctic waters (e.g., very low seawater temperatures, ice coverage, and complete darkness during several months over the year), these communities display high biomass and species diversity (Clarke and Johnston 2003), which makes Antarctic biodiversity on the continental shelf comparable with temperate and nontropical reefs (Clarke 2008; Gutt et al., ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" this volume) other important examples of animal forests are the assemblages dominated by bivalves (e.g., oysters or mussel beds), which are distributed almost everywhere. Submarine caves or abyssal planes can also harbor animal forests dominated by benthic suspension feeders, mainly occurring as communities in conspicuous, but scattered patches.

When defining the marine animal forests, we consider different levels of canopy/height, density, and diversity. Forests dominated by scleractinians, gorgonians, or large erect or massive sponges may be compared to truly terrestrial forests (which are by definition, dominated by trees). We used the term "forest" also for assemblages dominated by bivalves, bryozoans, sea pens, ascidians, or hydrozoans, which, due to their smaller dimensions (in most of the cases), could be more correctly compared with shrubby formations or even grasslands. As it occurs in terrestrial ecosystems, light irradiation and supply of resources can be different at different vertical levels of highly populated marine animal forests (Orejas and Jiménez, ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume; Riisgård and Larsen, ▶ Chap. 28, "Filter-Feeding Zoobenthos and Hydrodynamics" this volume; Rossi et al., ▶ Chap. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests" this volume), and canopy height and density are key factors to understand those vertical gradients. Diversity in a Caribbean coral reef dominated by gorgonians and scleractinians can be comparable to the diversity in a rain forest, whereas the boreal forests, frequently dominated by a single tree species, may be comparable to mussel beds, which are also frequently monospecific.

3 The Main Components of the Marine Animal Forests

The complexity of an animal forest depends on the structuring organisms. Indeed, coral reefs and sponge grounds can form highly complex and diverse three-dimensional structures, influencing hydrodynamics and supplying shelter and food to highly diverse associated fauna (Fig. 4). The most ancient animal forests were probably formed by the extinct group of *Rangeomorpha* which presented canopies of up to 2 m height in the precambrian oceans (Ghisalberti et al. 2014; Guizien and Ghisalberti, ▶ Chap. 18, "Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects" this volume).

Fig. 4 Epibiosis as an example of the complex interactions between different sessile organisms in the animal forest. The main structure (sponge, gorgonian, coral, etc.) may be the perfect substrate for other sessile organisms that take advantage of the three-dimensional structure of its host. (**a**) Gorgonian (*Paramuricea clavata*) with an epibiotic bivalve; (**b**) sponge (*Axinella damicornis*) with a zoanthid living between the folded structures (*Parazoanthus axinellae*); (**c**) White gorgonian (*Eunicella singularis*) completely covered by the alcyonarian *Alcyonium coralloides* (pink-yellow) (Photo credits: Sergio Rossi)

3.1 Sponges

Sponges were one of the first metazoans to form animal forests (Maldonado et al., ▶ Chap. 5, "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns" this volume). These organisms are present at all latitudes and depths, being common members of many marine benthic communities. In some cases, sponges can generate complex three-dimensional aggregations, which end up dominating the community (Gutt et al., ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" this volume; Maldonado et al., ▶ Chap. 5, "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns" this volume). The distribution of sponges, and their dominance in many ecosystems, is driven both by physical and biological factors, with depth, substrate type, and current regimes being among the most important (Bell 2008). Sponges, as active suspension feeders, play an important role in biogeochemical cycles, generating a flux of matter and energy from the pelagic to the benthic systems and vice versa (Reiswig 1971; Bell 2008; Coppari et al. 2016).

3.2 Cnidarians

The most studied group of marine ecosystem engineers are the scleractinian corals, which are the main builders of tropical and CWC reefs (Jordán-Dahlgren and Reyes-Bonilla, ▶ Chap. 2, "Caribbean Coral Reefs: Past, Present, and Insights into the Future" this volume; Orejas and Jiménez, ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume; Henry and Roberts, ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume). The three-dimensional structure of these organisms is based on their modular (clonal) growth, which has the polyp as the basic unit (Lartaud et al., ▶ Chap. 22, "Growth Patterns in Long-Lived Coral Species" this volume). Polyps are connected through the coenenchyme and are responsible for food uptake, metabolic processes, and reproduction. A similar modular growth of thousands of polyps takes place in gorgonians and black coral colonies, which can reach sizes as large as many scleractinian species, but with a protein-flexible axial skeleton (Sánchez, ▶ Chap. 4, "Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America" this volume). Most scleractinians, gorgonians, and antipatharians are fairly long-lived organisms that in some cases can exceed the age of 4000 years (e.g., black corals, Roark et al. 2006). Conversely, hydrozoans are fast growing species with marked seasonal cycles, generating patches with variable densities (Gili and Hughes 1995; Di Camillo et al., ▶ Chap. 14, "Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests" this volume).

Fig. 5 Active and passive suspension feeders. On the *left*, the active suspension feeder *Mytilus galloprovincialis* and the passive suspension feeder *Actinia equina*; on the *right*, the anthozoan the Parazoanthus image is distorted, a passive suspension feeder who depend on the currents to feed (Photo credits: Sergio Rossi)

3.3 Bryozoans, Ascidians, Polychaetes, and Bivalves

Bryozoans, ascidians, polychaetes, and bivalves can also form three-dimensional structures, building highly structured and dense communities (e.g., Försterra et al., ▶ Chap. 10, "Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters" this volume; Milazzo et al., ▶ Chap. 12, "Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean" this volume; Riisgård and Larsen, ▶ Chap. 28, "Filter-Feeding Zoobenthos and Hydrodynamics" this volume; Wood et al. 2012). Bryozoans are also clonal organisms with remarkable presence in some animal forests. They are more commonly distributed in warm- and cold-temperate seas, while their presence is scarce in tropical areas. Polar regions also have a significant presence of bryozoans (Wood et al. 2012). Ascidians can be solitary or colonial, whereas polychaetes and bivalves always occur in solitary form (or in some cases semicolonial forms). They can form massive three-dimensional structures, capable of modifying the near-bottom hydrodynamism. All of them are active suspension feeders, which may act as controllers of phytoplankton production (Riisgård and Larsen, ▶ Chap. 28, "Filter-Feeding Zoobenthos and Hydrodynamics" this volume) (Fig. 5).

4 Ecosystem Functions and Effects of Anthropogenic Impacts on the Animal Forests

Marine animal forests evoke images of beauty and biodiversity. However, tropical and CWC reefs or sponge grounds and all the previously mentioned different types of animal forests not only form beautiful seascapes, but they are in many cases biodiversity hotspots playing a paramount role in the functionality of the oceans and consequently in the welfare of human populations. Tropical coral reefs, for instance, provide food and leisure to human communities living in tropical coastal areas and contribute to dampening the effects of storms and hurricanes, dissipating up to 86% of the wave energy (Ferraio et al. 2014). Consequently, the destruction of coral reefs can have a dramatic impact both on the ecosystem (affecting the associated organisms and the biogeochemical cycles) and on the socioeconomical system (e.g., destruction of seascapes with cultural or spiritual value or depauperation of economically valuable species). Moreover, since ecosystems are highly interdependent on each other, the health of coral reefs is also directly related to the health of mangroves (Arias-González et al., ► Chap. 42, "The Animal Forest and Its Socio-ecological Connections to Land and Coastal Ecosystems" this volume; Polidoro et al. 2010), and the damages to one of the two ecosystems will impact the other. This relationship is still poorly understood, and increasing the knowledge in the connectivity (physical and functional) of the systems will be a key aspect to contributing to maintaining the productivity and biodiversity (Arias-González et al., ► Chap. 42, "The Animal Forest and Its Socio-ecological Connections to Land and Coastal Ecosystems" this volume).

Unfortunately, sustainable management and conservation of these systems is a challenging issue, well reflected in the "tragedy of the commons" (Hardin 1968). The lack of knowledge, as well as the perception of property that stakeholders have of the "ecosystem services," is especially problematic in the ocean, where boundaries and property are less clear than on land and where people have a less conscious perception of the impact of their actions. Several considerations that seem obvious in landscape conservation are not applied in seascape conservation, because the concept of property is better known and regulated in terrestrial ecosystems with respect to coastal and offshore areas (Rice 2011; Rice and Smith, ► Chap. 34, "Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest" this volume). This is even more dramatic in open ocean areas (but see Aguilar et al., ► Chap. 41, "Conservation and Management of Vulnerable Marine Benthic Ecosystems" this volume), and the extension of many benthic communities is in rapid decline. Despite the important advances in the scientific understanding on the interactions between marine ecosystems and human populations, and the improvement of management and conservation efforts at small and large spatial scales, the communities living on the ocean seafloor are rapidly changing, shifting from highly resilient complex structures to much more simplified communities (Bianchi et al., ► Chap. 43, "Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998" this volume; Rossi 2013).

Well-developed and structured animal forests can play an important role in carbon retention (Rossi et al., ► Chap. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests" this volume), which in ecosystems dominated by plants is known as "carbon sink." Despite their extension all over the world, the knowledge of the carbon retained in marine benthic ecosystems is basically limited to coral reefs (which are estimated to be a sink for 111 million tons of carbon per year, Kinsey and Hopley 1991). There is a much higher amount of information on the role of terrestrial forests as carbon sinks (Le Quéré et al. 2015); for example, the Amazonian forest can retain 1.02 t C ha^{-1} $year^{-1}$ (Grace et al. 1995) and coastal marine phanerogams up to 6.7 t C ha^{-1} $year^{-1}$ (Duarte et al. 2010), demonstrating that the loss of seagrass coverage may diminish the carbon retention capability of the ocean (Marbà et al. 2015). However, the amount of carbon retained by the great majority of marine animal forests is relatively unknown (Laffoley and Grimsdich 2009), as well as its possible decline due to the decrease in their complexity and maturity (Rossi 2013). For example, the decrease in coral calcification in the Great Barrier Reef (De'ath et al. 2009) or the replacement of these communities by fast-growing and less complex biogenic structuring organisms in the Caribbean Sea (Ruzicka et al. 2013; Lenz et al. 2015) indicates that the total amount of retained carbon may be much lower nowadays than in former times. Although the mechanisms of precipitation of $CaCO_3$ in coral skeletons are still not completely understood (Allemand et al. 2011), and there are different opinions regarding their net capacity of carbon sequestration (Ware et al. 1992), it is widely accepted that part of the CO_2 that enters in the water from the atmosphere is retained for millions of years in the skeleton of the bio-constructors (Allemand et al. 2011). In general, the extent to which the biogeochemical cycle of carbon will be modified due to the changes in the community composition and functionality is still largely unknown.

Biogeochemical cycles might also experience dramatic changes as the result of the impact of anthropogenic activities on the seafloor. For example, the destruction of animal forests caused by bottom trawling fishing (Fig. 6) (especially dangerous for CWC, sea pens, and sponge grounds) also results in dramatic changes in sediment load and infaunal composition, porosity, and nutrient content, with implications on the ecosystem functioning, in many cases to a point of no return, at least at human time scale (Puig et al. 2012). In soft-bottom communities affected by bottom trawling, important changes in the seston availability have been documented, with the homogenization of the substrate and the disappearance of three-dimensional structures being some of the most evident effects of this change (Sañé et al. 2013). The extent to which trawling-induced effects, such as bottom sediment excavation and resuspension occurs, has important implications for regional nutrient budgets in terms of the input of sedimentary nitrogen and silica into the water column. Sediment mixing and frequent bottom disturbance may also slow down or even completely prevent the regeneration of animal forests, especially in soft bottoms (Pilskaln et al. 1998). It is now widely recognized that bottom trawling has several impacts on marine ecosystems, including seafood stock impoverishment (Hinz, ▶ Chap. 37, "Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management" this volume).

Similar to deep coral communities, shallower animal forests (such as tropical coral reefs) are also suffering the destructive effects of fishing. Blast or dynamite fishing uses explosives to stun or kill fish, with extremely destructive effects on the surrounding habitats. Moreover, where economically valuable coral species are present, underwater animal forests are suffering the effect of their direct extraction (Jones et al., ▶ Chap. 36, "Harvesting and Collection of Animal Forest Species" this volume), which can alter the structure and the connectivity patterns of coral populations (Costantini et al., ▶ Chap. 38, "Genetic Connectivity and Conservation of Temperate

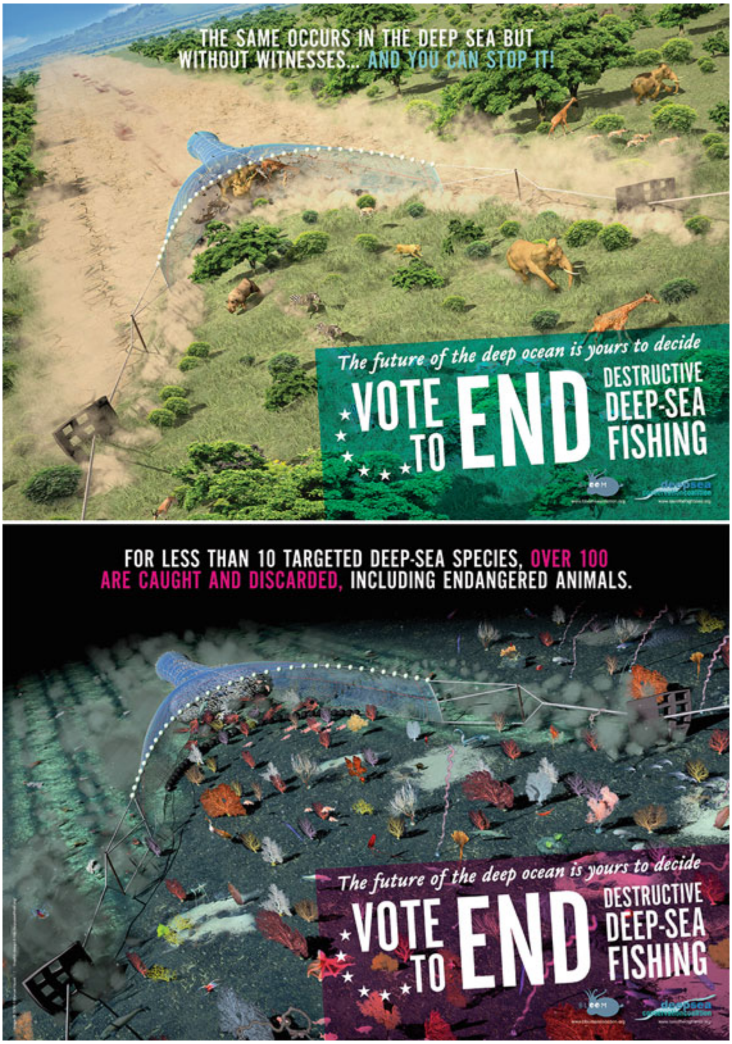

Fig. 6 Outreach campaign by Bloom Association (https://www.bloomassociation.org) to sensibilize people about what is happening in the seafloor, especially on the continental shelf, due to the intensive bottom trawling all over the world (Images courtesy of Bloom Association)

and Cold-Water Habitat-Forming Corals" this volume). Precious corals have been the target of harvesting for thousands of years due to their hard skeleton used in the jewelry industry (Tsounis et al. 2010). A paradigmatic example is the Mediterranean red coral (*Corallium rubrum*), target of the most ancient coral harvesting practice (see Jiménez and Orejas, ▶ Chap. 24, "The Builders of the Oceans – Part II: Corals from the Past to the Present (The Stone from the Sea)" this volume), and which populations have been depleted to the point that they look more like grasslands than like forests (Bramanti et al. 2009; Cau et al. 2016; Rossi et al. 2008).

The increase in seawater temperature caused by global climate change facilitates the spread of diseases in several corals species (Weil et al., ▶ Chap. 40, "Octocoral Diseases in a Changing Ocean" this volume) and is related to the massive bleaching of tropical corals (Altizer et al. 2013). Temperature shifts affect tropical, temperate, and polar animal forests, stressing species with narrow metabolic thresholds (Cerrano et al. 2000; Gutte et al. 2011; Schubert et al., ▶ Chap. 31, "Symbiotic Versus Nonsymbiotic Octocorals: Physiological and Ecological Implications" this volume) and causing changes in the composition of benthic communities (Sahade et al. 2015). Ocean acidification is also seriously threating several animal forests (Bramanti et al. 2013; Comeau and Cornwall, ▶ Chap. 39, "Contrasting Effects of Ocean Acidification on Coral Reef "Animal Forests" Versus Seaweed "Kelp Forests"" this volume) both at colony and at population level (acting in synergy with other environmental or anthropogenic stresses; Bramanti et al. 2014; Bramanti et al., ▶ Chap. 19, "Demography of Animal Forests: The Example of Mediterranean Gorgonians" this volume).

Marine animal forests (like most of the terrestrial forests) are mainly composed of long-lived organisms. Both trees and corals have similar growth patterns, in some cases are characterized by moderate or slow and modular growth, as it is the case for CWCs and Mediterranean gorgonians (Lartaud et al., ▶ Chap. 22, "Growth Patterns in Long-Lived Coral Species" this volume), and can display similar dispersal (Adjeroud et al., ▶ Chap. 20, "Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages" this volume) and reproductive strategies (Wangensteen et al., ▶ Chap. 21, "Reproductive Strategies in Marine Invertebrates and the Structuring of Marine Animal Forests" this volume). Corals and trees also share similar demographic structures so that population dynamics can be studied applying similar approaches (e.g., Linares et al. 2007; Bramanti et al., ▶ Chap. 19, "Demography of Animal Forests: The Example of Mediterranean Gorgonians" this volume). Millennial forests, as well as coral reefs, are characterized by a high resistance to natural perturbations, but when disturbances act in synergy (e.g., global climate change and human exploitation) or increase in frequency, these systems can collapse, and the slow dynamics of the species can make its recovery impossible, at least at human time scale. The challenge for ecologists is to identify the trends of these changes and be able to forecast the changes that the structure, composition, and functionality of these forests will experience in the future. Forecasting capacity depends not only on the knowledge of the biology, ecology, and environmental characteristics of the systems but also on the improvement of models suitable for long-living species such as trees and corals (Bramanti et al., ▶ Chap. 19, "Demography of Animal Forests: The Example of Mediterranean Gorgonians" this volume). Understanding the transformation of the animal forests will be essential to predict changes in the ecosystem functioning, as well as to implement effective management plans, conservation measures (Aguilar et al., ▶ Chap. 41, "Conservation and Management of Vulnerable Marine Benthic Ecosystems" this volume), restoration actions (Horoszowski-Fridman and Rinkevich, ▶ Chap. 45, "Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral

Transplantation" this volume), and sustainable use (Paoli et al., ▶ Chap. 44, "Ecosystem Functions and Services of the Marine Animal Forests" this volume).

The loss of the living three-dimensional structure implies changes in the seascape properties and in the availability of habitats and shelter for vagile and sessile species (e.g., Álvarez-Filip et al. 2011). Indeed, the presence of vagile fauna, like fishes or crabs, has been directly related to the presence of these complex three-dimensional structures (Baillon et al. 2012; Miller et al. 2012). Despite the evidence of the role of the biogenic structures in providing shelter and food for other organisms, these functions have only been rarely described quantitatively (Reaka-Kudla 1997; Álvarez-Filip et al. 2011).

Even if pristine animal forest probably no longer inhabits our oceans, highly diverse and functional animal forests would be more resilient to perturbations than degraded ones (Bianchi et al., ▶ Chap. 43, "Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998" this volume). Ecological resilience is defined as the capability of a community (or ecosystem) to return to a former state after disturbance, or the capacity to keep functioning after perturbations (see Bianchi et al., ▶ Chap. 43, "Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998" this volume for a review). For instance, in tropical coral reefs or in Antarctic benthic communities, high biodiversity increases the resilience (Bianchi et al., ▶ Chap. 43, "Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998" this volume). A higher number of species, in fact, results in a higher number of possible responses to perturbations. The maintenance of the biodiversity is then important to preserve ecosystem stability and balance (Sandin et al. 2008). However, once the stability is disturbed, the ecosystem could shift to an unstable state from which the return to a previous state could be difficult or even impossible, as already mentioned above. This is the case of CWC ecosystems, where the impacts of bottom trawling have long-term effects due to the slow growth rates and recovery capability of the structuring species (Althaus et al. 2009; Hinz, ▶ Chap. 37, "Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management" this volume; Aguilar et al., ▶ Chap. 41, "Conservation and Management of Vulnerable Marine Benthic Ecosystems" this volume; Ragnarsson et al., ▶ Chap. 35, "The Impact of Anthropogenic Activity on Cold-Water Corals" this volume).

The factors preventing the recovery of animal forests are not always clear; this is the case, for example, for the almost unprotected coral reefs in Mexico which show signs of recovery, while reefs dwelling in fully protected marine reserves in Belize do not present signs of recovery (Bruno 2014). The balance among environmental and biological constraints are different in different ecosystems; it cannot be forgotten that the recovery capacity of an animal forest is also linked to the reproductive strategies and growth patterns of its component (Galli et al. 2016), which may vary spatially and temporally according to food availability (e.g., the Mediterranean red gorgonian *Paramuricea clavata*, Cupido et al. 2009; Gori et al. 2013).

From another point of view, biodiversity plays an important role for tourism, which in turn provides economic benefits in several human societies. Global earnings from tourism can reach up to US$ 944 billion, and coastal tourism accounts for 85% of all tourism-related revenues (Klein et al. 2004). Because coastal tourism is directly related to the quality of the marine ecosystems, it follows that well-preserved animal forests will attract more tourism (White et al. 2000), generating higher income for local populations (Rodrigues et al. 2015). On the other hand, tourism also has an impact on the populations, as observed in the animal forests of the Mesoamerican Reef (the second largest coral reef in the world, extending from Mexico to Belize, Guatemala, and Honduras), which are suffering the increasing impact of touristic activities (Dietrich 2007; Arias-González et al., ▶ Chap. 42, "The Animal Forest and Its Socio-ecological Connections to Land and Coastal Ecosystems" this volume). In several touristic areas, economic revenue of local populations has been transferred from fishing to tourism. However, despite the interests of scuba diving tourism in preserving healthy animal forests, its massive use is endangering the fragile structures of several components of the animal forests (Sala et al. 1996).

Human-induced impacts are globally resulting in habitat reduction, degradation, and fragmentation. As a consequence of this, ecological connectivity among animal forest patches (sensu Taylor et al. 1993) can be deeply modified, with severe consequences on the population dynamics of the species which are part of those forests. Connectivity can take place through "corridors," which are linear connection elements, as well as through "stepping stones" acting as a bridge, or a "landscape matrix," which are parts of the surrounding landscape permeable to species dispersion. Analogous to terrestrial ecosystems, the relative importance of the different connectors depends on the kind of animal forest considered and the species harbored by those forests. The degree of connectivity is a critical factor for the maintenance of a good balance in the ecosystems. For instance, a low degree of connectivity can promote a decline in species and genetic diversity, as well as local extinctions. On the other hand, an excess of connectivity can lead to a homogenization of the ecosystem (with a decrease in β diversity), whereas a balanced connectivity level allows the coexistence of species that have different competition capabilities and dispersion potential. The role of ecological connectivity has been studied in terrestrial ecosystems over the last 20 years (Simberloff and Cox 1987; Gilbert-Norton et al. 2010), while its interest is more recent for marine ecosystems (e.g., Cowen et al. 1997 and references therein).

Even if marine defaunation (defined as depletion of animals) began tens of thousands of years later than on land (McCauley et al. 2015), humans have already deeply transformed all major marine ecosystems (Pimm et al. 2014; Thurstan et al., ▶ Chap. 33, "Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems" this volume), causing the ecological extinction of several species. This is, for example, the case of the precious coral *Corallium rubrum*, which is still frequent along the Mediterranean coast but which has completely lost its ecological role (Tsounis et al. 2010; Rossi et al., ▶ Chap. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests" this volume). Suitable and feasible management measures (Aguilar et al., ▶ Chap. 41, "Conservation and Management of Vulnerable Marine Benthic Ecosystems" this volume), meeting the compromise between animal forest conservation (Rice and Smith,

▶ Chap. 34, “Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest” this volume) and sustainable maintenance of the economy of local populations (Paoli et al., ▶ Chap. 44, “Ecosystem Functions and Services of the Marine Animal Forests” this volume), may only be achieved through the assessment of animal forest occurrence, distribution, and the study of the biology and ecology of the structuring organisms.

5 Perspectives and Challenges of Future Research

Even though the knowledge on several marine animal forests has greatly increased during the last century, many topics still need further exploration and understanding.

5.1 Distribution of the Animal Forests of the World

Extensive studies to assess the distribution and to quantify the biomass of the animal forests of the world are among the most urgent needs. Indeed, attempts to identify the more threatened coastal areas of the world oceans (Halpern et al. 2012) highlighted the very scarce amount of information on the benthic communities that are present along large extensions of coastal areas. Comprehensive information is currently available for very few well-studied coastal locations. For example, it is now accepted that 30–40% of the coral reefs have been severely damaged, and in 2030 probably more than 60% will be transformed or lost (Hughes et al. 2003; Hoegh-Gulberg et al. 2007). These studies deal in some cases with small and in other relatively large areas, but the complete map is still lacking. The knowledge about how the animal forest and other communities are distributed is important for this reason. Few decades ago, the deep ocean was considered almost a desert. Only after the achievement of technological advances, allowing deep-sea research with visual methods, as previously mentioned, the animal forests of the deep were discovered, changing our view of the capability of these organisms to survive in these environmental conditions. Not only the deep-sea communities have been neglected: the information available about the African coast, shelf and deep, is very scarce, as well as the knowledge about the deep animal forests of South America (but see de Soares et al., ▶ Chap. 3, “Brazilian Marine Animal Forests: A New World to Discover in the Southwestern Atlantic” this volume; Försterra et al., ▶ Chap. 10, “Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters” this volume; Montiel and Cárdenas, ▶ Chap. 9, “Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes” this volume) or the vast coast of Siberia. Also in areas that have been studied for a long time, there are still important gaps; in the Mediterranean Sea, data are available for some areas in the western and central part, with the eastern area being largely unknown. Within this framework, there is currently a strong need for quantitative exploration studies focused on megabenthic biodiversity, which are only possible after a serious reevaluation and appreciation of the importance of taxonomy for marine science. Also, it is worth to note that taxonomy expertise is disappearing from the scientific community, and only few researchers today are able to correctly identify sponges and cnidarian species, while for several other taxonomic groups, there are virtually no more experts.

5.2 Benthic-Pelagic Coupling Processes

Benthos has been regarded for years as a sink of the organic matter produced in the water column (but see the opposite vision in Arntz et al. 1999). In the late 1990s, the potential role of benthos was considered as a key factor in a novel approach by Gili and Coma (1998) who pointed out that benthic suspension feeders should be considered not only as "consumers" but also as organisms playing an important role in nutrient recycling. The role of particulate and dissolved organic matter in benthic-pelagic processes is still not fully understood, but the importance of benthic suspension feeders in the energy and matter processing (e.g., excretion, recycling, nutrient input for the microbial loop, etc.) has been already documented (e.g., Rossi and Gili 2009; Rossi et al., ▶ Chap. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests" this volume). Abundant literature has explored the trophic ecology of several components of marine animal forests (e.g., Graf 1992; Rossi et al. 2004; Houlbrèque and Ferrier-Pagés 2009; Jiménez and Ribes 2007; de Goeij et al. 2013). Current studies frequently combine different approaches to understand the links between food availability, capture and assimilation, and the role of benthic organisms in trophic food webs (Sebens et al., ▶ Chap. 29, "Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders" this volume). The role of animal forests in carbon and nutrient cycling has still not been completely understood. One of the main difficulties to approach this topic is the capacity of scaling up from physiology (i.e., carbon input, respiration, excretion, etc.) to community and ecosystem level (e.g., lack of precise data, lack of comparable experiments and protocols, etc.) due to the lack of the most basic knowledge on the biology of the different species (Fig. 7).

5.3 Photobiology and the Limits of Symbiosis

Photosynthesis is a highly regulated process that responds to variations in the availability of light at very different time scales. The mechanisms of interaction between animal host and symbiotic algae have been widely investigated in scleractinian corals. However, they are still largely unknown in other taxa, such as octocorals and, especially, sponges. Moreover, the processes involved in bleaching are still not fully identified as well as the potential influence of different clades of *Symbiodinium* in the resilience of scleractinians, octocorals, and sponges. In a fast-changing world, the high variability of clades which characterize octocorals and scleractinians may be

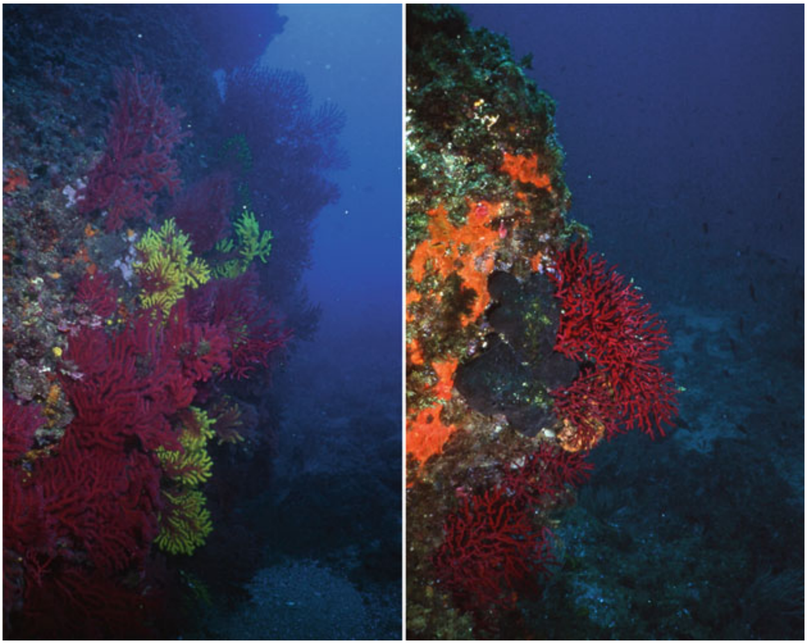

Fig. 7 Different morphology of similar animal forest depending on the surrounding hydrodynamics. The same gorgonian species (*Paramuricea clavata*) may have very different size and morphology depending on the exposition to the currents. On the *left*, tall *Paramuricea clavata* at 28 m depth; on the *right*, a patch of the same species but smaller (bus-like) colonies at 14 m depth. Both images have been taken in Cap de Creus (Spain) (Photo credits: Sergio Rossi)

a key point to understanding their ecological success in tropical waters (Schubert et al., ▶ Chap. 31, "Symbiotic Versus Nonsymbiotic Octocorals: Physiological and Ecological Implications" this volume), but also basic questions, such as photosynthetic adaptations, productivity and respiration rates, and even the presence of certain *Symbiodinium* clades in these organisms, are still pending to be resolved. Understanding the mechanism driving carbon translocation and photosynthetic efficiency (e.g., Tremblay et al. 2014) will help to better understand the distribution and resilience of symbiotic corals and sponges in shallow areas.

5.4 Metabolism and Biochemical Pathways: The Use of Energy

The basic metabolic pathways are still largely unknown for the vast majority of benthic engineer organisms. How energy is accumulated and mobilized in these species depends on the physiology of the organism, its developmental stage, growth, trophic ecology, and reproduction as well as on the environmental conditions. Free fatty acids, for example, are involved in the stress response in critical periods, such as reproduction (Viladrich et al. 2016), but the mechanisms involved in these biochemical pathways and their relationship with growth, stress, or reproduction are still unknown and depend on the trophic strategy (mixotrophic and heterotrophic, Viladrich et al. 2017). Seasonality in some geographical areas is a strong constraint that forces metabolic changes in suspension feeders (Rossi et al. 2006a, b), but there is still little information on how variations in food availability affect activity and thus the food consume and activity in sessile organisms (Barnes and Clarke 1995). Another energy-demanding process is the production of secondary metabolites; the composition and utilization of these products are still unknown for the majority of the species (Pawlik et al. 1995; Ianora et al. 2006; Ávila et al. 2008). However, it is known that these molecules are important for predatory deterrence or spatial competition and that great amounts of energy are necessary to synthetize them. However, a proper quantification of, for instance, how much energy is spent in spatial competition has not been properly calculated (Rossi and Snyder 2001). Part of this energy is probably used to the detriment of other important processes, such as growth or reproduction. The study of metabolism and biochemical pathways (also proteomics and metabolomics), and their modifications under stress conditions, are fundamental to understand the resilience of several animal forests to human-induced impacts and global climate change.

5.5 Reproduction

Reproduction is an extremely important life trait affecting species distribution and population recovery after a perturbation. It is very important to have a clearer picture about reproductive processes, especially for taxa like bryozoans, ascidians, and also sponges where information is scarcer than, for example, corals. Reproductive ecology has been studied in many scleractinian corals, mostly in tropical and temperate waters, but there is still no information available for many species living in all latitudes. Even less information is available on octocoral reproduction, in general. Considering the shift from scleractinian-dominated to octocoral-dominated communities observed in the Caribbean (Ruzicka et al. 2013; Lenz et al. 2015; Edmunds and Lasker 2016), reproduction in octocoral urgently needs dedicated studies to better understand the biology and ecology of these species and forecast their distribution under climate change scenarios (Kahng et al. 2011). It is fundamental to understand the factors that trigger reproduction and the metabolic pathways involved (Maldonado et al., ▶ Chap. 5, "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns" this volume; Wangensteen et al., ▶ Chap. 21, "Reproductive Strategies in Marine Invertebrates and the Structuring of Marine Animal Forests" this volume). Comparative studies in different areas are necessary in order to improve our knowledge about the role of the environmental factors in the species reproductive traits and strategies. Therefore, sound data on ecological and biological parameters are needed to better understand the dynamics and the potential survivorship of suspension feeder populations dwelling in different areas. There is also an important gap on environmental studies which are essential to explain why one place may be more suitable compared to another for reproduction, maintaining the populations and the genetic flux.

5.6 Connectivity and Resilience

Connectivity ensures the persistence of populations in a metapopulation framework (Hanski 1998). Knowledge about genetic fluxes and minimum viable population size (Costantini et al., ▶ Chap. 38, “Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals” this volume), as well as to consider deeper populations (Kahng et al., ▶ Chap. 6, “Mesophotic Coral Ecosystems” this volume; Gori et al., ▶ Chap. 7, “Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea” this volume) in the study of the population structure and dynamics in littoral communities, is essential nowadays to understand the resilience and diversity of animal forests. Connectivity of benthic populations depends, among others, on reproductive output, larval behavior, pelagic larval duration, and settlement success (e.g., Guizien et al. 2006, 2012; Martinez-Quintana et al. 2015). Therefore, energy investment in reproduction, feeding constraints, and energy storage capabilities, as well as larval nutritional condition and settlement success (Viladrich et al. 2016), are some of the topics that need further investigation. The final goal is to be able to understand and project into the future dynamics of the populations in the context of metapopulation systems. The development of metapopulation models will allow forecasting changes in community composition of the animal forests under future climate change scenarios (Guizien and Bramanti 2014).

5.7 Growth and Carbon Sink

Data on growth rates of the main structuring species of animal forest communities are not very abundant in shallow waters but are even scarcer in deep communities due to the difficulties associated with the work in the deep sea (Lartaud et al., ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species” this volume). Very little information is available on the annual increments in biomass for several taxonomic groups (e.g., sponges and bryozoans) or on the longevity of the majority of the species. An exception is represented by scleractinians and precious corals, for which growth and age determination have been extensively investigated due to the urgent need to develop management and conservation tools (e.g., Tsounis et al. 2010; Bramanti et al. 2014; Benedetti et al. 2016; Lartaud et al., ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species” this volume). The investigation of growth rates is fundamental to understanding the carbon retention capability of species populations (Coppari et al. 2016; Rossi et al., ▶ Chap. 30, “Benthic-Pelagic Coupling: New Perspectives in the Animal Forests” this volume). Growth is extremely variable between different taxonomic groups (even between different genera or species of the same taxon), being affected by environmental factors such as temperature and currents, which highly influence the amount of available food

(Grémare et al. 1997). The capability of the organisms to accumulate biomass is also related to its resistance, because the bigger the size, the higher the gonadal output, as has been suggested by Rossi et al. (2008). The study of the links between food inputs, environmental conditions, and community structure (and its role in the biogeochemical cycles) is still a pending subject in many of the animal forests.

Combining the information of experimental data sets on physiological parameters (e.g., respiration and feeding rates), growth rates, gamete output, etc., with studies *in situ* of occurrence, distribution, and demography of benthic populations could be a good approach to evaluate in a comprehensive way the sensitivity of benthic communities to environmental and anthropogenic disturbances (Coppari et al. 2016).

The analyses of the partial mortality, population structure, and reproductive success, at a population level, as well as the energy storage of organisms, could help to analyze and compare the health status of populations.

These approaches can be applied to test the direct (e.g., eutrophication, bottom trawling, etc.) and indirect (e.g., global warming, ocean acidification, etc.) impact of anthropogenic activities. Moreover, a standardized monitoring plan is necessary to forecast the recovery capacity of the populations.

Even if there are several oceanographic monitoring programs, at global (e.g., Global Ocean Observing system (GOOS)) and more regional level (e.g., MEDITS surveys), there is still an important need on the development of more programs to tackle different topics, including an important coordination effort among countries and researchers, as well as high amount of resources. Long-term monitoring program supplies fundamental data for the analysis and evaluation of ecosystem changes at long time scale.

5.8 Scientific Outreach

A properly informed society, which understands the importance of the natural ecosystems, is fundamental for the development and implementation of environmentally sustainable social and economic development. One of the aspects which frequently make difficult to bring research in the marine realm close to the society is the physical distance of common citizens to the oceans and seas.

To understand the negative impact of rainforest deforestation is relatively easy for the society; the images of bulldozers and the cutted giant trees are familiar to many people around the world. Human beings have direct and daily experience with trees and forests, and almost everyone has visited a forest, at least once in his life. Forests are also linked to the presence of animals, to wildness, and to something sacred. However, when the same devastating actions happen under the surface of the ocean, their importance and magnitude is impressively much less perceived (Fig. 6). There is a real need for a more direct contact between people, scientific organizations, and NGOs that emphasizes the role of these submarine animal forests for the overall planet functioning.

The concept of the animal forest allow to wake up the awareness of citizens linking their perception of the devastating effects of deforestation to other devastating actions that are less perceived, as reflected in Fig. 6. The concept of marine animal forest helps in explaining the needs for the conservation of marine ecosystem focusing on the already present experience and perception that people have in terrestrial forests. Animal forest is then a powerful image that could give strength and incisivity to outreach campaigns focused on marine ecosystems.

6 Conclusion

The concept of animal forests tries to unify some of the most important benthic ecosystems all over the world. The importance of a unifying theory, where the concepts are reduced as much as possible, is well recognized in the field of physics (Einstein 1940), but also ecology, due to its interdisciplinary nature, would greatly benefit from a similar approach. The goal of this book is to offer a broad overview about the marine benthic ecosystems dominated by sessile animals, stimulating researchers to go beyond their own disciplines toward a holistic and interdisciplinary approach.

Advances in science are not always the result of novel discoveries, but they often derive from the application of already developed concepts to new research fields. Therefore, interdisciplinarity have a major role in the advance of science. The important ecological role played by the ecosystems defined as “animal forests,” as well as their beauty, cultural, and spiritual value, requires strong interdisciplinary research and a direct connection with the society for their conservation for future generations. The ocean is still a pending subject, and the animal forest concept allows for a holistic and interdisciplinary approach to the problems faced by benthic ecosystems all over the world.

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Part I

Taxonomy, Biodiversity, Biogeography, and Evolution of Animal Forests

Caribbean Coral Reefs: Past, Present, and Insights into the Future

2

Héctor Reyes-Bonilla and Eric Jordán-Dahlgren

Abstract

Coral reefs are considered one of the more widely distributed "animal forests" in the tropical oceans. Notwithstanding, their status has been deteriorating in the last decades, and the Caribbean Sea is not an exception to this pattern. In this region, the joint effects of hurricanes, diseases, species introductions, and human activities (tourism, fisheries, and habitat loss) have caused severe decreases in coral cover, affecting the performance of the entire ecosystem. In this contribution, we began by reviewing the history of the reef coral faunas at genus level since the Eocene, under the perspective of functional diversity. The data show that, although regional origination and extinction modified the taxa composition, there has been a remarkable homogeneity in the number of functional groups present over time. However, the number of species per group has decreased and the lower redundancy makes current assemblage more fragile to perturbations. Finally, the recent status of Caribbean reefs is discussed, and models of random extinction and of loss of the most threatened species are applied. The results evidenced that, in both cases, at regional scale, no functional group may disappear, but reef systems in Cuba and the Lesser Antilles are the most susceptible to suffer direct damage by the loss of species. In particular, the main worry for the present and the future of the coral reefs of the Caribbean Sea may be the loss of the key reef builders (including *Acropora*, *Orbicella*), which are responsible for

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the construction of the reef structural framework, and consequently the drivers of many ecological processes and ecosystem services.

Keywords
Biodiversity • Caribbean • Cenozoic • Conservation • Coral reefs • Functional diversity • Perturbations • Resilience • Scleractinians

Contents

1 Introduction

Many scientific reports during the last two to three decades point out the stressful condition and catastrophic events on coral reef systems worldwide, both due to global change effects and local/regional impacts. The Caribbean Sea reef system is not an exception, and the reef seascape is changing drastically from what was reported before the 1980s; thus a reiterating question is about how much the Caribbean reef system is going to change on the short and medium term. Unfortunately, the extremely wide spatiotemporal framework on which the processes that shape the coral communities occur make difficult to address this sort of question in detail.

The aim of this work is to summarize both the historical and present-day condition of the Caribbean coral reef system as a whole, as well as discuss threats to the coral community. In particular, since they have an important role as reef builders, we will analyze biodiversity trends of scleractinian corals in the past, and its projection into the future. Both views will show the contrast of understanding we have regarding this reef system.

2 Caribbean Coral Reefs in the Past

The Coral reef biodiversity in the Caribbean has a complex history, driven by geologic and oceanographic changes related to tectonism that ended with the closure of the marine communication between the Caribbean and the Pacific Ocean by the rise of the Panama Isthmus. While the Caribbean Sea basically assumed its modern configuration by the late Miocene (Pindell 1994), some 10 million years ago, coral reefs were already present since lower Eocene in the proto-Caribbean Sea. The oldest reefs reported are from Barbados, around 40 million year ago, where two reef-builder genera of modern Caribbean reefs were already present: *Montastraea* and *Siderastrea* (Budd 2000), within a mixture of genera that originated in the Tethyan Sea during the Cretaceous, but some are apparently unique to the Caribbean (Budd 2000). Many works (i.e., Pandolfi and Jackson 2006) have reported well-developed reefs up to the Pliocene-Pliestocene in many Caribbean localities.

Notwithstanding the abrupt changes in climate and oceanic circulation along the Caribbean history that contributed to several extinction and speciation events (Budd 2000), coral reefs in the Caribbean had a long history of successful buildups (Haugh and Tiedemann 1998; Coates et al. 2003). However, large time lags in extinction events suggest that it was a long and complex process driven by many factors and not solely loss of productivity (O'Dea et al. 2007). The timing of the late coral extinctions in the Caribbean has been originally estimated to have initiated some 2–3 million years ago (Johnson et al. 1995; Jackson and Johnson 2001; Johnson et al. 2008; O'Dea et al. 2016), apparently within the geological time frame of the Panama Isthmus rise. Although Bacona et al. (2015) and Montes et al. (2012) proposed a much earlier loss of communication between the Pacific and Caribbean seas. Finally, after the Pleistocene the Caribbean symbiotic scleractinian coral richness is limited to around 70 species (a number that is being constantly revised by molecular and high-definition morphological techniques; Budd et al. 2012). Analysis of emerged Caribbean Pleistocene fossil shallow reefs showed a remarkable similarity in community structure (Pandolfi and Jackson 2006) between four different coral fossil assemblages, spanning from 104, 000 to 220, 000 years ago, with exception of the peak in abundance of the now extinct organ-pipe *Montastraea* in the 104 ka survey. The assemblages were dominated by *Acropora* and *Orbicella* (ex-*Montastraea*) just like modern counterparts all over the Caribbean before the onset of lethal coral diseases in the 1970s , suggesting that the extant relatively low-diversity reef coral fauna has been stable for the last 200, 000 years (Pandolfi and Jackson 2006).

The described changes in species composition (caused by events of extinction and speciation) had relevance in many aspects of the ecology of the coral assemblages, as well as for the functioning of the "reef forest." This is because, even when there is no formal correlation between coral cover, reef development, and species richness (Johnson et al. 2008), changes in composition are key to determine reef growth and relief aspects of relevance for the reef community functions (Alvarez-Filip et al. 2011). For instance, Renema et al. (2016) proposed that Acroporids became a dominant genera in Caribbean reefs as a result of their fast growing rates and local dispersal by fragmentation, traits that allow them to successfully cope with the drastic increase in glacioeustatic sea level dynamics occurred some 1.8 million years ago.

Table 1 presents the epoch (or epochs) of occurrence of the 68 coral genus that have been reported in the Caribbean Sea since the Paleocene. From the total number in each column it is evident how coral diversity increased from the Eocene (with excellent conditions of the sea temperature for the development of reefs and expansion of the tropical belts that allowed for the evolution of multiple coral lineages; Budd 2000; Gingerich 2006) to a peak in the Miocene, and then, afterwards, the diversity decreased somewhat gradually to the point that in the Recent we only have 27 genus in the region. These changes were well described and explained by Edinger

Table 1 Review of the presence (1) and absence (0) of coral genus present in the Caribbean Sea during the Cenozoic. Compilation of data from Budd et al. (1992, 1994), Budd (2000), and Budd and Wallace (2008)

Family	Genus	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Recent
Acroporidae	*Acropora*	0	1	1	1	1	1	1
	Astreopora	0	1	1	1	0	0	0
	Dendracis	0	1	0	0	0	0	0
	Montipora	0	0	1	0	0	0	0
Astrocoenidae	*Astrocoenia*	1	1	1	1	0	0	0
	Stephanocoenia	0	0	1	1	1	1	1
	Stylocoeniella	0	0	1	0	0	0	0
Pocilloporidae	*Madracis*	0	1	1	1	1	1	1
	Pocillopora	0	1	1	1	1	1	0
	Stylophora	1	1	1	1	1	1	0
Caryophylliidae	*Euphyllia*	0	0	1	0	0	0	0
Faviidae	*Agathiphyllia*	0	1	1	1	0	0	0
	Antiguastrea	0	1	1	1	0	0	0
	Antillophyllia	0	0	0	1	1	1	0
	Caulastrea	0	0	1	1	1	1	0
	Cladocora	0	1	1	1	1	1	1
	Colpophyllia	0	1	1	1	1	1	1
	Diploastrea	0	1	1	0	0	0	0
	Diploria	0	0	1	1	1	1	1
	Favia	0	1	1	1	1	1	1
	Favites	0	1	1	0	0	0	0
	Goniastrea	0	1	1	1	0	0	0
	Hadrophyllia	0	0	0	1	1	1	0
	Hydnophora	0	1	1	0	0	0	0
	Isophyllastrea	0	0	0	0	0	1	1

	Isophyllia	0	0	0	1	1	1	1
	Leptoria	0	1	1	0	0	0	0
	Manicina	0	0	0	1	1	1	1
	Scolymia	0	0	0	1	1	1	1
	Solenastrea	0	0	1	1	1	1	1
	Thysanus	0	0	0	1	1	1	0
Merulinidae	*Fungophyllia*	0	0	1	0	0	0	0
	Orbicella	0	0	0	0	1	1	1
Montrastraeidae	*Monstastraea*	0	1	1	1	1	1	1
Montlivalitidae	*Placosmilia*	0	1	0	0	0	0	0
Mussidae	*Antillia*	0	1	1	1	1	1	0
	Eusmilia	0	0	0	1	1	1	1
	Leptomussa	0	1	1	0	0	0	0
	Mussa	0	0	0	1	1	1	1
	Mussismilia	0	0	0	1	1	1	1
	Mycetophyllia	0	0	1	1	1	1	1
	Syzygophyllia	0	1	0	0	0	0	0
Trachyphylliidae	*Trachyphyllia*	0	0	1	1	1	1	0
Agaricidae	*Agaricia*	0	0	0	1	1	1	1
	Cyathoseris	0	1	0	0	0	0	0
	Gardineroseris	0	0	1	1	1	0	0
	Helioseris	0	0	0	0	1	1	1
	Leptoseris	0	0	1	1	1	1	1
	Pavona	0	0	1	1	1	1	0
	Trochoseris	0	1	0	0	0	0	0
	Undaria	0	0	0	1	1	1	1
Calamophyllidae	*Antilloseris*	0	1	0	0	0	0	0

(*continued*)

Table 1 (continued)

Family	Genus	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Recent
Siderastreidae	*Coscinaraea*	0	1	0	1	0	0	0
	Pironastrea	0	1	1	1	1	0	0
	Psammocora	0	0	0	1	1	0	0
	Siderastrea	1	1	1	1	1	1	1
	Sideroseris	0	1	0	0	0	0	0
Meandrinidae	*Dendrogyra*	0	0	0	0	1	1	1
	Dichocoenia	0	1	1	1	1	1	1
	Meandrina	0	1	1	1	1	1	1
	Placocyathus	0	0	0	1	1	1	0
Oculinidae	*Galaxea*	0	0	0	1	1	0	0
	Oculina							
Poritidae	*Actinacis*	0	1	1	0	0	0	0
	Alveopora	0	1	1	1	1	0	0
	Goniopora	1	1	1	1	1	1	0
Stylinidae	*Porites*	0	1	1	1	1	1	1
	Haimesastraea	1	1	0	0	0	0	0
Total		5	36	40	45	42	38	27

and Risk (1994), Budd (2000), and Maier et al. (2007), as a consequence modifications to in the regional productivity and oceanographic regimes (result of the closing of the interoceanic connection in Central America), combined with increased rainfall and river outflows.

The community and ecosystem effects of the faunistic changes brought upon by these switches can be measured in many ways, and in this case we will use functional ecology of the coral assemblages as a proxy, because reflects much better the status of species assemblages, than classic ecological indices (Gagic et al. 2015). Although there is plenty of information of how coral composition has shifted in time in the Caribbean (Budd 2000), and descriptions of the resultant modifications in life history patterns of the assemblages (Edinger and Risk 1994; Johnson et al. 1994), to the best of our knowledge there is no analysis that considered how the function of the reef coral species pool have also been modified. Differences and similitudes of morphological traits of fossil and recent Caribbean corals are analyzed, including information at colony and calicular level (Table 2), and applying a principal component analysis (PCA), which is a numerical tool that integrates all data to a number of numerical vectors (“axis”) that are representative of the data collection. While genus of the same families share many traits, they are not identical, especially in the ecologically important families Faviidae, Mussidae, and Agariciidae. Looking at the PCA (Fig. 1), 78% of the morphological variation was explained by the first five components, of which the first one is mostly influenced by calice width, the second by the presence of absence of a columella, the third by budding type and colony size, and the fourth by the presence or absence of paliform lobes, and the colony form, and the fifth by the structure of the wall. In broad terms, with some exception it appears that at the left side of the graph are the genera recognized as the main reef builders in the study region (Darling et al. 2012; Alvarez-Filip et al. 2013), while at the right we mostly observed corals with small sizes, solitary, or with relatively simple wall structure (parathecal).

From the same data (Table 2), we build a functional classification of the coral genera following the recommendations of Petchey and Gaston (2007) and Maire et al. (2015). The categorical traits were coded into numbers, and from the modified matrix a series of dendrograms were produced using clustering methods (UPGMA with single linkage) and three similarity measures (Gower, Euclidian distance and Bray-Curtis dissimilarity). The quality of the computed functional space of the six different options was determined from the cophenetic coefficient, and the level of stress from a nonmetric multidimensional scaling analysis of each combination. The best solution (UPGMA with Euclidian distance) was selected on the basis of the cophenetic coefficient value of 0.91. The final classification is shown in Fig. 2 and presents 10 groups based on morphology, that do not directly reflect a taxonomic classification. For example, in several groups there is a combination of genus from different families, and concurrently, most large families (with four or more species) are distributed in different sections of the tree. It is also important to notice that there are two monospecific groups (numbers 1 and 7, composed respectively by *Helioseris* and *Antilloseris*), four groups with six or less species, and the largest cluster (group 10) that includes 15 genera (less than 25% of the total number under study).

Table 2 Selected morphological traits from the fossil and recent Caribbean zooxanthellate coral genus present in the Cenozoic. Data obtained from examination of specimens in the National Museum of Natural History (Washington, D.C.) and the Museum of Paleontology of the University of California (Berkeley), publications by Wells (1957), Budd et al. (1994) and Johnson et al. (1995), and the web page "Neogene Marine Biota of Tropical America" (http://fossils.its.uiowa.edu/). Information for the genus *Haimesiastrea* was not available to complete the table and is not included

Genus	Colony size	Colony shape	Calice form	Calice width	Budding type	Wall structure	Columella	Pali	Septal lobes	Paliform lobes	Costae	Epitheca
Acropora	Large	Branching	Plocoid	Very small	Extramural	Septothecal	Absent	Absent	Absent	Absent	Absent	Absent
Astreopora	Intermediate	Massive	Plocoid	Small	Extramural	Septothecal	Absent	Absent	Absent	Absent	Absent	Absent
Dendracis	Intermediate	Branching	Plocoid	Small	Extramural	Septothecal	Absent	Absent	Absent	Absent	Absent	Absent
Montipora	Large	Branching	Plocoid	Small	Extramural	Septothecal	Absent	Absent	Absent	Absent	Absent	Absent
Astrocoenia	Large	Massive	Cerioid	Very small	Extramural	Septothecal	Styliform	Present	Absent	Absent	Absent	Absent
Stephanocoenia	Intermediate	Platy	Cerioid	Very small	Extramural	Parathecal	Styliform	Present	Absent	Absent	Absent	Absent
Stylocoeniella	Intermediate	Branching	Cerioid	Very small	Extramural	Septothecal	Styliform	Absent	Absent	Absent	Absent	Absent
Madracis	Intermediate	Branching	Plocoid	Very small	Extramural	Septothecal	Styliform	Absent	Absent	Absent	Absent	Absent
Pocillopora	Intermediate	Branching	Plocoid	Very small	Extramural	Septothecal	Absent	Absent	Absent	Absent	Absent	Absent
Stylophora	Large	Massive	Plocoid	Very small	Extramural	Septothecal	Styliform	Absent	Absent	Absent	Absent	Absent
Euphyllia	Small	Branching	Phaceloid	Medium	Extramural	Septothecal		Absent	Absent	Absent	Absent	Absent
Agathiphyllia	Intermediate	Massive	Plocoid	Large	Extramural	Synaptheculotecal	Trabecular	Absent	Absent	Present	Absent	Absent
Antiguastrea	Large	Massive	Subplocoid	Medium	Extramural	Parathecal	Lamellar	Absent	Absent	Absent	Absent	Absent
Antillophyllia	Small	Massive	Solitary	Very large	Absent	Parathecal	Trabecular	Absent	Present	Absent	Absent	Absent
Caulastrea	Large	Branching	Phaceloid	Medium	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Present	Present

Cladocora	Small	Branching	Phaceloid	Small	Extramural	Parathecal	Trabecular	Absent	Absent	Present	Present	Absent
Colpophyllia	Large	Massive	Meandroid	Very large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Present	Present
Diploastrea	Large	Massive	Subplocoid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Present	Present
Diploria	Intermediate	Massive	Meandroid	Medium	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Present	Present
Favia	Small	Massive	Plocoid	Small	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Favites	Large	Massive	Plocoid	Medium	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Goniastrea	Intermediate	Massive	Subplocoid	Medium	Intramural	Septothecal	Trabecular	Absent	Present	Present	Absent	Absent
Hadrophyllia		Massive	Flabelloid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Present	Present
Hydnophora	Intermediate	Massive	Cerioid	Medium	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Isophyllastrea	Intermediate	Massive	Cerioid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Isophyllia	Intermediate	Massive	Meandroid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Leptoria	Intermediate	Massive	Meandroid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Manicina	Small	Massive	Meandroid	Large	Intramural	Parathecal	Trabecular	Absent	Present	Absent	Present	Present
Scolymia	Small	Massive	Solitary	Very large	Absent	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Solenastrea	Intermediate	Massive	Plocoid	Small	Extramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Thysanus	Small	Massive	Flabelloid	Medium	Intramural	Parathecal	Trabecular	Absent	Absent	Present	Present	Present
Fungophyllia	Small	Platy	Solitary	Small	Extramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Orbicella	Intermediate	Massive	Plocoid	Small	Extramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Monstastraea	Large	Massive	Plocoid	Medium	Extramural	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Placosmilia	Small	Branching	Solitary	Very large	Absent	None	Absent	Absent	Absent	Absent	Present	Present
Antillia	Small	Massive	Solitary	Very large	Absent	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Eusmilia	Small	Branching	Phaceloid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Present	Absent	Absent
Leptomussa	Small	Massive	Plocoid	Large	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Present	Present
Mussa	Small	Branching	Phaceloid	Very large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent

(*continued*)

Table 2 (continued)

Genus	Colony size	Colony shape	Calice form	Calice width	Budding type	Wall structure	Columella	Pali	Septal lobes	Paliform lobes	Costae	Epitheca
Mussismilia	Intermediate	Massive	Plocoid	Very large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Mycetophyllia	Large	Platy	Meandroid	Large	Intramural	Parathecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Syzygophyllia	Small	Massive	Solitary	Medium	Absent	None	Absent	Absent	Absent	Absent	Present	Present
Trachyphyllia	Small	Massive	Flabelloid	Very large	Intramural	Parathecal	Trabecular	Absent	Present	Absent	Absent	Absent
Agaricia	Large	Platy	Meandroid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Cyathoseris	Small	Massive	Solitary	Small	Absent	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Gardineroseris	Large	Massive	Meandroid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Helioseris	Intermediate	Platy	Meandroid	Small	Intramural	Synaptheculotecal	Absent	Absent	Absent	Absent	Absent	Absent
Leptoseris	Intermediate	Platy	Meandroid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Pavona	Intermediate	Massive	Plocoid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Trochoseris	Small	Branching	Solitary	Small	Absent	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Undaria	Intermediate	Platy	Meandroid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Antilloseris	Small	Massive	Solitary	Very large	Absent	Synaptheculotecal	Absent	Absent	Absent	Absent	Present	Present
Coscinaraea	Intermediate	Massive	Cerioid	Medium	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Pironastrea	Intermediate	Massive	Cerioid	Small	Intramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Psammocora	Small	Massive	Cerioid	Small	Subplocoid	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Siderastrea	Small	Massive	Cerioid	Medium	Extramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Sideroseris	Small	Massive	Solitary	Medium	Absent	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Dendrogyra	Large	Massive	Meandroid	Small	Intramural	Septothecal	Lamellar	Absent	Absent	Absent	Absent	Absent

Dichocoenia	Intermediate	Massive	Meandroid	Medium	Intramural	Septothecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Meandrina	Intermediate	Massive	Meandroid	Large	Intramural	Parathecal	Lamellar	Absent	Absent	Absent	Absent	Absent
Placocyathus	Small	Massive	Flabelloid	Very large	Intramural	Parathecal	Lamellar	Absent	Absent	Absent	Absent	Absent
Galaxea	Large	Massive	Plocoid	Small	Intramural	Parathecal	Absent	Absent	Absent	Absent	Absent	Absent
Oculina		Branching	Plocoid	Small	Extramural	Parathecal	Trabecular	Present	Absent	Absent	Absent	Absent
Actinacis	Small	Massive	Plocoid	Small	Extramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Alveopora	Small	Massive	Cerioid	Small	Extramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Goniopora	Intermediate	Massive	Plocoid	Small	Extramural	Synaptheculotecal	Trabecular	Absent	Absent	Absent	Absent	Absent
Porites	Intermediate	Branching	Plocoid	Very small	Extramural	Synaptheculotecal	Trabecular	Present	Absent	Absent	Absent	Absent

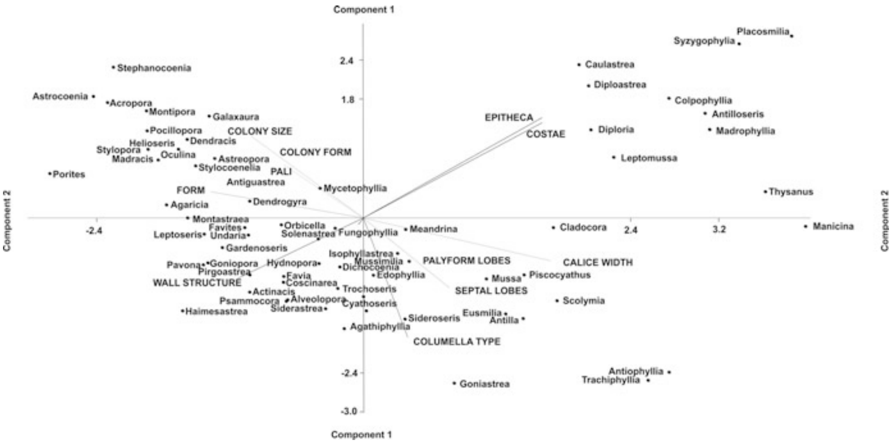

Fig. 1 Axis 1 and 2 of a principal component analysis; matrix of morphological traits of fossil and recent zooxanthellate corals of the Caribbean, presenting the characters that best typify each genus

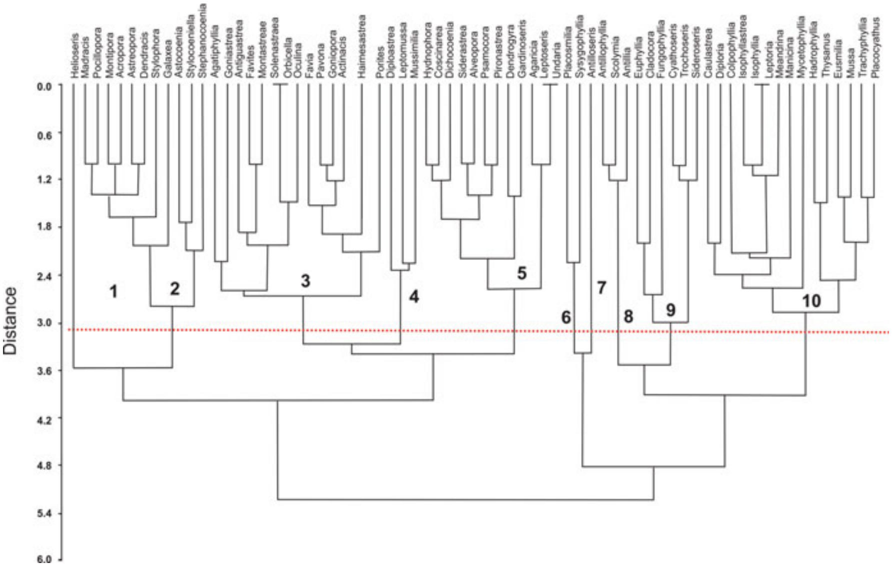

Fig. 2 Dendrogram depicting the morphofunctional classification of fossil and recent zooxanthellate coral genus in the Caribbean. The level of cut to determine the groups was defined at a Euclidian distance of 3.12

The finding of groups formed by a single taxonomic unit is relevant because as Mouillo et al. (2013) have shown, these organisms usually present the most atypical combination of traits, and thus, perform unique functions in the ecosystem. In our particular case, it is worthy of note that the two Caribbean genera that constitute isolated groups are of very limited presence in time; *Antilloseris* only occurred in the Eocene, while *Helioseris* is currently alive in the region (with a single species: *H. cucullata* (Ellis and Solander 1786), but its fossil history only dates from the Pliocene, less than 5 million years ago. These genera present very particular forms: *Antilloseris* is the only representative of the extinct family Calamophylliidae, was a small, solitary coral, and the only of its kind with septal lobes (Table 2), while *Helioseris* is the only agariciid in the Caribbean with no columella, platy morphology, and intermediate coral size (10 to 35 cm in maximum diameter; Johnson et al. 1994). We suggest that future studies should pay more attention to the status of this taxon: Even when the Red List of the International Union for Conservation of Nature deem *H. cucullata* in a low level of threat "Least concern," the phylogenetic analysis by Huang (2012) indicates that, among all agariciids of the western Atlantic, only *Agaricia lamarcki* Milne Edwards and Haime, 1851, represents a most endangered lineage. It should be not forgotten that in an ecosystem, once a rare element is lost it may not be easily substituted, and a good recent example seems to be that of *Acropora cervicornis* (*Pers. obs*).

Taking as a basis the classification in Fig. 4, the presence-absence matrix of genus versus time was rearranged by joining all components of each cluster, and from that array we observed how morphological diversity and richness of genus changed among epochs in the Cenozoic. In Fig. 3 it is apparent how both diversity indicators more than tripled when comparing the Eocene and Paleocene, and, although the numbers of genera have decreased since the Miocene in the region, the number of morphological groups has remained relatively stable, between 7 and 9. The association of both measures of diversity seems to follow a power relationship, suggesting that although about 30 coral genera are present in the Caribbean at any epoch, the number of morphological groups changes little (from 7 to 9). In analogous tests using species as independent variables, an asymptote in the graph is interpreted as niche saturation in the assemblage, which is then inferred as evidence of ecological redundancy, assuming that morphological similitude imply similar functionality, and hence a possible high level of ecological resilience (Micheli and Halpern 2005; Stuart-Smith et al. 2013). If this is the case, the results would point out that in the last 50 million years or so (since the Eocene), the level of macroevolutionary resilience in reef corals of the Caribbean has not changed much, even in the face of significant faunal turnover. If so, possibly, once 25–30 genera are present in the area the full set of reef building "related functions" would have been covered. But at the same time, the loss of some of the key ones would certainly place the assemblages and the entire reef ecosystems in a difficult situation.

A second much utilized measure of ecological resilience is the number of species represented in average per functional group (Mouillot et al. 2014). The idea is based on the concept that stability and diversity are functionally related; then high values of species indices would imply high potential resilience since there would be others that replace them and perform its ecosystem function (Guillemot et al. 2011). Following this concept, the value of the division of the number of genus and morphofunctional groups (MFG) for fossil and recent reef corals in the Caribbean Sea is shown in Fig. 3, and the results suggest that actually there seem to be differences in the degree of resilience in time. The figure for the Miocene (6.43 species per MFG) is the highest in the Cenozoic (Fig. 3), being four times greater than in the Eocene (1.67). After the Miocene, the quotient is decreasing in time, and remarkably the Recent

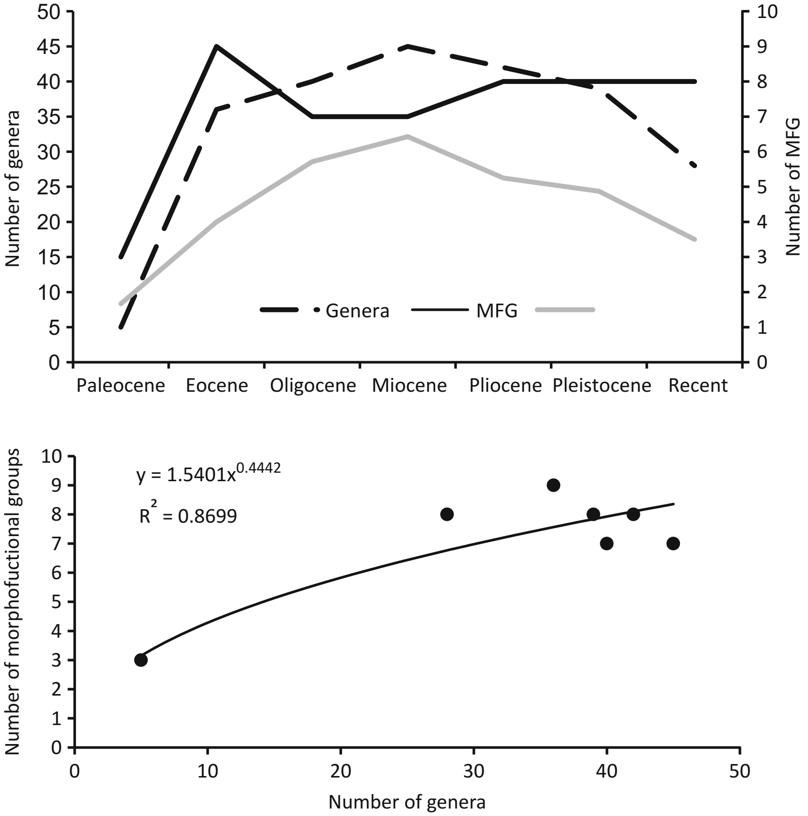

Fig. 3 Assessment of changes in richness and morphofunctional (*MFG*) diversity of coral genera in the Caribbean during the Cenozoic (*above*) and relationship of both indices (*below*)

presents the second to last value of this indicator (3.5 genus/group). This suggests that Caribbean reef coral assemblages are "naturally" more frail now than any other time in the last 65 million years; thus, the present decline witnessed in the last 50 years (Gardner et al. 2003; Jackson et al. 2014) may have an additional cause to the stressful anthropogenic influences over the reef ecosystem.

The next step in this study was to categorize the relative relevance of each MFG of reef corals in the Caribbean and western Atlantic during the Cenozoic, based on the number of genus per group and epoch, and in the proportion of the total coral fauna represented by each group in any time section. The results are presented in Table 3 and Fig. 5 and show an interesting trend: In general, the number of species in each group increased from the Paleocene to the Miocene and decreased afterwards. However, Group 1 (one species, discussed earlier in this section) appeared late (in the Pliocene), Groups 6 and 7 (including only three species in total) went extinct after the Eocene, and Group 4 only has one genus since the Miocene, and never more than two; the current representative (*Mussismilia*) is exclusive resident of Brazil (Leao et al. 2010).

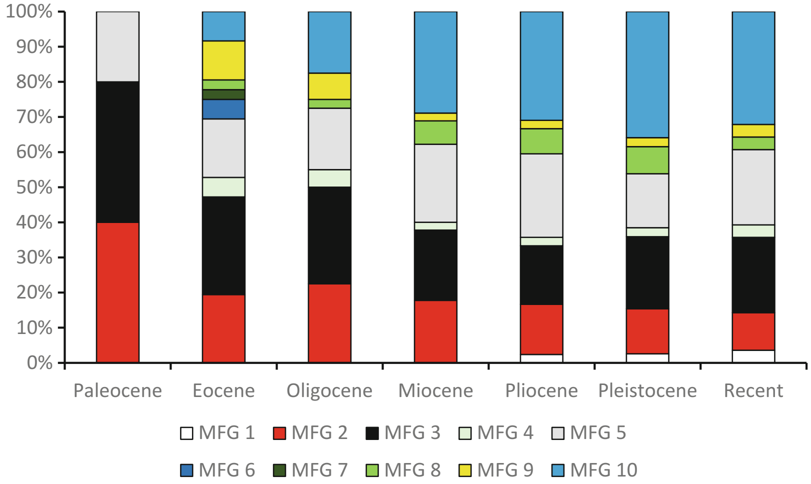

Fig. 4 Relative importance of each functional group of scleractinian corals of the Caribbean along the Cenozoic. *MFG* Morpho Functional Group

Notwithstanding, a chi-square test demonstrated no significant difference in the expected and observed number of genera per epoch, considering the 10 MFG (Xi = 52.42, $p < 0.01$). This means that no group has had radical changes in the number or representatives per epoch, independently of what are the trends in extinction and origination intensity (Budd and Johnson. 1999). The immediate conclusion is that after the Eocene, when the full set of about 7–9 functions have been fulfilled, the groups suffer some type of limitation in the ecological space of its constituent genera, probably because competition works as the factor to determine this outcome. The evidence for this conclusion is still scant, but nevertheless, these results call for a more profound examination of the fossil data, preferably at species level. Saturation of the ecological niche space is not unheard of and in the marine realm has been recognized to occur to strombid mollusks worldwide (Roy et al. 2001), and there is also an example in reef corals of the genus *Porites* (Mohedano-Navarrete et al. 2008); in this case, the morphological variability of the species (used as a proxy of function) reaches an asymptote when graphed against species richness present in the Pacific Ocean.

To finalize this section, it is important to pay attention to the paleontological trends presented by groups 2, 3, and 10, in which the key coral reef builders are located (e.g., *Acropora* in Group 2, *Montastraea* and *Porites* in Group 3, *Diploria* and *Colpophyllia* in Group 10), in comparison to the rest of genera. In Fig. 5 the reader can observe the number of genera present at each epoch in the Cenozoic, divided in "main reef builders" (the above cited groups), and a set of the seven remainder termed as "secondary reef builders"; also, the proportion of each category is shown. The graph evidences how from the Miocene to the Recent, the percentage of corals that function as "main reef builders" in the Caribbean region has been maintained from 61% to 69%, and consequently the other group always represents less than 40% of the total genus present in the study region. The regularity in these figures again called for

Table 3 Number of coral genera representative of each of the 10 functional groups shown in Fig. 5, as they occur along the Cenozoic. The relative relevance of each group at each epoch (percentage of the total fauna) is also presented

Group	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Recent	Number of genera (mean, sd)	Percentage (mean, sd)
1	0	0	0	0	1 (2%)	1 (3%)	1 (4%)	0.43 (0.53)	1.22 (1.56)
2	2 (40%)	7 (19%)	9 (23%)	8 (18%)	6 (14%)	5 (13%)	3 (11%)	5.71 (2.56)	19.65 (9.84)
3	2 (40%)	10 (28%)	11 (28%)	9 (20%)	7 (17%)	8 (21%)	6 (21%)	7.57 (2.99)	24.84 (7.81)
4	0	2 (6%)	2 (5%)	1 (2%)	1 (2%)	1 (3%)	1 (4%)	1.14 (0.69)	3.04 (1.87)
5	1 (20%)	6 (17%)	7 (18%)	10 (22%)	10 (24%)	6 (15%)	6 (21%)	6.57 (3.04)	19.57 (3.13)
6	0	2 (6%)	0	0	0	0	0	0.29 (0.76)	0.79 (2.10)
7	0	1 (3%)	0	0	0	0	0	0.14 (0.38)	0.40 (1.05)
8	0	1 (3%)	1 (3%)	3 (7%)	3 (7%)	3 (8%)	1 (4%)	1.71 (1.25)	4.34 (2.88)
9	0	4 (11%)	3 (8%)	1 (2%)	1 (2%)	1 (3%)	1 (4%)	1.57 (1.40)	4.19 (3.79)
10	0	3 (8%)	7 (18%)	13 (29%)	13 (31%)	14 (36%)	9 (32%)	8.43 (5.41)	21.96 (13.63)
Number of genera	5	36	40	45	42	39	28		
Number of morpho functional groups	3	9	7	7	8	8	8		

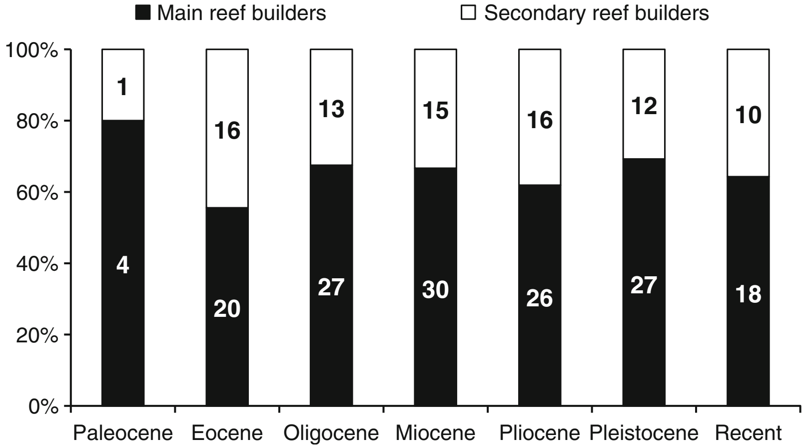

Fig. 5 Number of coral genera that are considered as "main reef builders" (morphofunctional groups 2, 3, and 10), and "secondary reef builders" (the other seven groups) and percentage that they represent in the total fauna at each epoch

a possible saturation of the macroevolutionary niche space (at genus level), which can probably be only explained by effects of competition. Another key point to address from Fig. 5 is that in the Recent, we have the least number of "main reef builder" genera (just 18) that have been present in any epoch since the Paleocene; this is another possible evidence that the current reef coral assemblages are naturally susceptible to deterioration from any kind of severe natural or anthropogenic disturbance.

As a general conclusion of this section, the analysis showed that the continuous extinctions and originations of reef coral genera in the Caribbean have significantly modified the composition of reef coral assemblages during the Cenozoic, but notwithstanding, the effect on the ecological function of the zooxanthellate scleractinians has not changed that much. There is a remarkable homogeneity in the number of morphofunctional groups in the region after the Eocene (once that the reefs recovered of the Cretaceous-Tertiary extinction), and that may be an evidence of saturation of the macroevolutionary niche space of the corals, both at the scale of the entire regional pool of genera and also in a more ecological level. One of the key possible consequences of these changes is that, as the reef coral assemblages in the Recent have very few functional groups and low redundancy, they are prone to be more easily disturbed if they are under the effect of a perturbation, being of natural or human-induced origin.

3 Caribbean Coral Reefs in the Present

The human impact on Caribbean reefs started as early as native Americans colonized the Caribbean shores, exploiting the reef resources they could reach, as evidenced by their impact on mean individual size of different fish populations (Wing and Wing 2001), and on the queen conch *Strombus gigas* (Stager and Chen 1996). With arrival of the Europeans, overexploitation of reef resources occurred due to much more efficient techniques. Turtles, manatees, and groupers were heavily impacted (Jackson 1997). Spaniards and other Europeans also made their forts with reef rock. During those periods, there are no written records describing the ecological damages impinged upon the coral ecosystem, but it was but was in several instances significant enough as to change community structures (Jackson 1997).

Scientific knowledge of Caribbean reefs remains lacking until the 1800s, when the works of Humboldt and Agassiz, among others, started to provide a formal view of what reefs are and how they may function. Knowledge that much later was greatly supplemented by the advent of SCUBA diving and drilling allowed researchers to infer reef functioning in an adequate time frame for these phenomena (Goreau 1959). This, together with paleobiological studies of Pleistocene raised reefs, has shown that although there are some 70 extant scleractinian reef-dwelling species, just a few have been truly reef builders in the past 200,000 years throughout the Caribbean: the branching *Acropora palmata* and *A. cervicornis*, the massive *ex- Montastraea annularis* species complex (*Orbicella annularis*, *O. faveolata*, *and O. franksi*), the massive *Pseudodiploria strigosa*, and the presently extinct *Montastraea nancy* (Pandolfi and Jackson 2006). Caribbean reefs were built up mostly by a combination of these few species, producing diverse reef types by geomorphologic criteria: atoll-like structures (Stoddart 1962; Milliman 1969), barrier reefs (James and Ginsburg 1979), and a wide array of fringing reefs, some showing a rather high level of development (Goreau 1959).

While in the past researchers considered that Caribbean reefs were poorly developed (as compared to Indo-Pacific ones), it is now recognized that, although reef development is variable within the Greater Caribbean, the accretion rates of the Caribbean reefs are not unlike those of reef regions with a much richer scleractinian coral diversity, as the Indo-Pacific (Birkeland 2015). Therefore, considering the difference in species richness between the Caribbean and the Pacific a simple relationship between coral diversity and reef development may not exist. We have to consider that some key species may be overwhelming contributors to reef development, as it had happened during the last couple of million years with Acroporids in the Caribbean (Renema et al. 2006). Actually, one of the fastest reef accretion rates ever recorded, in the order of 12 m per thousand years by *A. cervicornis*, was found on Alacranes reef in the Gulf of México (MacIntyre et al. 1977).

Due to strong environmental gradients, mostly wave impact and light penetration, coral reefs show a distinct zonation, basically in terms of protected and unprotected environments (to wave action). *A. palmata* is the only Caribbean scleractinian species able to grow, very successfully, on the wave breaking reef crest and shallow exposed and protected reefs. However, in a few localities as in Panamá reefs, the energy level of the breaking waves is too high for *A. palmata*, and then an algal ridge is found instead, not unlike the ones in Indo-Pacific reefs, a feature previously claimed to be a sign of difference between both reef realms (Glynn 1973; Adey 1978). The 3D structure created by the stands of the branching *A. palmata* play a rather important role in moderating the force of the incoming waves, and thus the shallow back reef environment becomes more suitable for the growth of many other species. The successful distribution relies on fast growth rates and dense basal skeletons, but also on an efficient local dispersal mechanism that take advantage of mild storms, as colony fragments detached by storms eventually may form new colonies if falling in adequate areas for their survival; thus locally enhance dispersal of the parent populations, a sort of asexual reproduction driven by the mechanical force exerted by the incoming stormy waves. The relevance of this process has been demonstrated by genetic analyses of the clonal structure, showing that a relatively few genotypes constitute *A. palmata* stands (Baums et al. 2006). In contrast, *A. cervicornis* (a very fast grower and prone to fragmentation as well) have a skeleton and colony shape that are not as robust to withstand wave impact as *A. palmata*; therefore it succeeds in protected environments from stormy waves, where it can form rather extensive and thick stands in either in shallow or deeper waters.

Usually the highest species richness assemblages are found in the so-called mixed coral zone at depths of 10–20 m, but, also when protected, back-reefs are relatively deep and coral species richness tend to be high as well. In euphotic reef zone, down from the surface to around 30 m, storm wave action and light gradients as well as temperature anomalies play an important role in the functioning of the communities. But in Caribbean reef environments with clear waters and other appropriate conditions, many of the mixed coral zone species are found down to more than 50 m (Goreau 1959 and many others), well into the realm of what is considered the mesophotic coral ecosystem, which can extend to depths beyond 100 m. However, in these areas the reef community tends to be dominated by sponges and azooxanthelate corals, and while some symbiotic shallow water coral species can be found on the deep zone, availability of photosynthetically active radiation is much decreased, both by attenuation and reduced spectral composition due to water column depth (Lesser et al. 2009), resulting in slow growth rates. Thus, although corals may be relatively abundant, no reef build up occurs because bioerosion exceeds accretion rates (Hinderstein et al. 2010). In comparison with the euphotic communities, scleractinian species richness is much reduced, but some euphotic water species such as *Montastraea cavernosa*, *Agaricia lamarki*, *A. grahamae*, and *Leptoseris cucullata* have been reported from the Bahamas at more than 100 m deep (Reed 1985), whereas *Stephanocoenia intersepta* and species of *Agaricia* and *Madracis* may be common at intermediate depths (Khang 2010). Bongaerts et al. (2015) found that mesophotic *Agaricia* species among others are associated with a deep-water *Symbiodinium* zooxanthelae, although most of these corals probably derive much of their energy requirements heterotrophically (Anthony and Fabricius 2000). However, although available light is the primary limiting factor for mesophotic symbiotic corals, Bongaerts et al. (2015), found that their lower limit may be strongly influenced by existing seawater temperature gradients, rather than light.

One rather important characteristic of the Caribbean reef environment is the abundance of gorgonians, which are found both in the protected and exposed reef zones, from the wave breaking reef crest to the limits of the mesophotyc zone, and beyond. Gorgonians are Octocorals that instead of forming a rigid aragonite skeleton as the scleractinia have a horny flexible central axis (some, like *Briareum asbestinum*, have the axis composed by compacted sclerites), and the colonies are branching and erect, mostly tree- or bush-like forms. The flexible central rod allows them to sway with passing waves, not unlike trees in the wind (Bayer 1961), thus the common Caribbean denomination of soft corals. Few species attain heights over 1 m and, when abundant, they resemble a tropical forest as gorgonian communities tend to be composed by many species. In the breaker zone only a few species, particularly the sea fans of the *Gorgonia* genus, dominate the gorgonian assemblages. While the spatial heterogeneity generated by the gorgonian "forests" is small, compared to that conformed by stony corals, it does create a complex environment where many small species and juveniles of larger species find shelter and nourishment (Kinzie 1973). Actually in the common and extensive hardground areas in the Caribbean, where no significant reef build-up occurs, gorgonians do grow abundantly (Goldberg 1973; Jordán-Dahlgren 1989). Unlike many scleractinian corals, few gorgonian species are clonal, and due to their relatively soft constitution their life span rarely exceeds a few decades, even if not detached from the substrate by storms (the main cause of natural mortality, Kinzie 1973). Gorgonians depend on sexual reproduction for dispersal, and because of their limited life-span, many species can be good indicators of ecological connectivity in real time (Jordán-Dahlgren 2002).

To complement the previous description of the status of the reef corals of the Caribbean, we followed the idea developed in the first part of this document, and performed a numerical analysis of the condition of the "reef forests" based on the morphological characteristics of the species that inhabits the region. To make a more thorough study, here it was included both the Greater Caribbean (Gulf of Mexico, Florida, and the Caribbean), subtropical areas like Bermuda and from northern Florida to South Carolina in the United States, and also the coast of Brazil, in the southern hemisphere. The final database (including 81 species) was constructed by joining the information from Horta-Puga et al. (2007), Table S4 in Miloslavich et al. (2010), and supplementary material of Huang and Roy (2015; http://datadryad.org/resource/doi:10.5061/dryad.178n3). There were small differences among these sources regarding the nomenclature of the species, so the definite list is presented in Table 4. It is important to notice that a recent paper indicates the presence of 23 species in Brazil (Leao et al. 2016), instead of 18 as mentioned by Miloslavich et al. (2010), but that list included azooxanthellate species; the number of zooxanthellate ones is 18, and for that reason we kept the latter figure for further analyses. Finally, for the analysis of the records, each species was assigned to a purported functional group related to reef building to which its genus belongs (Fig. 3).

Initially, the 81 corals were grouped into eight groups which, in turn, have very different number of species each; groups 10 and 3 (comprising species of *Montastraea*, *Porites*, and *Diploria*) have 22 and 20 taxa respectively, while group 1 has a single species (*Helioseris cucullata*) and group 9 has just two (*Cladocora* spp.). Groups 4 (*Mussismilia* spp.) and 8 (*Scolymia* spp.) contain three species each. As mentioned in a previous section of this paper, the occurrence of single-species functional groups makes them quite relevant in the assemblages, because if they are

Table 4 Review of the presence (1) and absence (0) of zooxanthellate corals in the western Atlantic. Key for locations: (1) Subtropical USA (north Florida to South Carolina); (2) Bermuda; (3) Flower Garden Banks; (4) Veracruz, Campeche Bank; (5) Mexican Caribbean; (6) Belize; (7) Bahamas and south Florida; (8) Cuba; (9) Puerto Rico; (10) Hispaniola; (11) Jamaica; (12) Cayman Islands; (13) Guatemala; (14) Honduras; (15) Nicaragua; (16) Costa Rica; (17) Panamá; (18) Lesser Antilles; (19) Curacao, Aruba, and Bonaire; (20) Colombia; (21) Venezuela; (22) Trinidad and Tobago; and (23) Brazil. FG: Morphofunctional group to which the species belongs. Species are arranged on the basis of their morphofunctional group

Species	MFG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Helioseris cucullata	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0
Acropora cervicornis	2	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Acropora palmata	2	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Acropora prolifera	2	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	0
Madracis auretenra	2	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	0
Madracis carmabi	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Madracis decactis	2	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Madracis formosa	2	1	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	0	0
Madracis myriaster	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Madracis pharensis	2	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	0
Madracis senaria	2	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	0
Stephanocoenia intersepta	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Favia conferta	3	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Favia fragum	3	0	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Favia gravida	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Favia leptophylla	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Montastraea annularis	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Montastraea cavernosa	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Montastraea faveolata	3	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0
Montastraea franksi	3	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Solenastrea bournoni	3	0	0	0		1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0
Solenastrea hyades	3	1	0	0		1	0	1	1	0	0	1	0	1	1	1	1	1	0	0	1	1	0	0

(*continued*)

Table 4 (continued)

Species	MFG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Oculina diffusa	3	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0
Oculina valenciennesi	3	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Oculina robusta	3	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Oculina varicosa	3	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Porites astreoides	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Porites branneri	3	1	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Porites colonensis	3	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0
Porites divaricata	3	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Porites furcata	3	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	0
Porites porites	3	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Mussismillia braziliensis	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Mussismillia hartii	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mussismillia hispida	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Agaricia fragilis	5	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1
Agaricia grahamae	5	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1
Agaricia lamarcki	5	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	0
Agaricia undata	5	1	0	1	0	1	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	1
Leptoseris cailleti	5	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Undaria agaricites	5	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Undaria carinata	5	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0
Undaria crassa	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Undaria danae	5	1	0	0	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	0	0	1	0	0
Undaria humilis	5	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Undaria purpurea	5	0	0	0	0	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	0
Undaria pussilla	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Undaria tenuifolia	5	0	0	0	0	1	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0

Dendrogyra cylindrus	5	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	0
Dichocoenia stellaris	5	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0
Dichocoenia stokesii	5	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Siderastrea radians	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Siderastrea siderea	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Siderastrea stellata	5	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scolymia cubensis	8	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Scolymia lacera	8	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Scolymia wellsi	8	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocora arbuscula	9	1	0	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0
Cladocora debilis	9	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Colpophyllia amaranthus	10	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0
Colpophyllia natans	10	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Diploria clivosa	10	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0
Diploria labyrinthiformis	10	0	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0
Diploria strigosa	10	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Manicina areolata	10	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Manicina mayori	10	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	0
Eusmilia fastigiata	10	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Meandrina braziliensis	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Meandrina caribbaea	10	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	0
Meandrina danae	10	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	1	0	0	1	0	0
Meandrina meandrites	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Meandrina memorialis	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isophyllastrea rigida	10	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Isophyllia multiflora	10	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Isophyllia sinuosa	10	0	1	0	0	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0
Mussa angulosa	10	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0

(*continued*)

Table 4 (continued)

Species	MFG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Mycetophyllia aliciae	10	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	1	0	0
Mycetophyllia danaana	10	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	0	0
Mycetophyllia ferox	10	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0
Mycetophyllia lamarckiana	10	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0
Mycetophyllia reesi	10	0	0	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0
Total species richness		32	25	31	40	53	43	67	57	59	58	57	53	25	58	40	40	62	59	55	54	64	31	18
Total number of MFG		7	5	7	6	7	7	7	7	7	7	6	6	6	7	6	7	7	8	7	7	7	7	6

lost no other element can provide the same function in the ecosystem, and, in addition, the rarity itself tends to make them prone to local extinction (Hobbs et al. 2010; Mouillo et al. 2013). That may well be the case of the isolated population of *Mussismilia* residing in the Lesser Antilles, which will be discussed in more detail in the following paragraph.

The total species richness and number of assumed morphofunctional groups found at each region appears in Fig. 6, as well as the ratio richness/MFG. As

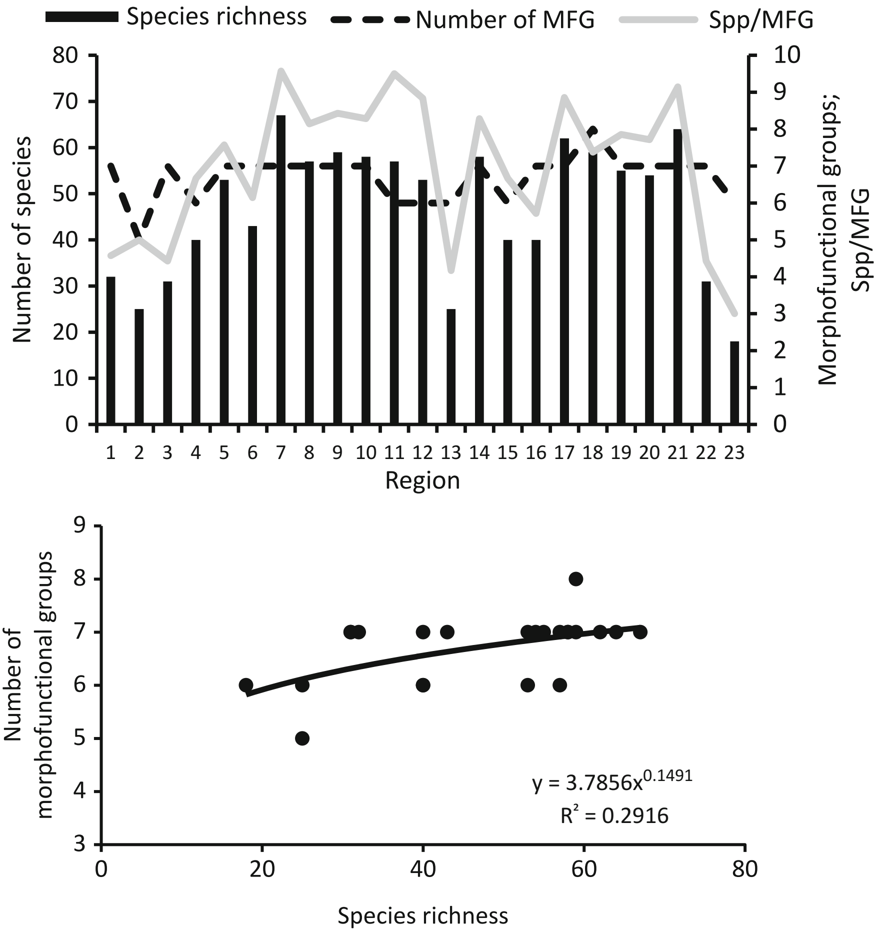

Fig. 6 Assessment of richness, morphofunctional (*MFG*) diversity and the quotient spp./MFG of coral assemblages of the western Atlantic (*above*), and relationship of richness and functional diversity (*below*). Key: (1) Subtropical USA (north Florida to South Carolina); (2) Bermuda; (3) Flower Garden Banks; (4) Veracruz, Campeche Bank; (5) Mexican Caribbean; (6) Belize; (7) Bahamas and south Florida; (8) Cuba; (9) Puerto Rico; (10) Hispaniola; (11) Jamaica; (12) Cayman Islands; (13) Guatemala; (14) Honduras; (15) Nicaragua; (16) Costa Rica; (17) Panamá; (18) Lesser Antilles; (19) Curacao, Aruba, and Bonaire; (20) Colombia; (21) Venezuela; (22) Trinidad and Tobago; and (23) Brazil

observed, the highest number of species are reported in Bahamas and south Florida (67), Venezuela (64), and Panama (62), while the lowest appear in Brazil (18), Bermuda (25), and Guatemala (25). Budd and Pandolfi (2010), Miloslavich et al. (2010), and Veron et al. (2015) discuss the origin of these differences, and conclude that the lowest species richness might be caused by a relative isolation of the reefs in the southern hemisphere due to current patterns and the presence of the outflow of the Amazon and Orinoco rivers, while the maximum richness may be due to speciation in peripheral regions such as the Caribbean island arc. On the other hand, the number of functional groups have a minimal variation, from 6 to 7 in all regions excepting Bermuda (5) and the Lesser Antilles (8). This last area, encompassing from the Virgin Islands to Barbados and Grenada (the entire island arc of the Caribbean), is the only one that actually covers the full set of reef coral morpho "functions" in the western Atlantic, and this condition is due to the fact that in the area there is a report of *Mussismilia braziliensis*, (Miloslavich et al. 2010), a representative of the morphofunctional group 4, that otherwise is exclusive of Brazilian waters. Unfortunately, the number of studies conducted on reef corals in the Lesser Antilles is still very limited (Jackson et al. 2014), but the relevance of the presence of this unusual coral in the region merits more research effort.

There is no similar analysis in the literature to compare the results presented above, but the noteworthy stability in number of functional groups of corals anywhere in such a large geographic realm calls for an explanation. We suggest that like the low beta diversity of coral communities along the region (average of 0.79 in Bray-Curtis similarity and over 0.86 units of the Dice coefficient; Reyes-Bonilla 2004; Veron et al. 2015), the pattern of uniformity in the number of morphological groups is another example of how well homogenized is the coral fauna in the western Atlantic. We suggest that the high faunal similarity of corals, which translates to a very similar number of MFG per region along the western Atlantic, may be a consequence of the complex oceanographic patterns in the region, that may transport larvae in several directions during the year, and depending upon the season (Wood et al. 2014; Qian et al. 2015). Also, after the region became isolated after the closing of the Tethys Sea, time has been enough for populations of most species to spread along the eastern coast of the Americas.

The regression curve between species richness and number of morphological groups (Fig. 6) follows a power trend ($p = 0.031$) and indicates how limited is the influence of changes in richness to the quantity of functions that a coral assemblage in the western Atlantic may perform. According to the model, a region with 22 coral species would have 6.01 morphological groups, while another with 60 species is predicted to present as much as 6.97. In short, the great homogeneity in morphological group composition and occurrence mentioned before is also reflected in this case. The interpretation of this finding, in agreement with the macroecological theory and complemented with the paleoecological results previously presented in this chapter, is that the biogeographic unit has covered the available ecological niche under current oceanographic and biological conditions, and because of the great connectivity in the Gulf of Mexico and Caribbean Sea, the same pattern of MFG's richness is presented at each region. The only possible exception is Brazil, with very low number of MFG and noticeable qualitative differences in species composition. Saturation of niche space is not the general trend in nature at local scales (Wiens 2011); nevertheless, the pattern changes when the area is extended to embrace a full biogeographic region (Russell et al. 2006), and these instances are usually found in taxonomic groups in which competition is intense (Beaugrand et al. 2013), like it occurs with reef corals (Chadwick and Morrow 2011). As a final point, it is unknown how evolutionary processes may increase or decrease the morphological variability and modify the physiology of reef corals in the future, and thus what would be their potential functions in reefs. The possibility clearly exists if we consider that global change and other strong drivers may be increasing the speed for speciation in the sea (Laugen et al. 2014). For instance, in the genus *Pocillopora*, a shift of zooxanthellate type was observed in the Eastern Pacific due to a mass mortality of symbiont populations of clade C (LaJeunesse et al. 2010).

The relation of the number of species present in a region and the amount of morphological groups (Fig. 7) behaves very differently to what was observed with the total number of groups per region. The average number of species per MFG in all regions of the western Atlantic is 6.97 (sd = 1.93), assuming this implies high ecological redundancy and high resilience to perturbations. Following this line of thought, it is possible that, for this reason, it took over 500 years of continuous

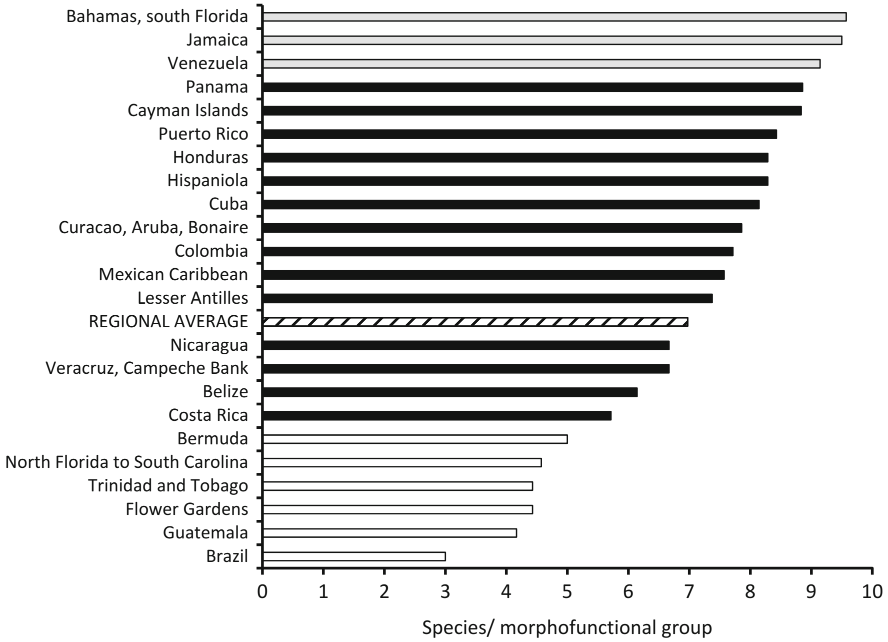

Fig. 7 Quotient of the number of species and of morphofunctional groups of reef corals present at each region of the western Atlantic. *Black bars* are values included in an interval of one standard deviation from the mean, *white bars* are those reefs in which the quotient is one deviation lower than the average or less, and *gray bars* are regions with values higher than one deviation from the mean

human use and natural perturbations, to cause significant ecological modifications to the system, like the ones we observe since the 1970s but that actually have been accumulating in time (Jackson 1997; Jackson et al. 2014). However, the ecological view, based on just a few decades observations, also points out that the system functioning thrives on just a few builder species and wiping out any of them seems to generate an ecological catastrophe. In this sense present species diversity seems more a result rather than a structuring driver, and therefore there seems to be little or no functional redundancy at the ecological time frame.

In a smaller scale, the highest values of species/MFG occur at Bahamas and south Florida (9.57), Jamaica (9.5), and Venezuela (9.14), while the lowest are in Brazil (3.00), and also there are four regions with 4.17–4.57 spp./MFG (the subtropical USA, Flower Gardens Bank, Guatemala, and Trinidad and Tobago). This evidence calls for a very different level of tolerance to perturbations depending on the region of the western Atlantic. To address this observation, we used the average and standard deviation values of the quotient species/morphofunctional groups, in order to classify which regions are in a best condition from the perspective of their redundancy (Fig. 8); those with values of spp./MFG higher than one deviation are considered as the most resilient, while if the region value of the quotient is lesser than one deviation, it may be much more susceptible to suffer ecological changes either by the loss of species or the reduction of their abundances to a level that the population is not able to adequately fulfill its role in the ecosystem, as has been the case with sharks (Ferretti et al. 2010) and probably sea turtles and other large vertebrates (Jackson 1997). Figure 8 shows the result of this test. As observed, there are six regions where resilience of the zooxanthellate coral assemblages may be less than average: Brazil, Guatemala, Flower Garden Banks, Trinidad and Tobago, the subtropical USA, and Bermuda. All are either placed in the northern or southernmost limit of presence of

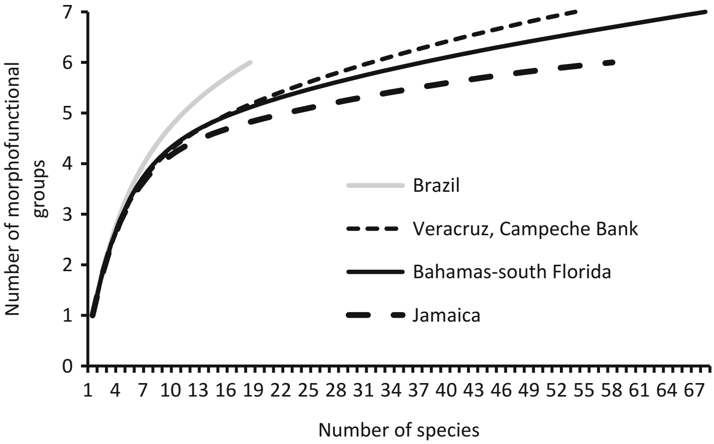

Fig. 8 Curves showing the number of morphofunctional groups of reef corals left in four regions of the western Atlantic, in relation to local extinction of species. The graph should be read from *right* to *left*, in order to consider the consecutive loss of taxa

corals in the region, or instead (the case of Guatemala), the local environmental conditions are deleterious for the development of reefs (Fonseca and Arrivillaga 2003). In these regions, there are at least three morphological groups with just one representative species (usually groups 1, 8, and 9, including species such as *Helioseris cucullata*, *Scolymia* spp., and *Cladorora* spp.; Table 4). This way, the loss of only three species would cause a 43% reduction in the number of morphological groups (Trinidad and Tobago, subtropical USA, and Flower Gardens; from 7 to 4 MFG) and a 60% depletion in Bermuda (from 5 to 2 groups). Other 14 regions are around the average in their species/MFG quotient, indicating that they may be considered as in the same level of resilience to stress. Finally, three areas were pointed out as potentially the most resilient to perturbations: Jamaica, Bahamas and south Florida, and Venezuela.

The latter two cases are interesting because the status of the reefs at Bahamas and Venezuela has usually been taken as good (Pandolfi et al. 2005; Rodríguez-Ramírez et al. 2008), even in the face of bleaching events (Eakin et al. 2010; Bastidas et al. 2012). This may be because the level of human pressure on the systems is not elevated or management is very adequate (in Bahamas), or because in Venezuela the reefs are not exposed to the effects of hurricanes and conservation is successful, to the point that there are no differences in reefs on the mainland or in insular marine parks (Cróquer et al. 2010). On the contrary, the status of Jamaican corals is completely opposed and has been poor since decades ago (Jackson et al. 2014), because of the unusually high level of human use, combined with natural perturbations like the mass mortality of the sea urchin *Diadema antillarum*, coral diseases, and the mass mortalities of *Acropora* spp. populations (Wilkinson 2006; Jackson et al. 2014). The discrepancy of our results and the current situation may be due to the fact that data from Table 4 do not include relative cover of the species, and there is no reported local extinction of any coral species in the island. Only with qualitative information it is improbable to have a clear idea of the local level of coral reef resilience. For these reasons, the logical next step to improve our findings is to repeat this analysis more in depth, taking coral species abundance in order to best quantify the ecological status of the "reef forests" in the western Atlantic.

A final comment related to the relationship between species richness and the number of morphological groups present in a given region is that they behave linearly ($a = 0.8974$, $b = 0.1292$, $r^2 = 0.92$, $p = 0.013$), and thus, the number of corals in a regional species pool can be taken as a good indicative of the quantity of functions that they perform. Similar results have been presented for other marine taxa (Mora et al. 2011; Rojas-Montiel et al. in press) and reinforce the use of species richness as proxy for system function, making evident that this is a simple but powerful measure of biodiversity.

The numerical analysis executed showed that coral reefs in the western Atlantic have probably filled its ecological space (considering current environmental and biological conditions), and that because of the wide dispersal of most species along the region, the number of morphofunctional groups present at each one is about the same everywhere. The average number of coral species per MFG in the biogeographic region investigated is almost 7, which allows to infer high ecological redundancy and hence resilience to perturbations. Notwithstanding, some areas in the northern and southern margins of the western Atlantic have much less resilience, as the number of species per MFG is of 4.6 or less; there, as three groups are represented by only one species, the probability of the regional ecosystem to suffer damages for any perturbation is high.

4 Current Threats Affecting Caribbean Coral Reefs

The last 50–30 years evidence that corals and coral communities are facing a severe stress due to deterioration of their environment. The degree of deterioration is locally variable and multifactorial, but surface ocean warming, acidification, eutrophication, pollution, and overexploitation seem to be the main drivers (IPCC reports). The suspected increase in hurricane intensity (Bender et al. 2010) due to global warming, in combination with the other drivers of environmental degradations, may represent a further threat as local recovery capacity may be further diminished by suboptimal environmental conditions.

More likely, the major effect of this negative environmental change is the proliferation of lethal emergent diseases in corals that, whether pathogenic or environmental such as thermal bleaching (Glynn 1993), are able to produce mass killings of key species (Harvell et al. 2007; Peters 2015), generating catastrophic community changes. The severe impact of these diseases and syndromes seem to be related to depressed immunity induced by the new suboptimal, stressful environmental (Reed et al. 2010; Palmer et al. 2011).

The two major ecological disease-driven catastrophes, ever registered, occurred in the 1970s and early 1980s affecting all reefs in the Greater Caribbean. One was the mass mortalities of *Acropora palmata* and *A. cervicornis* (Aronson and Precht 2001), perhaps the most important scleractinian reef-builder corals in the region by a syndrome named white band disease (Peters et al. 1983). The other was the mass mortalities of the sea urchin *Diadema antillarum* (Lessios 1982), one of the most important herbivores in the region. Both events were presumably caused by pathogens, that are still unidentified, but the massive mortalities amounted to an ecological catastrophe, which may even have serious economic repercussions. The main ecological role of *A. palmata* and to a lesser degree that of *A. cervicornis* has been explained above, but its loss also affects the environmental services that the reef provides (Alvarez-Filip et al. 2009). Whenever fringing and extended fringing reefs are present (the most common reef type in the Caribbean Sea), this species plays a major role in protecting the shoreline by stabilizing beaches and minimizing damage to infrastructure, but at the same time generates an adequate environment for the many beach and water recreational activities that constitute one of the main services for the tourism industry in the region.

The impact of *D. antillarum* mass mortalities amounted to a potential phase shift from coral-dominated to algal-dominated reefs (Lessios et al. 1984), because this sea urchin became a key species in controlling algal growth as overfishing of herbivorous fishes, all over the Caribbean, resulted in a loss of algae controllers (Jackson et al. 2014). In the absence of herbivores macroalgae are able to overgrow and or smooth scleractinian corals, while at the same time preempting successful recruitment of coral larvae due to the extensive mats covering the hard substrate (Jackson et al. 2014). For many authors this has led to community phase shifts (Hughes 1994; Dudgeon et al. 2010), which may be long lasting as eutrophication of the coastal zones enhanced algal growth, which is much faster than that of scleractinian corals. However, there are reports that question the generalization of these phase shifts Caribbean wide (Croquer et al. 2016). Recent reports of recovery of *D. antillarum* (Jordán-Garza et al. 2008) as well as of *A. palmata* are appearing (Zubillaga et al. 2008; Rodríguez-Martínez et al. 2014), while *A.cervicornis*. However, environmental conditions do not improve, and further catastrophic impact by emergent diseases can't be ruled out. In fact, the other major reef builders in the Caribbean, the species of the massive genus *Orbicella*, are being gradually decimated by the yellow band syndrome (Cervino et al. 2008), a slow-spreading disease killing a rather slow-growing host. Aside from scleractinians, many other important species in the reef ecosystem are being severely impacted by emergent diseases including gorgonians, algae, particularly the important reef-binder crustose coralline algae, fishes, sponges (Harvell et al. 2009), and important fisheries species as lobster (Lozano-Álvarez et al. 2008).

But unfortunately there are other additional threats to the well-being of coral communities in the form of invading species. One is the lionfish, *Pterois volitans*, an efficient predator from Pacific reefs, which was irresponsibly introduced in the temperate western Atlantic (Schofield 2009) and that eventually invaded the Caribbean, where it has no natural enemies. The main concern with the lionfish is the potential overpredation of small fish, mostly juveniles, that can cause severe damages an already overfished system which icthiofauna was already depleted (Paddack et al. 2009).

Another threat is the formation of dead zones in base erosional platforms normally adequate for coral biota, in areas of heavy eutrophication and poor water movement. Although most known areas are related to the Mississippi area, a nonreefal zone in the Gulf of México, several personal observations, not yet published, indicate the existence of dead zones in Caribbean islands and the Panamá coast.

And yet another less understood phenomena and its effects on the shallow reef communities are the recent and sporadic formation of massive drifting masses of Atlantic *Sargassum* species that reach Caribbean shores, clogging small embayments and pileup on beaches. Although drifting *Sargassum* spp. is not uncommon in the Caribbean, these very large masses seem to arrive from a new "Sargasso sea," north-west of the Lesser Antilles (Gower et al. 2013). Decomposition of these large masses result in the release of noticeable amounts of H_2S and nutrients, and darkening of the clear-crystalline Caribbean shore waters may have a strong impact on photosynthetic organisms. All these effects have already have had a serious deleterious effect on the tourism industry in many Caribbean localities all over the region, because recreational beach activities are seriously impaired.

What would be the effect of all these stressors and catastrophes? To address this point of interest we extended the morphological analysis into the future, with a straightforward question: What would be the effect of the loss of species to the structural completeness of the reef forests of the western Atlantic? To do so, we used two approaches; the first one was to apply a model of random extinction of species at each one of the 23 study regions, in order to quantify the rate of loss of functions per species locally extinct. In this case, we used the method proposed by Fonseca and Ganade (2001), whose basic equation is analogous to that of a rarefaction curve, and simulate the expected number of morphological group's loss at any number of species extinctions. The basic data for each region of study corresponded to the total number of species, the total amount of morphological groups present, and the correspondent number of species at every group. The original method proposes to perform comparisons of the curves on the basis of the percentage of morphological groups disappeared after a 10%, 50%, or 90% loss of species, but in our case we changed this perspective, and took in consideration the whole curve. To do so we fit the data from the simulation to an exponential curve (model: number of morphological groups = ordinate + [(slope * ln(number of species)], because in all cases, the determination coefficient was higher than 0.98. Then, the slope was taken as the indicator of the effect of extinctions because a higher value represents the loss of more functions in the system when a certain number of species are gone.

The second procedure was based on the evaluations presented by the Red List of the International Union for Conservation of Nature. A series of studies (Isaac et al. 2007; Mace et al. 2008; Mooers et al. 2008) have translated the level of danger in which a species was classified, into the probability of extinction by the year 2100 using fuzzy logic, and all coincide in affirmation that the most imperiled taxa are those catalogued in the following status: critically endangered, endangered, and vulnerable (see http://www.iucnredlist.org/ for explanation of the criteria used to qualify the taxa in these categories). Under this supposition, we deleted from the database the 10 species that fulfill the criterion of highest probability to be extinct during this century: critically endangered: *Acropora cervicornis*, *A. palmata*; endangered: *Orbicella annularis*, *O. faveolata*; vulnerable: *Agaricia lamarcki*, *Dendrogyra cylindrus*, *Dichocoenia stokesi*, *Orbicella franksi*, *Mycetophyllia ferox*, *Oculina varicosa*. The combination of the classification in the Red List (numerically translated into the probability of extinction) and the level of rarity of each species determined by the number of million years of evolutionary history that each lineage represents in a cladogram including all species of interest is known as the "EDGE index" (meaning "evolutionary distinct and globally endangered"), and was applied by Huang (2012) to resolve which coral species might have priority in conservation efforts. Huang and Roy (2013) use it to determine that the loss of species due to bleaching and disease would cause the largest negative effect on the phylogenetic history in Scleractinia (as the most susceptible species to these agents are corals with relatively old lineages). Further, Huang and Roy (2015) assert that ecoregions with very high phylogenetic diversity but with low number of species (like Hawaii or the eastern Pacific) would be much more affected by loss of species in high levels of the Red List, than those with the highest species richness, in which the loss is minor.

An example of four curves produced by the simulation of random extinctions is presented in Fig. 8. The graph indicates how in the case of Veracruz-Campeche Bank, the Bahamas and south Florida, and Jamaica the local disappearance of about half of the resident coral species would only cause the loss of about one morphological group; this is a direct consequence of the high ecological redundancy of the local reef coral assemblages. However, in all cases if richness is reduced to about 15 species, then the community would be put in a very difficult situation, as the loss of local populations of any species may have much stronger relative effects. In the case of Brazil, with a total richness of only 18 species in six morphological groups, the effect of local extinctions is amplified. The main message here is that considering the coral assemblages in full, the model predicts that it would take an event (or several events) of large magnitude to extirpate enough species in any single region, in order to evidence a real modification of the functioning of the reef forest. As we mentioned earlier, so high resilience can explain why we are seeing clear damages on the reefs until these days and after centuries of indiscriminate exploitation of the ecosystem. This conclusion seems to be at odds with what we have witnessed in many Caribbean reefs (phase shifts from live coral to algae, diminished rate of carbonate production, virtual local extinction of *Acropora* spp.; Alvarez-Filip et al. 2013; Perry et al. 2013); however let's not forget that the scale does not directly correspond and that the analysis presented here may be more adequately interpreted thinking in areas of large sizes, where metapopulation dynamics control connectivity and recovery (Foster et al. 2012). The results then might indicate that although local damages occur, the possibility to maintain enough colonies in an impacted region can serve as an insurance, if the sources of the metapopulations are, for example, nearby and in protected areas (Mumby and Harborne 2010), and if coral cover is relatively low (to lower competition for space; Graham et al. 2011). It is possible that this hypothesis helps explaining why even when the situation is dire, nevertheless there are positive signs like the increase in abundance and size of *A. palmata* in Colombia, Venezuela, and at the Veracruz reef system, in Mexico (Zubillaga et al. 2008; Bayraktarov et al. 2013; Rodríguez-Martínez et al. 2012; Larson et al. 2014).

Returning to the results of this paper, and considering the random extinction model of reef corals, the slopes of the exponential model for all regions of interest are presented in Fig. 9, and for interpretation and as in other sections of this chapter, we used the average value for all 23 regions and its standard deviation (1.528 ± 0.188) as the measure of which sites would be in better or worse condition than the rest. The data indicate that in three areas, random extinction of species would have the lesser impact (Jamaica, Cayman Islands, Bermuda), while the opposite occurs in the case of Brazil, Flower Gardens, the subtropical USA, Trinidad and Tobago, and the Lesser Antilles. In these late cases the slope is more than 40% higher than in the previously cited three areas, indicating that the local extinction of any coral would have a much more relevant relative impact.

The second method, in which the scenario stipulates the extinction of the 10 more endangered coral species that inhabit the western Atlantic (Fig. 10), reveals that the

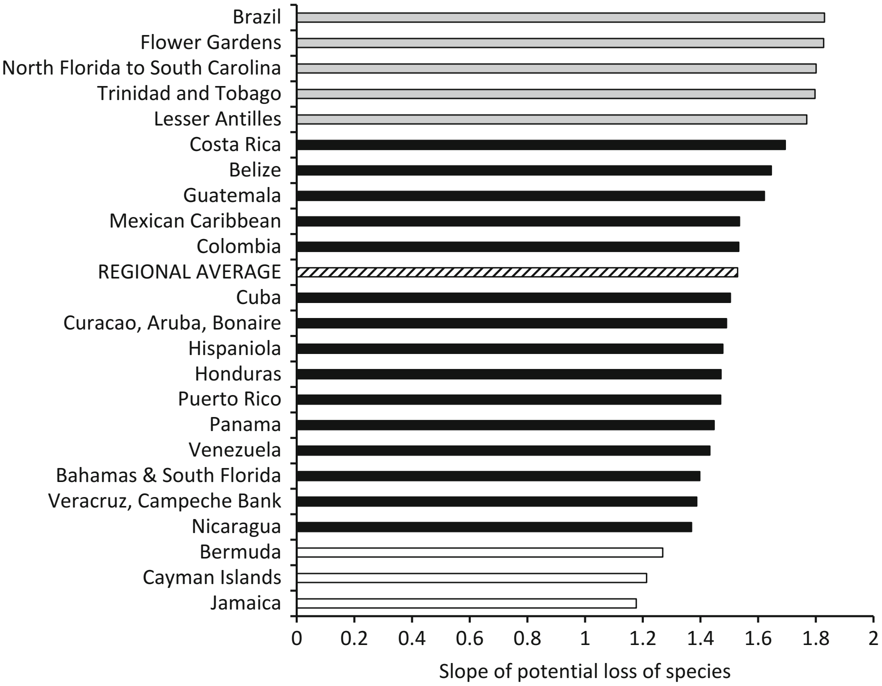

Fig. 9 Slope of the exponential regression that best modeled the extinction curve of reef corals in all studied regions of the western Atlantic

average number of species per region would change from 47.0 to 39.6 (a mean of 7.4 species less per region), but notwithstanding, no region suffers the loss of a single morphological group under this scenario. The basic reason why this occurs is that the species considered belongs to clusters with many representatives (groups 2, 3, 5, and 10; see Fig. 2). The four most impacted regions would be Bahamas and south Florida, Cuba, Puerto Rico, and Venezuela, where the 10 most threatened species resides, and the subtropical USA, Bermuda, Guatemala, the Flower Gardens, and Costa Rica would decrease its species richness in just 3–5 species. And in contrast Brazil's diversity will not decrease at all under this circumstance. The operative conclusion reached is that the effect of the elimination of the endangered corals may not have a distinct effect on general function of the reefs, but nevertheless the result should be taken with care, as specific functions are relatively more conspicuous or relevant than others in an ecosystem view (e.g., carbonate production vs. feeding to associate invertebrates). For that reason, future analyses should be conducted looking specifically for indicators of each specific function and pondered.

To present a final view of this section, we hierarchized the position of the regions for both the extinction slope and the number of Red List species lost, and summed the ranks; this way, regions with the highest value can be considered as more resilient to extinctions (random or directed) than others. The gradation was done using the mean and standard deviations of all data. The results appear in Fig. 11 and show that

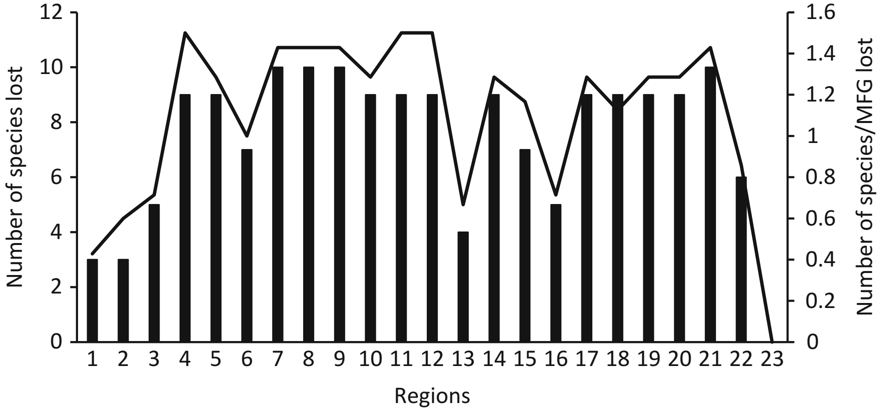

Fig. 10 Number of species loss, and change in the resilience (indicated by the number of species per functional group), if the ten most endangered reef coral species of the western Atlantic (according with the Red List of IUCN) become extinct. Key for locations: (1) Subtropical USA (north Florida to South Carolina); (2) Bermuda; (3) Flower Garden Banks; (4) Veracruz, Campeche Bank; (5) Mexican Caribbean; (6) Belize; (7) Bahamas and south Florida; (8) Cuba; (9) Puerto Rico; (10) Hispaniola; (11) Jamaica; (12) Cayman Islands; (13) Guatemala; (14) Honduras; (15) Nicaragua; (16) Costa Rica; (17) Panamá; (18) Lesser Antilles; (19) Curacao, Aruba, and Bonaire; (20) Colombia; (21) Venezuela; (22) Trinidad and Tobago; and (23) Brazil

Bermuda, Nicaragua, Jamaica, and the Cayman Islands are the reef regions with more probabilities to resist human and/or naturally induced extinctions, while the Lesser Antilles and Cuba are in the worst position. From the analysis, and the susceptibility of the last two regions, we suggest that conservation efforts have to be conducted taking the priority on the entire western Atlantic.

5 General Conclusion

Given that the rate of human population growth in coastal reef-areas is not diminishing and neither are eutrophication, pollution, overfishing, and global climate change stresses, unavoidable questions about the future of the coral reef system in the Caribbean prevail in both scientific and management practitioners. However, coral reef science capability to predict the possible outcomes, with some acceptable likelihood, is still hampered by evolving theoretical concepts and by insufficient knowledge of the dynamics of key processes in ecological and biogeographic coherent spatial time frames.

The historical and biogeographic models presented here provide a fundamental input into our view of the Caribbean reef at large scales. The dynamics of millions of years suggest that it would take an event (or several events) of large magnitude to extirpate enough species in any single region to evidence a real modification of the functioning of the Caribbean reef system; the metapopulation dynamics likely determine the extent of connectivity and recovery. This historical based line of

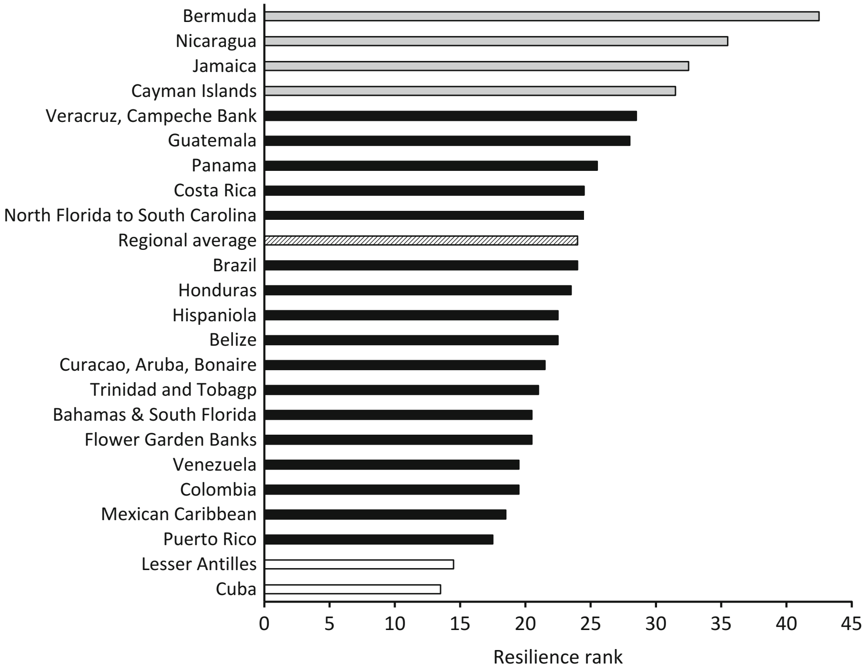

Fig. 11 Results of the sum of ranks from the analyses of random and directed local extinction of corals, for the 23 studied regions of the western Atlantic

thought suggests also that it is unlikely that corals, or coral biota, will disappear, but to what extent the Caribbean reef scleractinian fauna as a whole will be resistant to present changes in environmental conditions remains an open question.

Although coral reefs are rather complex high diversity systems, functionally the Caribbean reefs, at least at the local scale, resemble more to a forest than a jungle, in the sense that there are few key structural species. Therefore, local condition and abundance of these few key species determine, or heavily influence, the extent of many ecological processes and in the much shorter economical time frame reef services and goods, upon which the tourism economy of many reef sites in the Caribbean heavily depends, may be locally affected threatening local livelihoods.

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Brazilian Marine Animal Forests: A New World to Discover in the Southwestern Atlantic

3

Marcelo de Oliveira Soares, Tito Monteiro da Cruz Lotufo, Leandro Manzoni Vieira, Sula Salani, Eduardo Hajdu, Helena Matthews-Cascon, Zelinda M. A. N. Leão, and Ruy Kenji Papa de Kikuchi

Abstract

The Southwestern Atlantic Ocean is the final Brazilian maritime frontier. The Brazilian authorities refer to this marine area as the “Blue Amazon,” being rich in biodiversity and ecosystem services and similar in extension to the country’s rainforest. This area is possibly one of the most important benthic biodiversity hotspots in the world; however, there is a lack of scientific knowledge about its marine biodiversity. Interestingly, these benthic communities generate three-dimensional structures along the Brazilian coast, similar to the trees in the Amazon rainforest. The Brazilian marine animal forests (BRAF) in the “Blue Amazon” can be compared to their rainforest counterpart: an ecosystem with high

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diversity but relatively unknown. This chapter presents a review of the environmental characteristics and benthic habitats along the tropical coast of Brazil (coral reefs, intertidal sandstone reefs, benthic communities in rocky shores, continental shelf communities, oceanic islands, etc.). Furthermore, it presents synthetic information regarding the ecology and diversity of the benthic suspension feeders (sponges, scleractinian corals, octocorals, zoanthids, mollusks, ascidians, and bryozoans) in Southwestern Atlantic. Major knowledge gaps remain the baseline research on benthic communities in mesophotic and deep-sea reef ecosystems in this marine region. Finally, this chapter reviews the major anthropogenic threats (urbanization, aquaculture, invasive species, mining, climate change, and petroleum and gas exploration) and makes recommendations for further research and conservation programs.

Keywords
Marine environments • Tropical ecosystems • Benthic biodiversity • Conservation • Brazil • Southwestern Atlantic • Coral reefs • Benthic suspension feeders • Sponges • Ascidians • Bryozoans • Mollusks • Cnidarians

Contents

1 Introduction

The Southwestern Atlantic (SW Atlantic) Ocean is the final Brazilian marine frontier. The Brazilian authorities refer to this marine area as the “Blue Amazon,” being rich in biodiversity and ecosystem services and similar in extension to the country's tropical rainforest. This marine area is one of the most important (and largely unknown) benthic biodiversity hotspots in the world. Improving the knowledge of species diversity is a major challenge, particularly given the geographic size of the area, environmental diversity, and the high rates of benthic endemism (Longo and Amado-Filho 2014). There is in fact a lack of scientific knowledge regarding the biodiversity, biomass, abundance, and ecosystem services (e.g., fisheries, tourism value, or three-dimensional structures such as carbon sinks) of the area.

For terrestrial environments, the general concept of forests is defined as an ecological system in which trees (plants) are abundant and dominate the landscape (e.g., rainforest). In marine environments, many benthic ecosystems show the same level of three-dimensional complexity, biodiversity, and ecosystem services (carbon sinks, nursery, or refuge areas), but seascapes are dominated by sessile animals. Rossi (2013) referred to these animal-dominated ecosystems as animal forests, including sponges, cnidarians (hydrocorals, hydrozoans, anthozoans), bryozoans, mollusks, and ascidians, which are considered "eco-engineering" or "foundation" species based on their ability to modify seafloor habitats. These benthic species are primarily responsible for the structuring of animal forests, which may have high biodiversity, are unknown, and are threatened ecosystems, including those of the SW Atlantic Ocean.

The Brazilian marine animal forests (BRAF) (Fig. 1) in the "Blue Amazon" can be compared to their rainforest counterpart, an ecosystem with high diversity and biomass but relatively unknown. In recent decades, research in the Amazon rainforest has increased due to national and international interest in tropical biodiversity and the importance of the ecosystem services offered (e.g., climate regulation); however, this has not been the case for BRAF. Therefore, BRAF needs increased public attention and funding for the development of basic applied research and conservation programs. The Brazilian population (with over 200 million people) is unevenly distributed; unlike the low population density in the Amazon, the coastal zone has a high population concentration, especially Northeast and Southeast Brazil. Most large cities are located on the coast and have shown rapid urbanization and tourism growth, which combined with other human activities, such as overfishing and oil exploration, creating significant cumulative human impacts (Halpern et al. 2015). These anthropogenic activities need more effective environmental planning to mitigate their impacts, considering the importance of ecosystem services provided by marine animal forests (sensu Rossi 2013).

In this chapter, the environmental characteristics (tides, currents, sedimentology, waves, etc.) of the tropical coast of Brazil and the diversity of coastal benthic habitats will be described to present a synthesis of the current knowledge. The chapter also presents information on the ecology and knowledge of biodiversity related to benthic suspension feeders in different marine ecosystems (coral reefs, sandstone reefs, benthic communities in rocky shores, continental shelf communities, oceanic islands, etc.). Ascidians, sponges, bryozoans, hydrocorals, zoanthids, scleractinian corals, octocorals, and mollusks are among the most important animal ecosystem

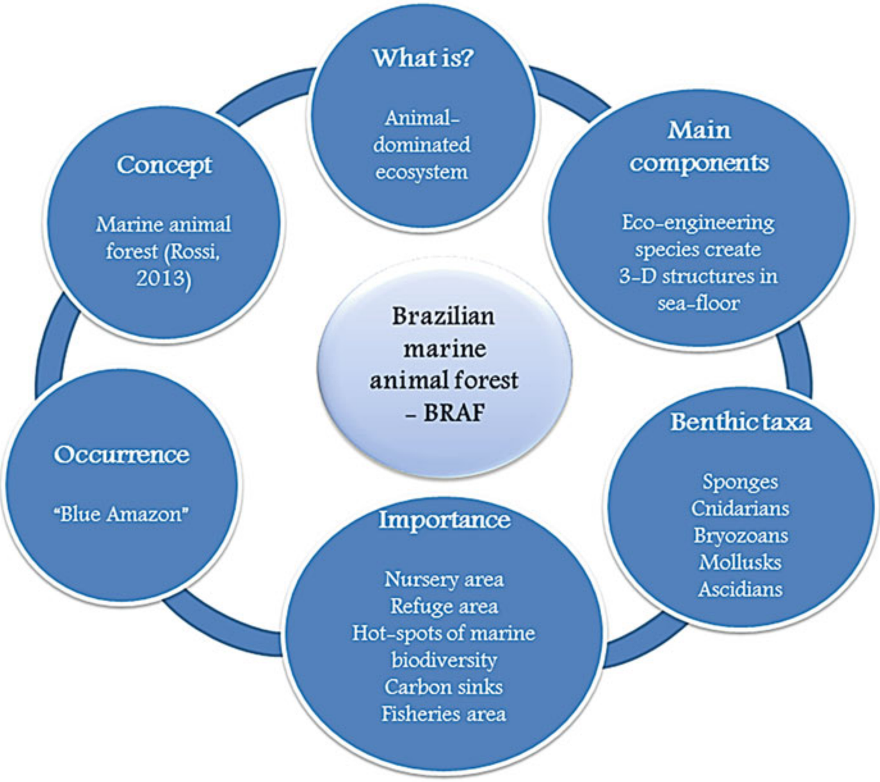

Fig. 1 Brazilian marine animal forest (BRAF): concepts, definition, benthic taxa and occurrence

engineers in the tropical coast of Brazil. The study of benthic communities in mesophotic and deep-sea reef ecosystems in this region still has major knowledge gaps in baseline and applied research. We aim to provide keys to develop future research and conservation plans related to these poorly known areas. Considering the local and global human impacts, the major threats to BRAF are reviewed, such as coastal urbanization, aquaculture, exotic species, mining, fishing, and the effects of climate change. Recent developments such as the emerging industry of petroleum and gas in deep waters and the environmental impacts at the land-sea interface are discussed to improve the knowledge regarding the need to adopt conservation programs for BRAF. Considering the lack of knowledge of basic aspects, the chapter makes recommendations for further research using new oceanographic technologies. Finally, important conservation programs for public policies are discussed, such as the effective implementation and expansion of marine protected areas (MPAs) and rigorous environmental monitoring in the large "Blue Amazon."

2 Tropical Coast of Brazil: Environmental Characteristics and Benthic Habitats

One of the most important aspects in understanding the diversity and distribution of BRAF is the environmental characteristics (geography, tides, currents, waves, and sedimentology) that affect benthic habitats. The continental shelf along the tropical region of Brazil, from 3° S to about 20° S is an oligotrophic environment with little influence from river runoff and only locally subjected to eddy-induced shelf-edge upwelling (Fig. 2). Thus, it is among the least productive ocean margins of the world (Dominguez et al. 1992). It comprises two sectors in terms of the shelf width, namely, the Northeast and East. The Northeast sector can be further subdivided into three parts considering the coastline trend and wave regime: northern, central, and southern Northeast. The narrow part (Northeast sector) spreads from the region of the Parnaíba River (3° S) mouth to the Jequitinhonha River mouth (15° S) and the wide sector, from there to the Doce River mouth (20° S). The whole region is mesotidal and influenced by the South Equatorial Current that bifurcates at 10° S to form the North and South Brazil Current. Thus, the northern and central Northeast sectors are influenced by the North Brazil Current (flows northwestward), while the

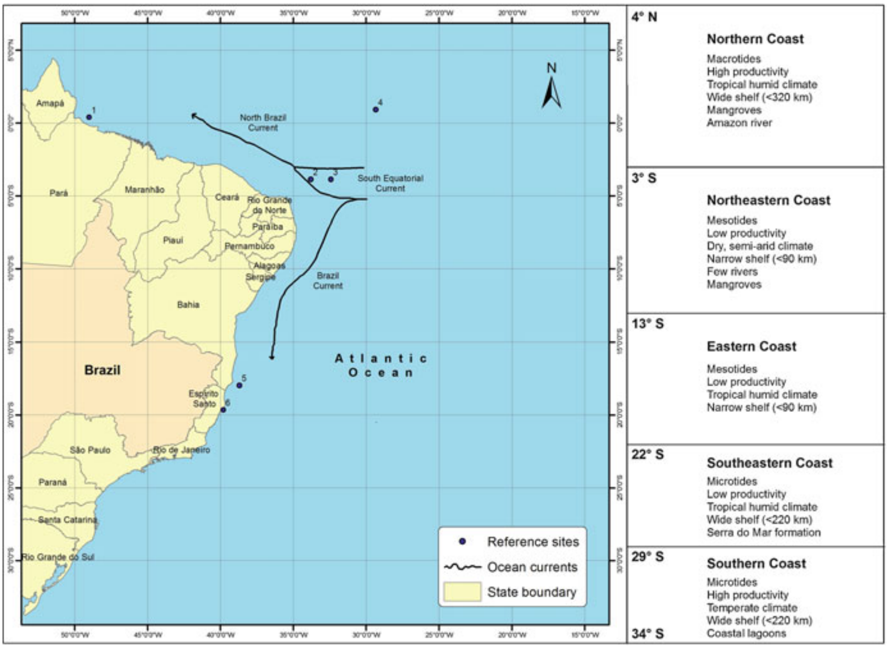

Fig. 2 Main oceanographic and climate characteristics of the Brazilian coast, including the tropical Southwestern Atlantic (Modified from Santos et al. (2008))

East sector is within the range of the Brazil Current, flowing southward. Along most of its narrow extension, the shelf is about 50 km wide. However, the East sector widens forming two banks called the Royal Charlotte and Abrolhos Banks, where its width reaches approximately 200 km. The shelf break is generally at a depth of 80 m.

The Brazilian Current (BC) and the North Coastal Brazilian Current (NCBC) are the main surface currents on the Brazilian continental margin (Stramma 1991; Silveira et al. 1994; Fig. 2). They originate from the South Equatorial Current at about 5–6° S and flow to the south (BC) with average velocities of 50–70 cm s^{-1} and to the north and northwest (NBC) attaining velocities of 30 cm s^{-1}. Data from the Atlas de Cartas Piloto (DHN 1993) show that between 10 and 13° S, during July and August (austral winter), a reverse flow to the north can occur. North of 5° S, the NCBC becomes strong because of combining with the South Equatorial Current.

The oceanographic and climatic processes that occur in the tropical region of Brazil are controlled by three elements: (i) trade winds associated with air masses generated in the South Atlantic high-pressure (SAHC) cell, (ii) advances of polar air masses, and (iii) the Intertropical Convergence Zone (ITCZ). A divergence zone of trade winds occurs in the southern part of the SAHC, and northeasterly winds dominate in the south of this zone. A seasonal variation of this cell produces a north-south oscillation of the divergence zone between 10° S and 20° S. This divergence zone moves northward during summer and southward during winter. Thus, easterly and southeasterly winds dominate year-round the coast north of 13° S (Northeast sector), with speeds ranging from 5.5 to 8.5 m s^{-1} (US Navy 1978). South of 13° S (East sector and the southernmost part of the Northeast sector), the easterly and southeasterly winds blow during fall and winter (April to September), and the northeasterly winds prevail during spring and summer (September to February), with the wind speed rarely above 5.5 m s^{-1} (US Navy 1978). The Antarctic polar front moves northward across the South American continent, east of the Andes Mountains, as great anticyclones, and splits into two branches. The eastern branch moves along the coast toward the Equator and can reach as far as 10° S during winter but, rarely, reaches latitudes lower than 15° S in summer (Dominguez et al. 1992). The advance of this polar front also generates additional south-southeasterly winds, which reinforce the southeasterly winds generated by the anticyclone high-pressure cell (Dominguez 2009).

Wave patterns are controlled by variations in the trade winds, in relation to movements of the offshore high-pressure centers. This region is mainly dominated by sea waves (periods of <7 s). Those with heights >1 m account for more than 50% of the observations referred to in the U.S. Navy Marine Climatic Atlas (U.S. Navy 1978). In the Brazilian north and northeast coasts, the waves moving from the southeast dominate all year-round, and the waves from the east are important from January to May (summer–fall) and September to November (spring). However, the southernmost part of the northeast and east coasts is dominated by waves moving from the east during the whole year. Waves from northeast are only important from November to February (summer), and waves from southeast occur from March to August (winter). Thus, waves effectively enhance water circulation in the southern part of the northeast and east coasts. The north coast and the northernmost part of the northeast coast are protected from the main wave train year-round, affected only by a secondary wave train (waves from the east) from September to May.

Carbonate environments occur over the middle and outer shelves and in the inner shelf away from riverine influences. Reefs are common in shallow water along most of the shelf. In depths >30 m, mesophotic reefs and rhodolith beds are common, not only over the shelf but also on the surface of seamounts and oceanic islands (Amado-Filho et al. 2016, Magalhaes et al. 2015). Bioclastic carbonate gravel and sands (free-living non-articulated coralline red algae, maërl, *Halimeda*, benthic Foraminifera, and mollusk debris) are also important constituents in the inner shelf in many areas (Coutinho 1980; Dominguez and Leão 1998; Testa 1997; Testa and Bosence 1998, 1999) and not only in the middle and outer shelves, as was previously thought. More commonly, the inner shelf constitutes a typical mixing zone of siliciclastic and carbonate sediments; siliciclastic sediments originate from river discharge, coastal erosion, and reworked relict deposits of former lower sea-level stands, whereas carbonate sediments originate from locally produced grains produced by the growth and transport of calcareous organisms, such as red and green algae. Near the São Francisco River mouth (10°30′ S) (Fig. 2), the largest river in Northeastern Brazil, the carbonate sediment production is interrupted. In addition, the inner shelf of the south part of the eastern region, between the Jequitinhonha (15°00′ S) and Doce (19°40′ S) Rivers, is influenced by river discharges, and plumes of fine sediments occur up to 50 km offshore. In these areas, bioclasts occur only in the middle and outer shelves, and the main carbonate sediments are mollusk shells, benthic Foraminifera, debris of calcareous algae, bryozoans, echinoids, and more rarely, coral gravel. Reefs occur along the entire carbonate province. In the northernmost part, reef buildups are logistically more difficult to find and difficult to map in turbid waters. Near the shore patch and bank, reefs occur commonly within siliciclastic sandy to muddy sediments, both in the northeast (Testa 1997) and in east (Araujo 1984; Leão 1982; Nolasco 1987) sectors. Milliman and Barreto (1975) and Kikuchi and Leão (1998) documented the occurrence of drowned reefs at the shelf break.

Another important benthic habitat where animal forests occur is the Brazilian oceanic islands in the tropical SW Atlantic. The islands include Fernando de Noronha Archipelago, Rocas Atoll (the only atoll in South Atlantic), and Saint Peter and Saint Paul Archipelago (Fig. 3). These islands vary in size (e.g., the largest is Fernando de Noronha) and distance from the mainland (e.g., the most remotely located is St. Peter and St. Paul) and have a particular diversity and ecology of benthic suspension feeders. These environments in the tropical region of the youngest of the world's oceans (South Atlantic) constitute one of most important biodiversity hotspots worldwide. After decades of research, knowledge of insular diversity and biogeography is developing, with an increase in published scientific literature since 2000. These oceanic islands can provide evolutionary and ecological insights regarding the high biodiversity and numbers of benthic endemic taxa (e.g., sponges and ascidians).

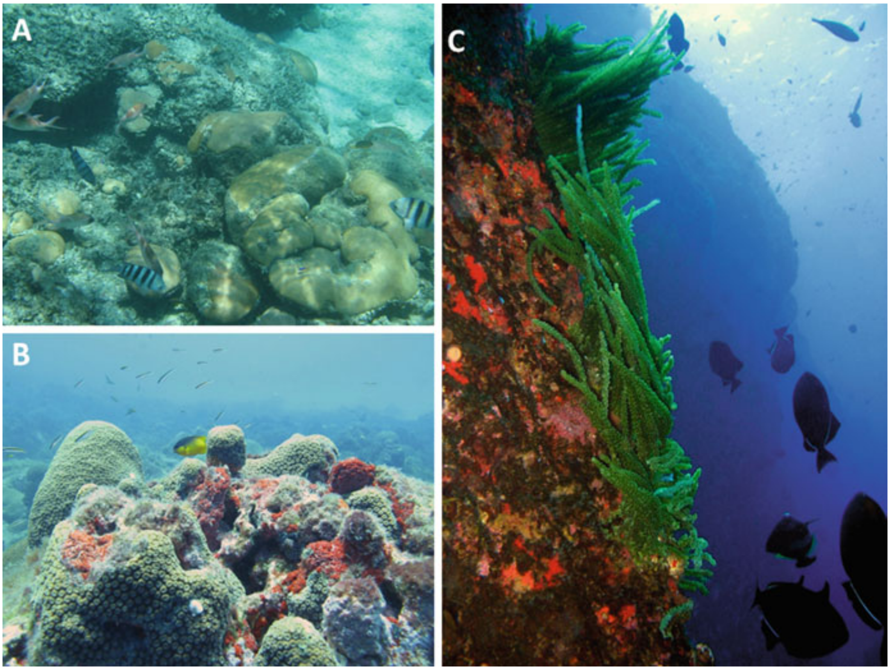

Fig. 3 Oceanic islands in Tropical Southwestern Atlantic (Brazil). (**a**) Rocas Atoll lagoon with reef fishes associated with endemic coral *Siderastrea stellata*. (**b**) Reef fishes and scleractinian coral in the Fernando de Noronha Archipelago. (**c**) Seascape of the remote Saint Peter and Saint Paul Archipelago (Photos from: M.O. Soares, T.M. Lotufo)

3 Benthic Ecology and Diversity: Eco-Engineers in BRAF

Sponges, cnidarians, bryozoans, mollusks, and ascidians, which are considered eco-engineering species, comprise the animal forests (Rossi 2013) that are present in shallow and deep waters in the coast of Brazil. In this section, the diversity and ecology of these animal groups in Brazilian waters are reviewed.

3.1 Porifera

Sponges are considered the oldest metazoans, with an origin estimated at about one billion years ago (Li et al. 1998), and are known for their beauty, species diversity, and variety of shapes and colors. They are exclusively aquatic, mostly marine, with some freshwater species. Widely distributed from the tropic to the polar regions, and the intertidal zone to greater depths, sponges are currently classified in five classes: Archaeocyatha (fossil), Calcarea, Demospongiae, Hexactinellida, and

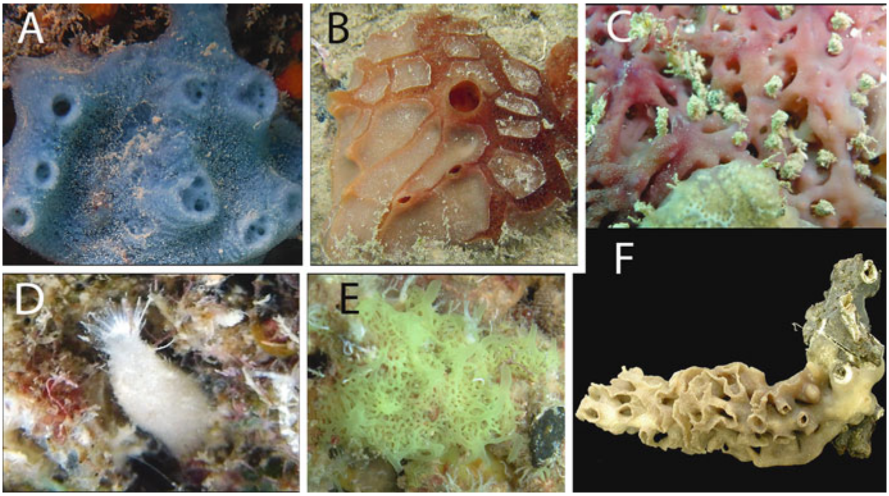

Fig. 4 Samples of Porifera class from Brazil. (**a**, **b**) Demospongiae (**a** – *Haliclona caerulea*, **b** – *Placospongia* sp.), (**c**) Homoscleromorpha (*Oscarella* sp.), (**d**, **e**) Calcarea (**d** – Sycon, **e** – *Clatrina aurea*), (**f**) Hexactinellida (*Farrea herdendorfi*). Photos from: (**a**) E. Hajdu, (**b**) S. Salani, (**c**) S. Salani, (**d**) B. Condor, (**e**) E. Hajdu, (**f**) D. Lopes

Homoscleromorpha. More than 8,700 species of sponges have been described to date, but their true diversity is certainly much greater (Van Soest et al. 2016; Fig. 4).

As comparatively simple, multicellular, sessile animals, their functional units are mobile and totipotent cells. The majority of sponges do not exhibit true tissues, with all known exceptions in the Homoscleromorpha (Ereskovsky et al. 2009). Most have a skeleton made of spicules (calcium carbonate or silica) and/or spongin fibers, sometimes reduced to spiculoids. They are mostly filter feeders, but carnivory also occurs in species that use particular spicules to trap prey, usually microcrustaceans (Vacelet and Boury-Esnault 1995).

The main reef builders in the present are corals and algae, but this has not always been the case. Sponges were the dominant constructors in the Paleozoic and Mesozoic (Hooper and Van Soest 2012) and can form banks similarly structured to coral reefs. Such sponge-dominated grounds are of great importance in some regions such as off the mouth of the Amazon, western Canada, Antarctic, and various areas of the boreal Atlantic. Sponges are associated with several microorganisms, algae, and metazoans, which use this habitat for shelter, nursery grounds, camouflage, and feeding. Sponges have developed powerful chemical mechanisms to defend themselves and mediate these relationships with other organisms (Pawlik 2011).

The frequency and variety of these ecological relationships are reflected in the important roles of increasing environmental three-dimensional complexity and consequently, biodiversity in general, notably in sciophilous habitats. Sponges can erode calcareous and other kinds of substrates, as well as cement reefs, transfer nutrients through the benthic–pelagic coupling processes (Bell 2008), participate in biogeochemical cycles (silicon and calcium carbonate), or contribute to primary production and nitrification by means of symbiotic cyanobacteria or unicellular algae (Rützler 1990). De Goeij et al. (2013) recently estimated that the role played by sponges in retaining DOM and releasing POM to the benthic food chain in reef environments, the "sponge loop," is the most important mechanism of carbon cycling in these ecosystems.

Deep-sea sponge does not have a detailed bio-regionalization as a result of the fragmented knowledge of their distribution patterns. Sponges have a marked preference for consolidated (or semi-consolidated) substrates as the ones near coral reefs, which generally have steeper slopes, and are on hills, submarine canyons, and the continental slope (Hogg et al. 2010). As the fossil record of sponges consists primarily of fused skeletons, and the majority of living sponges has disarticulated skeletons, investigations about their evolutionary history are mostly based on relationships inferred from the study of recent species (Reitner and Wörheide 2002).

Sponges exhibit the greatest biodiversity in the tropics. The greatest distribution pattern observed in sponge genera is Tethyan, i.e., occurring in all three oceans with distinct warm tropical diversity centers (van Soest 1994). Other important distribution patterns exhibited by sponge genera are austral, boreal, bipolar, and discontinuous. Some large distributions are repetitively seen in sponge species in the Atlantic-Mediterranean, Indo-West Pacific, and Tropical West Atlantic. Poriferans are essential for biogeographical cohesion in the latter region, because they form a structured environment at intermediate depths, considerably expanding environmental three-dimensionality, allowing the establishment and transit of species underneath the freshwater plume of the Amazon River, in a region dominated by muddy water flowing from the massive river system, and forming a biogeographic corridor for gene flow between the Caribbean and Brazilian fauna (Moura et al. 2016; Fig. 9).

According to Muricy et al. (2011), about 450 species of sponges have been described from Brazil. The state with the largest number of reported marine sponges is Bahia (141 species, with the Abrolhos archipelago), followed by São Paulo (98 species), Pernambuco (65 species, excluding Fernando de Noronha), and Rio de Janeiro (62 species). The states with the least species are Piauí (one species) and Paraná (three species). These numbers possibly reflect different sampling efforts and highlight the fragmented nature of the assessments. The main macroscale, shallow-water, distribution patterns of Brazilian marine sponges are the Tropical West Atlantic and endemic. The first reflects the large number of species currently shared with the Caribbean region (e.g., Van Soest and Hajdu 1997), and the second denotes a particular evolutionary history, where distinct barriers were expressed at different times, starting with the collapse of Gondwana and early opening of the Atlantic in the Cretaceous (Fernandez et al. 2012).

At least 108 species of marine sponges have already been identified from Brazilian oceanic islands, but many species still await detailed taxonomic study in scientific collections. The majority of these species (60%) is shared with the Caribbean region, and 16% are endemic (Moraes 2011; Muricy et al. 2011). Fernando de Noronha has the largest number of species (70 species), followed by Rocas Atoll

Fig. 5 Sponges from Brazilian coast. (**a**) *Desmapsamma anchorata*, (**b**) *Mycale angulosa*, (**c**) *Haliclona melana*, (**d**) *Monanchora arbuscula*. Photos from: (**a**) S. Salani, (**b**) E. Hajdu, (**c**) A. Bispo, (**d**) C. Castello-Branco

(47 species), Saint Peter and Saint Paul Archipelago (27 species), and Trindade Island (20 species). Despite the proximity of some islands, the number of shared species is relatively low. Rocas Atoll and Fernando de Noronha are 150 km apart but share only 30% of their sponge fauna. The large component of fauna shared with the Brazilian northeast (about 58%) is explained by the E–W direction of the South Equatorial Current and W–E direction of the respective countercurrent, which assures a relatively fast pathway for larval interchange between islands and the continent, no matter their preferred bathymetry.

However, at smaller scales, an irregular patchy pattern is observed, which translates into distributional heterogeneity, generating markedly different frequencies of occurrence in neighboring localities. Often, important gaps occur, even in the distribution of abundant species. For example, *Desmapsamma anchorata* and *Mycale angulosa* are very common in Bahia (and toward the north) and Angra dos Reis Bay (RJ) but are unknown in the Cabo Frio region (RJ). In part, these heterogeneous Patterns generally reflect the low dispersion capacity of sponge larvae (Hajdu et al. 2011). The southern distribution limits of some species of sponges south of Bahia are different (e.g., *Callyspongia vaginalis*, Bahia; *Haliclona melana*, São Paulo; *Tedania ignis*, Santa Catarina) (Fig. 5). These multiple southernmost limits in the distribution of tropical species have caused the area to the south of Bahia down to Santa Catarina to be considered transitional between the Tropical West Atlantic and subtropical Patagonian fauna (Hajdu et al. 2011).

Despite a recent increased effort in mapping Brazilian marine sponge diversity, the known species lists for the different sectors of the coast, including the deep sea, are still incomplete.

3.2 Cnidarians

Cnidarians are an important taxonomic group in marine biology, considering the importance of benthic (e.g., corals, octocorals, hydrocorals) and pelagic specimens (e.g., Scyphomedusae and Cubomedusae). The scleractinian corals, hydrocorals, octocorals, and zoantharians have a major function in marine animal forests due to the abundance and diversity of colonial species and the occurrence in tropical coral reefs, temperate coralligenous, mesophotic, and deep-sea ecosystems. Among the cnidarians, the scleractinian corals are the major framework reef builders (eco-engineers) that provide most of the structural complexity in the reef ecosystems. These corals grow into rocklike colonies that form the basic structure of coral reefs (Guest et al. 2012). Their symbiotic relationship with dinoflagellate algae (*Symbiodinium* sp.), provides sufficient energy to the coral polyps for survival and helps in the production of their calcium carbonate skeleton.

The Brazilian scleractinian coral fauna has the following three distinctive characteristics: (i) it is a low diversity coral fauna (23 corals and 5 hydrocorals) compared to that of the North Atlantic reefs, (ii) the major reef builders are endemic species to Brazilian waters, and (iii) it is predominantly composed of massive forms. These Brazilian corals were first described from species collected during scientific expeditions to Brazil in the nineteenth and twentieth centuries, with 18 coral and three hydrocoral species (Hartt 1868, 1869, 1870; Laborel 1967, 1969a, b). More recently, new coral and hydrocoral species have been described (Amaral et al. 2007, 2008; Neves et al. 2008, 2010). Two invasive coral species have also been included in the list of Brazilian coral fauna: *Tubastraea tagusensis* and *T. coccinea.* These invasive coral species have been described from reefs in Todos os Santos Bay (Miranda et al. 2016; Sampaio et al. 2012), rocky shores in Rio de Janeiro State (Creed 2006; Creed and De Paula 2007; De Paula and Creed 2004, 2005; Ferreira et al. 2013), and incrusting oil platforms in the states of Santa Catarina (Mantelatto et al. 2011; Riul et al. 2013) and Espirito Santo (Costa et al. 2014). To date, the cnidarian fauna of Brazil comprises 23 species of stony corals and 5 species of hydrocorals.

Hermatypic coral species are distributed along the coast of Brazil in four major geographic regions: northern, northeastern, eastern, and southeastern (Fig. 2). The northern marginal area occurs between the Amazon River mouth and Cape São Roque (0°30′ S to 5°29′ S). The northeastern area extends from Cape São Roque to the mouth of the São Francisco River (5°29′ S to 10°30′ S). The eastern area comprises the entire coast of the state of Bahia, from the mouth of the São Francisco River to the Doce River (10°30′ S to 19°40′ S), and the southeastern marginal area extends from the mouth of the Doce River to the coast of the Santa Catarina State

(19°30′ S to 27°30′ S). The major reef core area comprises the northeastern and eastern regions. The two marginal regions (northern and southeastern) were described as the north and south regions of impoverishment in hermatypic corals by Laborel (1969a).

Among the endemic species (Fig. 6), *Mussismilia braziliensis* and *M. leptophylla* show the greatest geographical confinement, because they are described only along the coast of the state of Bahia (the eastern region). However, *M. hispida* has the largest spatial distribution, occurring from Rocas Atoll (northeastern region) to the coast of Santa Catarina State (southern region). *Siderastrea stellata* and *Favia gravida* are the most common coral species in shallow intertidal pools of the reef tops and are considered resistant to variations in temperature, salinity, and water turbidity. *S. stellata* has a broad distribution along the Brazilian coast, from the reefs of the northern region to the coast of the state of Rio de Janeiro. *F. gravida* is a common species on the reefs from the northeastern and eastern regions. The cosmopolitan species *Porites astreoides*, *P. branneri*, *Agaricia agaricites*, *A. fragilis*, *Montastraea cavernosa*, and *Madracis decactis* are found in both Brazilian and Caribbean reefs. In Brazilian reefs, they have a secondary role in the construction of the reefs located on the northeastern and eastern regions. *M. cavernosa* shows phenotypic variation with depth. The shallow forms (<5 m) are hemispheric, and those found on the lateral walls of the reefs at depths >5 m may be flattened and encrusting. *Meandrina braziliensis* has two morphological variations: a free-living form that inhabits sandy bottoms and a fixed form, attached to the reef walls. It has a wide distribution along the Brazilian coast, from the northern region to the southernmost portion of the eastern region. The small corals *Scolymia wellsii*, *Phyllangia americana*, *Astrangia braziliensis*, and *A. rathbuni* do not contribute significantly to the construction of the reef structures. *A. rathbuni* occurs in the southern region (from the state of Rio de Janeiro to the coast of the Santa Catarina State), at depths of a few meters to 90 m, attached to skeletal fragments.

Of the four species of *Millepora* reported from the Brazilian reefs, three are considered endemic (*M. braziliensis*, *M. nitida*, *and M. laboreli*). They exhibit two major growth forms: branching and encrusting. Delicate, fingerlike branches are characteristic of low-energy environments. Irregular, short, rounded branches are common on the edges of the reefs, with the thick, massive branches in zones of higher energy. Encrusting forms are seen on reef tops or encrusting the axes of gorgonians. The cosmopolitan species *M. alcicornis* is predominant on the windward borders of the reefs, a reef region that corresponds to the *Acropora palmata* zone of the Caribbean reefs, and it is found along the entire tropical Brazilian coast. The endemic species *M. braziliensis* (Fig. 6) was first described by Verrill in 1868 and confirmed by Boshma (1961). More recently, Amaral et al. (1997), using molecular methods, validated the species. In zones of high hydrodynamism (currents and waves), the colonies of this hydrocoral are more massive, but in protected zones, their branches are flattened. Laborel (1969a) located the zone of *M. braziliensis* immediately below the zone of *M. alcicornis. M. alcicornis* are commonly found on the reefs from the northeastern and eastern regions. *M. nitida* (Fig. 6) is also considered an endemic species to Brazil and has only been recorded only along

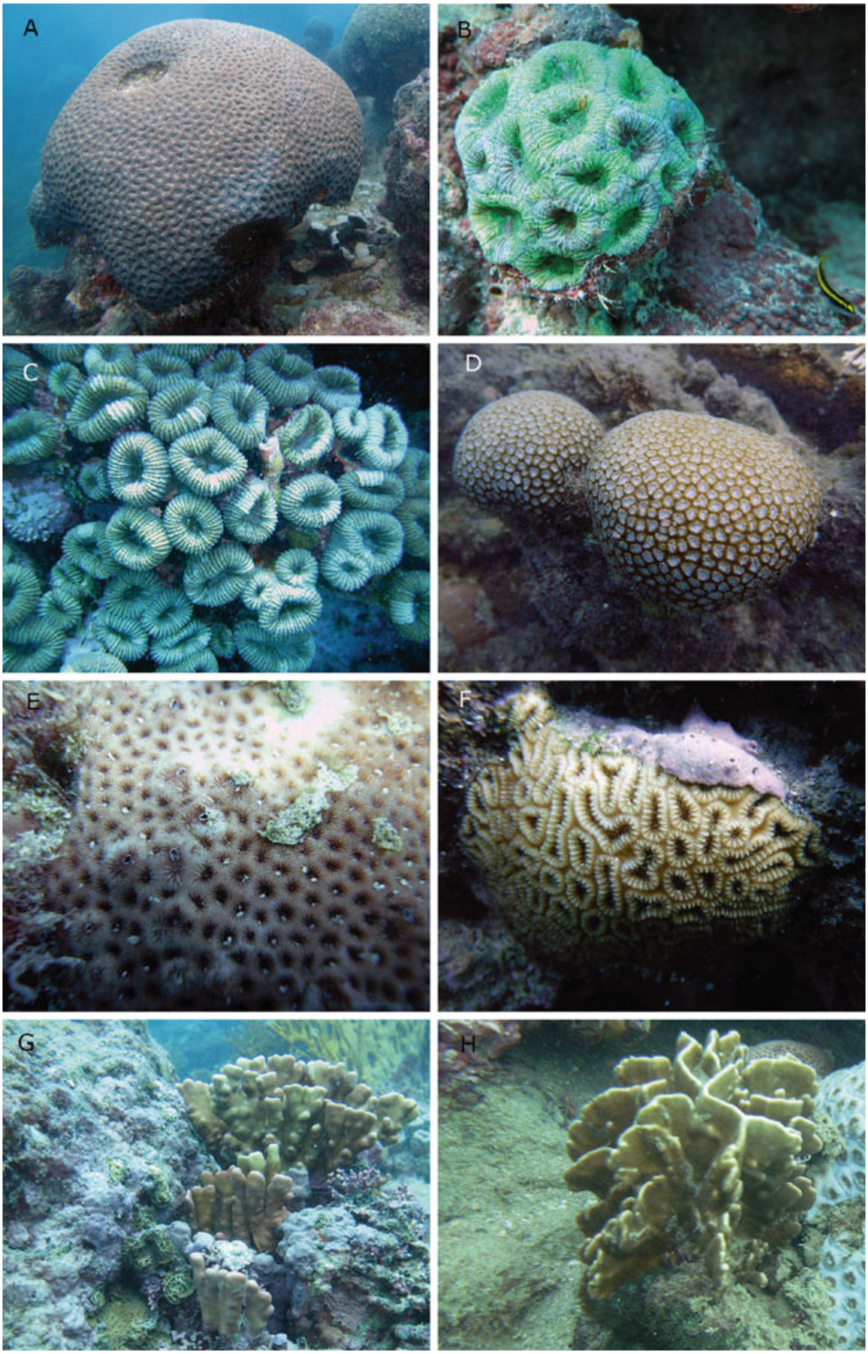

Fig. 6 Endemic corals from Brazilian coast: (**a**) *Mussismilia braziliensis*. (**b**) *Mussismilia hispida*. (**c**) *Mussismilia harttii*. (**d**) *Mussismilia leptophylla*. (**e**) *Siderastrea stellata*. (**f**) *Favia gravida*. (**g**) *Millepora nitida*. (**h**) *Millepora braziliensis* (Photos from: R.K. Kikuchi)

the coast of Bahia State. *M. laboreli* has been described on the Parcel de Manuel Luis reefs, coast of Maranhão State, and in the north region (Fig. 2). Apart from the millepores, a small hydrocoral, *Stylaster roseus*, has been found in protected reefs from the northeastern and eastern regions.

Octocorals are soft-bodied cnidarians found throughout the world's oceans, including the Brazilian coastline. Octocorals add structural complexity to animal forests and are abundant in many benthic ecosystems. There are approximately 3,200 species of octocorals globally, but only approximately 110 species have been recorded in Brazilian waters (Pérez et al. 2011; Almeida et al. 2014), with recent findings in deep waters (Cordeiro et al. 2015). Castro et al. (2010) performed a review and suggested only 17 reef species occurred in Brazil. Recently, Moura et al. (2016) found a high diversity of octocorals (26 species) in the reef system of the Amazon mouth. These studies suggest that octocorals have an important function in Brazilian coral reefs, and further studies regarding their ecology and diversity, mainly in the tropical coast, are needed.

Zoantharians play a considerable ecological role in animal forests in Brazil, considering their diversity and function in benthic ecosystems. They are represented by 13 colonial species in Brazilian waters (Santos et al. 2015) and are commonly used for protection, shelter, and food for other animals. The genera *Zoanthus*, *Palythoa*, and *Protopalythoa* have a wide distribution in Brazilian waters, occurring in coral reefs, intertidal sandstone reefs, and rocky shores along the coastal and oceanic islands. The zoantharians are especially abundant in intertidal and shallow coastal reefs, acting as a good competitor for space (Soares et al. 2011b; Rabelo et al. 2013, 2015).

Considering the geographic distribution of coral reefs, no known reefs are present in the southeastern and southern regions, from the mouth of the Doce River (19°30′ S) to the coast of São Paulo State, although corals have been found in these regions and at Arraial do Cabo in Rio de Janeiro State, in the "Laborel's coral oasis" (Laborel 1969a), including *Siderastrea stellata* and *Mussismilia hispida* on several rocky shores (Castro et al. 1995; OigmanPszczol and Creed 2004, 2006). *M. hispida* has also been observed along the coast of São Paulo State (Migotto 1997).

At depths below 30 m (mesophotic reefs) in drowned reef structures with low coral coverage, the coral *Montastraea cavernosa* is predominant, whereas *Siderastrea* spp., *Agaricia* spp., *Porites* spp., *Madracis* spp., *Favia* spp., *Scolymia* spp., and the black corals, such as *Cirripathes* and *Antipathes* are limited (Bastos et al. 2013; Moura et al. 2013).

3.3 Mollusca

Mollusks are one of the most successful animal taxa in terms of biodiversity and geographic distribution. Most mollusks are marine organisms and occupy a vast range of marine habitats, from the polar seas to tropical ecosystems, such as mangroves and coral reefs. Among the various sessile benthic taxa present in the marine animal forests, mollusks stand out for their ecological importance. These animals play a key role in benthic environments as they represent much of the biomass of these ecosystems and include taxa recognized as eco-engineering species, such as gastropods and bivalves. For example, a reef formed by vermetid gastropods is a biogenic structure, which can reduce the action of the waves on the shore and provide shelter for a variety of organisms (Chemello and Silenzi 2011). Some reef mollusks, such as vermetids, may participate in the construction of coral reef environments, including oceanic atolls (Soares et al. 2011a). The Vermetidae act as biological engineers creating a complexity of habitats; in Abrolhos Reef, Northeast Brazil, *Dendropoma irregulare*, which is associated with calcareous algae, represents a considerable portion of the reef (Spotorno-Oliveira et al. 2015).

The tropical coast of Brazil is a large area with a wide range of habitats that with a considerable mollusk diversity. However, despite significant knowledge on mollusk diversity on the Brazilian coast, further studies are still needed. Mollusks are well represented in all coastal habitats including reef ecosystems (coral reefs, sandstone, and rocky shores), sandy and muddy environments, sea-grass meadows, and estuarine areas. In reef areas, the malacofauna generally consists of epifauna including mostly gastropods, cephalopods, and polyplacophorans but also some bivalves. A survey of Brazilian reef ecosystems found 400 species of mollusks in coral reefs, 500 in intertidal reefs, and 200 in infralittoral reefs (Lewinsohn 2006).

Mollusks also comprise an important part of the biomass of marine phanerogam meadows, which serve as nurseries for various bivalve and gastropod species. In a study on the malacofauna associated with a *Halodule wrightii* meadow, Barros and Rocha-Barreira (2013) registered 24 species, 11 of them Bivalvia and 9 Gastropoda, the latter being the most abundant mollusk class.

Mollusks are also common in environments with unconsolidated sediments and may be dominant in some of these areas. In muddy environments, mollusks play an important role in sediment bioturbation, modifying sediment structure by mixing the different layers, and consequently changing the original hydrodynamic properties (Pereira and Soares-Gomes 2002; Soares-Gomes and Pires-Vanin 2003).

At least 500 mollusk species have already been recorded in unconsolidated substrates along the Brazilian coast (Lewinsohn 2006). A survey of intertidal sandy substrates in Northeastern Brazil found a great diversity of gastropods and bivalves with the representative species being *Olivella minuta* and *Donax striatus* (Matthews-Cascon and Lotufo 2006).

In estuarine environments, mollusks, especially gastropods and bivalves, are among the most representative groups. Oysters in the estuary can build a reef forming dense populations that could alter the environment (e.g., *Crassostrea brasiliana* and *C. mangle*). These eco-engineering species can present dense populations, building reefs that are important for the ecosystem structure and function and providing habitat for other animals. A study of the spatial and temporal distribution of the malacofauna in an estuary found that the greatest diversity of species occurs in areas with higher marine influence and that *Anomalocardia brasiliana* and *Neritina virginea* were the most abundant species (Barroso and Matthews-Cascon 2009).

In a workshop held in 2010, the categories and criteria established by the International Union for the Conservation of Nature (IUCN) were used to assess the conservation status of the Brazilian species of marine mollusks. Six species were considered threatened: five gastropods—*Eustrombus goliath*, *Aliger costatus* (Strombidae), *Olivancillaria contortuplicata*, *O. teaguei* (Olividae), and *Petaloconchus myrakeenae* (Vermetidae), and the bivalve *Euvola ziczac* (Pectinidae). The species *E. goliath* and *A. costatus* were considered vulnerable, whereas *E. ziczac* was considered endangered, and *P. myrakeenae*, *O. contortuplicata,* and *O. teaguei* were considered critically endangered. The other species evaluated were assessed as least concerning or near threatened, or there was insufficient data for a thorough species assessment.

Further research is needed to increase the knowledge of mollusk biodiversity and conservation status along the tropical coast of Brazil, especially in deep-sea ecosystems, including the continental slope. This knowledge is fundamental for further studies and direct conservation and management measures for the mollusks in BRAF.

3.4 Bryozoa

The phylum Bryozoa comprises one of the most abundant sessile invertebrates in the ocean, with approximately 6,000 living species described globally. Bryozoans are colonial, suspension feeders that often remain attached to hard surfaces, with important biomass in sessile communities, forming colonies ranging from a few millimeters to more than 50 cm in size. Bryozoans are good competitors for space and food and may grow on natural or artificial substrata with other fouling communities. Therefore, some important exotic species have been widely reported in marinas, ports, and harbors worldwide. There are few free-living species (e.g., Cupuladriidae), with the majority of taxa growing as encrusting sheets (unilaminar to multilaminar), massive forms, and erect (flexible or rigid) forms. These bryozoan colonies are useful in providing environmental information in both recent and paleoenvironmental studies. These growth forms are often controlled by competition pressure and environmental parameters, such as depth, salinity, temperature, nutrient supply, water energy, substrate, and sedimentation rate. Like corals, some bryozoans may develop rigid three-dimensional colonies, increasing available substrata in the seafloor for other encrusting organisms (algae and animals) and providing microhabitats for other invertebrates, such as crustaceans, polychaetes, mollusks, and echinoderms.

Despite the importance of bryozoan fauna in benthic communities, few studies have been carried out on bryozoans along the Brazilian coast compared with the tropical and subtropical waters of the Pacific and Indian Oceans. Until the end of the twentieth century, only 346 bryozoan species were reported from Brazil (Vieira et al. 2008), mostly in the southeastern coast (Rio de Janeiro and São Paulo). However, since the last decade, the number of bryozoan species reported in Brazil has increased owing to the resumption of recent studies made on the

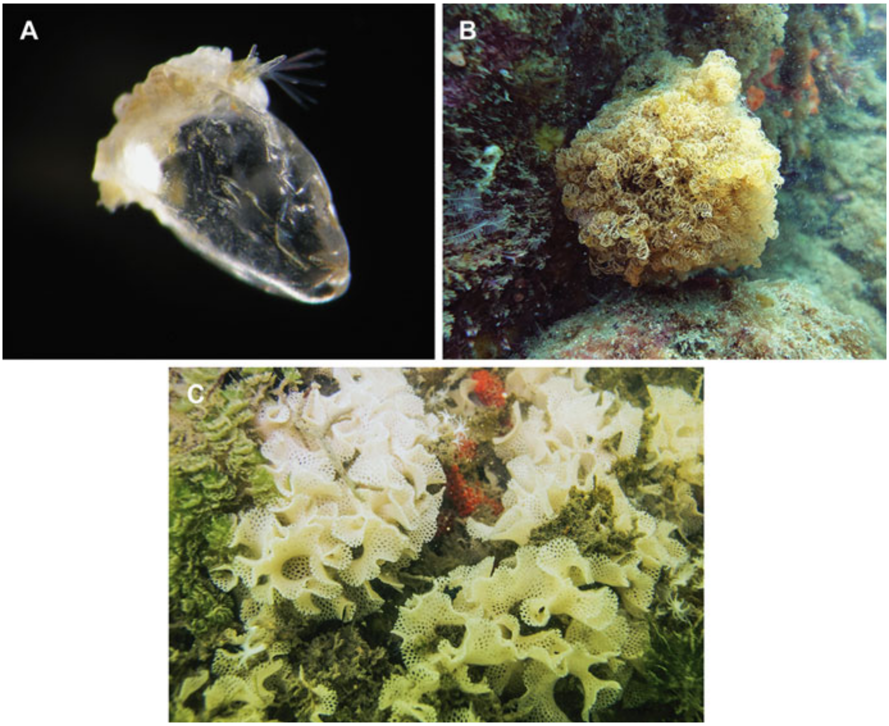

Fig. 7 Bryozoans from Brazilian coast. (**a**) *Rosulapelta rosetta*. (**b**) *Catenicella uberrima*. (**c**) *Triphyllozoon arcuatum* (Photos from: A.E Migotto, R.J Miranda)

phylum. Today, the total number of known bryozoan species in Brazil's exclusive economic zone is 460 (Vieira et al. 2016). In some localities, such as the northern São Paulo coast, recent studies on marine biota have revealed higher bryozoan species richness than that of other sessile invertebrates (Amaral and Nallin 2011). In addition, the São Paulo coast has one of the few interstitial bryozoan fauna known (Winston and Vieira 2013), including endemic taxa inhabiting the surface of mineral grains and sand- to gravel-size shell fragments (Fig. 7a). The interstitial bryozoan fauna is also known from one other subtropical latitude in the US coast (Florida), and it is expected to occur in other shelf locations around tropical and subtropical latitudes with mixed terrigenous and carbonate sediments, relatively high energy, and lacking in silt that include the northeastern coast of Brazil and their oceanic islands.

In Brazil, there is a huge inconsistency in the species richness in both latitudinal and depth gradients. The majority of bryozoan species are reported between latitudes 18 and 25° S (Southeastern Brazil), with few studies performed in North and Northeast Brazil. Comparing the well-known area in SE and NE Brazil, São Paulo and Bahia have 210 and 135 species, respectively. This lack of studies also leads to a very low bryozoan diversity toward the northern coast. For example, between latitudes 7 and 4° N that comprise about one third of the Brazilian coastline, less than 15 species are known. It is worth noting that while Southeastern Brazil has the highest proportion of species reported, including rocky shores and continental shelf communities, the knowledge on bryozoan fauna associated with coral reefs and sandstone banks is limited. This is also reflected in the number of new bryozoan taxa and endemic species expected to be found on coral reefs and sandstone bank communities compared with rocky shore communities. In some remote areas in the northern coast of Brazil with a high degree of endemic marine species, including the Parcel Manuel Luiz Marine State Park, no studies on bryozoan fauna have been carried out. However, in Rocas Atoll, 24 bryozoan species were reported, but there is no ecological information on these species. Bryozoan fauna from the oceanic islands is one of the least known among Brazil territories (Vieira et al. 2008). There is also limited ecological information regarding this fauna in both Trindade Island and Fernando de Noronha, with no information on endemic or ecologically important species in the benthic community. However, in Saint Peter and Saint Paul Archipelago, considered the most isolated archipelago of the Brazilian territory, the bryozoan fauna is better known than that in the other oceanic islands, with 22 bryozoan species reported, including at least eight endemic species (Vieira et al. 2012). In this archipelago, important relationships between bryozoans and other organisms exist, including calcareous algae, corals, black corals, gastropods, and sponges. At least one bryozoan, *Margaretta buski*, is considered an ecosystem engineering species and is abundant and regularly distributed between 10–45 m depths, below the *Caulerpa racemosa* (Forsskal) belt. Characteristically, this bryozoan forms three-dimensional erect colonies, increasing the complexity of substrata and number of microhabitats that may provide shelter to small invertebrates (e.g., crustaceans, sea spiders, and echinoderms) and serving as substrate for hydroids, sponges, and other bryozoans. From NE to SE Brazil, other bryozoans may also form erect three-dimensional colonies, including flexible arborescent species of cheilostomes, such as bugulids and catenicellids (Fig. 7b) to well-calcified colonies, as those of the exotic phidoloporid *Triphyllozoon arcuatum* (Almeida et al. 2015; Fig. 7c).

In Brazil, considering the depth gradient of bryozoan fauna, only 114 species have been reported at depths of 100 m or greater, with the majority species found at depths between 0 m and 50 m. In contrast, among the shallow water bryozoan fauna, which is better known in the southeastern coast of Brazil, no records of bryozoans exist at depths >700 m in South and Southeast Brazil. Only 34 species have been reported at depths >700 m from a latitude of 8° S (off Recife, Pernambuco, Northeastern Brazil) (Vieira et al. 2010). With the exception of very few localities in the Brazilian coast, such as north of São Paulo, it is not possible to estimate the species richness of bryozoans from shallow waters or the relationship between bryozoans and benthic communities. Recent studies have suggested that there are new species to be discovered, even in well-studied areas (Vieira et al. 2014); the real bryozoan diversity in Brazil is underestimated, with very limited knowledge of the coral reefs.

3.5 Ascidiacea

Ascidians are among the least studied groups of marine hard bottom sessile benthic suspension feeders. However, these animals may be abundant and diverse in many regions and habitats. As typical active filter feeders, ascidians are abundant in productive coastal waters and may even dominate fouling in urbanized areas. Ascidians are usually rare in offshore underwater reefs but may be more diverse in these habitats than in the intertidal zone.

As is the case with many other marine invertebrates, most of the available knowledge is concentrated in Europe and North America, including the Caribbean region. In Brazil, there is a lack of knowledge about this group. Until the beginning of the twenty-first century, there were very few published reports specifically on the ascidian fauna (Dias et al. 2012). The typically tropical coast was almost completely neglected, with very limited surveys performed along this region. Recent efforts directed on the northeastern coast have revealed a diverse ascidian fauna, with many cases of endemism.

The first comprehensive account of ascidians from the tropical shallow areas of Brazil was presented by Lotufo (2002), with collections along most of the southeast and northeast coasts. This first account revealed marked transitions in the ascidian fauna composition along these regions. Recently, with an increase in the number of trained specialists, several other assessments were made available; since 2002, more than 40 new studies have been published about ascidians, covering all regions of the Brazilian coast.

The hard bottom habitats along the southeastern coast, including São Paulo, Rio de Janeiro, and Espírito Santo States, are dominated by typical rocky shores with a granitic/gneissic nature. This region is also influenced by the colder and richer waters of the South Atlantic Central Water mass, with upwelling and intrusions related to wind regimes, especially off Rio de Janeiro. The ascidians from São Paulo have been studied in more detail, with 66 species described until 2011 (Rocha et al. 2011). For Rio de Janeiro and Espirito Santo, the available information is still limited, and further assessments are needed.

From Espirito Santo toward the equatorial margin, crystalline rocks become rare, and the hard substrate available is almost exclusively arenitic (sandstone reefs), marking a transition of the ascidian faunal composition. However, even important regions, such as the large reef formations in the Abrolhos region, lack information on the ascidian fauna. In addition, most of the surveys are restricted to the intertidal region, with limited surveys of underwater reefs. From the data available and personal observations, ascidians are more abundant in the intertidal region and scarcer in underwater reefs. Most ascidians are cryptic animals and may constitute important elements in the reef matrix, which is not sampled during typical surveys.

No true transition was noted from the central to northeast coast, and the faunal composition is very similar (Lotufo 2002; Moreno et al. 2014). However, the Brazilian oceanic islands present a more peculiar ascidian fauna, with >40% endemic species (Paiva et al. 2015).

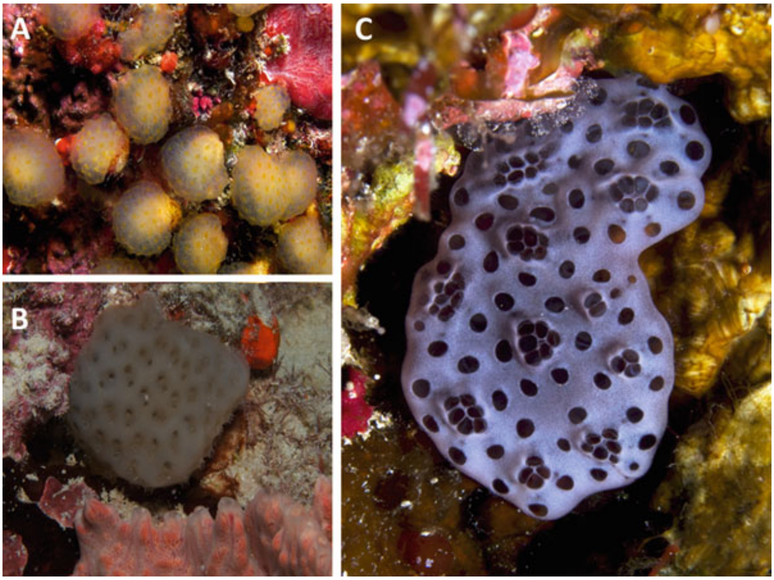

Fig. 8 Ascidians from Brazilian coast. (**a**) *Eudistoma vannamei*. (**b**) *Stomozoa gigantea*. (**c**) *Eudistoma versicolor*

Regarding composition, the didemnids are the most diverse ascidian group throughout Brazil. In the tropics, polycitorids (especially *Eudistoma*) are the second most diverse taxon, whereas in the southeastern rocky shores, styelids occupy this position. Large solitary forms are particularly rare in the reefs, where colonies predominate.

The beach rocks (sandstone reefs) along the northeast shores also have a very diverse ascidian fauna. Didemnids are also abundant, especially *Didemnum galacteum*, *D. psammatodes*, *D. granulatum*, and *Polysyncraton* aff. *amethysteum.* Regarding biomass, polycitorids from the genus *Eudistoma* (Fig. 8) are very important, particularly *E. vannamei* and *E. versicolor.* Styelids are also frequently found on the underside of loose rocks, especially botryllids and *Eusynstyela tincta*.

In the northeastern underwater reefs, two species stand out in the seascape because of their abundance and size: *Stomozoa gigantea* and *Eudistoma saldanhai. S. gigantea* (Fig. 8) may form large globular colonies, sometimes with a diameter of >20 cm.

In the oceanic islands, didemnids are further diverse, and *Trididemnum maragogi* is the most abundant species. Contrarily to other didemnids, this species is usually present in areas exposed to light, where they may form aggregates of colonies >50 cm in diameter. This species harbors microalgae of the genus *Prochloron*, in an association similar to *Symbiodinium* in cnidarians. The ascidian fauna from Fernando de Noronha Archipelago was recently surveyed, and revealed a diverse assemblage, with potentially several new endemic species. The islands of Trindade and Martin Vaz and the Vitória-Trindade seamount chain, connecting them to the coast, have not been thoroughly surveyed. A small number of samples have been collected from Manuel Luís reef, off Maranhão State, but there is a need for more thorough assessments in that region, including other reefs that have not been mapped in detail. There are also many deeper banks and seamounts off Ceará and Rio Grande do Norte States, which have not been adequately sampled since the surveys are more expensive and difficult to conduct.

Ascidians have limited dispersal during the short period of free-swimming larval stages, ranging from minutes to a few hours. As such, these animals provide an interesting model to evaluate connectivity between subpopulations. However, ascidians could also be dispersed by rafting, through attachment to flotsam, and other floating debris. Increased shipping traffic at regional and international scales is also reshaping the ascidian assemblages through bioinvasion, especially near harbors and marinas with more intense activities.

When all these aspects are considered, the need for further surveys is clear, especially of the underwater reefs. The use of various tools, including molecular genetics, is crucial in the detection of cryptic species. Following the more traditional morphological analyses, more than 40 new records or species were described from Brazil in the past 20 years (Rocha et al. 2011). Hence, more records and species descriptions are expected as new tools become available for taxonomists, and the ascidian diversity in marine animal forests can be thoroughly evaluated.

4 Threats to BRAF

The sessile three-dimensional living structures of animal forests are currently under threat from direct and indirect effects of human activities such as urbanization, aquaculture, invasive species, overfishing, bottom trawling, climate change, and mining (petroleum, gas, and minerals). In this section, these major threats to BRAF are discussed, considering that a current lack of knowledge contributes to their rapid degradation (Rossi 2013).

4.1 Urbanization

The Brazilian population is highly dense in the coastal areas, stemming from the occupation process, especially after European colonization and the establishment of cities. About 16 of the 27 capital cities are located on the coast, and rapid urbanization has occurred in the last few decades based on urban and tourism growth. Marine urbanization is increasing, and the impacts of artificial structures have been widely documented in the last decades (Dafforn et al. 2015). Dafforn et al. (2015) described the major environmental impacts, such as direct and indirect physical disturbances, artificial habitat, and pollution. Despite increasing global urbanization, their environmental impacts on marine animal forests, including those of Brazil, remain poorly understood (Rossi 2013). Recent data (Scherner et al. 2013) demonstrated that urban areas on the Brazilian coast had significantly lower calcareous algal cover and seaweed diversity. These data show that coastal urbanization in the SW Atlantic is a driver of seaweed biodiversity loss and causes shifts in the benthic assemblage structure. Shifts in benthic primary producers propagate through marine trophic webs and can cause significant changes in biomass and biodiversity of benthic suspension feeders. Another problem is that coastal urbanization increases contaminated water runoff, lowering the water quality in urban areas. This affects the environmental factors, which affects the benthic–pelagic coupling processes and benthic diversity of marine animal forests. Therefore, further research is necessary to investigate the recent urbanization of the Brazilian coast and its effects on animal "ecosystem engineers" along a latitudinal gradient.

4.2 Aquaculture

Aquaculture has grown in Brazilian waters in the last decades, supported by public and private funding, and it is expected to grow further, driven by increasing domestic demand and public support. The favorable climatic conditions, extensive available coastal areas, and inexpensive labor, as well as an increasing domestic demand have stimulated the production of food and the consolidation of aquaculture on the Brazilian coast (Queiroz et al. 2013). The expansion of aquaculture production may increase the seafood supply for the human population, but management aimed at expanding aquaculture in coastal environments needs rigorous monitoring and environmental planning owing to potentially negative impacts on marine animal forests.

In Northeastern Brazil, public and private policies encourage the rapidly growing industry of shrimp farming (exotic species, *Litopenaeus vannamei*). Shrimp farming has grown in the last decades in Latin America and has become the main mariculture industry in Brazil, commonly located in important transitional ecosystems, including mangroves. The environmental and socioeconomic importance of mangrove forests is well established in scientific literature, but the effects of aquaculture on marine animal forests are limited. Mangrove forests provide many ecosystem services to coastal zones, such as the sustainability of fisheries stocks, acting as carbon sinks, reducing contamination, acting as nursery habitats for marine biodiversity, and protecting the coastal zone against natural disasters (Polidoro et al. 2010). However, mangrove ecosystems may be situated in close proximity to the shrimp farms and could be negatively affected by anthropogenic activities (e.g., continuous nutrient discharges, pollution, deforestation, and the introduction of exotic species and diseases) (Queiroz et al. 2013; Almeida et al. 2016). The mangroves in estuaries commonly export organic matter to the marine environment. The destruction of mangroves by unplanned aquaculture and urbanization can exert strong environmental impacts on marine animal forests, by affecting the benthic–pelagic coupling processes (i.e., changing the organic matter fluxes and biogeochemical cycles), causing habitat destruction and shifts in reproductive cycles. However, these possible effects are not yet well understood.

Mollusk culture is another mariculture activity expected to develop in Brazilian waters. Mollusk culture, by definition, is the activity of producing clams,and is carried out in Brazilian federal waters with the majority of the producers located in Santa Catarina State (South of Brazil). *Perna perna* is the main mollusk species cultivated for food (approximately 90%) throughout this subtropical coast, followed by oysters (exotic species *Crassostrea gigas*, and native species *C. brasiliana* and *C. rhizophorae*). The environmental effects of intensive production (such as artificial eutrophication) and of the introduction of exotic species (such as the invasive species *C. gigas*) on marine animal forests are not yet well known.

4.3 Invasive Species

Biological invasions of “ecosystem engineers” (such as benthic suspension feeders) are ecological phenomena with obvious negative consequences for marine animal forests and public health and lead to frequent economic issues. Considering that the South Atlantic is the most recent ocean, as well as a hotspot for tropical biodiversity, the information on invertebrate bioinvasions in this region is insufficient. The Brazilian coast has experienced significant transoceanic ship traffic since the sixteenth century, but the consequences of maritime transport on bioinvasions have only recently received higher academic and governmental attention (Rocha et al. 2013). Recent data show the presence of invasive species in BRAF, including mollusks, ascidians, bryozoans, and corals. Rocha et al. (2013) discussed the available data and suggested that the list of exotic species (265 species) has many problems and requires taxonomic and biogeographic detailed analyses, since it comprises 42 nonindigenous, 187 cryptogenic, 25 native, and 11 native benthic invertebrates.

Mollusks are one of marine groups of invasive species in the Brazilian coast. *Leiosolenus aristatus* is a borer species that lives in hard bottom ecosystems and the shells of other mollusks. Another important invasive species is the bivalve *Isognomon bicolor*. This mollusk is well distributed in the tropical SW Atlantic and competes for the same habitat as other commercially valuable benthic species in rocky habitats of Brazil. The ascidians (e.g., *Styela plicata* and *Phallusia nigra*) are another important component of biological invasions (Skinner et al. 2016) in marine animal forests. There are few studies recording exotic bryozoans in Brazilian coast. Recently, two bryozoans species were reported in Brazil, *Licornia jolloisii* (Audouin, 1826) (Vieira et al. 2013) and *Triphyllozoon arcuatum* (MacGillivray, 1889) (Almeida et al. 2015), but there are no studies on their in impact on native fauna or on economy. In Brazil, however, there are a high number of bryozoans assigned as cryptogenic due absence of data on the origin of species; thus, more studies are needed to detect exotic species and study of their impacts in the coast.

The orange cup corals *Tubastraea coccinea* and *T. tagusensis* are the first invasive scleractinian species to be introduced to Brazil and exert negative effects on marine animal forests. They alter the native benthic assemblages and the ecological interactions among species. A recent study by Silva et al. (2014) demonstrated that in the last 11 years, these corals transitioned from rare to dominant in the benthic ecosystems of the Rio de Janeiro coast and increased their distribution range by 2.1 km per year along the Brazilian coast. These invasive "ecosystem engineers" modify marine animal forests by competing with native benthic species and displacing native species (e.g., native scleractinian corals). Moreover, they alter the benthic–pelagic coupling processes, affecting the ecosystem services, often introducing new diseases and/or toxic substances that affect the marine environments. These corals are azooxanthellate and can alter the trophic structure of animal forests, displacing native autotrophic corals (e.g., scleractinians) by their heterotrophic colonies. Considering the high biodiversity of BRAF and the value of ecosystem services, understanding the dispersal of invasive "ecosystem engineers" and their impacts is fundamental for their effective management.

4.4 Fishing and Bottom Trawling

Bottom trawling is one of the main threats to marine animal forests globally (Rossi 2013), also present in the Brazilian coast. Despite the knowledge of the negative impacts on marine benthic ecosystems worldwide (e.g., Mediterranean Sea), the effects on BRAF need further investigation. Bottom trawling is a large-scale fishing activity along the Brazilian coast. Bottom trawling in deep waters off the Brazilian coast (>200 m) has been increasing in the last two decades, but the effects in coastal and deep marine animal forests have not yet been studied. Prantoni et al. (2013) found an increase of benthic infaunal density after bottom trawling. The authors suggested that the overall increase was correlated with the reworking of the sediment matrix and an increase in food availability from the resuspension of the sediment for suspension feeders. However, this research only evaluated the short-term effects of bottom trawling. The medium- and long-term effects on infaunal assemblages are not fully understood and may be negative. Furthermore, bottom trawling could cause shifting of benthic macrofauna such as suspension feeders and depletion of top predators in tropical Brazilian waters. Despite the lack of information, recent research has shown the possible impact of bottom trawling and fishing, especially in deep areas; Kitahara et al. (2009) showed through board observer reports, the capture of large quantities of deep-sea corals as "bycatch." The researchers showed that a great quantity and diversity of corals (Scleractinia, Octocorallia, and Antipatharia), such as colonies of *Lophelia pertusa*, *Solenosmilia variabilis*, and *Madrepora oculata*, were captured as bycatch. Many countries are banning deep bottom trawling to prevent further destruction of marine animal forests not exploited by the fishing industry. It is essential and urgent to implement similar measures in the tropical Southwestern Atlantic, and since the fishing industry does not exploit these deeper regions, the measures would have no socioeconomic effects.

4.5 Climate Change

In the context of global environmental changes (acidification, sea surface temperature anomalies, sea-level rise, and shifts in rainfall), little is known about the resilience of BRAF with respect to climate change. The increase in recent research about coral bleaching and sea surface anomalies in Brazilian waters has been concentrated on the eastern Brazilian coast (e.g., Abrolhos Bank) and oceanic islands (Fernando de Noronha and Rocas Atoll). Coral bleaching associated with the first semester (summer) is a phenomenon that has been observed in the South Atlantic, induced by El Niño/Southern Oscillation (ENOS) events (Ferreira et al. 2013; Leão et al. 2010; Soares and Rabelo 2014). These events are related to anomalies in sea surface temperature (SST), including several weeks of above average temperatures, high temperatures on the sea surface, and positive hotspot values. It is assumed that there is a relationship between coral bleaching, irradiation, and SST in the South Atlantic reefs. The nearshore coral reefs of Bahia State are the most impacted by the effects of eutrophic waters associated with coastal pollution, high sedimentation in the land-sea interface, turbidity, and the most exposed to the effects of coral bleaching and infectious diseases. In the offshore area of the Abrolhos complex, bleaching rates were milder, but the reef ecosystems are threatened by an increase in coral diseases in recent years. Despite increased bleaching rates and coral diseases, the mass mortality in Brazilian coral reefs has not been detected until now. These results indicate a hypothesis of stronger resilience with climate change. However, the natural disturbances (e.g., turbidity, sedimentation) associated with the effects of global climate changes (e.g., sea surface anomalies) and human-induced activities (e.g., urbanization and contamination) could lead to higher levels of degradation on the reefs (Leão et al. 2010).

One of the least investigated environmental factors is the change in the rainfall pattern and its effect on BRAF. Rainfall commonly controls the estuarine water flow processes and the transfer of materials from the mainland to the sea. The Intergovernmental Panel on Climate Change (IPCC) is expecting shifts in the pattern of rainfall in the Brazilian coast, including reduced rainfall in Northeast Brazil, a region with scarcely known tropical ecosystems. Reduced rainfall could decrease the fluvial contribution to the ocean. Multiple effects include an increase of particulate contaminant accumulation in estuarine environments and increase of dissolved Hg export to the marine environment (Lacerda et al. 2012). Shifts in organic matter, contaminants, and nutrients can have drastic effects in benthic marine animal forests. These environmental effects and scenarios of climate change should be studied in further research. The cumulative impacts of climate change (acidification, sea surface temperature, and rainfall anomalies) in BRAF are one of most important research themes to be developed in the future.

4.6 Mining (Petroleum, Gas, and Minerals)

The mining and extraction of mineral resources occurs in continental and marine environments. In the Brazilian coast, the oil and gas industries have had a strong private investment and support from public policies, especially exploration in deeper waters. The recent discovery of pre-salt at depths >1,000 m is expected to develop the mining industry continuously, considering the scarcity of resources such as oil and gas worldwide. It is important to carefully evaluate the exploitation of these marine resources and the environmental risk associated with the transportation of these materials (e.g., oil spills). The lack of information about the diversity and distribution of BRAF in the deep sea are an important aspect to consider. It is important to note that these activities are subject to environmental licensing in Brazil, requiring a detailed description of the benthic communities and the effect of the proposed activities.

Mining activities established in continental areas can affect marine animal forests via estuarine environments, e.g., one of the biggest environmental disasters in Brazil was caused by a Samarco mining waste dam collapse. In November 2015, approximately 50 million cubic meters of iron waste entered the Doce River after the dam collapsed, reaching the Atlantic Ocean 2 weeks later and possibly affecting the biodiversity of the continental shelf and the largest reef complex in Brazil (Abrolhos Bank). One controversy that remains unresolved is whether the sludge was contaminated with heavy metals, including arsenic, copper, and mercury, and if this contamination will persist, delaying environmental recovery (Escobar 2015). Another hypothesis is that the huge brown plume (with silting) and mining waste could affect primary production and thereby reduce benthic diversity. This could occur with an increase in water turbidity, reducing the penetration of light, and consequently primary productivity. The total impact on marine animal forests (Miranda and Marques 2016) and the environmental consequences to the river and adjacent ocean is still unclear.

In conclusion, the threats to BRAF are increasing in the Brazilian coastline, induced by multiple economic activities and the rapid expansion of urban areas. Moreover, it is necessary to understand the indirect effects of climate change in benthic diversity and ecology. Addressing the local, regional, and global impacts, it is possible to analyze the cumulative negative effects on eco-engineering species and the oversimplification of benthic ecosystems (Rossi 2013).

5 Mesophotic and Deep-Sea Ecosystems Along the Brazilian Coast: A Lack of Knowledge and Clear Legal Framework for Management

Mesophotic ecosystems (30–150 m) have been recognized as one of most important marine animal forests, based on the diversity of corals, sponges, ascidians, and other organisms found in the “twilight” zone. There is a growing interest among the scientific community toward the ecological role of mesophotic ecosystems and eco-engineering species (corals, gorgonians, sponges, etc.) occurring in the coastal zone, as stress refuge areas, such as from the thermal anomalies resulting from climate change, and their ecological connectivity between the shallow and deep ecosystems. However, the knowledge of these important animal forests is limited in many aspects, including diversity and biogeography in the SW Atlantic, because the research has been mainly conducted in the Caribbean and Indo-Pacific regions (Loya et al. 2016).

Owing to the extensive Brazilian coastline, lack of taxonomists, and high operational costs of these surveys (such as the use of remotely operated vehicles (ROVs, Trimix diving, and submarines), such research projects have only recently been carried out on the Brazilian coast, focusing mainly on bathymetric distribution and benthic diversity. Recently, the research of Meirelles et al. (2015), Magalhaes et al. (2015), Moura et al. (2016) and Amado-Filho et al. (2016) generated advances in the knowledge of mesophotic reefs, mainly in seamounts (Vitória-Trindade Seamount), oceanic islands (Rocas Atoll and St. Peter and St. Paul Archipelago), and an extensive reef ecosystem at the mouth of the Amazon River.

These advances are important based on various environmental threats, such as overfishing and oil exploration in offshore Brazil. According to Meirelles et al. (2015), the mesophotic reefs of the Vitória-Trindade Seamount are a mosaic of reef systems and include major fleshy algae dominated by rhodolith beds, crustose coralline algae (CCA) reefs, and turf algae that are present on rocky reefs of different health levels. The animal forests comprise mainly sponges and corals such as *Siderastrea* sp., *Montastraea cavernosa*, and the endemic species, *Mussismilia hispida.* Tissue necrosis and bleaching affected >90% of the coral colonies in the shallow waters of Trindade Island. However, >90% of the coral colonies at the mesophotic sites (rhodolith beds and rocky reefs) were healthy. An important area for investigating the marine animal forest is the oceanic area. Recent research (Amado-Filho et al. 2016) described the mesophotic reefs in the Rocas Atoll. In this study, the rhodolith beds were the main ecosystem, composed mainly of crustose coralline algae and presented different reef structures, such as the formation of carbonate reefs by the coalescence of rhodoliths. Other research (Magalhaes et al. 2015) described the shifts in benthic assemblages from shallow waters to the “twilight” zone in one remote oceanic island (St. Peter and St. Paul Archipelago). These authors found a mesophotic benthic ecosystem (30–60 m) dominated by crustose coralline algae and marine animal forest components, such as bryozoans and scleractinian corals. These recent results demonstrate the need to increase research in the coastal and oceanic South Atlantic, considering the importance of mesophotic reefs.

The recent research of Moura et al. (2016) at the mouth of the Amazon River found a reef ecosystem in a large area of the northern region of Brazilian coral reefs. These results suggest the presence of a reef comprising eco-engineering species of 9,500 km^2 at mesophotic depths. This reef comprised three sectors: northern, central, and southern (Fig. 9). Each sector has a specific composition of benthic suspension feeders and the structure and functioning of the animal forest. This ecosystem is colonized by large sponges and other benthic filter feeders (hydroids, octocorals,

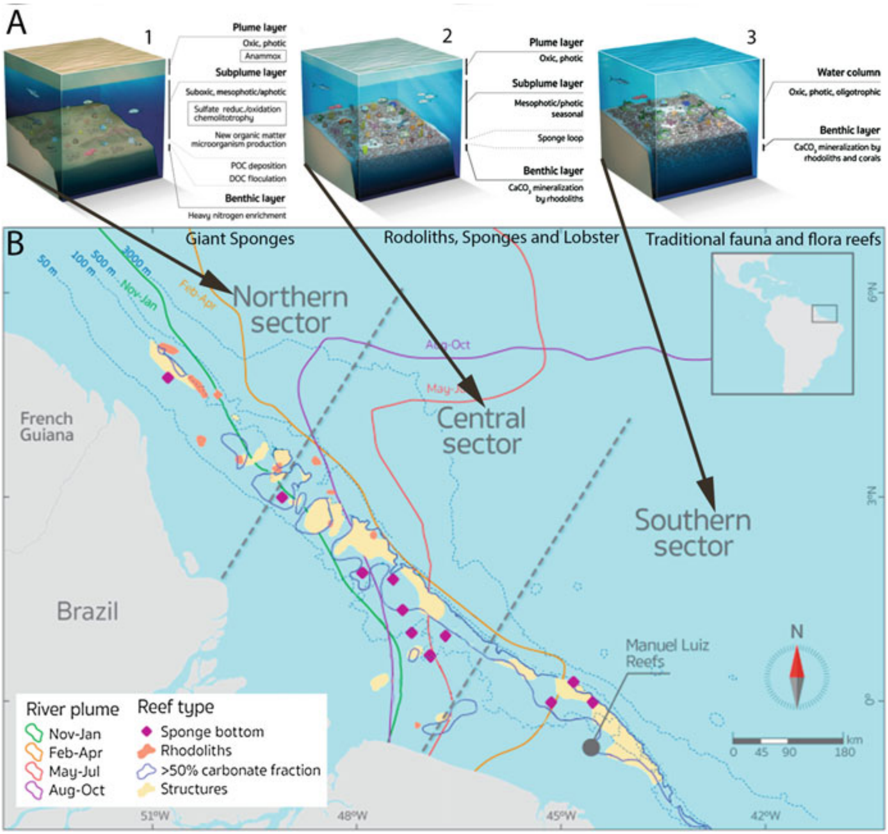

Fig. 9 Map of the Amazon shelf showing the benthic megahabitats and seasonal influence of the river plume. (**a**) (one to three) Main structural and functional traits of the reefs in the Northern (120 m), Central (55 m), and Southern Sectors (25 m), respectively. (**b**) Distribution of reef biodiversity types and plume river. The plume lines represent the outer edge of the plume during that season (Figure adapted from Moura et al. 2016)

black corals, and scleractinians) that survive in low light and high levels of particulates from the Amazon River plume. This suggests that the absence of information on diversity and distribution of BRAF (mainly in deeper areas) is due a lack of research.

Another important ecosystem (largely unknown) is the BRAF in deeper areas. Kitahara et al. (2009) analyzed the diversity and distribution of deep corals (22 species) along the Brazilian coast, at sites up to 1,000 m deep. The researchers found that at lower latitudes (toward the equator), there was an increase in species richness, as well as between the outer continental shelf and 500 m deep, which may be related to the increased availability of hard substrates. Despite these advances, the knowledge of the tropical Southwestern Atlantic is very scarce, considering that research has been carried out in the south platform of Brazil (between the 24 and 34° S).

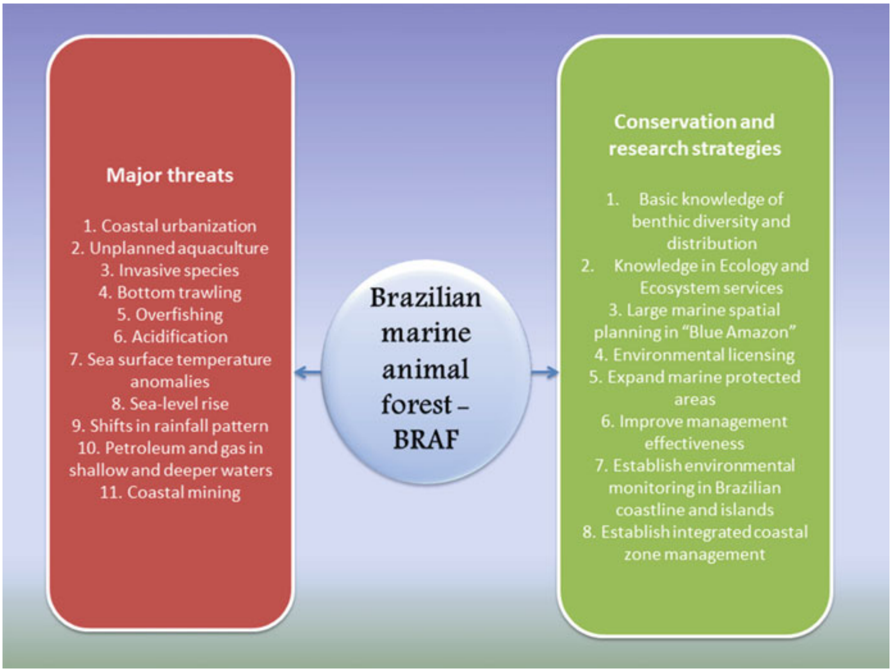

Fig. 10 Brazilian marine animal forest (BRAF): threats and conservation strategies

6 Conclusions and Future Directions

With the uncontrolled advance of human occupation in the Brazilian coastal zone (Halpern et al. 2015), it is necessary to propose measures that preserve its biodiversity and, simultaneously, offer alternative ways of sustainable exploitation of its natural resources (Fig. 10). However, it is necessary to understand the diversity and ecology of the marine animal forests, particularly their population dynamics and reproductive cycles for effective environmental management. Therefore, two aspects are important: knowledge about the BRAF and conservation programs with direct measures.

To understand benthic diversity and ecology, Longo and Amado-Filho (2014) carried out an extensive review and observed that although the Brazilian coast is recognized as one of the areas with the greatest species richness, efforts to increase knowledge of this marine biodiversity have been inadequate compared with that of other countries. As a result, a large portion of the Brazilian coast, continental shelf, and deep ocean remain unknown. The review suggested possible factors that contribute to this: the extensive length of coast, high diversity of ecosystems, lack of specialized systematic specialists, and species richness, with a high rate of endemism, all of which present challenges for field research. The combined use of technological tools such as side-scan sonars, ROVs, and technical diving is vitally important in acquiring knowledge of ecosystems and their functions, especially in areas like mesophotic and deep regions (Longo and Amado-Filho 2014). It is expected that new studies will result in other discoveries about the BRAF of these underexplored areas, such as the recent findings of Moura et al (2016) about the Amazon biogenic reef.

Considering the need for applying direct conservation measures to BRAF, one important aspect is the implementation of effective marine protected areas (MPAs). Creating MPAs intended to counteract the effects of anthropogenic pressures on the coastal and oceanic environment is a significant step toward conserving biodiversity and ecosystem services (Almeida et al. 2016). Schiavetti et al. (2013) analyzed the MPAs along the Brazilian coast and discussed that the protected marine region has not reached the 10% recommended protection proposed at the Seventh Conference of the Parties to the Convention on Biological Diversity (COP7). Brazil is protecting only 60% of the minimum established by COP 7. Eastern Brazil has more MPAs (predominantly sustainable areas) than the North and South Continental Platform. One of the reasons for this, according to Schiavetti et al. (2013), is that there are more coral reefs, including the largest reef complex in the South Atlantic Ocean (Abrolhos Bank). Mapping of the sea floor along the Brazilian coast is necessary to understand the distribution and diversity of marine animal forests, including coastal and oceanic ecosystems. This information is fundamental to promote specific strategies for the protection of benthic marine ecosystems and expand the MPAs, including the poorly known mesophotic ecosystems and deep-sea benthic communities off the Brazilian coast. Establishing new and expanding existing MPAs in ecosystems with the occurrence of marine animal forests are important but insufficient in the context of the Brazilian National System of MPAs. It is also necessary to improve the effective management of MPAs on the Brazilian coast, both on land and the oceanic islands (Soares et al. 2010; Almeida et al. 2016). Gerhardinger et al. (2011) identified the major flaws in the Brazilian conservation system, including poor inter-institutional coordination of coastal governance, institutional and financial crisis, poor management within individual MPAs, problems with regional networks of MPAs, and an overly bureaucratic management and administrative system. Rectifying these is an urgent priority to establish the effective management of MPAs because of the increasing urbanization and human impacts along the Brazilian coast.

Considering that Brazil is generally far from reaching the international targets of COP7, this discussion highlights the importance in accelerating the establishment and management of MPAs to promote the protection of marine animal forests, among other valuable ecosystems. Moreover, another international conservation priority is improving environmental planning (Rego et al. 2016), large marine spatial planning, and monitoring of marine biodiversity with recent and growing environmental impacts. One of the main public policies is increasing the number and size of MPAs and simultaneously implementing strong conservation efforts outside MPAs using environmental licensing; the subsequent planning of human activities that can affect the BRAF must complement this effort.

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7 Cross-References

- ▶ Animal Forests of the World: An Overview
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Growth Patterns in Long-Lived Coral Species
- ▶ Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages
- ▶ Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998
- ▶ Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns

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Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America

4

Juan Armando Sánchez

Abstract

Octocoral animal forests (Gorgoniidae and Plexauridae: Octocorallia) at both sides of tropical America provide a unique and characteristic seascape. They can reach over 2 m in height and even form a closed "canopy" in the densest communities. As a functional forest, gorgonian corals provide feeding substrate and habitat for diverse associated biota. This shallow-water fauna was evidently affected by the closure of the Isthmus of Panama, which provided new and different ecological opportunities at both sides. The different ecological settings provided opportunities for these groups to undergo separate adaptive radiations. New ecological conditions could lead to diversification in this group. At the Tropical Eastern Pacific (TEP), new planktonic resources provided new niches for suspension-feeding organisms, such as azooxanthellated gorgonian corals, and could have driven an adaptive radiation to exploit the new food sources. In the Caribbean, there is evidence of ecological speciation in some genera, and the scenario of ecological divergence as a major driver of gorgonian coral diversification is very likely. Thus far, the developmental phenotypic plasticity that we see today in transisthmian gorgonian corals is not just the product of speciation but adaptive developmental plasticity, and it needs further study. Gorgonian corals are today affected by many of the stressors predicted by global change, such as an increase in the frequency and intensity of tropical storms, rising seawater temperatures, and invasive species, yet these cnidarians seem highly resilient to bleaching and ocean acidification conditions. However, there is a link between high thermal anomalies and gorgonian coral immunity, which is associated to disease outbreaks and mass mortalities in sea fans in the Caribbean since the 1980s and more recently in the TEP.

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Octocorals • Gorgonian corals • Ecological speciation • Adaptive radiation • Ocean acidification • Octocorallia • Zooxanthellae • Global climate change • Emerging marine diseases • Aspergillosis

Contents

> “While I was comparing the longitudinal sections of the young branch of trees with those of the *Gorgonia*, I was surprised to find such a similitude between the pith of a branch of walnut tree, of a year’s growth, and that of *Gorgonia*. . .” John Ellis, 1776, “On the Nature of the *Gorgonia*; that is a real marine animal, and not a mixed nature, between animal and vegetable.” *Phil.Trans.R.Soc.Lond.*66:1–17

1 Introduction

To introduce marine ecology, an easy strategy is to stress the fact that the continent is a “green world” dominated by plants, including many inedible organisms like pine or gum trees, whereas the ocean is an “animal world.” The first thought about life in the sea is most likely a fish school. With a few exceptions, e.g., kelp and sea grass communities, or intertidal algal beds, marine ecosystems have a more representative biomass in animals. Plants in the ocean are usually tiny, unicellular, and edible, and countless planktonic organisms efficiently consume their blooms, which energy end up in larger invertebrates, fishes, birds, or mammals. On the ocean floor, sessile animals occur everywhere, even at extreme depths. Sessile animals usually feed on suspended particles and organisms from the water column, and in some regions, they form dense communities. These are the “animal forests," jungles of dense suspension feeders including cnidarians such as hydroids, anemones, corals, and octocorals (including gorgonians), among others. For a long time, many cnidarians were actually considered plants. Around 1776, John Ellis was the first scientist to convince his colleagues that gorgonian corals were actually animals and not plants.

The "animal forest" analogy probably gets closer to its implied meaning at some tropical coral and rocky reefs. The trees of these forests are mostly octocorals of the gorgonian type (Octocorallia: Holaxonia: Gorgoniidae and Plexauridae), which are highly branched treelike polypal colonies (Sanchez 2004). In contrast with their Indo-Pacific, soft and fleshy octocoral counterparts (Fabricius and Alderslade 2001), gorgonian octocorals have little area of attachment to the substrate besides a holdfast; they have erect, branching, or sea fan shapes; and most of their biomass is over the substrate, in the water column. This strategy provides access to resources in the water column, reducing species competition at the substrate level (Jackson 1977). Gorgonian corals can reach over 2 m in height and can almost form a closed "canopy," i.e., you cannot see the substrate from above their branches, at the most dense communities in the shallow exposed habitats in the Caribbean Sea (Cadena and Sánchez 2010; Gambrel and Lasker 2016).

Dense gorgonian communities have been explicitly proposed as animal forests that promote stock recruitment, where gorgonian larvae concentrate beneath the canopy (Privitera-Johnson et al. 2015). This type of community is common at both coasts of tropical and subtropical America, Brazil, the west coast of Africa (Grasshoff 1988), and even some temperate areas in the Atlantic (Devictor and Morton 2010; Perez et al. 2011) and the Mediterranean Sea (Previati et al. 2010). This chapter focuses on the gorgonian coral communities at both sides of tropical America. Biogeographically, these communities belong to the Tropical Eastern Pacific (TEP) with some species spanning from Peru to California (Grigg 1977) and in the Tropical Western Atlantic (excluding Brazil) including the Caribbean, Bahamas, southern Gulf of Mexico, and Florida (Bayer 1961).

2 Octocoral Animal Forests Assemblages and Diversity

A major question in biology is why tropical ecosystems are so diverse (Bowen et al. 2013). Octocorals in the tropical shallow seas are remarkably diverse. Over 10 species from the same genus can be found in sympatry within just a 10 m^2 area in the Caribbean Sea, for example (Sánchez 2009; Sánchez et al. 2005). However, these highly diverse gorgonian coral communities at both sides of tropical America have unknown origins. The sea fans from the genus *Pacifigorgia* (Octocorallia: Gorgoniidae), for instance, have only one species in the Atlantic and over 34 species at the TEP (Vargas et al. 2008). The rise and closure of the Isthmus of Panama induced dramatic oceanographic changes at both sides of tropical America with major effects on marine diversity (Coates et al. 1992). The ultimate goal of this chapter is to provide testable hypotheses on the evolutionary forces that affected the origin and diversity of gorgonian coral communities in this region.

3 Caribbean Octocoral Communities

The marine animal forests at both sides of tropical America provide a unique and characteristic seascape, where their differences in diversity of species and assemblages are immediately noticeable (e.g., Fig. 1). The Caribbean gorgonian coral assemblages, typical reef-dwelling communities, have clear zonation patterns in terms of water motion, topographic relief, depth, and sediment transport (Alcolado 1981; Kinzie 1973; Sanchez et al. 1997; Yoshioka and Yoshioka 1989). The types of assemblages vary considerably depending on the conditions at each reef, which include contrasting assemblages at the extremes and a myriad of overlapping associations in between (Lasker and Coffroth 1983a; Sanchez 1999; Sanchez et al. 1997). In Caribbean reefs, zooxanthellate gorgonian octocorals from the families Gorgoniidae and Plexauridae dominate the landscape above 30 m depth with about 51 species present (Sánchez and Wirshing 2005). Below this depth, other azooxanthellate families such as Ellisellidae become more abundant (Sanchez 1999; Velásquez and Sánchez 2015).

Gorgonian populations in the Caribbean have mean densities between 1 and 10 col m^{-2}, and roughly half (~50%) of the colonies are plexaurids rivaled only by sea feathers *Antillogorgia* spp. (Etnoyer et al. 2010; Lenz et al. 2015; Sánchez and Pizarro 2005). Caribbean wide, *Antillogorgia americana* is one of the most common species (Fig. 1f), whereas the northern and western Caribbean have localities with dense populations of *A. bipinnata* (Fig. 1b, c). A common plexaurid assemblage includes species of *Plexaura, Pseudoplexaura*, *Plexaurella*, and *Eunicea* (Fig. 1d), and a shift to species with larger polyps (*Eunicea* sea candelabra) occurs at siliciclastic reefs with continental influence (Velásquez and Sánchez 2015). Sea fans (*Gorgonia* spp.) were once a dominant octocoral on the reef crest and fore-reef areas around the wider Caribbean (Birkeland 1974; Lasker and Coffroth 1983b), but today, their populations are greatly decimated in many localities due to fungal and other diseases (Smith and Weil 2004).

Gorgonians are flexible treelike structures that can withstand different levels of water motion. This flexibility is related to the ratio between elastic and hard (calcium carbonate) axial structures in the different species (Boller et al. 2002; Esford and Lewis 1990a, b; Shirur et al. 2014). In addition, the complex positioning of coenemchymal sclerites, which projecting structures collide to stiffen the branches (Lewis and Wallis 1991; West 1997, 1998), allows a species-specific tolerance to particular water motion levels. For example, the southwestern Caribbean atoll Courtown Cays, in Colombia (Fig. 2a), includes all kinds of reef geomorphological settings, an emergent windward barrier reef separating the wave-exposed and gently sloping windward fore-reef terrace, from the protected lagoon basin with patch reefs, and the leeward terrace (Diaz et al. 1996). This type of reef provides ideal environmental gradients for the different Caribbean gorgonian species tolerances. A transect along the gorgonian communities of an atoll clearly shows that there are some species with specific environmental tolerances, whereas there are some generalist species found in all environments (Fig. 2b). This revealing observation (Sanchez et al. 1997) points out the importance of phenotypic plasticity to colonize diverse environments in gorgonians, which is remarkable in some Caribbean species present in most environments.

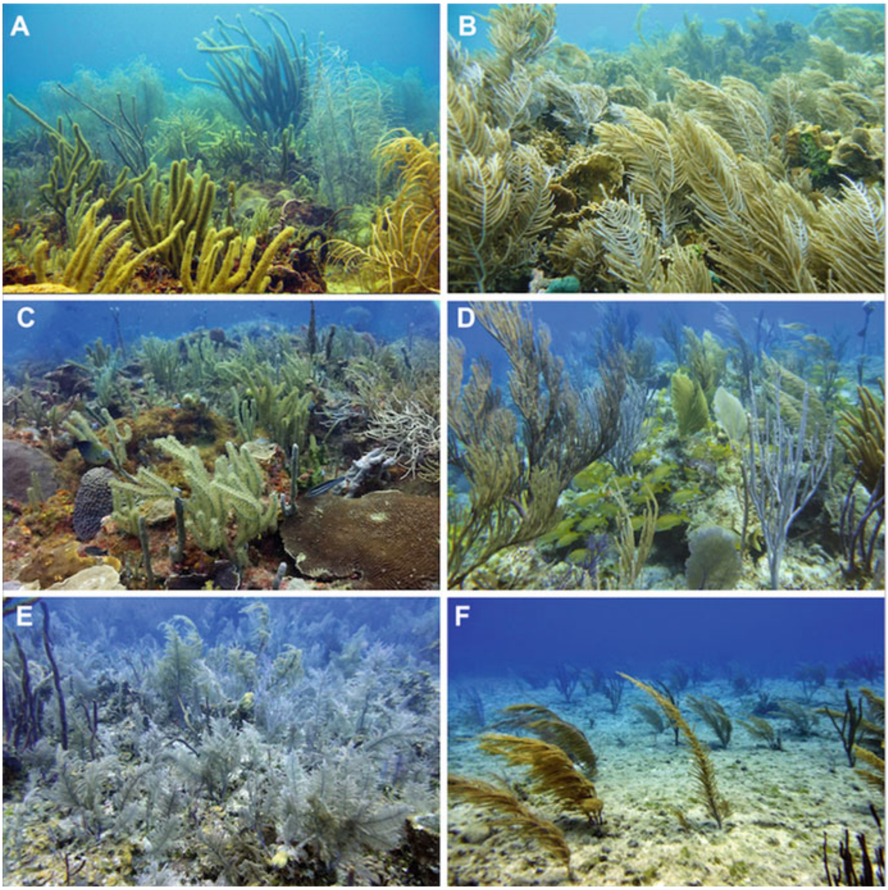

Fig. 1 Octocoral animal forests in the Caribbean Sea. (**a**) Large colonies of *Pseudoplexaura, Eunicea*, and *Antillogorgia* at Isla Fuerte, Colombia (10 m). (**b**) Dense forests of *Antillogorgia bipinnata* at Crawl Cay, Bocas del Toro, Panama (5 m). (**c**) Diverse sea candelabrum species (*Eunicea* spp.) at the plateau from Imelda Bank, Barú Island, Cartagena, Colombia (**d**) Large colonies of *Plexaura, Eunicea, Gorgonia*, and *Pseudoplexaura* off Abaco Island, Bahamas (10 m). (**e**) Diverse species of sea feathers (*Antillogorgia*) off Gorda Cay, Bahamas (15 m). (**f**) Dispersed tall colonies of sea feathers (including *A. americana*) and candelabrum octocorals (*Eunicea*) off Abaco Island, Bahamas (15 m) (Photos: Juan A. Sánchez)

4 Eastern Pacific Octocoral Communities

In contrast to research of Caribbean gorgonian assemblages, with over four decades of observations, the first surveys on TEP communities started in the last few years. Despite the paucity of studies on this area, there is enough information to understand how different these octocoral communities are with respect to their Atlantic counterparts. Although the number of species could be similar to the Caribbean, TEP gorgonian octocorals are clearly dominated by *Pacifigorgia*, *Leptogorgia*, and

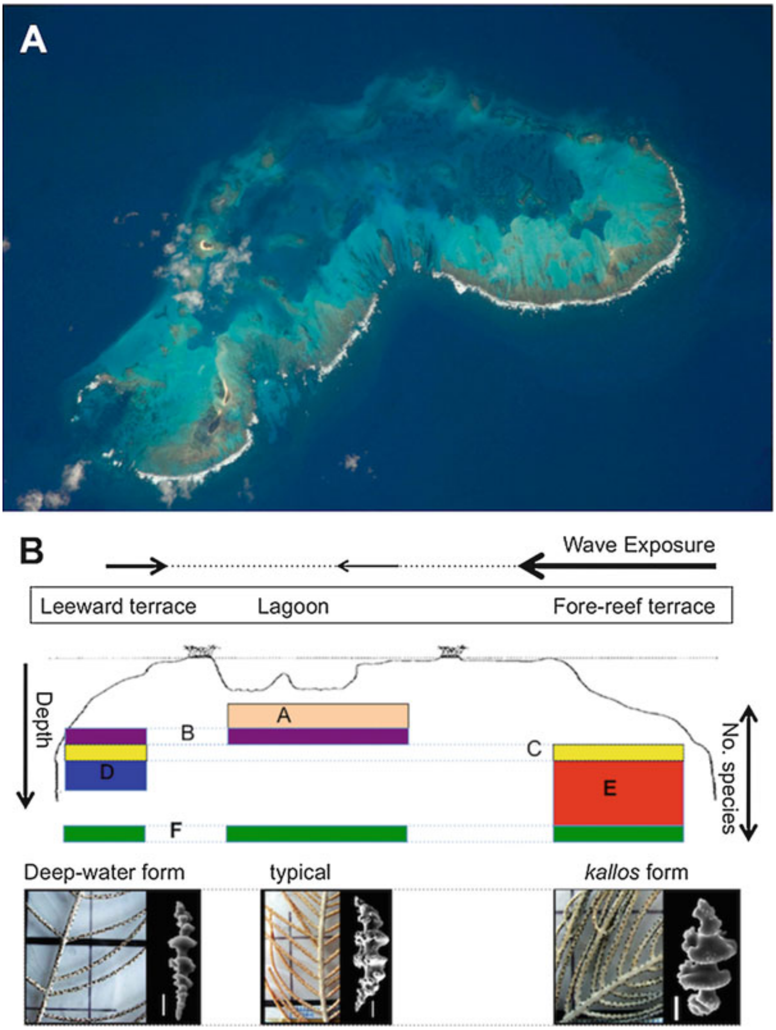

Fig. 2 Octocoral assemblages at different environment from a Caribbean atoll. *A*. Species found only in lagoon patch reefs (e.g., *Pseudoplexaura porosa, Ps. crucis, Plexaura homomalla, P. kuekenthali*). *B*. Leeward terrace and lagoon patch reefs (e.g., *Eunicea fusca*). *C*. Leeward and fore-reef terraces (e.g., *Eunicea flexuosa, E. succinea, Pseudoplexaura crucis, Ps. wagenaari*). *D*. Leeward terrace only (*Antillogorgia hystrix*). *E*. Fore-reef terrace only (e.g., *Antillogorgia acerosa, Pterogorgia citrina, E. tourneforti, Plexaurella grisea, Pl. fusifera, Gorgonia ventalina, Pterogorgia anceps*). *F*. Found in all environments (e.g., *Antillogorgia Americana, A. bipinnata + A. kallos, Briareum polyanthes-asbestinum, Pl. dichotoma, Muriceopsis flavida*). Below is one species found in all atoll environments, *Antillogorgia bipinnata*, exhibiting both colony and sclerite plasticity across habitats (Data on species assemblage from Sánchez et al., 1997; *A. bipinnata* photos from Sánchez et al. 2007, Biomed Central)

Muricea species together with a few species from *Eugorgia*, *Heterogorgia*, and *Psammogorgia*.

With a few exceptions (e.g., *Eugorgia auriantiaca, Muricea californica*, and *P. stenobrochis*), most gorgonian corals in this region are below 50 cm in height or width (Gomez et al. 2014). Species diversity in shallow-water assemblages can be as high as 38 species in Las Perlas Archipelago, Panama (Guzman et al. 2008), 23 species along the coast of Costa Rica (Breedy and Cortés 2015; Breedy and Guzman 2003), 15 species in Coiba Island (Panama), 10–17 species along the Pacific coast of Mexico (Abeytia et al. 2013), 16 species in Gorgona Island and Cabo Corrientes, Colombia (Sánchez et al. 2014), and as low as three to four species in Oceanic islands such as Cocos (Costa Rica) and Malpelo (Colombia) (Breedy and Cortés 2008; Sánchez et al. 2012). Areas with high octocoral diversity in shallow waters, but no formal surveys available, include several habitats along the coast of Ecuador (Manabi region, including Isla de la Plata) and Mancora, Perú (personal observations). There are some taxonomic surveys from the Galapagos Islands reporting 11 similar species (Williams and Breedy 2004) and unpublished collections deposited at the National Museum of Natural History (Washington DC, USA) from the coast of El Salvador and Easter Island, Chile (personal observation). New species are frequently found in this region; consequently the accounts on octocoral diversity can change in the following years.

All the TEP octocoral fauna is azooxanthellate, including the aposymbiotic genus *Muricea* lacking zooxanthellae only in the TEP. Therefore, they are all suspension feeders, with subtle changes in form optimized for capturing certain size particles. This is an obvious speculation when comparing the slight differences from dozens of mesh-like *Pacifigorgia* sea fans (Breedy and Guzman 2002, 2003). *Pacifigorgia stenobrochis*, for instance, has the mesh size of over an order of magnitude wider than *P. irene*, and there is a continuum of forms and sizes in between (Breedy and Guzman 2002). As most gorgonian octocorals requiring a hard substrate for attachment, the TEP fauna usually settles on rocky substrates covered with crustose coralline algae instead of areas with scleractinian reef development (Guzman et al. 2008; Sánchez et al. 2012, 2014).

Two particular features of TEP gorgonian assemblages are their high densities and species hyperdominance, i.e., the local dominance of a few species in the community (Fig. 3). There are peak colonial densities of about 100 colonies m^{-2} in Coiba Island (Gomez et al. 2014) and 30 colonies m^{-2} in Gorgona Island (Sánchez et al. 2014). Although most surveyed sites in those regions have densities ranging between 1 and 15 colonies m^{-2}, the gorgonian density can suddenly increase due to the invasion of the exotic snowflake octocoral *Carijoa riisei* (Sánchez and Ballesteros 2014) as well as episodic mass recruitment of some species (Gomez et al. 2014), including *Leptogorgia alba* (Fig. 3d). The latter species is equivalent of a habitat generalist species (such as *A. bipinnata* in

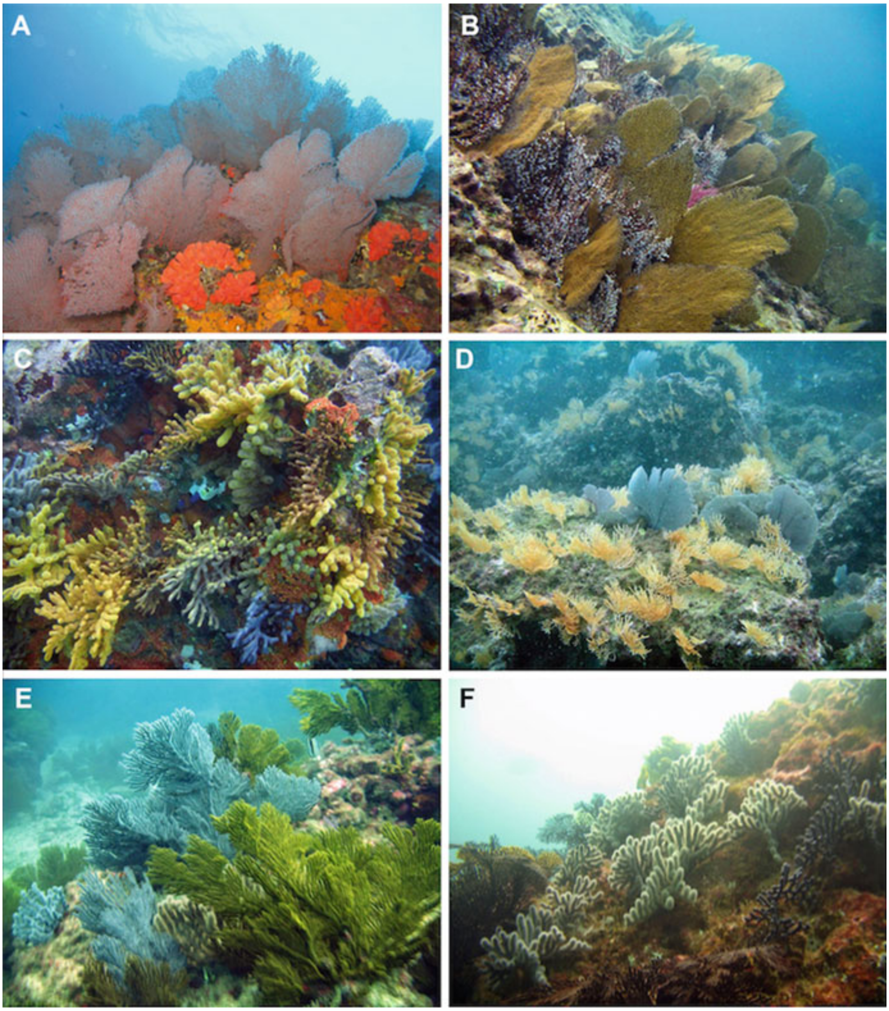

Fig. 3 Octocoral animal forests at the Tropical Eastern Pacific. (**a**) Rocky outcrop with a dense population of *Pacifigorgia cairnsi*, Malpelo Island, Colombia (20 m). (**b**) *P. firma* sea fans in contact with the invasive snowflake coral *Carijoa riisei* at Gorgona Island (La Montañita), Colombia (8 m). (**c**) Dense stands of candelabrum colonies (*Muricea*) at Cabo Corrientes, Choco, Colombia (12 m). (**d**) Juvenile sea whips (*Leptogorgia alba*) and sea fans (*P. irene*) at La Roñosa, Cabo Corrientes, Choco, Colombia (10 m). (**e**) Large colonies (above 50 cm in height) of *Muricea* (including *Muricea californica*, yellow) at Los Ahorcados, Puerto Lopez, Ecuador (20 m). (**f**) Candelabrum colonies (*Muricea* spp.) at La Roñosa, Cabo Corrientes, Choco, Colombia (5 m) (Photos: Juan A. Sánchez)

the Caribbean) extending from the beginning of the subtidal to a depth of 70 m (Abeytia et al. 2013).

Gorgonian assemblages in the TEP are locally dominated by either sea candelabrum species (*Muricea* spp., Fig. 3c, e, f), sea fans (*Pacifigorgia* spp. Fig. 3a–b), or sea whips (*Leptogorgia* spp. Fig. 3d). In a region such as Cabo Corrientes, Choco, the subtidal habitat can be dominated by thick-branched *Muricea* species of several colors (Fig. 3c) or the sea whip *L. alba* and occasionally the green sea fan *Pacifigorgia bayeri*. At an intermediate depth of about 5 m, clumps of *P. firma* can be occasionally found. Then, about a depth of 10 m, sea fans (*Pacifigorgia eximia*, *P. irene*, and *P. sculpta*) dominate the seascape, and as depth increases, a more diverse assemblage is found including *Eugorgia*, *Heterogorgia*, different species of *Muricea* (including *M. crassa* and *M. fruticosa*), and *Pacifigorgia* (including *P. rubicunda, P. sculpta*, and *P. stenobrochis*). Finally, around 30 m *L. alba* is seen again together with *M. fruticosa* and rare sea fans (e.g., *P. senta*) and other organisms such as black corals. Despite an apparent faunal zonation structure, the patterns could be quite different at intermediate depths, other regions, or at oceanic islands. With the exception of widespread species, such as *L. alba*, the available literature suggest a species replacement pattern at the different TEP regions (from hundreds to thousands of kilometers) but with clear dominance of some of the local species (Abeytia et al. 2013; Gomez et al. 2014; Sánchez et al. 2014).

5 Symbiosis

5.1 Microorganisms

As a functional animal forest, gorgonian octocorals at both sides of tropical America provide feeding substrate, habitat, and protection for diverse associated biota; therefore, they are truly foundation species. Although microorganisms have not been fully studied in this fauna, traditional and recent approaches call the attention on the great potential of gorgonian corals as highly diverse holobionts including viral, bacterial, fungal, and protozoan associates (Barrero-Canosa et al. 2012; Hewson et al. 2012; Zuluaga-Montero et al. 2010b; Correa et al. 2013). Their microbiota could be responsible of the rich and diverse secondary metabolites found in octocorals, which have been known to carry promising pharmacological applications (Lei 2016; Wei et al. 2004).

As mentioned above, only the gorgonians from the Atlantic engage in symbiosis with zooxanthellae (*Symbiodinium*: Dinophyta) (Van Oppen et al. 2005), where >85% of species host *Symbiodinium* clade B, followed by a few species with clade C (Goulet and Coffroth 2004). Yet, it is known that juvenile stages of Caribbean octocorals can have many different kinds of *Symbiodinium* before maintaining a single type (Poland et al. 2013), which could be very specific in some species (Parkinson et al. 2015; Prada et al. 2014). Thus far, it is known that under stress, a change of symbiont is possible (Lewis and Coffroth 2004). It is also known that gorgonian coral species with higher amounts of lipids contain higher densities of *Symbiodinium*, which can be as high as 7×10^6 cells cm^{-2} in *Pseudoplexaura* (Shirur et al. 2014).

5.2 Invertebrates

Many invertebrates are closely associated to gorgonian corals. In the Caribbean, at least 21 species of octocorals host *Ovulidae* cowries and egg cowries (Mollusca: Gastropoda). The aposematic flamingo tongue snail, *Cyphoma gibbosum* (Fig. 4a), predates most shallow-water species, while the fingerprint flamingo tongue, *C. signatum*, is a *Plexaurella* spp. specialist (Reijnen et al. 2010). The Caribbean egg cowries, *Cymbovula acicularis* and *Simnialena uniplicata,* are mimetic ectoparasites from most Gorgoniidae and sea fans (*Gorgonia* spp.), respectively (Lorenz and Fehse 2009; Reijnen et al. 2010). Most TEP sea fans and sea whips (*Pacifigorgia, Eugorgia*, and *Leptogorgia*) have also mimetic egg cowries, *Simnia avena* (=*S. aequalis*) and *Simnialena rufa*, remarkably faithful to their hosts' polyps and color patterns (Fig. 4b), which comprise model cases of masquerade camouflage (Sánchez et al. 2016; Sánchez 2013). Sessile invertebrates also colonize the bare gorgonian skeleton after injury and predation and contribute to tissue and colony mortality. Predators such as the flamingo tongue or the fire worm (*Hermodice carunculata*: Fig. 4e) expose the gorgonian skeleton after removing the live tissue (Vreeland and Lasker 1989). Partial tissue mortality due to disease also opens new bare endoskeleton for algae and other invertebrate colonization. This is a preferred substrate for many solitary and colonial organisms in the Caribbean, such as bivalves (e.g., *Pteria colymbus*), hydrocorals, and other hydroids, sponges, and tunicates (Fig. 4c).

In contrast, living branches of gorgonian corals in the TEP are the habitat for colonies of brittle stars, *Ophiactis savigny*, *Ophiothrix spiculata*, and *Ophiothela mirabilis* (Cantera et al. 1987; Neira et al. 1992, 2005), which can colonize entire colonies (Fig. 4d). Crustaceans, sometimes in large numbers, like colonies, are also associated (and mimetic) to *Muricea*, *Leptogorgia*, and *Pacifigorgia*, including the shrimps *Neopontonides* and *Veleronia* (Pontonidae) together with cirripedes, amphipods, and caridean shrimps (Cantera et al. 1987; Ramos 2015), which most of them remain understudied.

5.3 Reef Fish

Reef fish, mostly predators, also associate closely with gorgonian corals. The TEP longnose hawkfish (*Oxycirrhites typus*: Fig. 4f) and coral hawkfish (*Cirrhitichthys oxycephalus*) exhibit sea fanlike camouflage, which is likely an ambush strategy (Sánchez et al. 2016). The TEP king (passer) angelfish (*Holacanthus passer*) has been seen feeding in large groups on the invasive octocoral *Carijoa riisei* (Sánchez and Ballesteros 2014). The Caribbean butterfly fish *Chaetodon capistratus* preferably feeds on gorgonian corals with mature gonads (Lasker 1985). Large surgeonfish schools have been observed targeting single large sea fan colonies biting it all over frenetically for a short time and then moving away leaving no clear signs of tissue damage (E. Weil, personal communication). Are they just consuming excess mucus with organic particles trapped in it? Other fishes in the Caribbean, such as the

Fig. 4 Common associated species to shallow-water octocorals at both sides of tropical America. (**a**) Flamingo tongue, *Cyphoma gibbosum*, on *Eunicea tayrona*, Caribbean Sea, Bocas del Toro, Panama (7 m). (**b**) Egg cowrie, *Simnia avena*, on *Pacifigorgia cairnsi*, Malpelo Island, Colombia (20 m). (**c**) Tunicate, *Clavelina picta*, on *Antillogorgia americana* branch, Abaco Island, Bahamas (15 m). (**d**). *Pacifigorgia stenobrochis* sustaining a colony of *Ophiothela mirabilis*, Cabo Corrientes, (12 m). (**e**) Fireworm, *Hermodice carunculata*, feeding a branch of *Pseudoplexaura porosa*, Isla Fuerte, Colombia (12 m). (**f**) Longnose hawkfish, *Oxycirrhites typus*, with a sea fanlike background camouflage beside *Pacifigorgia media*, Cabo Corrientes, Choco, Colombia (15 m) (Photos: Juan A. Sánchez)

trumpet fish *Aulostomus maculatus*, oftentimes align with gorgonians to ambush prey (Aronson 1983) or simply use them as background camouflage or shelter seeking protection, like the slender filefish *Monacanthus tuckeri* (Ben-David and Kritzer 2005). The TEP leather bass, *Dermatolepis dermatolepis*, has been commonly seen scrapping its body against sea fans, *P. cairnsi*, at Malpelo Island, which is an unknown behavior.

6 Gorgonian Animal Forests Demography

6.1 Growth

The typical gorgonian corals at both sides of tropical America, families Gorgoniidae and Plexauridae, have slow growth rates and are moderately long lived. Gorgonian colonial size, rather than age, is the most reliable indicator of their survivorship and growth, where large colonies have higher survivorship (Yoshioka 1994) and small colonies higher growth rates (Cadena and Sánchez 2010; Gomez et al. 2014). Growth rates (branch linear extension) in gorgonian corals can be as low as 1 cm year^{-1} in TEP (*Leptogorgia alba*: Gomez et al. 2014) and Caribbean species (*A. elisabethae*: Lasker et al. 2003) and up to 5 cm year^{-1} in the Caribbean black sea rod *Plexaura homomalla* (Kim and Lasker 1997) and 15–30 cm year^{-1} in Caribbean sea feather (*A. acerosa:* Cadena and Sánchez 2010).

Colony growth in gorgonians is a complex yet self-organized process (Sanchez et al. 2004; Sanchez 2004), in which other modules in addition to the polyps (twigs and branchlets) have determinate growth (Lasker et al. 2003) but the sum of the parts follows an adaptive growth program (Lasker and Sánchez 2002). The development of a gorgonian colony (astogeny) has arranged relationships between global (whole colony) and local properties (main stem and holdfast), e.g., the number of total branches correlate with the number of stem canals, which suggests that the adaptive colonial growth has a coordinated integration (Cadena et al. 2010; Morales Pinzon et al. 2014; Sánchez and Lasker 2004). Consequently, integrated colonial features, such as the main stem, together with seasonal productivity pulses, can provide a demographic record of the colony (Goffredo and Lasker 2006), which has been successfully used as an age proxy to develop individual-based models of population growth and response to clipping (Goffredo and Lasker 2008). The Caribbean gorgonian species, *Antillogorgia elisabethae*, reach sexual maturity in about 4–7 years and can live between 20 and 40 years (Goffredo and Lasker 2006, 2008). The TEP species *Muricea fruticosa* and *M. californica* reach maturity at 5–10 years, respectively, and can live over 50 years (Grigg 1974, 1975). Given the centennial ages of most deep- and cold-water octocorals (Tracey et al. 2007), these fauna should be considered moderately long lived. Estimates on the maximum ages and growth rates from most gorgonian corals remain unknown and need to be studied.

6.2 Reproduction

The reproductive strategies of gorgonian corals at both sides of tropical America are closely linked with the demography and population genetics of their species. Sexual reproduction strategies in the species of this area include broadcast spawners as well

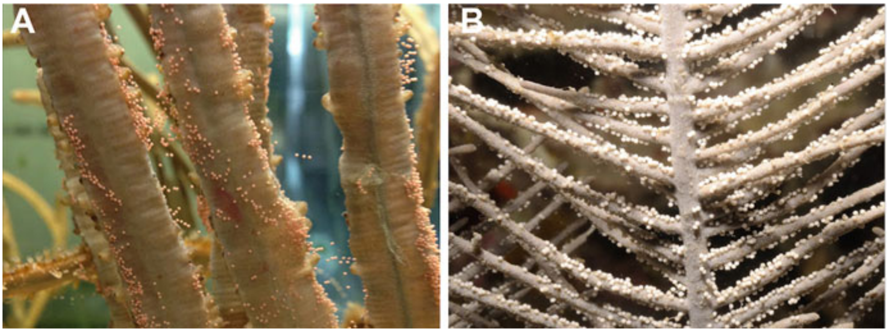

Fig. 5 Surface brooding in Caribbean octocorals. (**a**) *Pterogorgia guadalupensis* in lab conditions. (**b**) *Antillogorgia bipinnata* at Crawl Cay, Bocas del Toro, Panama (6 m) (Photos: Juan A. Sánchez)

as internal and surface brooders (Fig. 5), with most species being gonochoric (Kahng et al. 2011). From the TEP species, the only reproductive study goes back to Grigg (1979), on two brooder species of *Muricea* (*M. californica* and *M fruticosa*). The reproductive mode of the over 35 species of the TEP sea fans *Pacifigorgia* is uncertain; if guessing for their phylogenetic affinity to *Leptogorgia* (Aguilar and Sanchez 2007; Ament-Velásquez et al. 2016; Sanchez 2007), they could be broadcast spawners (Beasley et al. 2003; Gotelli 1991; Kahng et al. 2011).

In contrast, several gorgonian corals have been studied for their sexual reproduction in the Caribbean. Most plexaurids (*Eunicea, Plexaura*, and *Pseudoplexaura*) and sea fans (*Gorgonia ventalina*) are gonochoric broadcast spawners and some sea feathers (*Antillogorgia*) and sea ribbons (*Pterogorgia*) surface brooders (Kahng et al. 2011). Caribbean broadcast spawners octocorals (*Eunicea*) have among others the largest egg diameters and volumes (Sánchez 2009), which could be related to long larval dispersal. As in Caribbean broadcast-spawning corals (Foster et al. 2012), panmixia among distant populations has also been found in gorgonian corals with this strategy (Andras et al. 2013; Prada and Hellberg 2013). Surface brooders, which larvae do not travel far (Gutiérrez-Rodríguez and Lasker 2004), have shown a strong genetic structure among hundreds to thousands of kilometers (Gutierrez-Rodriguez et al. 2005, 2009; Lasker and Porto-Hannes 2015) and even tenths of meters (Smilansky and Lasker 2014), which suggests that gorgonians with this strategy tend to have a philopatric distribution.

The density of gorgonian corals increases considerably due to the different sexual and asexual reproductive strategies. The few recent studies on gorgonian coral recruitment in this area have revealed high densities of settlement for both brooders and broadcast spawners (Gomez et al. 2014; Lasker 2013; Privitera-Johnson et al. 2015), which agrees to what is known for other types of octocorals and gorgonian corals elsewhere (e.g., Brazeau and Lasker 1992b; Gotelli 1988). Clonality, a strategy to increase population size, is another common property between plant and animal forests. In the Caribbean, it is long appreciated the contribution from asexual colony propagation to population maintenance and growth (Lasker 1990),

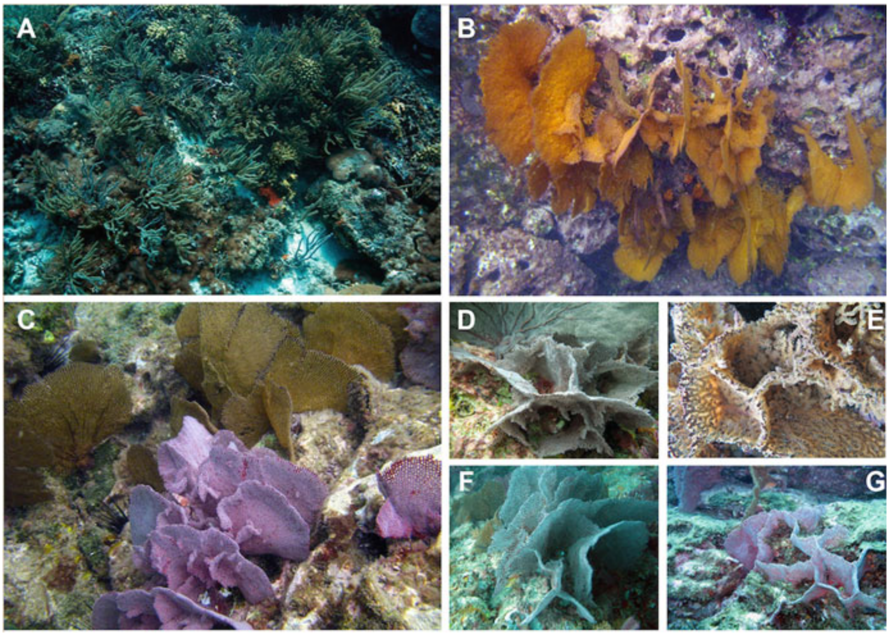

Fig. 6 Examples of clonality at some shallow-water octocorals at both sides of tropical America. (**a**). Fragmentation leading to dense zones of *Eunicea fusca* at Curacao (water factory reef, 12 m). (**b**) Multiple connected sea fan colonies of *Pacifigorgia firma* at Gorgona Island (12 m). (**c**) Two stands of connected sea fans, *P. firma* and *P. rubicunda* at Gorgona Island (12 m). Comblike configurations in different sea fan species (Cabo Corrientes, Choco, Colombia): (**d**) *Pacifigorgia* sp., (**e**) *P. bayeri* (**f**) *P. cairnsi* (**g**) *P. rubicunda* (Photos: Juan A. Sánchez)

which is a disturbance-sensitive process clearly influencing the genetic diversity in a population (Coffroth and Lasker 1998; Lasker and Coffroth 1999). In the Caribbean, fragmentation is promoted by the gorgonin skeletal properties, such as constrictions in *Plexaura kuna*, that make possible breakage under certain drag forces (Boller et al. 2002). Vegetative propagation is also common in the sea candelabrum corals *Eunicea* (Sánchez 2009), the most speciose genus in the Caribbean, where *E. fusca* is probably the most extreme example of clonality (Fig. 6a: Sarmiento, A. & Sánchez, J.A., in prep.).

There are no records of vegetative propagation for TEP gorgonian corals. High gorgonian densities seem related to episodic sexual recruitment in broadcast spawners such as *Leptogorgia* (Gomez et al. 2014) and likely philopatry in brooders like *Muricea* (e.g., Fig. 2c). However, several TEP *Pacifigorgia* sea fans exhibit connected stands of colonies in a comblike shape (Fig. 6b–f), which clearly extends a genotype beyond the normal space required for single sea fan colony. It is well known that sea fan colonies, such as *Gorgonia ventalina*, have random orientations when small, but adult ones accurately orientate perpendicular to the prevailing water flow direction (Wainwright and Dillon 1969). It is of great interest to know why sea fans like *Pacifigorgia* choose to grow in multiple directions, particularly whether it is a response to turbulent flow or if it is a vegetative growth strategy (or both). It certainly increases efficiency of food capture in any direction the water is flowing. It could also provide structural strength and increase survivorship.

7 Animal Forests in a Changing Ocean

7.1 Effects of Storms

One of the predictions of global climate change is the increase in frequency and intensity of storms (Church et al. 2013), which has been a particular concern in the Atlantic Ocean (Goldenberg et al. 2001). Natural disturbances, such as hurricanes in the Caribbean, comprise a major factor structuring coral reef communities (Gardner et al. 2008). Reef-building corals distributed in the hurricane belt are quite more clonal than those from protected regions (Foster et al. 2013). Although it is known that disturbance leads to fragmentation and vegetative propagation in some Caribbean gorgonians (Coffroth and Lasker 1998; Lasker and Coffroth 1999), a pattern of hurricane-driven clonality for these corals has not been explored. Two major hurricanes (category 5), such as David in 1979 and Allen in 1980, were responsible for up to 100% gorgonian's mortality in localized reef areas along their pathways, though the extent of gorgonian mortality was highly variable (from 0% to 100%) and unpredictable (Woodley et al. 1981; Yoshioka and Yoshioka 1987). The effects of Hurricane Michelle (2001, category 4) in the gorgonian corals from San Salvador, Bahamas, can be seen in Fig. 7a–b. In this occasion, huge reef areas were covered with a layer of sand over 30 cm thick, suffocating all reef organisms including many gorgonian corals (Fig. 7b). In addition, hundreds of large gorgonian skeletons accumulated under reef crevices (Fig. 7a), which included members of nearly each species seen in the reef (personal observation). A testable prediction is that long-lived gorgonian species distributed along the hurricane belt have reduced maximum sizes with respect to populations from protected areas.

7.2 Global Warming

One of the most worrisome outcomes from climate change is the effect of warming seawater temperatures on marine biodiversity with the following loss of ecosystem services (Hoegh-Guldberg et al. 2007; Rutterford et al. 2015). Caribbean reefs have experienced the "sum of all fears" in recent years with two major widespread thermal anomalies in 2005 and 2010 that produced region-wide intense bleaching and disease outbreaks that caused high coral and octocoral mortalities (see details in Chap. 40, "Octocoral Diseases in a Changing Ocean" by Weil et al., this volume). The year 2005 was a record hurricane season, with four category 5 storms, including Katrina (Eakin et al. 2010). Even though disease prevalence in octocoral populations increased significantly, no major octocoral mass mortalities were reported, except for *Plexaurella* spp. (Quinn and Kojis 2007), which is the only Caribbean gorgonian

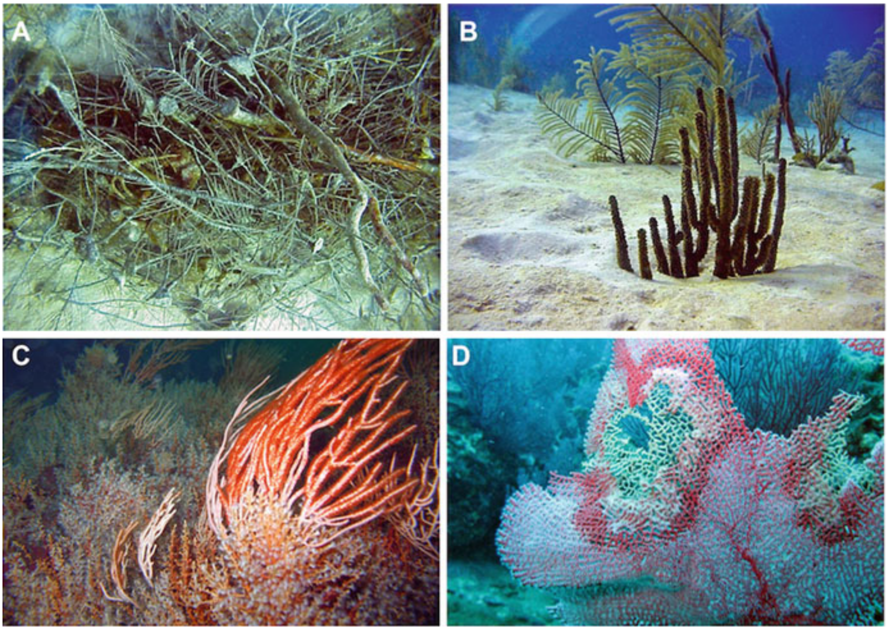

Fig. 7 Some common treats on octocorals at both sides of tropical America. (**a**) Remains of multiple tall gorgonian corals accumulated after Michelle hurricane (2001, category 4) at San Salvador, Bahamas (10 m). (**b**) Living remains of *Eunicea* and *Antillogorgia* covered with >20 cm thick layer of sand after Michelle hurricane (2001) at San Salvador, Bahamas (10 m), (**c**) The snowflake invasive octocoral, *Carijoa riisei*, monopolizing space and overgrowing *Leptogorgia alba*. (**d**) *Pacifigorgia rubicunda* colony with aspergillosis-like fungal disease (c-D, colonies at Cabo Corrientes, Choco, Colombia, 12 m) (All photos: Juan A. Sánchez)

coral genus carrying *Symbiodinium* clade C (Van Oppen et al. 2005). Clade B, which is prevalent in most Caribbean gorgonians, is more bleaching resistant (Lewis and Coffroth 2004; van Oppen et al. 2009). Although Caribbean gorgonian octocorals normally bleach under prolonged thermal stress, monitoring of bleached gorgonian corals has shown negligible mortality and resilience after bleaching (Lasker 2003; Prada et al. 2010). These observations can be explained by the fact that Caribbean gorgonians tend to be heterotrophic and do not rely as much on *Symbiodinium* for their energetics (Baker et al. 2015). This mixed strategy render most Caribbean gorgonians in sort of a "safe ground" with regard to future thermal anomalies if no disease outbreaks impact their populations.

The effects and dimensions of rising seawater temperatures have been also related to emerging marine diseases (Harvell et al. 2004; Miller and Richardson 2015), which affect a number of coral reef organisms including octocorals (Weil et al. 2006; Weil 2004). Coral reef scientists in the early 1980s were not prepared to completely understand the causes and drivers of unexpected Caribbean-wide mass mortalities such as the case of the black sea urchin *Diadema antillarum* (Lessios et al. 1984) and the acroporid corals (Gladfelter 1982). Actually, the spread of the sea urchin mortality was systematically and timely followed through the Caribbean, whereas the mortalities of corals such as *Acropora* and the sea fans *Gorgonia* spp. were unnoticed in many places and reported several years after (Dustan and Halas 1987; Garzón-Ferreira and Zea 1992; Guzmán and Cortés 1984; Nagelkerken et al. 1997). The major fungal disease causing widespread sea fan mortalities in the early 1990s and 2000s is still around, infecting a number of Caribbean gorgonian corals (Ward et al. 2006b), and is caused by the cosmopolitan fungi *Aspergillus sydowii* and *A. flavus* and is termed aspergillosis (Alker et al. 2001; Smith et al. 1998; Smith and Weil 2004; Toledo-Hernández et al. 2013; Zuluaga-Montero et al. 2010). The populations of *Gorgonia ventalina* have recovered in some localities, and their genetic diversity appeared unaffected (Andras et al. 2011; Bruno et al. 2011). Twenty years after the 1982–1983 Caribbean sea fan mortality, TEP gorgonian corals (*Pacifigorgia* and *Leptogorgia*) were seen and reported with an aspergillosis-like disease (Sánchez et al. 2011, 2014), which have very similar epizootiology and fungal associates (Barrero-Canosa et al. 2012). A mass mortality of at least four *Pacifigorgia* species occurred during 2008, and the disease still prevails in several TEP locations (Sánchez et al. 2014). This disease outbreak provided more questions than answers on the infectious biology, given the great differences in the host species and geographic settings between the Caribbean and TEP.

The common feature of diseases in aquatic organisms is a link between environmental drivers, including temperature change and immunity (Mydlarz et al. 2006). Despite the complexity of immunocompetence in a gorgonian coral such as *Gorgonia ventalina* (Couch et al. 2008), temperature has been found to compromise disease resistance in this sea fan (Ward et al. 2006a), which suggests that fungal diseases like aspergillosis could be of opportunistic nature (Burge et al. 2013). Although seawater temperatures during El NIño Southern Oscillation (ENSO) events can be as high as 30–32 °C (Mora and Ospina 2001), temperatures are usually below 27 °C at TEP locations experiencing sea fan mortalities. However, there is considerable variation (~10 °C below) during the upwelling season (February to April), which was warmer during 2008 (Sánchez et al. 2014). Although it seems counterintuitive, increases in water vapor, the main greenhouse gas, affect upwelling favorable wind stress at the TEP, which explains major climate anomalies in the area including ENSO (Bakun et al. 2010). The disease outbreak in TEP gorgonian corals opens a whole new perspective to understand and interpret marine diseases in an area not as altered as the Caribbean Sea.

7.3 Invasive Species

One of the most detrimental and pervasive impacts of human-induced global change is the appearance of invasive species (Simberloff et al. 2013), which involves unwanted cascade effects altering natural ecosystems (Walsh et al. 2016). Recently, octocorals at both sides of tropical America have been targeted by the invasion of pest species. In the Caribbean, the Indo-Pacific species of soft coral *Xenia membranacea*, which is part of the aquarium trade, was found in reefs from

Venezuela a few years ago (Ruiz Allais et al. 2014). This is of great concern given the invasive capacity of *Xenia* (Putra et al. 2014), together with the vulnerability to invasions of altered ecosystems such as Caribbean reefs (Albins and Hixon 2008, 2013). At the TEP, the Western Atlantic snowflake coral *Carijoa riisei* (Telestidae) was recently reported as an invasive species, which was already a pest in regions like Hawai'i (Kahng and Grigg 2005). The snowflake octocoral quickly monopolizes hard bottoms and overgrows and kills native species (Fig. 7c) at a lineal rate of 12 cm year^{-1}, which has threatened the native gorgonian octocorals in this area (Sánchez and Ballesteros 2014). The candelabrum octocorals, *Muricea*, are the most susceptible to the contact with the snowflake coral, leading to local extinctions of this genus in several localities of the Colombian TEP. The snowflake octocoral is closely associated with a cytotoxic sponge, *Desmapsama anchorata*, allowing it to successfully overgrow other invertebrates (Calcinai et al. 2004). While the snowflake octocoral can disappear as sudden as it appears, it can wipe out all the gorgonians in a single colonization event. Although turtles and the passer angelfish have been seen predating on this invasive species, their populations are increasing along the Colombian TEP, and it has recently appeared in Ecuador (K. Jaramillo, personal communication). There are no successful strategies to eradicating this species so far (Wagner et al. 2009).

7.4 Ocean Acidification

Among the predictions of global change, ocean acidification is another stressor associated with climate change, a consequence of increases in carbon dioxide emissions ($p\mathrm{CO}_2$) (Gattuso et al. 2015). Of great concern are the predicted effects of undersaturated $\boldsymbol{\Omega}_{\mathrm{aragonite}}$ on reef-building coral skeletons (Fantazzini et al. 2015). At the Great Barrier Reef, for instance, there is already evidence of a decline in scleractinian coral calcification (De'ath et al. 2009). So far, gorgonian octocorals from the Caribbean have demonstrated to be resistant to ocean acidification (Enochs et al. 2016), even under undersaturated $\boldsymbol{\Omega}_{\mathrm{calcite}}$ (Gómez et al. 2015). Other octocorals, such as species of soft corals in the Red Sea, have also shown to be fine under high $p\mathrm{CO}_2$ values due to protective properties of their tissues (Gabay et al. 2013, 2014). At naturally acidified reefs, like in Iwotorishima Island in Japan, octocorals clearly have become the dominant cnidarians over scleractinian corals (Inoue et al. 2013). As in many other aspects, TEP octocorals have not been studied under ocean acidification conditions, yet given that the TEP is one of the more naturally acidified areas in the tropics (Gattuso et al. 2015), their abundant presence in this area supports the hypothesis of gorgonians being highly resistant to high $p\mathrm{CO}_2$ environments. Overall, gorgonian octocorals seem to be highly resistant to thermal anomalies, bleaching, and, in general, diseases. Their populations have not suffered mass mortalities as extensive as those reported in Caribbean scleractinian corals, and remain in good shape with a tendency to increase (Lenz et al. 2015). Gorgonian octocorals at both sides of tropical America seem to be more resistant to thermal anomalies, acidification, and disease outbreaks (but see Weil et al. 2016) than their scleractinian counterparts; therefore, they belong on the list of potential survivors under rapid global change.

8 Evolutionary Biology

Gorgonian octocorals separated by the Isthmus of Panama have a recent diversification in both sides of the barrier. TEP gorgonids seem more related to the subtropical western Atlantic (and Gulf of Mexico) and the western coast of Africa, where *Leptogorgia* is a dominant lineage (Aguilar and Sanchez 2007; Sanchez 2007), than the shallow-water Caribbean. The most abundant octocoral species at the TEP are closely related and sympatric, such as *Pacifigorgia* and *Muricea* (Ament-Velásquez et al. 2016). There are very few cases of clear geminate species, e.g., separated by the isthmus, like *Heterogorgia* (Vargas et al. 2010). Likewise, most modern Caribbean species belong to Caribbean-endemic genera: *Antillogorgia, Eunicea*, and *Plexaura* (Aguilar and Sanchez 2007; Grajales et al. 2007; Sanchez et al. 2003). The Caribbean has an outstanding number of endemic lineages, *Antillogorgia*, *Eunicea*, *Gorgonia*, *Plexaura*, *Plexaurella*, *Pseudoplexaura*, and *Pterogorgia*, which all have symbiosis with zooxanthellae, whereas no TEP octocorals have symbiotic zooxanthellae (van Oppen et al. 2009). The great mystery is the aposymbiotic nature of *Muricea* in the TEP, while its Caribbean conspecifics have *Symbiodinium*.

Zooxanthella-bearing Caribbean octocorals (Sánchez and Wirshing 2005) exhibit community-wide patterns of phenotypic plasticity. Within each species, most individuals in shallow waters have smaller surface sclerites and shorter branches (Velásquez and Sánchez 2015), such as the case of *Eunicea flexuosa* (Prada et al. 2008). The contemporary Caribbean gorgonian community certainly resembles the product of ecological speciation, involving sympatric genera such as *Eunicea* with up to 16 species (Grajales et al. 2007; Sánchez 2009). Ecological conditions not only have structured gorgonian communities, but they have likely influenced diversification in many lineages. As seen in Fig. 2, most gorgonian coral species occupy a narrow environmental range, where species with wide ranges (e.g., *Antillogorgia americana*, *A. bipinnata* + *A. kallos*, *Briareum polyanthes-asbestinum*, *Eunicea flexuosa*, *E. succinea*, *Muriceopsis flavida*, and *Pl. dichotoma*) have been considered to be cases of exceptional plasticity. This could be related with the diversification of the group. Species that are usually in most environments, including contrasting conditions (e.g., deep and shallow), are exposed to additional environmental challenges for which the same genotype cannot be at its optimum adaptive peak (Fig. 8). Although this scenario can lead to divergent selection in contrasting environments, ecological speciation occurs when reproductive isolation takes place among adapted morphotypes (Fig. 8). This is usually assumed to happen as a byproduct of selection acting on genomic regions with pleiotropic effects (Nosil 2012; Rundle and Nosil 2005). One major driver for ecological divergence could be the identity of the cryptic *Symbiodinium* species, which are known to vary greatly with depth in scleractinian corals (Bongaerts et al. 2015), and there seems to be cryptic variation in gorgonian corals as well (Prada et al. 2014). However, the predicted high frequency of

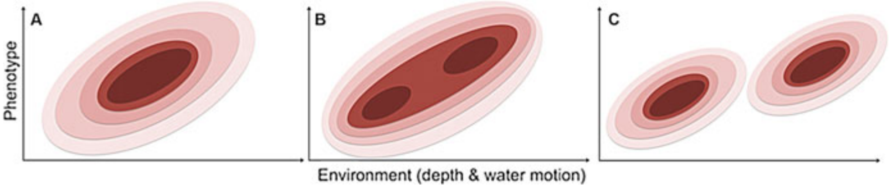

Fig. 8 Adaptive hyperspace of a gorgonian coral phenotype (higher fitness as progressively darker). (**a**) The species through time develops larger plasticity as populations grow and colonize new benthic areas (t_{x+1}). (**b**) The adaptive peak of the original species shifts toward contrasting conditions exhibiting ecological divergence (t_{x+2}), (**c**) which leads to differential distribution of traits around distant and divergent fitness optima (t_{x+3})

ecological and sympatric speciation in gorgonian corals suggests a more general mechanism promoting reproductive isolation.

Species distributing in most reef environments provide unique opportunities to study ecological divergence and habitat-induced selection, the process leading to ecological speciation. For instance, *Briareum polyanthes and B. asbestinum* are two soft corals encompassing most reef environments, one branching and other encrusting, yet these have been topic of debate on whether they are one or two species (Bilewitch et al. 2010; Brazeau and Harvell 1994; Brazeau and Lasker 1992b; West 1997). *Eunicea flexuosa* is one of the model species for ecological speciation due to its shallow-deep divergence (Kim et al. 2004; Prada et al. 2008; Prada and Hellberg 2013). *Antillogorgia bipinnata and A. kallos* (Fig. 2) are also closely related species with a morphological cline. These corals distribute in most reef environments (1–45 m) with about an order of magnitude difference in morphological characters between bathymetric extremes (Sánchez et al. 2007). Likewise, *Plexaurella dichotoma* and *P. fusifera*, distributing between 0.5 and 30 m deep, are the two morphological (sclerite wart shape) extremes between low and high water motion (Alcolado 1985). Given the habitat preferences of Caribbean gorgonian corals, in addition to the evidence of ecological speciation in some species, the scenario of ecological divergence as a driver of gorgonian coral diversification is promising, but it needs further study.

The Caribbean and the Eastern Pacific have endemic octocoral faunas, which diversification rates probably accelerated after the closure of the Isthmus of Panama. The rise of the isthmus induced dramatic oceanographic changes at both sides, the Caribbean turned oligotrophic with an impoverishment of plankton greatly noted with the nearly absence of radiolarians and diatoms (Coates et al. 1992). The Eastern Pacific, on the other side, turned into a mesotrophic ocean with cooler waters and localized upwelling allowing a luxuriant diversity and biomass of plankton (Fernández-Álamo and Färber-Lorda 2006). The offer of new resources created new ecological opportunities for suspension-feeding organisms, such as azooxanthellate gorgonian octocorals, and could have driven an adaptive radiation to exploit the new food sources. Numerous closely related species of *Eunicea, Antillogorgia*, *Plexaura-Pseudoplexaura*, *Muricea*, and *Pacifigorgia* exhibit signatures of recent radiations (e.g., high morphological differentiation, niche partitioning, and low genetic divergence). The different ecological settings at both oceans also point out the possibility of these groups undergoing separate adaptive radiations. New ecological opportunities can lead to rapid ecological speciation (Schluter 2016). This idea can develop from the same gorgonian (modular) property, phenotypic plasticity (Lande 2015), but played out differently on the two sides of the isthmus in response to the different dominant ecological conditions. Preliminary data suggest that *Pacifigorgia* and *Muricea* exhibit niche divergence, which supports an adaptive radiation hypothesis for the origin of TEP gorgonian corals. With only one *Pacifigorgia* species in the Atlantic (Vargas et al. 2008), it is clear that since the closure of the isthmus of Panama, a few ancestral species turned into over thirty species in the last few million years (Sánchez J.A. et al., unpublished data). Likewise, *Muricea* has a few symbiotic species in the Caribbean but more than a dozen aposymbiotic ones in the Eastern Pacific (Breedy and Guzman 2016).

The large morphologic variation and plasticity that we see today in transisthmian gorgonian corals is not just the product of speciation. New phenotypes do not arise at random, rather by adaptive developmental plasticity (West-Eberhard 2003, 2005). The underlying mechanisms promoting morphologic novelties can provide the basis to understand the bridge between phenotypic plasticity and speciation in gorgonian octocorals (Schluter 2016). Rapid evolution and speciation is usually based on mechanisms already acquired by the species, where natural selection acts on pre-adaptations (Turner 2002). Figure 9 shows the Caribbean Sea ribbon corals, *Pterogorgia guadalupensis* and *P. anceps*, and the flamingo tongue *C. gibbosum*, a gorgonian specialist grazer. Given the negligible genetic variation between *Pterogorgia guadalupensis* and *P. anceps* (Wirshing and Baker 2015), these species can be considered to be the same taxon. The only difference between these two nominal species is the presence of an additional angular ribbon in *P. anceps*, which roughly increases one third, e.g., an additional row of polyps perpendicular to the ones found in the blade, the number of polyps in the colony (Sánchez, J.A., unpublished data). Assuming a fixed number of gametes per polyp, this is an increase in reproductive output and fitness in *P. anceps*, but on the other hand, it may slow colony growth with respect to the flat ribbon *P. guadalupensis* due to production of an additional row of polyps.

For *C. gibbosum*, it is easier to prey on a flat ribbon, such as *P. guadalupensis*, than upon the angular ribbon *P. anceps*. The morphological change into a ribbon or an angular ribbon is hypothesized here as a stable evolutionary strategy (ESS) (Smith 1974). An ESS is ruled by game theory, and it predicts that two or more different, oftentimes competing strategies, coexist in a population, which in the *Pterogorgia* case is likely triggered by *C. gibbosum* at the early stages of colony growth. Colonial organisms usually expend their energy and resources in growing because size is evolutionary advantageous. It increases feeding surface, reproductive output, competition abilities, and survivorship. A large colony will not be significantly affected by the predation activity of the flamingo tongue. Whereas if a colony gets grazed when small, its chances of surviving are lower, unless it can heal and then grow the angular ribbon shape as a response to predation to prevent further

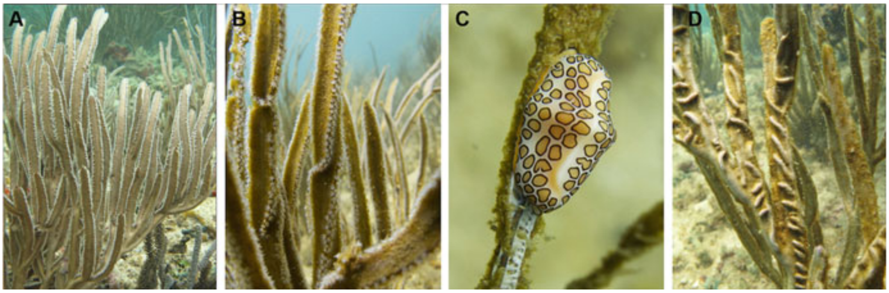

Fig. 9 Sea ribbons from the Caribbean Sea (Bocas del Toro, Boca del Drago, Panamá, 3 m). (**a**) *Pterogorgia guadalupensis*. (**b**) *P. anceps*. (**c**) Flamingo tongue, *Cyphoma gibbosum*, predating on *P. guadalupensis* branch. (**d**) Unusual *Pterogorgia* morphotype (Photos: Juan A. Sánchez)

attacks. Overfishing of *Cyphoma* predators, such as spiny lobster and hogfish, has significantly increased its abundance and grazing on gorgonian corals (Burkepile and Hay 2007; Chiappone et al. 2003). Phenotypic plasticity, starting as an EES, can turn into a major evolutionary force in gorgonian corals.

9 Conclusions

Gorgonian octocorals at both sides of the tropical America are foundation species that assemble in shallow habitats (coral reefs and rocky environments) and form structurally complex, animal forests of high diversity and density. As an analog animal forest, gorgonian octocorals provide feeding substrate, habitat, and protection for a highly diverse associated biota. There is a myriad of understudied vertebrate and invertebrate fauna associated to gorgonian corals, together with the less-known microbiota. Gorgonian holobionts in the Tropical Eastern Pacific do not harbor zooxanthellate symbionts. Their trophic ecologies therefore are basically different. There are notable differences between the octocoral communities from the Caribbean Sea and the TEP summarized in Table 1.

Population genetics composition and diversity of gorgonian octocorals depend largely on their sexual and asexual reproductive strategies as well as their dispersion capabilities. Gorgonian recruitment observations have revealed high densities of settlers for both brooders and broadcast spawners. Surface brooders, which larvae do not travel far, have shown a genetic structure along hundreds to thousands of kilometers and even tenths of meters, which suggest that gorgonians with this strategy have a philopatric distribution. Clonality through fragmentation, a strategy to increase population size and gain substrate, is another common property between plant and animal forests. In the Caribbean, the contribution to clonality from asexual colony propagation to population survivorship, expansion, and growth is very important. No similar mechanisms have been observed in the TEP. Observations on these mechanisms and population genetic information are needed for the main

Table 1 Comparison between common attributes of octocoral communities from the Caribbean Sea and the Tropical Eastern Pacific. Please refer to text for details and references

Octocoral community attribute	Caribbean Sea	Tropical Eastern Pacific
Number of species above 30 m	~61 spp. (Bocas del Toro, Panama)	~38 spp. (Las Perlas Archipelago, Panama)
Percentage of zooxanthellate species above 30 m	98%	none
Most speciose genus	*Eunicea*: 16 spp.	*Pacifigorgia*: 34 spp.
Species with largest bathymetric range	*Antillogorgia bipinnata*, 1–45 m	*Leptogorgia alba*, 1–70 m
Tallest species	*Antillogorgia acerosa*, ~ 5 m	*Eugorgia* spp., ~ 2 m
Maximum densities	30–100 colonies m^{-2}	~10 colonies m^{-2}
Associated specialist ectoparasite	*Cyphoma gibbosum* (aposematic)	*Simnia*/*Simnialena* (mimetic)
Maximum growth rates	*Antillogorgia acerosa*: 15–30 cm $year^{-1}$	*Leptogorgia alba*: 1 cm $year^{-1}$
Maximum life-span	*Muricea fruticosa* and *M. californica*: ~50 years	*Antillogorgia elisabethae*: ~40 years
Surface brooders	*Muricea*	*Antillogorgia, Pterogorgia*
Broadcast spawners	*Leptogorgia, Pacifigorgia* (?)	Plexauridae, *Gorgonia ventalina, Antillogorgia americana*
Most common disease	Aspergillosis	
Invasive species	*Carijoa riisei*	*Xenia membranacea*

octocoral species in the TEP, including the sea fan *Pacifigorgia* and, especially, how they propagate their colonies in a comblike fashion.

Many of the stressors associated to climate change, such as increase in frequency and intensity of tropical storms, rising seawater temperatures, more disease and bleaching events, and increase in invasive species, have already affected in different ways gorgonian populations around the world. It is predicted that Caribbean long-lived gorgonian octocoral species that distributed along the hurricane belt will show a reduction in their maximum sizes with respect to populations from sheltered regions. Although Caribbean gorgonian corals normally bleach under prolonged thermal stress, monitoring of bleached gorgonians has shown negligible mortality and higher resilience after high thermal anomalies and bleaching. However, there is a link between thermal anomalies and gorgonian immunity, with diseases producing mass mortalities in sea fans and other species across the Caribbean from the 1980s to the 2000s (*Gorgonia*) and, more recently, in the TEP (*Pacifigorgia*). It is unknown why unrelated sea fans (e.g., reticulated branching) are more prone to fungal diseases than hierarchical branched gorgonian octocorals. One hypothesis is that the wider, exposed surface area is prone to capture the water-suspended, dispersing hyphae or spores of the fungus. Gorgonians from the Caribbean have shown experimentally to be highly resistant to ocean acidification; this together with their resistance to bleaching will probably help them survive the rapid global change conditions. No studies on this aspect have been carried out in TEP species.

10 Future Directions

Studies on many aspects of the biology of gorgonian octocorals, such as growth rates, forms, trophic ecology, minimum reproductive size, maximum colony ages, reproductive biology and ecology, health status and susceptibility, and mortality rates, are needed for both the TEP and Caribbean–Atlantic regions.

There are intriguing evolutionary trends in gorgonian corals, which are also worth paying more attention. Giving their ecological preferences, in addition to the available evidence of ecological speciation in some genera, the scenario of ecological divergence as a driver of octocoral diversification is compelling. In the Caribbean, there are species distributed in most reef environments, providing unique opportunities to study ecological divergence and/or habitat-induced selection, the process leading to ecological speciation if there is reproductive isolation. However, the predicted high frequency of ecological and sympatric speciation in gorgonian octocorals suggests a more general mechanism promoting reproductive isolation, which is unknown at the moment and requires further study. Yet, a general model should be outlined and tested to see if these cases are the mainstream or just rare examples.

Future octocoral studies in this region should take advantage on the fact that the Caribbean and Eastern Pacific have endemic, yet highly diverse, faunas. With a few seemingly allopatric-generated species, numerous closely related species of *Antillogorgia, Eunicea, Muricea*, *Pacifigorgia*, and *Plexaura-Pseudoplexaura* exhibit signatures of recent radiations (e.g., high morphological differentiation and low genetic divergence). The different ecological settings at both oceans also point out the possibility of these groups undergoing separate adaptive radiations. New ecological opportunities could lead to rapid ecological speciation. At the TEP, the offer of new planktonic resources created new ecological opportunities for suspension-feeding organisms, such as azooxanthellate gorgonian corals, and could have driven an adaptive radiation to exploit the new food sources. Yet, the developmental phenotypic plasticity that we see today in transisthmian gorgonian corals is not just the product of speciation and needs further study.

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Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns

5

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Abstract

This chapter reviews the major known monospecific and multispecific sponge aggregations in the world's oceans. They are shown to occur from the intertidal to abyssal depths, in tropical, temperate, and high latitudes and sometimes to create spectacular formations, such as glass sponge reefs, lithistid reef-like fields, and carnivorous sponge grounds. Sponge aggregations are recognized as singular vulnerable habitats that deserve special research attention and legal protection. However, this review reveals that there is only a poor and fragmentary understanding of the main biological, environmental, and geochemical factors that

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favor and maintain these systems, including the food supply, which is fundamental knowledge. There is also a particular lack of information regarding reproductive biology, growth rates, life spans, and the main factors causing mortality, all crucial drivers for understanding population and community dynamics and for developing conservation strategies. The sponge aggregations have been shown to increase the structural complexity of the habitats, attracting a larger variety of organisms and locally enhancing biodiversity. From the very few cases in which sponge biomass and sponge physiology have been reliably

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approached jointly, phenomenal fluxes of matter and energy have been inferred. Through their benthic-pelagic coupling, some of the densest sponge aggregations have a significant local or regional impact on major biogeochemical cycles and food webs. Physical damage and habitat destruction derived from man-driven activities along with epidemic diseases facilitated by global environmental alterations emerge as major threats to the future of the sponge aggregations.

Keywords
Porifera • Benthic-pelagic coupling • Food chains • Reef • Mangrove • Deep-sea benthos • Arctic benthos • Antarctic benthos • Conservation biology • Vulnerable habitats

Contents

1 Introduction

Sponges are common members of many marine benthic communities. Under circumstances that are not yet well understood, they may undergo exceptional proliferation, forming spectacular aggregations that can be constituted by either a single species or mixed species assemblages. Sponge aggregations are known to occur at virtually all depths, from the intertidal (Fig. 1a–c) to the abyssal zone, and sometimes in quite extreme environments (Fig. 1d). Their extension can range from a few hundreds of m^2 to hundreds of km^2. More importantly, whenever sponges aggregate, they do not only substantially increase the tridimensional structure of the benthic habitat and its associated biodiversity, but they also affect the hydrodynamics of the deep boundary layer, the circulation and recycling of crucial marine nutrients and, in general, the matter and energy transfer between the water column and the benthos. This chapter summarizes the most remarkable types of sponge aggregations known in the ocean to date. It compiles and reviews information on their particular geographical and environmental settings, taxonomic composition, basic organization features, and ecological significance.

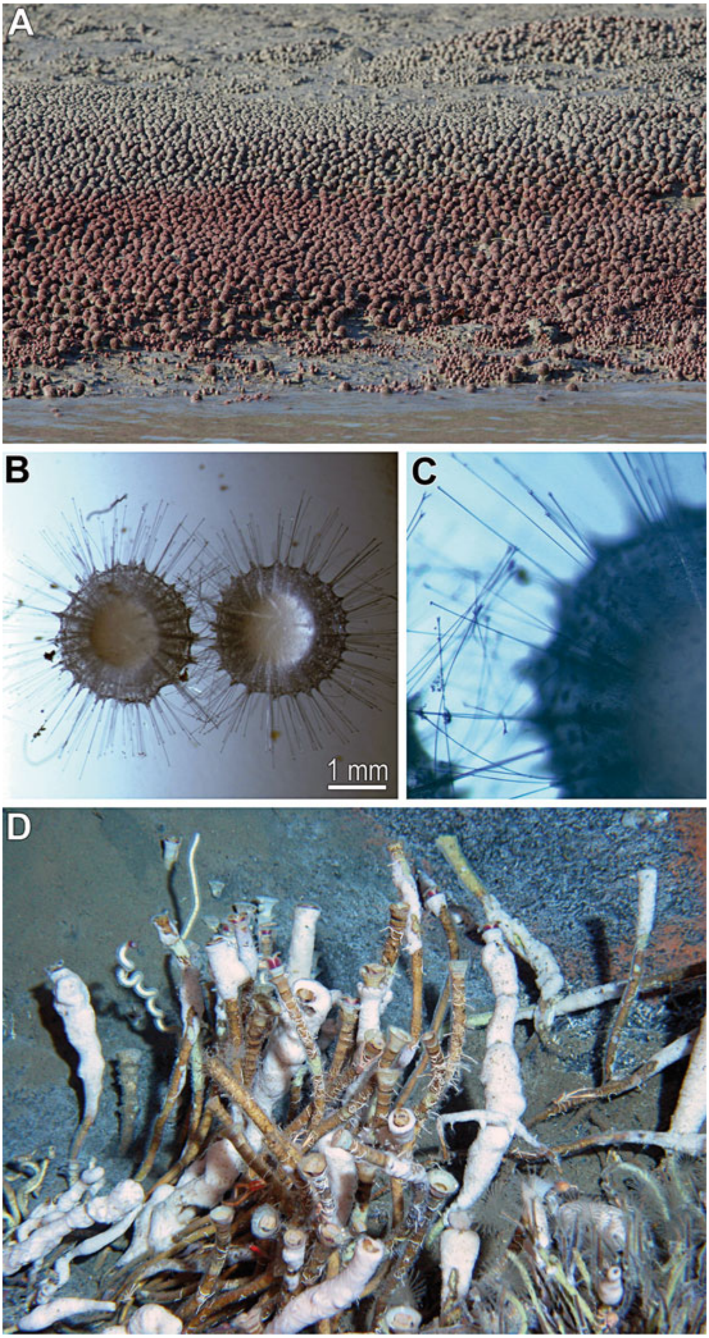

Fig. 1 **Examples of sponge aggregations at unusual habitats**. (**A**) View of an extremely dense monospecific aggregation of spirophorid demosponges (preliminarily identified as *Craniella* sp. by

2 Coral Reef Sponge Aggregations

There are two major coral reef areas in the world ocean. One is the tropical and subtropical Atlantic Ocean (TSAO). The "Greater Caribbean," from Bermuda in the North to Venezuela in the South, probably has the lushest reef development in the TSAO. The other major reef area is the Indo-Pacific, which includes the Great Barrier Reef (GBR) in Australian waters and the "Coral-Triangle" (CT) region, which encompasses areas in the western Pacific Ocean and eastern Indian Ocean.

Sponges of the class Demospongiae are important components, both in diversity and biomass, throughout the world's coral reefs. Typically, coral reefs develop on the continental and island coasts where sea surface temperatures do not fall below a yearly average of 21 °C, practical salinity oscillates between 30 and 40, and sediment input is low. Physicochemical and biological factors (wave action, sediment, light, substrate, oxygen, nutrients, competition, predation, and symbiosis) further shape patterns of sponge distributions across reef systems.

Across Caribbean coral reefs, massive demosponges in the forms of tubes, fans, vases, branches, or balls from genera such as *Agelas*, *Aplysina*, *Xestospongia*, *Callyspongia, Niphates, Mycale*, and *Geodia* flourish. Nevertheless, much of the diversity is comprised of sciophilous species, primarily crusts and small cushions dwelling on the underside of coral plates, inside reef crevices and caves, and excavating substrata. These cryptic habitats harbor hundreds of sponges, many still undescribed. Sponge abundance in the Caribbean varies across coral reef profiles. Below 6 m depth, where sponges are not exposed to wave surge and heavy sedimentation, but still enjoy sufficient nutrient transport, the highest biomass occurs, particularly peaking around 20 m depth where competing reef corals thin out due to the reduced light and the increased particulate organic matter concentration. Forereefs host an average sponge biomass that is typically twofold to threefold higher per unit area than on patch reefs (Table 1). However, in some lagoon settings,

Fig. 1 (continued) J. Fromont) while exposed to air during low tide at Porosus Creek, a tributary of the Hunter River in the Kimberley Region of Western Australia. (**B**, **C**) Juveniles of *Craniella* sp. (from Norway) upon hatching from the mother sponge, where they had been produced sexually through direct development (i.e., in absence of a larval stage). The spicules (protriaenes and anatriaenes) protruding out of the body of the released juveniles tangle easily (**C**) with those of the adults, favoring settlement in aggregation. Nevertheless, if resuspended by turbulences, these unattached juveniles can be easily dispersed by horizontal flows as well. Their persistence in the water column is facilitated by the protruding spicules, which act as buoyancy devices favored by water viscosity at low Reynolds numbers. This physical mechanism is also exploited by another holoplanktonic and meroplanktonic organism, the floatability of which is due to the protrusion of long skeletal structures out of the body, such as radiolarians and unciliated hoplitomella larvae of sponges. (**D**) View of a dense population of *Myxilla (Ectyomyxilla) methanophila* highly exposed to toxic methane flows at hydrocarbon seeps of the upper Loussiana slope (Gulf of Mexico). The sponge grows as an encrusting epibiont on vestimentiferan tubeworms. It is able to survive in these unusual conditions through symbiosis with methylotrophic bacteria of the genus *Methylohalomonas* and polycyclic aromatic hydrocarbon-degrading bacteria of the genera *Cycloclasticus* and *Neptunomona* (Arellano et al. 2013)

Table 1 Biomass (volume in $cm^3\ m^{-2}$) of the most common siliceous demosponge and homosclerophorid species (53 spp.) occurring at the fore reef (n = 99; 1 × 1 m quadrats) and the patch reef (n = 64) of the barrier reef around Carrie Bow Cay (Belize). Data for mangroves (n = 111) in a nearby area of the reef lagoon are also included for comparative purposes. Mangrove densities were calculated as the sponge fauna growing on the roots intersected by the plane of a 1 m^2 quadrat placed orthogonal to the water surface. Only the most external roots were considered in the spatial measurements, since the high density of root in some area made inner roots unapproachable to divers

	Forereef		Patch reef		Mangrove			Forereef		Patch reef		Mangrove	
Sponge species	*Avg*	*SD*	*Avg*	*SD*	*Avg*	*SD*	Sponge species	*Avg*	*SD*	*Avg*	*SD*	*Avg*	*SD*
Agelas clathrodes	4.8	26.3	2.4	13.5	0.0	0.0	*Holopsamma helwigi*	0.0	0.0	51.7	127.7	0.0	0.0
Agelas conifera	195.4	990.6	42.5	284.5	0.0	0.0	*Hymeniacidon* sp.	0.4	3.0	0.0	0.0	0.0	0.0
Agelas sceptrum	25.7	139.7	18.8	150.0	0.0	0.0	*Iotrochota birotulata*	4.1	33.4	119.1	257.9	0.0	0.0
Agelas wiendermayeri	42.0	281.5	0.1	0.3	0.0	0.0	*Lissodendorix isodictyalis*	0.0	0.0	0.0	0.0	89.9	330.8
Amphimedon compressa	4.8	24.4	0.0	0.0	0.0	0.0	*Lissodendoryx colombiensis*	5.5	54.3	0.0	0.0	0.0	0.0
Biemna caribea	0.0	0.0	0.0	0.0	3.4	16.5	*Monanchora barbadensis*	0.4	1.8	0.3	0.9	0.0	0.0
Biemna sp.	0.0	0.0	0.6	4.7	0.0	0.0	*Mycale laevis*	1.4	9.2	2.5	8.0	0.0	0.0
Callyspongia fallax	0.4	3.6	0.0	0.0	0.0	0.0	*Mycale laxissima*	1.5	14.5	2.8	16.1	8.0	60.0
Callyspongia plicifera	35.8	147.3	0.0	0.0	0.0	0.0	*Mycale microsigmatosa*	0.0	0.2	0.0	0.0	9.2	46.2
Callyspongia ramosa	0.0	0.0	1.9	11.6	0.0	0.0	*Niphates digitalis*	54.2	209.4	19.9	128.6	0.0	0.0
Callyspongia sp.	4.6	45.2	0.0	0.0	0.0	0.0	*Niphates erecta*	7.8	22.3	29.6	118.4	0.0	0.0
Callyspongia vaginalis	11.5	61.7	45.4	172.3	0.0	0.0	*Petrosia pellasarca*	18.5	145.3	0.0	0.0	0.0	0.0

Chalinula molibta	0.0	0.0	0.0	0.0	23.7	103.8	*Petrosia weinbergi*	52.8	499.9	0.0	0.0	0.0	0.0
Chondrilla nucula	0.2	1.4	0.0	0.0	0.0	0.0	*Plakinastrella onkodes*	6.9	27.7	0.0	0.0	0.0	0.0
Cinachyrella apion	6.3	59.2	8.3	66.3	0.0	0.0	*Plakortis angulispiculatus*	0.9	8.8	0.0	0.0	0.0	0.0
Cliona caribbaea	0.3	1.9	76.6	196.5	0.0	0.0	*Plakortis halichondroides*	10.4	69.9	0.0	0.0	0.0	0.0
Cliona delitrix	0.6	4.4	0.0	0.0	0.0	0.0	*Pseudoaxinella lunaecharta*	0.2	1.3	0.0	0.0	0.0	0.0
Cliona varians	3.9	19.6	0.8	4.0	0.0	0.0	*Scopalina ruetzleri*	3.4	9.7	4.3	9.1	1.4	9.3
Cryptotethya cripta	16.3	161.7	11.2	67.3	0.0	0.0	*Siphonodyction coralliphagum*	2.3	14.9	0.0	0.0	0.0	0.0
Ectyoplasia ferox	29.2	196.5	0.0	0.0	0.0	0.0	*Tedania ignis*	0.0	0.0	0.0	0.0	1709.2	3640.3
Geodia neptunii	491.1	2682.9	250.6	2004.8	0.0	0.0	*Teichaxinella* sp.	0.0	0.0	0.3	1.8	0.0	0.0
Halichondria magniconulosa	0.0	0.0	0.0	0.0	78.6	276.5	*Timea* sp.	0.0	0.3	0.0	0.0	0.0	0.0
Haliclona implexiformis	0.0	0.0	0.0	0.0	53.9	191.0	*Xestospongia carbonaria*	0.9	9.0	0.0	0.0	0.0	0.0
Haliclona manglaris	0.0	0.0	0.0	0.0	5.5	19.3	*Xestospongia* cf *rosariensis*	5.1	49.4	0.0	0.0	0.0	0.0
Haliclona sp.1	0.0	0.0	0.0	0.0	1.0	8.9	*Xestospongia muta*	3846.2	20189.2	830.5	6644.0	0.0	0.0
Haliclona sp.2	0.2	1.1	0.0	0.0	0.0	0.0	*Xestospongia proxima*	12.7	126.6	0.0	0.0	0.0	0.0
Haliclona tubifera	0.0	0.0	0.0	0.0	0.1	0.5	**TOTAL AVERAGES**	**4908.0**	**20607.9**	**1520.1**	**6947.0**	**1984.0**	**3691.7**

on patch reefs, certain sponges thrive. For example, thick crusts of *Chondrilla caribensis* form remarkable aggregations at some Caribbean patch reefs, occupying on average 44.7% ± 10.3% of the hard substratum and even overgrowing corals (Fig. 2a). On forereefs, sponge volume has been estimated at 3 L m^{-2} in Discovery Bay, Jamaica (Reiswig 1973) and at 4.9 ± 20.6 L m^{-2} on the Belize Barrier Reef (Table 1; Fig. 2b). The latter biomass is made up by 53 common species (Table 1). Scattered, large individuals of *Geodia neptuni* and *Xestospongia muta* (Fig. 2c) are responsible for the large variability in sponge volume per m^2 of forereef. This latter species, with sizes between 1 and 200 L, occurs at densities ranging from 1 to 27 individuals per 100 m^2 on deep reef sites in the Bahamas, the Florida Keys, Colombia, and Belize. At Conch Reef, in the Florida Keys, average mean biomass of *X. muta* alone is estimated at 1.4 L m^{-2}, and it appears that biomass is increasing over time.

The Indo-Pacific coral reefs, particularly the “coral triangle” region, support the most diverse sponge assemblages in the world, with a probable very high number of yet undescribed species. While sponges are very abundant on the reef slopes, they also dominate cave and overhanging reef environments. Similar to Caribbean reefs, many large, conspicuous sponges are present, such as the giant barrel sponge *Xestospongia testudinaria* (Fig. 2d), but again, the diversity levels are often driven by high abundance of very small (<2–3 cm^2), encrusting species. Sponge genera absent from the Caribbean reefs, such as the large *Ianthella* fans and plate-shaped phototrophic sponges (*Lamellodysidea*, *Phyllospongia*, and *Carteriospongia*), are also conspicuous on these reefs. As an example, in the Wakatobi Marine National Park, in Sulawesi, over 130 sponge species have been reported to date with abundance estimates of more than 200 individuals m^{-2} and occupying more space than corals. In this area, reef degradation has occurred reducing coral cover, while the sponge *Lamellodysidea herbacea* (Fig. 2e) has increased in abundance (up to 100 individuals m^{-2}) and now covers more than 75% of the substratum in some locations. This species, common throughout the Indo-Pacific, is indeed currently proliferating in a number of locations.

Another striking example is Palmyra Atoll in the central Pacific, where there are contrasting patterns of abundance and diversity in the atoll lagoons compared to outer atoll reefs. The lagoons were heavily modified in the 1940s during World War II and virtually all the coral was removed or destroyed. The hard substratum in the lagoon is now dominated by sponges. Sponge diversity is low, with only 24 species reported, but sponge cover ranges from 20% to 50%. This contrasts with the nonlagoon reefs, which are considered among the most pristine in the world, and have very few conspicuous sponge species and very low sponge abundance (<1% cover).

Sponge populations on the Great Barrier Reef are also rich, having lower overall diversity than the Indian Ocean region but higher diversity than the Pacific Islands. On the Great Barrier Reef, sponge biomass ranges from 0.45 kg m^{-2} on inner reefs to less than 0.2 kg m^{-2} on outer reefs. Importantly, the distribution of sponge biomass in Australian reefs appears to contrast with that in the Caribbean. In a comparative study (Wilkinson and Cheshire 1990), the estimated sponge biomass on

Fig. 2 **Views of coral reef sponge aggregations**. (**A**) A dense population of *Chondrilla caribensis* on a Belizean patch reef covering a large area of substratum, including coral. (**B**) General view of a shaded overhang on the forereef off Carrie Bow Cay in Belize, dominated by large, orange individuals of *Agelas* spp and an additional variety of smaller sponges. (**C**) A mid-size individual of *Xetospongia muta* on the Belizean forereef. (**D**) A mid-size individual of *Xetospongia testudinaria* at Wakatobi Marine National Park (Indonesia), the pumping activity of which is revealed by the injection of fluorescein. (**E**) View of a large individual of *Lamellodysidea herbacea* at Wakatobi Marine National Park

relatively healthy reefs of the Great Barrier Reef was six times lower than that in Belize, with the highest biomass on inner (lagoon) reefs (1–2.4 kg wet weight m^{-2}), followed by barrier back reefs (0.9–1.3 kg m^{-2}), and outer reefs (0.3–0.7 kg m^{-2}). Whether food availability could be limiting sponges is a hypothesis that needs further exploration and has been proposed in the past to explain the large sponge biomass differences between the Caribbean and Great Barrier Reef forereef assemblages.

In Western Australia, some of the richest sponge assemblages have been reported from Ningaloo Reef Marine Park (Schönberg and Fromont 2012). Estimates suggest that there are more than 500 species on the shelf (at 30–100 m depth) in this region. The highest biomass averages at some sites up to 0.5 kg wet weight m^{-2}, which is about 12 times lower than maxima at the Great Barrier Reef forereefs.

Reef sponges have an impact on the ecosystem as powerful space competitors with feeding-deterrent chemistry and through physiological functions. Coral reef sponges compete for space with sessile invertebrates and algae and live in association with a large spectrum of microbes, algae, invertebrates, and fishes through epibiosis, endobiosis, and symbiosis (Rützler 2012). Furthermore, they are preyed upon by several invertebrates (polychaetes, molluscs, echinoderms, etc.), fishes, and sea turtles. These factors have driven the evolution of natural products chemistry (mostly toxic) among coral reef sponges, which show a comparatively larger diversity of compounds than those characterizing deep-sea sponge assemblages. Through their filter feeding activity, sponges may help to keep reefs in oligotrophic conditions favorable to corals. Indeed, the densest sponge fauna of a Jamaican forereef (15–50 m) has been estimated to filter daily a volume of water equivalent to the entire water column over the reef bottom, retaining nearly 100% of the picoplankton and suspended detritus (Reiswig 1974). Sponges also profoundly affect the food chain of coral reefs through additional mechanisms. They take up dissolved organic matter (DOM) that is unavailable to other invertebrates and generate, in exchange, an outflow of particulate organic matter (POM) resulting from metabolic waste and cellular renewal that feeds other invertebrates at basal and intermediate levels of the reef trophic chain (de Goeij et al. 2013; Maldonado 2015). Reef sponges, being consumed by different invertebrates and vertebrates, are also an important resource for higher levels of the food chain in coral reefs. Additionally, sponges influence biogeochemical cycling of dissolved nutrients on coral reefs, particularly of nitrogen and silicon. Many sponges contain a high density of prokaryotes in their mesohyl, which makes them able to either incorporate nitrogen from the water (via aerobic fixation) or to release nitrogen to the water column (via annamox) or both. Often, they are also net sources of nitrate and ammonium that facilitate local primary productivity and the general reef microbial loop. The majority of reef sponges belong to the class Demospongiae, most of which produce siliceous skeletons in such large amounts that make the whole reef ecosystem function as net silicon sink, even more important than diatom primary productivity (Maldonado et al. 2010).

A number of species (mainly belonging to the family Clionaidae) participate in limestone destruction (bioerosion) that may weaken reefs. The excavation process produces very fine sediments that fill crevices in the framework but may also lead to the smothering of other sessile reef organisms. Interestingly, the information to date suggests that many tropical reef sponges, and particularly the excavating ones, would tolerate and even be favored by the predicted scenarios of ocean warming, acidification, and coral decimation for the next 100 years. The general trend is that the abundance of reef sponges may be rising in areas with regressing coral covers (Bell et al. 2013). Yet local examples of sponge decline also occur. A 14-year census in the Panamanian Caribbean revealed the steady disappearance of the less common species (51.3%) and a 42.6% drop in the local sponge biomass (Wulff 2006). The causes of such local sponge declines remain unclear, but diseases emerge as a major factor of mortality for tropical sponge assemblages.

This section summarizes information for the best known reef systems, but many others known to occur still remain poorly investigated.

3 Mangrove Sponge Aggregations

Mangroves are tropical or subtropical coastal, intertidal plant communities dominated by certain species of trees that have specialized root systems allowing them to cope with anoxic mud substrata. Their distribution parallels that of coral reefs, except that they are more tolerant to temperature and salinity fluctuations, and therefore they extend between 25° N and 25° S latitude. Among the many species of mangrove trees, those belonging to the genus *Rhizophora* have stilt roots that provide stable substrates within a soft-mud environment where sessile organisms, such as sponges, hydroids, bivalves, polychaetes, barnacles, and tunicates, can attach. Although factors such as temperature, salinity stress, and limited water renewal influence the abundance of sessile invertebrates on the roots, their abundance and distribution is mostly determined by the tidal regime and the tolerance of the species to aerial exposure and solar radiation. Sponges, in particular, do not have protective shells and therefore have limited tolerance to low-tide exposure. This explains why early reports from Indo-Pacific mangroves earned them a reputation for supporting a poor sponge fauna because the large tidal ranges (approximately 1–3 m) are too stressful. There are however exceptions, such as mangroves in certain marine lakes and along coastal islands in the Berau region of Indonesia (Becking et al. 2013). A total of 119 sponge species have been described from these habitats, some even tolerating unusually long air-exposure times.

In the Caribbean, the mean tidal range is much lower (about 15 cm), which allows more sponge species to settle and survive on mangrove stilt roots and peat banks. Out of the 550 invertebrate and alga species found living as epibionts of mangle roots in the Caribbean (Guerra-Castro and Cruz-Motta 2014), sponges are estimated to contribute about 10–70% of the species richness on submerged roots (Diaz and Rützler 2009). Some of these Caribbean mangrove sponges, which are well adapted to live near the mean low tide mark (Fig. 3a), can also survive temporary exposure during very low spring tides (Rützler 1995), such as *Lissodendoryx isodyctialis* (Fig. 3a, f) *Haliclona manglaris* (Fig. 3b), and *H. implexiformis* (Fig. 3e). Up to 127 sponge species have been reported inhabiting mangrove roots in eight Caribbean countries (Belize, Colombia, Cuba, Guadalupe, Jamaica, Panama, Trinidad, and Venezuela), although most mangrove systems remain unexplored (Guerra-Castro and Cruz-Motta 2014). In Belize, where a number of mangrove forests have been studied (Rützler et al. 2000; Maldonado et al. 2010), Twin Cays, which is a mangrove island inside the barrier reef west of the field station on Carrie Bow Cay, supports 57 sponge species (see Table 1 for most common species; Fig. 3a–f). The nearby mangrove ponds of the Pelican cays, only 16 km to the southwest, where

Fig. 3 **Views of mangrove sponge aggregations**. (**A**–**F**) Views of sponges on red-mangrove roots lining a Twin Cays canal. (**A**) Massive *Tedania ignis* (red) and *Lissodendoryx isodictyalis* (blue) growing on roots at the lower limit of low tide; (**B**) *Haliclona manglaris* (blue) growing on mangrove oysters, *Isognomon alatus*, while fully exposed to air during low tide; (**C**, **D**) roots almost entirely dominated by massive *T. ignis* in the "Sponge Haven" area of Twin Cays; (**E**) Root covered by massive *Haliclona implexiformis* (purple), thickly encrusting *Scopalina ruetzleri* (yellowish orange), and a small patch of *H. manglaris* (bright blue); (**F**) A typical combination of dominant sponge species on roots at Twin Cays: *L. isodyctialis* (blue), *H. implexiformis* (purple), and *Halichondria magniconulosa* (yellow), along with the bright orange tunicate *Distaplia corolla*. (**G**, **H**) Two general views of the very diverse sponge assemblage on roots in a Pelican Pond mangrove. Sponges seen are *Mycale microsigmatosa, Mycale laxissima, Mycale laevis, S. ruetzleri, Iotrochota birotulata*, *Aplysina* cf. *cauliformis*, *Dysidea etheria*, *Chelonaplysilla* sp., *Desmapsamma anchorata*, and *Amphimedon compressa*, among others

the barrier reef is broken up and allows oceanic water to flush the lagoon, supports more than 147 species (Fig. 3g–h), according to a revision of the census in progress.

Although mangrove specialist sponges do exist, such as *Haliclona manglaris* (Fig. 3b, e) that rarely grows in habitats other than mangrove, most of the sponge fauna in Caribbean mangroves consists of generalist species that, because of their resistance to desiccation, siltation, and salinity stress, are able to colonize this habitat from adjacent reefs and seagrass meadows (see Table 1 for examples of shared species). Nevertheless, these mangrove-colonizing generalists develop abundance patterns different from what they show in adjacent reefs and seagrasses; coupled with the presence of some mangrove specialists, this makes the sponge fauna of mangroves systems across the Caribbean globally distinct (Diaz 2012). Unlike coral reefs, where large tubular, vase, and ramose species dominate, mangroves are rich in thin crusts and thick massive sponges. Demosponges from the orders Poecilosclerida (*Clathria*, *Tedania*, *Lissodendoryx*, and *Mycale*) and Haplosclerida (*Haliclona*, *Niphates*) have a high diversity and dominate the mangrove sponge fauna (Fig. 3). When mangrove systems are altered by natural or man-induced disturbance (e.g., clear cutting and increased sediment in water) opportunistic species, such as *Tedania ignis* (Fig. 3c, d) and *Clathria curacaoensis* (senior synonym of *C. schoenus*), tend to increase in abundance over more mangrove-specialized species.

Significant spatial variability in species composition has been reported at four spatial scales within southern Caribbean mangroves: among roots, sites, localities, and regions. Yet since mangrove stilt roots can extend underwater by up to 2–3 m, the composition and abundance of sponge species also varies along the submerged length of the root. Collectively, these patterns suggest high regional and local β diversity. Local colonization events and succession have been shown to be important factors explaining a large portion of the spatial variation in these communities. Competition for space and predation from asteroid echinoderms and fishes is also important in shaping the structure of mangrove sponge assemblages.

Accurate quantifications of mangrove sponge biomass are scarce. Estimates at Twin Cays mangrove islands (Belize) provided an average of 1.9 ± 3.9 L of sponge m^{-2} (Table 1), a value that, although restricted to the small extension of the mangrove habitat, runs parallel to or even surpasses the biomass average of sponges living in adjacent patch reefs and seagrass meadows (Table 1). On the leeward sides of the islands, sponges are more abundant, covering 10–50% of the root surfaces, followed by sea anemones, ascidians, and algae. The bulk of biomass is typically provided by few, locally dominant species. For example, an assessment of total root coverage at four distinct sites in Bocas del Toro (Panama) revealed that the six most common sponge species out of the 65 identified species contributed 87–99% of the total coverage.

What ultimately favors sponges to aggregate at extremely high densities on some mangrove roots remains unclear, but physiological benefits could mediate such a sponge-mangrove-root association. Indeed, sponges growing on mangrove roots have been shown to incorporate DOM from the root (Ellison et al. 1996), possibly through unique sponge-associated microbes capable of processing mangrove-derived DOM. Furthermore, an apparent transfer of sponge-fixed nitrogen has been detected on mangrove leaves, suggesting that the exchange of multiple organic compounds can take place between the sponges and the mangrove trees.

4 Deep-Sea Astrophorid and Hexactinellid Grounds

Dense aggregations of astrophorid demosponges and hexactinellids are common at lower shelf, bathyal, and/or abyssal depths. At the shallowest zones, these aggregations often also incorporate a mixture of other demosponges. In the Northern Hemisphere, these sponge aggregations are well known in the North Atlantic, within the 40°–75° N latitude belt, a zone coincidental with elevated levels of dissolved nutrients and primary production in surface waters. The absence of continental margins in the equivalent 40°–60° S latitude belt (Southern Ocean) has limited benthic research, leaving it unknown whether analogous bathyal and abyssal sponge aggregations occur, except on the Kerguelen Plateau.

In the North Atlantic, extensive "astrophorid sponge grounds" are found from the western Barents Sea along the Norwegian shelf to the Faroes, the Shetlands and the western banks, south of Iceland, along the Reykjanes Ridge, to southern Greenland, and in the northwest Atlantic along the continental shelf and slopes off Labrador and Newfoundland (Klitgaard and Tendal 2004; Murillo et al. 2012; Knudby et al. 2013; Beazley et al. 2015). These sponge grounds typically occur on gravel and coarse sand bottom and at depths from 150 to 1,700 m. The fauna is dominated by large species of the genus *Geodia* (Fig. 4a), with additional astrophorids in the genera *Stryphnus*, *Stelletta*, and *Thenea* and the axinellid *Phakellia* (Table 2). The association is found over a vast geographic area, and depending on local conditions of topography, bottom type, and hydrography some variation in dominance of species, taxonomic composition, and densities occurs. This is most clearly seen in fjord areas, where the number of species lowers significantly when ascending to depths as shallow as 60–80 m. On the Norwegian continental shelf, the combined density of the five most dominant sponge species, *Geodia barretti, G. atlantica, G. macandrewii, G. phlegraei*, and *Stryphnus fortis* peaks up to six individuals m^{-2}, with an average value of 0.43 ± 0.08 individuals m^{-2} (Kutti et al. 2013). The first-mentioned three *Geodia* species together constitute more than 50% of the total sponge abundance, and individuals may exceed 1 m in diameter. At some sites of the Norwegian shelf, estimates of *G. barretti* wet biomass alone average 1.4 kg m^{-2} but can be as high as 45 kg m^{-2}. Grounds in the same area may also be totally dominated by *Stryphnus fortis*, reaching a similar biomass per m^{-2} (Fig. 4b). Density of habitat forming sponges on the grounds in the northwest Atlantic ranges from 5 to 25 sponges m^{-2}, with more than 15 sponges m^{-2} triggering a significant increase in the number of associated fauna (Beazley et al. 2015). Indeed, the astrophorid grounds are biodiversity hotspots (compared to non-sponge habitats) across the northern Atlantic, where sponges can constitute about 90% of the benthic biomass, excluding fishes (Klitgaard and Tendal 2004; Murillo et al. 2012). Such sponge biomasses are responsible for significant carbon and nitrogen cycling processes. For instance, average carbon consumption by *G. barretti* alone at the northern Norwegian shelf is estimated at 200 mg C m^{-2} d^{-1}, ranging between 30 and 400 mg C m^{-2} d^{-1}. It means that the shelf population of *G. barretti* can filter approximately 250 million m^3 of water and consume 60 t of carbon daily (Kutti et al. 2013). The *Geodia* grounds extend into the Arctic, from north of Spitzbergen to

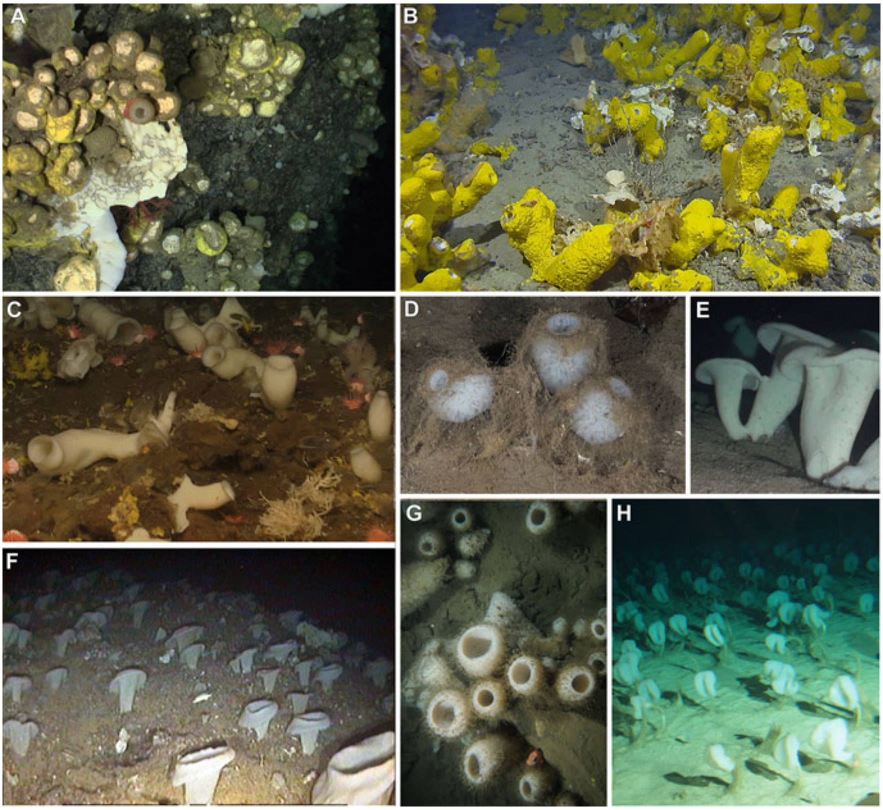

Fig. 4 **Views of deep-sea astrophorid and hexactinellid sponge grounds**. (**A**) Bathyal sponge ground at Flemish Cap (Canada), typically dominated by *Geodia barretti* and *G. phlegraei,* and with common occurrence of *Stryphnus* spp. (**B**) View of an aggregation dominated by *Stryphnus fortis* at the Norwegian deep shelf. In (**A**) and (**B**) grounds, the astrophorids are often covered by the yellow, encrusting sponge, *Hexadella detritifera*. (**C**) A dense aggregation of *Trichasterina borealis* and *Schaudinnia rosea* forming on a seamount at the Arctic Mid-Ocean Ridge. In between the hexactinellids, *Geodia hentscheli*, *G. parva*, and *Thenea valdiviae* occur intermingled, collectively resulting in a dense sponge coverage and favouring a substantial spicule mat on the bottom. (**D**) View of aggregated *Pheronema carpenteri* on soft bathyal bottoms in the North Atlantic. (**E**, **F**) View of *Asconema setubalense* fields on bathyal seamounts at the Alboran Sea (Mediterranean) and around the Canary Islands (North Atlantic). Note a small individual in (**E**) formed by budding from the base of a large adjacent individual. (**G**) View of a bathyal aggregation of *Vazella pourtalesi* on the north-western continental margin of the Atlantic. (**H**) Views of an aggregation of the parachute-like *Sericolophus hawaiicus* at the Kona slope (Hawaii, USA), showing all individuals oriented in the direction of the prevailing current for facilitated suspension feeding

the Fram Strait and along the East Greenland shelf edge into the Denmark Strait and north of Iceland in the east, and in the Davis Strait and into the Canadian Archipelago in the west. There the sponge fauna also includes species of the hexactinellid genera *Asconema*, *Trichasterina*, *Schaudinnia*, and *Scyphidium*, along with an abundance of the astrophorids *Stelletta* and *Thenea* (Fig. 4c, Table 2).

Table 2 Most common sponge species in the North Atlantic deep-sea aggregations. Main habitat builders are referred to as "XXX", common accompanying species as " XX", less common but yet frequent species as "X". *Stryphnus ponderosus* has often been reported in the literature on boreal sponge grounds, but most records probably correspond to *S. fortis*

Sponge species	Boreal *Geodia* grounds	Arctic *Geodia* grounds	*Thenea* grounds	*Thenea-Radiella* grounds
Asconema foliata	X	XXX		
Caulophacus arcticus				XXX
Cladorhiza gelida		X		XXX
Forcepia topsenti				XXX
Geodia atlantica	XXX			
Geodia barretti	XXX	X	X	
Geodia hentscheli		XXX	X	
Geodia macandrewii	XXX	XX		
Geodia parva	X	XXX	X	
Geodia phlegraei	XXX	X		
Hymedesmia stylata				XXX
Phakellia robusta	XXX	X		
Phakellia ventilabrum	XXX	XX		
Radiella sol		X		XXX
Schaudinnia rosea		XXX	X	
Scyphidium septentrionale		XX		
Stelletta normani	XXX	X		
Stelletta rhaphidophora		XXX	X	
Stryphnus fortis	X			
Sycon abyssale				XXX
Tentorium semisuberites	X	X		XXX
Thenea abyssorum		X		XXX
Thenea levis	XX		XX	
Thenea muricata	XX	X	XXX	
Thenea valdiviae	X	XX	XXX	
Trichasterina borealis		X		

Thenea grounds occur in deep fjords in Norway, Iceland, and East Greenland, as well as along continental shelves and on seamounts in the northeast Atlantic and the Arctic at 100–900 m depth. The preferred substratum is mud, often charged with large amounts of released sponge spicules that form mat-like structures. *Thenea muricata* is the most common species (Table 2), with a body size reaching up to

50 cm diameter. Below 2,000 m depth in the basins of the Greenland, Iceland, and Norwegian Seas, grounds of *Thenea abyssorum* and the hadromerid *Radiella sol* occur, including spirophorid species of *Craniella* at combined densities of up to 20–24 individuals m^{-2}. Dwarfed species of the genera *Radiella*, *Tentorium*, *Forcepia*, and *Hymedesmia* also occur, together with a constant presence of smaller calcareous sponge species (Table 2). Abyssal populations of *T. abyssorum, Tentorium semisuberites*, and *Craniella* spp. account for about 90% of sessile biomass and are estimated to process 1–6 mg C m^{-2} d^{-1}, with a substantial coupled oxygen demand (Witte and Graf 1996). Thus, these sponge grounds have a significant role in the deep-sea turnover of organic carbon, although their flux is one to two orders of magnitude lower than those in *Geodia* grounds. *Thenea* spp. reproduce both sexually and asexually by budding, which could facilitate aggregated growth. The growth of oocytes in the abyssal populations of *T. abyssorum* is rapid and synchronous, triggered by a seasonal input of particulate organic matter from the photic ocean (Witte 1996). These patterns suggest that sexual reproduction and other metabolic activities in abyssal sponge grounds may be markedly connected to events and cycles of the photic ocean.

At lower latitudes than the high-production belts described above, several different types of aggregation of deep-sea astrophorid demosponges have been described. In the eastern North Atlantic and in the Mediterranean Sea, the astrophorids *Pachastrella monilifera* and *Poecillastra compressa* have been reported to reach densities of up to 10 ± 0.7 individuals m^{-2} and a wet weight biomass of up to 0.315 kg m^{-2}. The axinellid *Phakellia ventilabrum* may also contribute to these aggregations with average densities of up to 0.27 ± 0.01 individuals m^{-2}, as has been recorded for the Cantabrian Sea.

Also at temperate latitudes, hexactinellids may form dense sponge aggregations. However, they differ from the astrophorid demosponges in that they typically form monospecific grounds. The hexactinellid *Pheronema carpenteri* probably forms the most extensive sponge aggregation, occurring from south of Iceland and west of Scotland, across the Porcupine Seabight, Azores, northern Spain, Portugal, Canary Islands, and off Morocco at 800–1,350 m depth. The substrate is mud with large amounts of sponge spicules often forming mats. The sponges are nest shaped, up to 25 cm high and 30 cm across, and can be more than 200 g in wet weight. They are anchored in the mud by rooting tufts of long spicules (Fig. 4d), with aggregations of up to 475 individuals 1,000 m^{-2}, and peak abundances and wet weight biomass up to six individuals m^{-2} (average 1.5 individuals m^{-2}) and 1.1 kg m^{-2} (average 372 g m^{-2}), respectively (Rice et al. 1990). Sexual reproduction remains unknown, with budding from the lower part of the sponge suggested to give rise to clumps of individuals.

Three other kinds of hexactinellid-dominated sponge grounds, but of smaller spatial extent, are known from several areas of the North Atlantic. Off the Canary Islands, off Portugal, and at the Alboran Sea (Mediterranean Sea), small fields of the large (up to 1 m tall) vase-shaped *Asconema setubalense* have been found on seamounts at bathyal depths (Fig. 4e, f). Details of the extension, biomass, and densities have not been obtained, but clumps of up to five individuals m^{-2} have been recorded, with average density of about 0.5 individuals m^{-2} at the densest areas of the aggregation. On the eastern Scotian Shelf off Nova Scotia, *Vazella pourtalesi*, a barrel-shaped sponge up to 30 cm (commonly known as “Russian hats”) forms large monospecific aggregations with densities of up to eight individuals m^{-2} on muds with sponge spicules at 100–600 m depth (Fig. 4g). It is a rare species only known elsewhere from the Gulf of Mexico and the Azores where it has been reported at low densities. Similarly, the cup-shaped up to 40 cm high *Nodastrella asconemaoida* forms aggregations with densities up to six individuals m^{-2} at 560–630 m depth on cold-water coral reefs on Rockall Bank west of Ireland. It is a rare species, with only a few specimens known from off Florida and possibly from the Mid-Atlantic Ridge (Dohrmann et al. 2012).

At tropical latitudes, dense, monospecific aggregations of hexactinellids have also been described in the bathyal zone. *Sericolophus hawaiicus* forms a 300 km-long population that encircles the island of Kona (Hawaii) at 350–450 m depth (Fig. 4h), forming a 100 m-wide belt on the slope. The upper bathymetric limit of the sponge population is imposed by the presence of the 10 °C permanent thermocline, while the lower depth limit is set by the occurrence of a minimum oxygen layer. The sponge is about 50 cm in total height, consisting of a 20 cm-wide cup-like body with an outward-folded margin that becomes inflated as a parachute by the horizontal currents. The body is anchored to the fine sand bottom by a flexible stalk consisting of a bunch of up to 50 cm-long parallel spicules. The maximum sponge density in central areas of the population is 10–14 individuals m^{-2} and 0–2 individuals m^{-2} near the edges of the band, with the overall density averaging 2.3 individuals m^{-2}. Nothing is known about the reproduction, although small juveniles are often seen adjacent to the stalk of the adults. The dense sponge aggregation appears to feed not only on deep-sea bacteria but also on abundant cyanobacteria brought from the photic zone by a down-slope current. These sponges, with their parachute-like body and a stalk of twisting spicules that allows reorientation to shifts in the prevailing current, are particularly suited to capture the suspended food provided by horizontal flows. The sponge aggregation is estimated to consume about 55 mg C and 7.3 mg N m^{-2} d^{-1}, being a significant regional player in the deep-sea microbial food web (Pile and Young 2006). Likewise, the population is estimated to contain a silica standing stock of about 2.7 t per linear km of sponge band, becoming a massive regional silicon sink (Maldonado et al. 2005).

At the abyssal plains, low-density fields of scattered hexactinellids may extend over vast areas. For instance, extensive fields consisting of two flat, mat-like species, *Bathydorus laniger* (21 cm diameter on average) and *Docosaccus maculatus* (12 cm diameter on average), and the stalked *Hyalonema bianchoratum* occur at 4,000 m in the northeast Pacific, 220 km west of the central California coast. Over the years, average individual size and density in these sponge fields fluctuate as a result of shifts in the input of POC into the benthic boundary layer. The variability of POC inputs may range over two orders of magnitude, from 0.22 mg C m^{-2} d^{-1} during years of low primary productivity in the overlying photic ocean to 20 mg C m^{-2} d^{-1} or more during years of high productivity. An increase in size and sponge density appears to occur with a time lag of 13 months after arrival of the POC pulse to the benthic layer. Average density of the two mat-like species was about 91.2 ± 12.4 individuals ha^{-1} from 1989 to 2006. The greatest density was 363.5 individuals ha^{-1} in 2004. Nevertheless, although moderate seasonal POC inputs appear to stimulate sponge recruitment, large food influxes modify drastically the community structure, increasing the density of a few species, while often decreasing the overall diversity. Between 2006 and 2012, two major inputs of organic carbon in the form of phytodetritus (in 2006) and carbon-rich salps (in 2012) occurred, followed by a community shift from a sponge-dominated community to a mobile, detritus-feeding, holothurian-dominated community. In parallel to the decline of filter-feeding sponges, carnivorous sponges increased (Kuhnz et al. 2014). These dynamics provide strong evidence that even abyssal sponge aggregations can be significantly impacted by natural and man-driven changes taking place in the photic ocean and that the concept of slow growing and long lived for abyssal hexactinellids may not be universal.

This section summarizes information for the best studied astrophorid and hexactinellid aggregations but others, still poorly investigated, are known, such as the bathyal aggregations of *Aphrocallistes beatrix* around the Canary Islands, the *Geodia* spp. grounds in the North Pacific, the *Monoraphis chuni* grounds off New Caledonia, the *Thenea* spp. grounds in the Indian Ocean, and the *Euplectella* fields in the Sagami Bay off Japan. For virtually all aggregations described herein (but see Beazley et al. 2013, 2015; Knudby et al. 2013) how the reproductive biology, growth rates, longevity, and the environmental conditions (food supply, hydrography, sea-floor traits, etc.) contribute to develop and maintain the aggregation of the habitat-forming species remain poorly investigated or completely unaddressed.

5 Glass Sponge Reefs

As summarized in the previous section, hexactinellid sponge aggregations occur at bathyal and abyssal depths worldwide, but those in the form of biohermal reefs are exceptional. Biohermal sponge reefs were only known from the fossil record in mid-Jurassic to early-Cretaceous seas (Ghiold 1991; Wiedenmayer 1994), until to everyone's surprise, analogous hexactinellid reefs were discovered alive (Conway et al. 1991, 2005; Krautter et al. 2001) on the western Canadian continental shelf in the 1980s (Fig. 5a–b). In water depths from 90 to 240 m massive framework reefs are built by sponges of the order Hexactinosida, particularly by the species *Aphrocallistes vastus*, *Heterochone calyx*, and *Farrea occa*, all of which have secondary silicification to fuse their spicules into a rigid 3D silica framework (Fig. 5c–f). The young sponges attach to the skeletons of dead sponges leading to biohermal growth. Other hexactinellid species from the order Lyssacinosida are found among the reefs where the reef is less dense. The reefs may be up to 25 m in height and up to 9,000 years old and mantle hundreds of km^2 of the seabed (Conway et al. 2005). Sponge reefs in the Strait of Georgia occur in clumps 35–70 m in diameter and, within clumps, individual sponges usually have several oscula (filtration units). Because the base of individuals is often hard to discern, reef density is gauged by oscula density (Fig. 5d). Densities of oscula are 23–46 m^{-2} and each sponge osculum may be 15–40 cm high. It is calculated that living sponge biomass (skeleton and tissue) in the living portion of three well-studied reefs in this area averages 17–26 kg m^{-3}, with approximately 20% being organic tissue and 80% forming the siliceous skeleton.

Glass sponges are long lived, with growth rates up to 6 cm yr^{-1} (Leys and Lauzon 1998) and a projected age of 220 years for 1 m large individuals. Those growth rates are very similar to estimates made for reef-forming sponges (1–9 cm yr^{-1}) from images captured in sequential years (Kahn et al. 2016). Both of these North-Pacific estimates are an order of magnitude higher than one made by dating the silica skeleton of a single dried specimen of *Rosella racovitzae* collected from Antarctica, which showed a growth rate of 2 mm yr^{-1} and an estimated age of 440 years (Fallon et al. 2010). The faster growth rate of reef sponges may be an adaptation to outgrow sediment deposition in the siliciclastic reef environment.

Glass reef sponges filter almost continuously, and the density of oscula in reefs means that the sheer volume of water filtered by sponge reefs is astounding. Each osculum filters at a rate of 1–3 cm s^{-1}, and for the range of sizes of oscula measured (15–40 cm^2) the filtration rate is 1.3–10.3 m^3 d^{-1} per osculum (Kahn et al. 2015). The grazing (filtration) rate of sponge reefs in the Strait of Georgia was estimated to be 85–198 m^3 m^{-2} d^{-1}, more than twice the rate of the next most intense suspension feeding community known, mussel beds in shallow bays (Kahn et al. 2015). The sponges daily clear the equivalent of the entire water column above them (170 m) of all bacteria, while new bacteria are supplied by prevailing currents, but exactly what the source is (whether from sinking of marine snow or from deep water brought in onto the shelf) is still to be determined. Sponge filtration not only clears the water column of vast numbers of bacteria, but it also recycles wastes to the water in the form of ammonium and CO_2. Additionally, reef sponges excrete particulate wastes as 50–60 μm aggregates that could be eaten by deposit feeders, but such a putative fueling of the food chain awaits to be empirically proved. These heavily silicified sponges also take up an important amount of silicate from the water column to form the skeletal framework. Silicon uptake rates are estimated to be one to two orders of magnitude lower (3.5 mmol Si m^{-2} d^{-1}) than those of other silicifiers, such as diatoms, but, over the long lifetime of these sponges, it leads to substantial accumulation of silicon in the skeletons. In the living portion of three well-studied reefs in the Strait of Georgia, the biogenic silica standing stock averages 7–12 kg m^{-2} (Chu et al. 2011). Since up to 25 m of biohermal structure may lie below the surface, a lot more silica is locked below ground, and therefore sponge reefs form a regionally important silicon sink.

Glass sponges reproduce sexually, with spermatocysts and embryos being found in winter months, and juveniles less than 5 cm high being common on skeletons of dead sponges (Kahn et al. 2016). Genetic studies show high gene flow within and across the Strait of Georgia but not with glass sponges on the west side of Vancouver Island (Brown 2015). Sponges adjacent to one another in a clump are also genetically distinct. Therefore, reef sponge larvae are not necessarily long lived, but the flow regime that feeds the reefs also manages to disperse larvae well.

Reef initiation is dependent on the long-term stability and relict nature of the deep shelf seafloor where coarse glacial deposits occur. Organic rich, mainly biogenic

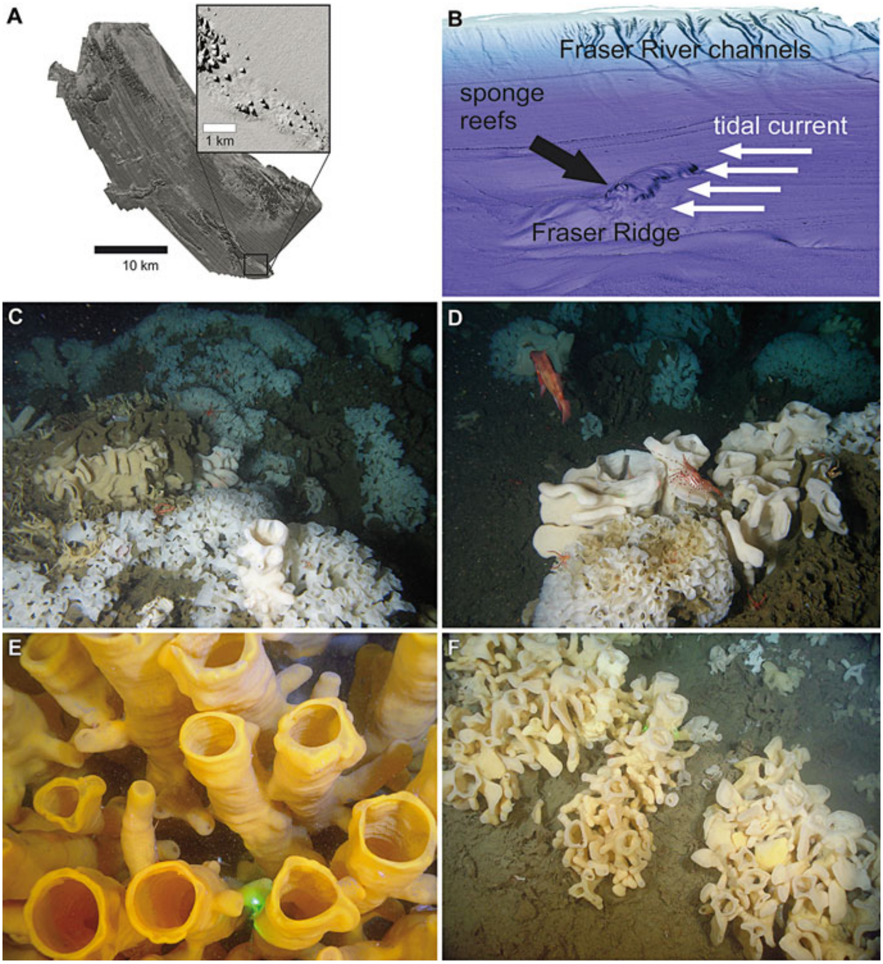

Fig. 5 **Views of glass sponge reefs**. (**A**, **B**) 3-D digital models created using multibeam data show the location and shape of glass sponge reef formations: (**A**) A chain of sponge reefs sits on a rough glacial seabed at the south end of the very large reef complex in Hecate Strait; (**B**) Fraser Ridge reef, very close to the channels of the Fraser River in the Strait of Georgia (SoG). (**C**) General view of a reef in Hecate Strait, a substantial component of which is *Farrea occa* (white) with individuals of *Aphrocallistes vastus* and *Heterochone calyx* often growing out of it. Red galatheid crustaceans are frequent inhabitants of the *F. occa* clumps. (**D**) Detail of clumps of *F. occa* and *H. calyx,* with crustacean and fish fauna in Hecate Strait. (**E**, **F**) Views of the Fraser Ridge Reef, showing oscula tubes of *H. calyx* (**E**) *A. vastus* (**F**) both characterized by lateral projections, which can result in the formation of new oscula

flocs (marine snow) and resuspended shelf sediments delivered by tidal currents (Fig. 5b) cement gaps and interstices in the reef surface. The reefs form large aggregations and develop into clusters with diverse forms, such as bioherms, ridges, and sheets or meadows that coalesce as the reefs form even larger complexes over millennia. It is thought that reefs develop in response to the ambient seabed currents and the availability of glacial substrate. Reefs may develop in areas of elevated suspended sediment concentration, such as at river deltas, but in all cases reef initiation requires a nondepositional seabed. This is somewhat contradictory and suggests a finely balanced system where sediment is required in order to provide the reef matrix, but too much sediment will smother the filter feeding sponges. Laboratory experiments showed that whereas the lyssacine glass sponge *Rhabdocalyptus dawsoni* arrests its filtration when sediment concentrations reach 11 mg L^{-1}, the reef forming *Aphrocallistes vastus* is more tolerant and only arrests filtration at sediment concentrations of 35 mg L^{-1} (Tompkins-MacDonald and Leys 2008), which is significantly higher than the normal concentrations of suspended solids measured at the Fraser Ridge reef, 8.25 mg L^{-1}.

The reefs may have developed preferentially in the Pacific because of the rich hexactinosidan sponge fauna in this region and are probably found in shallow waters in the Pacific because of relatively high silicate levels which do not normally occur in shelf depths elsewhere. Other factors that correlate with dense aggregations of glass sponges in shallow waters are low temperatures (below 12 °C), low light, and high food availability.

In functional terms, the accumulative 3D growth of reef sponges leads to complex habitat formation. The biohermal topography provides shelters and smooths the local hydrodynamic patterns, while the biological activity of sponges increases the exchange of energy and matter between the water column and the benthos, all of which favors benthic biodiversity. Fish, crustaceans (Fig. 5c), nudibranchs, and infaunal polychaetes are all more abundant in reef habitats than in nonreef areas. These unique hexactinellid sponge reefs are vulnerable habitats and raise important conservation concerns.

6 Lithistid Aggregations

The “lithistids” are demosponges of diverse phylogenetic affinity but which are characterized by the common possession of hypersilicified desma spicules. The desmas interlock to form a rigid, massive silica skeleton that renders these sponges stony. Lithistids were present in the Cambrian (>540 mya) forming dense assemblages in reefs that thrived through the Paleozoic (>254 mya). A second major radiation and diversification took place in the Mesozoic, particularly from the late Jurassic (163–145 mya) through most of the Cretaceous (145–65 mya), when impressive “silica reefs” built by lithistids and hexactinellids (see Sect. extant glass sponge reefs) developed on continental shelves. These sponge reefs started to decline in the late Cretaceous (93–65 mya) and progressively disappeared through the lower Tertiary (65–23 mya). Present-day lithistids are considered to be remnants of that Mesozoic fauna, some taxa partially or totally having lost their rigid desma skeletons. During the Cretaceous (144–65 mya) over 150 reef-building genera were known. Today only 46 living genera are known, many of which only have one or two living representatives. They mostly occur in temperate and tropical latitudes; only one species is known from a polar region (Kelly 2007). They typically occupy deep habitats such as shelf breaks, steep slopes, seamounts, hydrothermal vents, and volcanic fields, but in some locations they are also common in shallow caves.

Two significant regional faunas of lithistids are known worldwide: the slope and continental shelf fauna of the tropical and subtropical Atlantic (Pomponi et al. 2001; this work) and the southwest Pacific seamount fauna including that of the Norfolk Ridge south of New Caledonia (Lévi 1991) and New Zealand (Kelly 2007; Kelly et al. 2007). In both regions lithistids dominate the fauna (along with hexactinellids), but the structure and taxonomic composition of the communities differ. In the tropical western Atlantic, lithistids form dense, low diversity communities dominated by species of genera *Discodermia* and *Corallistes* on vertical faces of shelf margins or old horizontal carbonate shelf reefs. Equivalent lithistid assemblages, but probably most important in terms of biomass, have recently been discovered on seamounts in the temperate eastern Atlantic (Fig. 6a–c). The seamount system of the Norfolk Ridge and New Caledonia harbors a much richer, unique lithistid fauna that appears largely unchanged from the Mesozoic, about 60–70 mya (Lévi 1991). These sponges dominate the benthic seamount macrofauna, being the only area in the modern ocean where the lithistid assemblages rival in taxonomic diversity with those from the Mesozoic. An important component of this fauna has been described from New Zealand and surrounding areas (Kelly 2007), with abundant populations at Wanganella and Pandora Banks, Three Kings Ridge, outer Bay of Plenty (Fig. 6d) and southern Kermadec Ridge, and North Taranaki Bight.

Although lithistids were significant members of Paleozoic and Jurassic reefs, they appeared unable to develop analogous aggregations in the modern ocean. This view has been challenged by the discovery of a monospecific reef-like formation around the top of a deep seamount at 800 m in the Mediterranean Sea (Maldonado et al. 2015). Individuals of the foliose species *Leiodermatium pfeifferae*, which grows as erect, contorted, 0.3–0.9 cm thick plates, up to about 80 cm in height, and 100 cm in width (Fig. 6e), occur at high densities, becoming intertwined. The massive lithistid skeletons neither disaggregate nor easily dissolve after sponge death, persisting as an available substrate for new lithistid individuals to recruit. The accretive, clumped growth produces sponge mounds on the seabed (Fig. 6f), conservatively estimated to reach a maximum height of about 180 cm, but being on average at a height of 114 ± 35 cm. Because of the superimposing and intertwined nature of the aggregation, density is difficult to accurately estimate and tentative counts at the top layer of the formation indicate from 1 to about 16 individuals m^{-2}, with sponges covering from 5% to virtually 100% of the seabed, and averaging about 41.6 ± 29.5% cover. Such a dense and complex 3D “reef-like” aggregation attracts a diverse vagile fauna dominated by fish and macroinvertebrates.

The particular circumstances that have favored the dense reef-like aggregation of *L. pfeifferae* at one particular seamount, but not on other adjacent seamounts where the species has also been recorded, remain unclear. At 800 m depth, silicate concentration (averaging annually 8.50 ± 0.6 μM) and inputs of particulate food are only modest. As many other lithistids, *L. pfeifferae* is able to cope with intense siltation, promoting the accumulation of sediment on its inhalant layer. It is

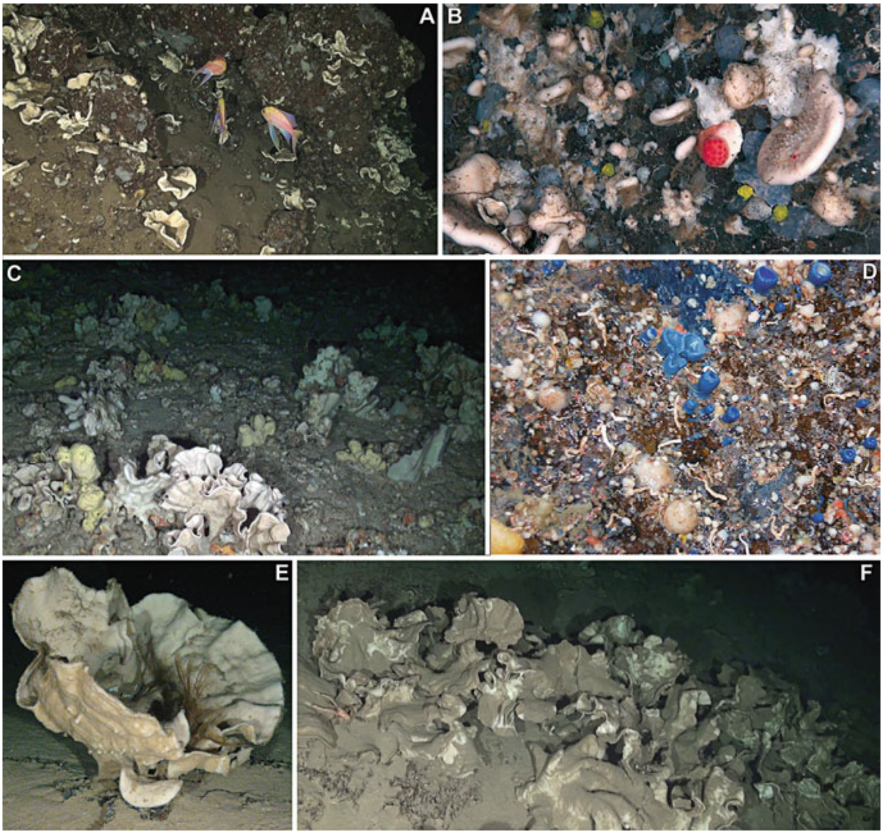

Fig. 6 Views of lithistid aggregations. Lithistid aggregations. (**A**, **B**) Assemblages of lithistid sponges dominated by corallistids recently discovered at seamounts around the Canary Islands (Eastern North Atlantic, Spain). (**C**) View of a sponge aggregation dominated by lithistids of the genera *Corallistes*, *Macandrewia*, *Neophrissospongia*, and *Discodermia* at the Gorringe Bank (Eastern North Atlantic, Portugal). Often, large astrophid demosponges in the genera *Characella* (covered by the yellow encrusting sponge *Hexadella detritifera*) and *Pachastrella* and haplosclerids in the genus *Petrosia* also occur. (**D**) Lithistid sponges on the surface of a boulder at 160 m, Rungapapa Knoll, Bay of Plenty, New Zealand. Bright blue cup sponges are immature specimens of *Reidispongia coerulea*, cream knobs are *Macandrewia spinifoliata*. (**E**, **F**) View of an isolated individual of *Leiodermatium pfeifferae* and view of a small patch of the impressive reef-like aggregation formed by this species around the apex of the “Stone Sponge Seamount” in the Balearic Sea (Mediterranean), respectively

hypothesized that the sediment deposits, rich in organic content derived from decaying diatoms and other phytoplankton, could be used as both a medium to culture bacteria from which the sponges would subsequently feed and potentially a pathway to reuse silicate released from the dissolution of the accumulated diatom frustules.

In general, lithistids occupy a similar ecological niche to other deep-water sponges and are renowned for their associations with fungal and bacterial symbionts, many of which are the source of rich bioactive metabolites in these sponges. Factors that are thought to affect the distribution and abundance of lithistids include availability of hard substrate (steep-sided seamounts, continental margins, carbonate rubble), ocean circulation, food, and silica availability (hydrothermally active sites high in silica vs. oceanic waters low in silica, etc.), but direct evidence of the particular role of those factors is not generally available. We do have direct evidence of the role of climate change; however, the distribution of New Zealand fossil and living lithistid faunas are remarkably disjunct; a rich fossil fauna existed off the South Island during the Late Eocene, but these species and genera only occur north of Chatham Rise today (Kelly 2007). Likewise, reproductive processes and how they might impact the formation of dense aggregations or diverse assemblages remain largely unknown. Nevertheless, a first molecular approach indicated that populations of several lithistids stay relatively well connected across distant deep seamounts off New Caledonia (Ekins et al. 2015), suggesting that at least some lithistids have unknown mechanisms for long-distance dispersal.

7 Carnivorous Sponge Grounds

Carnivorous sponges (Class Demospongiae, Family Cladorhizidae) are a group of typically deep-water sponges that feed on live macroscopic prey (Vacelet and Boury-Esnault 1995) rather than filter feed; they lack the aquiferous system and special feeding cells (choanocytes) considered to be diagnostic for the Porifera. They are often shaped to increase surface area and consequently the chances of passively contacting prey; they are either asymmetrical, divaricating in a tree-like shape, or are symmetrical with profiles resembling those of feathers, palm trees, dandelions, or sunflowers. Most possess lateral filaments covered by “C”-shaped microsclere spicules that act as tiny hooks to capture small crustaceans by their bristles. Digestion is intracellular, accomplished by the migration of cells to the site of struggle, overgrowth phagocytosis, and encapsulation of the prey.

Carnivorous sponges are distributed globally but seem to be most common in deep-water environments such as hadal trenches, seamounts, mid-ocean ridges, volcanic arcs, methane seeps associated with accretionary prisms and hydrothermal vents. The deep southwest Pacific waters surrounding New Zealand present a highly diverse and frequently novel fauna, with over 30 species representing almost all known genera. Numerous sites on the Macquarie Ridge are dominated by cladorhizid sponges (Fig. 7a, b) unusually diverse in genera and species, and many other invertebrates live in close proximity. They contrast with monospecific aggregations described for *Euchelipluma pristina* (Fig. 7c) at the Lilliput hydrothermal vent field southeast of Ascension Island at a depth of 1,500 m (Koschinsky et al. 2006), *Abyssocladia lakwollii* (Fig. 7d, e) at hydrothermal vents around 1,000 m near the Solomon Islands (Vacelet and Kelly 2014), and

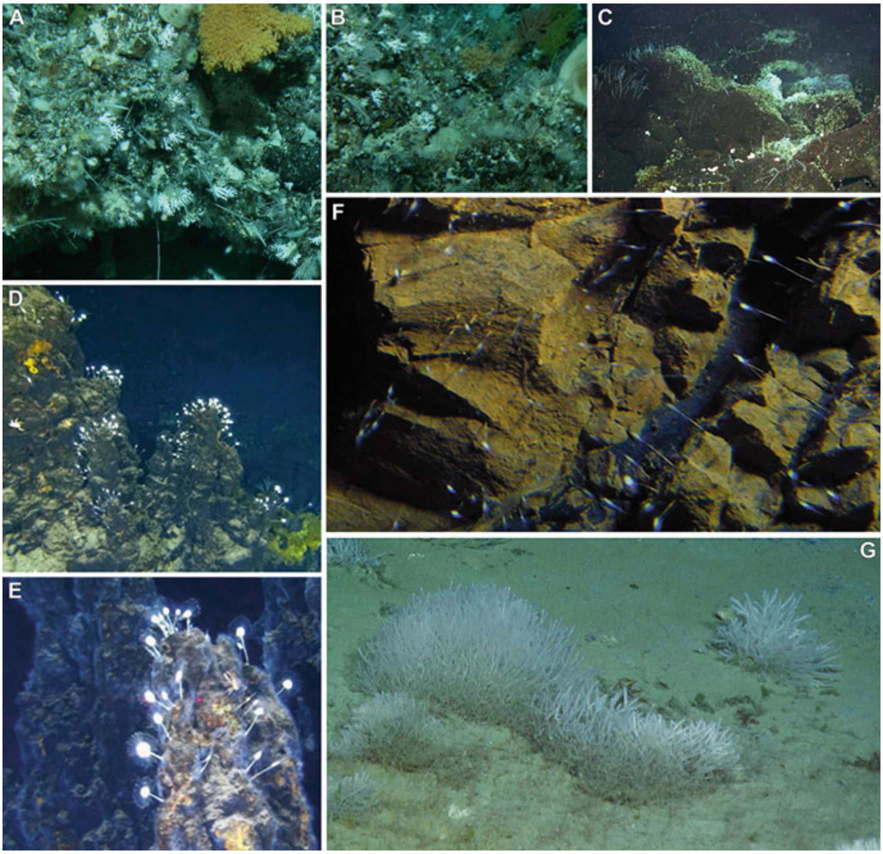

Fig. 7 **Views of carnivorous sponge aggregations** (**A**, **B**) Cladorhizidae garden on Seamount 7 at Macquarie Ridge (Australian Exclusive Economic Zone around Macquarie Island), 53.430° S, 159.075° E, 845–900 m. The sponges grow on a bottom substrate comprised of boulders, cobbles, gravel, sand, and shell fragments. (**C**) Field of *Euchelipluma pristina* on Candelabrum Meadow, a diffuse vent site at 1,500 m depth, on the Lilliput hydrothermal vent field on the southern mid-Atlantic Ridge (*MAR*) to the southeast of Ascension Island. Reproduced with permission from InterRidge News (2006) 15: 9–15 where it was first published. (**D**, **E**). *Abyssocladia lakwollii* in situ, images taken from remote-operated vehicle (*ROV*), far eastern Solomon Islands: (**D**) sponges clustered on hydrothermal chimneys; (**E**) close-up image of sponges showing halo of lateral filaments. (**F**) Aggregation of *Abyssocladia* cf. *bruuni* attached to pillow lava in the southwest breach of Vailulu'u Seamount off American Samoa. (**G**) Dense gardens of methanotrophic sponges, *Cladorhiza methanophila* at a deep site of methane seepage (5,000 m, Atalante, Barbados accretionary prism)

Abyssocladia cf. *bruuni* (Fig. 7f) near vents off American Samoa (Staudigel et al. 2006). Densities of carnivorous sponges have seldom been estimated quantitatively. The abundance of *Chondrocladia lampadiglobus* on the east Pacific Rise between 2,586 and 2,684 m depth was estimated at 1–2.6 individuals km^{-1}, whereas on a Pacific abyssal plain rich in polymetallic nodules, density has been estimated at 16, 4, and 5 individuals ha^{-1} for *Chondrocladia*, *Cladorhiza*, and *Asbestopluma*, respectively.

A remarkable example of much denser monospecific aggregations is provided by the stalked *Abyssocladia* cf. *bruuni* (Fig. 7f) at 600 m depth on the rim of Vailulu Seamount, an active underwater volcano east of Tau in American Samoa (Staudigel et al. 2006). Significant portions of the seamount's flank, rim, and caldera were explored, but cladorhizid sponges were found only in a single shallow breach (low area of the rim) on the southwest side. A current meter deployed for 2 months near the sponges revealed semidiurnal tidal cycles with long periods of inflowing current (15–30 cm s^{-1}) alternating with short periods of export at slower current speed (10 cm s^{-1}). Sponges were oriented in such a way as to present the maximum exposure of their filaments to the prevailing currents, suggesting that sponges may rely on plankton transported into the volcano from the surrounding ocean.

The ecology of carnivorous sponges in mid-ocean habitats is poorly understood. Their populations are remote, isolated, and usually not the primary focus of the expeditions that lead to their discovery. However, an easily accessible Mediterranean cave population of *Lycopodina hypogea* (Vacelet and Boury-Esnault 1995) has afforded researchers a remarkable model for the study of feeding, digestion, longevity, and reproduction. The ability to culture these shallow cladorhizids will potentially help us understand the success of carnivorous sponges in the deep sea.

While most sponge aggregations increase habitat complexity and biodiversity, aggregations of carnivorous sponges may function in the opposite way. Although the observational evidence of carnivorous sponges capturing invertebrate larvae is very limited, it cannot be ruled out that fields of carnivorous sponges may reduce the likelihood that larvae of other invertebrates will reach the bottom. Preliminary feeding experiments of *Lycopodina hypogea* with larvae of the polychaete *Malacoceros fuliginosa* revealed that a few larvae were trapped and digested, but trapping success was low compared to that of copepods or mysids, probably because polychaete larvae have scarce and few setae. Whether carnivorous sponges can also be cannibalistic on conspecific larvae remains unknown. Genetic characterization of material ingested by *L. hypogea* showed that its prey belong to a large taxonomic range, including copepods, polychaetes, brittle stars, and nematodes (Rastorgueff et al. 2015). Some carnivorous sponges may complement their diet by symbiosis with methanotrophic bacteria (Vacelet et al. 1995), a feeding ability that probably allows them to aggregate around vent and seep habitats as well as other extreme environments that are uninhabitable to most other sponges. Methanotrophic sponges were discovered at 5,000 m depth on the edge of the Barbados accretionary prism, where extensive aggregations of *Cladorhiza methanophila* (Fig. 7e) were only found in areas of methane seepage, generally associated with sea anemones and the methanotrophic clam *Abyssogena southwardae*.

The reproduction of cladorhizids is poorly known, but it is suspected that some reproductive traits may facilitate the establishment of aggregations. Carnivorous sponges appear to be hermaphrodites that brood embryos and larvae. Unlike all other sponges, the sperm cannot be spawned in the water outflow because carnivorous sponges lack functional aquiferous canals. Rather the cysts in which the spermatozoids become mature develop a thick envelope that incorporates spicules sticking out of its surface. These spermatophore-like structures migrate through the mesohyl and leave the sponge body. The protruding spicules operate as buoyancy devices, but also allow spermatophores to be captured easily by conspecifics. Local hydrodynamics must therefore be important in establishing aggregations and determining population structure. It is suspected that oocytes may remain arrested in an early stage of oogenesis and that oocyte maturation is triggered by spermatophore capture (Lee et al. 2012). Although this mechanism, if confirmed, will increase the probability of fertilization, an even more interesting idea is that large mature zygotes may remain in developmental arrest awaiting some cue of a favorable environment (e.g., increased frequency of prey capture), so that juvenile sponges would be produced only during times of adequate food availability. Massive release of arrested zygotes could also favor the formation of aggregations. Most factors that help maintain aggregations including dispersal abilities of the larvae, longevity, predators, and other mortality sources remain unknown.

8 Antarctic Aggregations

After more than 100 years of research, over 400 species of sponges are known from the Southern Ocean. Most records come from the continental shelves and slopes (Janussen and Downey 2014), but abyssal plaines have also started being explored (Janussen and Tendal 2007; Göcke and Janussen 2013). The Antarctic sponge fauna shows some special traits and covers a broad diversity in many parameters. The endemism is pronounced (about 60% of the species) and the taxonomic homogeneity of the fauna along the almost 40,000 km long coastline is remarkable (Downey et al. 2012), favored by the circumpolar current and the eurybathy of many sponges species. These general patterns are suspected to be modified in the still poorly known deep-sea Antarctic environments (Brandt et al. 2007), because the barrier effect of the polar front (PF) reduces with depth and allows some faunal exchange. As to diversity, some species are minute while others reach a height of up to 2 m. While most species are white, yellow, beige, or grey, some are black, brown, carmine, or intensive green. A broad variety of substrates, among them sponge spicule mats that vary from 1 cm to 1 m in thickness, are often utilized, and a few species live buried in the sediment. Most are free living, others live as epibionts on other sponges, clams, and even on brittle stars, as is the case of *Iophon radiatum* growing on the ophiuroid *Ophioplinthus* spp. (Gutt and Schickan 1998). The great majority are filter feeders, but there are also some carnivorous species. Around the continent, sponge grounds occur both as almost monospecific and as quite diverse assemblages. The composition of the last mentioned is unique and heterogeneous, and their occurrence covers extreme ranges from absence in some Antarctic subregions to world records in biomass caused by ecological drivers of which some Antarctic specific are well known, while others still are to be deciphered.

It has been estimated that, on the relatively well-known Antarctic shelf, the sponge assemblages occupy about 10% of area and host an average biomass of about 12.7 kg of sponge wet weigh m^{-2} (Gutt et al. 2013). Some local studies also provide a more detailed description of the local patterns in sponge biomass distribution. A benthic biomass survey in the southeastern Weddell Sea shelf found three faunistic clusters of which two had only proportions between 0.5% and 4.2% of sponges. In the third, sponges were dominant with 43.3% of the total biomass (Gerdes et al. 1992). Values varied, especially in the sponge community with striking differences between stations. The sponge community had 3 out of 21 stations with no sponges at all, 8 stations had less than 10 g m^{-2}, 6 had 10–100 g m^{-2}, 3 had 100–1,000 g m^{-2}, and the highest value was 1.4 kg m^{-2}. Different studies on the composition of the sponge fauna in the same area showed that hexactinellids, *Rossella* and *Anoxycalyx* species (Fig. 8a–c), as well as demosponges, most dominant *Cinachyra* spp. (Fig. 8d), contribute to such biomass values with highly variable patchiness between both groups and within these taxa (Barthel and Gutt 1992). Independent of the abundance, the sea floor was almost totally covered by sponges where biomass was highest. Similarly, a study based on nine stations north and south of King George Island (South Shetland Islands) between 120 and 2,000 m depth found values of >100 and 10–100 g of sponge biomass m^{-2} at one station each, while four stations had no sponge at all (Piepenburg et al. 2002).

These Antarctic sponge populations also show surprising dynamics. At McMurdo Sound, a very dense recruitment of the demosponge *Homaxinella balfourensis* (Fig. 8e, f) covered up to 80% of the bottom surface over 1 km. The population explosion occurred over a few years in the 1970s when there was reduced anchor ice formation in the 15–30 m depth zone but, when the anchor ice returned, it carried the entire population away. In this case, no *Homaxinella* settled in the deeper habitats covered with a spicule matrix (Dayton 1989). In subsequent years, *Homaxinella* settled ubiquitously but only on artificial substrata (old cages, floating settlement surfaces, and even on pipes marking transects), rarely in the disturbed zone, and never on deeper natural surfaces. It would appear that the larvae are very motile and well dispersed but do not survive well when settling on natural surfaces because of postsettlement predation. In other areas and below 30 m depth, *Homaxinella* spp. recolonize areas disturbed by grounding glaciers or by scouring icebergs. They can dominate an initial low-diversity pioneer assemblage but are rare in more mature and diversified communities.

Another McMurdo Sound species, the less opportunistic, very large hexactinellid *Anoxycalyx joubini* showed no detectable recruitment from the 1960s through 1989, but then it had a population explosion in which it settled only on artificial substrata, sometimes in such large numbers that their growth pushed them off the structure onto the bottom where they almost always die as a consequence of predation (Dayton et al. 2013). Here, the lack of settlement on natural substrata suggests very effective predators (potentially all the predators from foraminifera, polychaetes, crustaceans, to echinoderms) on the small larvae and recruits. There are other almost monospecific aggregations in deeper water of large *Rossella* spp. that appear to result from asexual reproduction of recruits that escape predation (Fig. 8b). On the southeastern Weddell Sea shelf, sea-bed images showed a size-depending proportion of budding specimens of the species complex *Rossella nuda* or *A. joubini* ranging

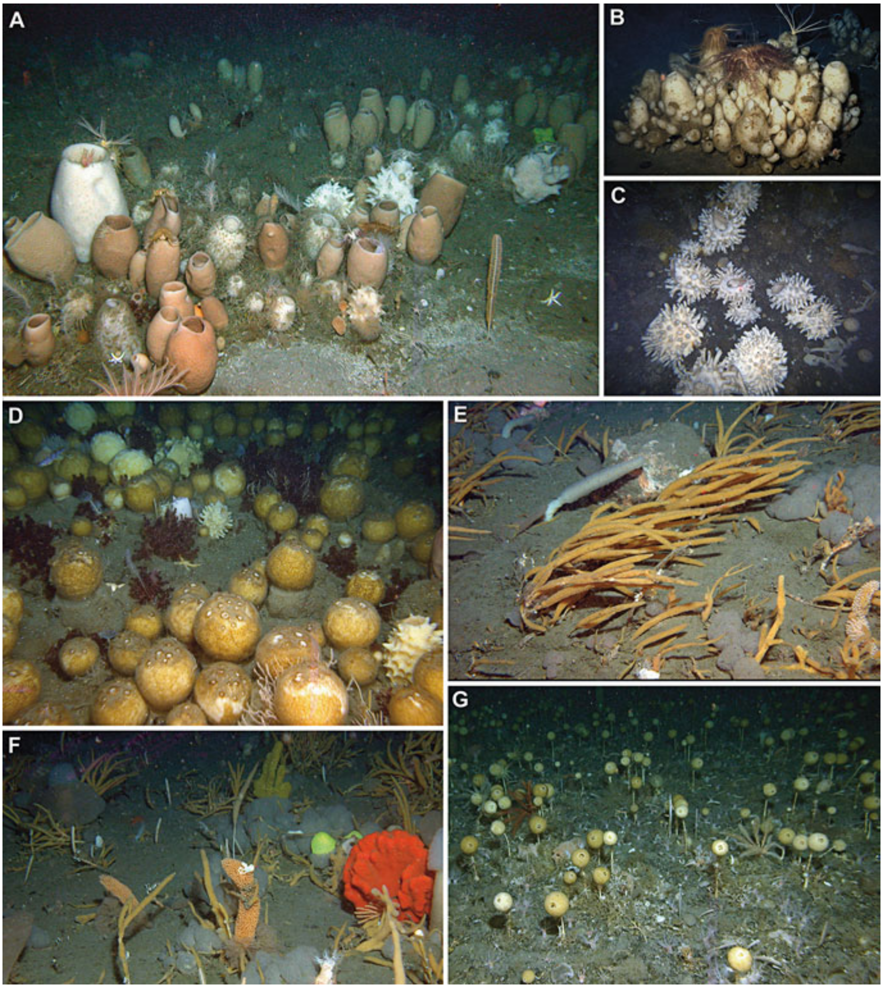

Fig. 8 Views of Antarctic aggregations. (**A**) A benthic assemblage in the Southeastern Weddell Sea (Antarctica) at approximately 233 m water depth. It is dominated by glass sponges, *Anoxycalyx joubini* and *Rossella* spp, with a rich associated fauna of echinoderms and cnidarians, indicating that this habitat has not been disturbed by ice scouring for a relatively long period. (**B**) Detail of a large clump of *Rossella podagrossa* formed by budding and photographed at 50 m in 1974 in the Ross Sea. Reproduced with permission of Magnolia Press from Zootaxa (2015) 1: 169–177, where it was first published. (**C**) Detail of a small aggregation of the spiky hexactinellid *Rosella racovitzae* or *R. nuda* photographed using a small ROV designed to go down through 12 cm holes drilled in the ice. (**D**) A nearly monospecific aggregation of the demosponge *Cinachyra barbata* s.l., in the Southeastern Weddell Sea at 250 m depth. (**E**, **F**). Benthic assemblage east of the Antarctic Peninsula at 210 m. They are dominated by *Homaxinella balfouriensis*, with abundance of other erect demosponges, including the reddish *Kirkpatrickia variolosa*, and a rich associated fauna of compound sea-squirts (translucid white) and sea-fans. (**G**) Aggregation of “lollipop” sponges (herein *Stylocordyla chupachups*) with associated bryozoans, ascidians, and cnidarians. These assemblages are common at an intermediate stage of bottom recolonization after iceberg scouring

from approximately 3–76% and small-scale patches of budding *R. racovitzae* specimens (Barthel and Gutt 1992).

Also in McMurdo Sound, *Rossella podagrosa* has been observed to disperse by small buds that break off and float away in the currents. In areas with reduced currents, this asexual reproduction results in patterns of clumped specimens that tend to characterize the distribution of the species (Fig. 8b). This mode of reproduction might also have been evolutionary advantageous for other rossellids during ice ages, when most of the Antarctic shelf was covered by grounded inland ice. Budding, although reducing genetic diversity and favoring endogamy in the long term, would enable the successive generations of the shelf species to establish in small refuge areas and not being drifted away as larvae to hostile deep-sea environments. Indeed, as larvae of most hexactinellids, rossellids included, remain “unseen”, molecular studies should confirm that those so-called “asexual buds” are not juveniles derived from a process of sexual reproduction by direct development (i.e., lacking a larval stage), as is known for spirophorid demosponges. Sphirophorids, of which the genera *Cinachyra* and *Tetilla* form extensive sponge grounds in some Antarctic shelves, lack the larval stage, and rely for propagation on nonswimming “bud-like” propagules (Fig. 1b, c), which, indeed, are juvenile sponges grown within the maternal body through a process of sexual reproduction with internal fertilization, brooding, and direct development. As these unciliated propagules, charged with a heavy spicule skeleton at the time of crawling out of the maternal body, often fall right by the side of the mother sponge, they favor the formation of dense aggregations.

Iceberg scouring shapes sponge grounds significantly, a phenomenon well studied in the Weddell Sea. Above all, it causes high mortality and formation of sponge spicule mats that serve as a substratum for other organisms. Scouring also buries biogenic silicon in the sediment. It is an open question whether the lower limit of high-diversity sponge grounds coincides by chance with the lower limit of abundant scouring by icebergs or whether iceberg-scouring stimulates the development of sponge grounds. It has been shown that iceberg scouring shapes the diversity of coexisting stages of recolonization by sponges (Fig. 8g), characterized by demosponges, sometimes by hexactinellids, and in some areas by fast growing species or, in other areas, by long-lived species. Benthic communities beneath ice shelves were often assumed to be poor in diversity and biomass, as inputs into the local trophic chain were restricted to limited external food arriving by advection. Interestingly, carnivorous species are found in these areas. Ocean and atmospheric warming is also favoring that 23,000 km^2 of such continental shelf areas start developing high levels of primary production upon ice shelf disintegration. Such a food inflow caused in the Larsen A area after 12 years, but not yet in the Larsen B embayment after 5 years, a sudden recruitment of hexactinellid sponges (Gutt et al. 2011). After a further 4 years, a twofold to threefold increase in number of individuals and a dry biomass increase of hexactinellids and demosponges from 17.5 to 32.5 g m^{-2} was described (Fillinger et al. 2013). These new findings suggest that hexactinellids can be ecological pioneers. These species also appear to be able to arrest their growth and reproductive activity for decades until favorable conditions return and trigger explosive body growth and reproductive activity. The regression of the ice cover is making evident that Antarctic sponge aggregations may be substantially shaped by not only ice scouring and predator abundances but also by food delivery patterns. Reciprocally, the explosive growth and decline of the sponge populations is thought to have a nonnegligible impact on the benthic-pelagic coupling of major flows of particulate food and silica at the habitat level (Maldonado et al. 2012; Gutt et al. 2013; Sañé et al. 2013).

From the rare occurrence of adult glass sponges in still or formerly ice-shelf covered areas, we learn that they do not necessarily need much food. When ice shelves disintegrate, some species recruit very successfully, indicating that higher food supply supports their success. A general conclusion from these observations is that such specimens reach such remote areas as larvae that are brought in by currents and experience high mortality, because juveniles are especially sensitive to food limitation. Such complexity in ecological demands and life performance could also explain their highly unpredictable occurrence in non-ice-covered habitats.

.The role of sponges and other macroinvertebrates in adding three-dimensional structure to Antarctic benthic habitats and increasing the biodiversity of their associated fauna is described in detail in ▶ Chap. 11, “Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems” by Gutt et al.

9 Conservation Concerns for Sponge Aggregations

The main threats to the structure and ecological functioning of virtually all types of sponge aggregations are mechanical damage and general habitat destruction derived from either physical damage or pollution. In many aggregations, the risk of mechanical damage is primarily from bottom-fishing activities (e.g., longlining, benthic gillnets, benthic traps, trawling, etc.). For some aggregations, particularly glass sponge reefs, longlining may be just as problematic as trawling, because very long fishing lines easily slice through sponges. In areas where trap or pot fishing is used, they may damage sponge aggregations during recovery. In addition to these direct impacts caused by physical contact, sponges may suffer indirect impacts of chronic trawling through increased sediment loads causing smothering.

Until recently, physical damage of benthic habitats and organisms mostly occurred as a result of fishing activities. However, more recently the causes have expanded to include other industrial activities, such as dredging, oil and gas prospecting and exploitation, and deep-sea mining. The latter activity in particular is threatening a number of pristine sponge aggregation types found on shelf breaks, slopes, seamounts, and hydrothermal vents. A striking example is the lithistid reef-like formation recently discovered on a Mediterranean seamount that is the target of imminent plans for prospecting and exploitation of oil and gas (Fig. 9). Preservation of seamount habitats is also important for carnivorous sponges, a small but fascinating group of sponges that are critically important for seamount ecology. Direct habitat destruction is also a major concern for mangroves worldwide and, consequently, to their distinct associated underwater sponge communities.

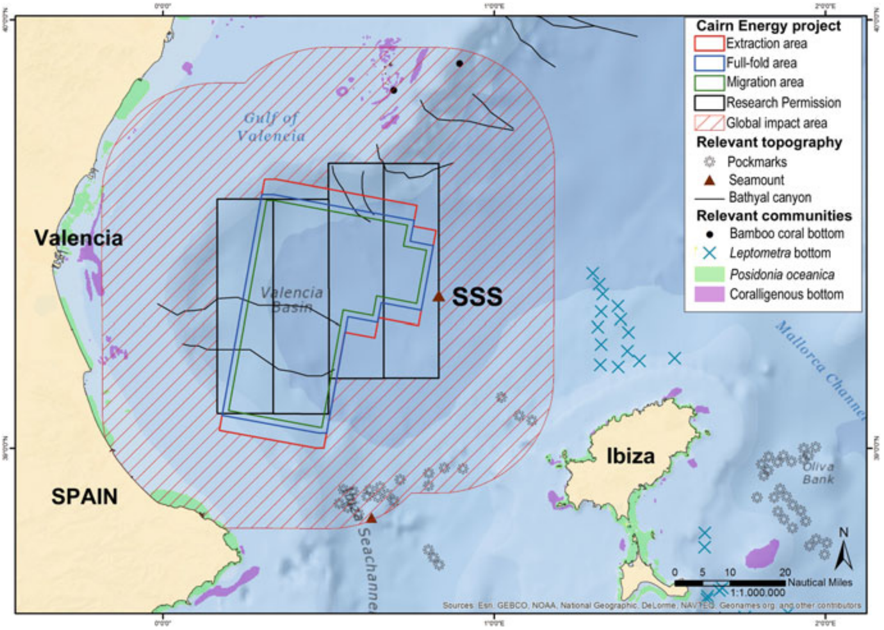

Fig. 9 Example of interaction between commercial exploitation of seamounts and vulnerable sponge aggregation in the Western Mediterranean. The map has been elaborated using public information available from the Spanish Ministry of Industry, Energy and Tourism, published in the Spanish Boletín Oficial del Estado (*BOE*) and at the Ministry webpage:http://www6.mityc.es/aplicaciones/energia/hidrocarburos/petroleo/exploracion2014/mapas/inicio.html. The company Cairn Energy has requested permission (i.e., Cairn project) to seismic prospecting, to research, and to extract hydrocarbons from a large bathyal area between the Spanish Coast and the Balearic Island of Ibiza (Mediterranean Sea). The area of interest includes the SSS seamount, that is, the site where the unique lithistid reef-like aggregation, reminiscent of analogous Jurassic formations, occurs. The global impact area is estimated as an outer, 30 km-wide belt around the zone of activity

While physical damage to sponge aggregations and their habitats is relatively easy to identify at shallow depths through direct observation, the conservation status of deep-water sponge aggregations is often hard to evaluate due to their remoteness. In the northwest Atlantic, important *Geodia*-dominated sponge grounds have been protected by the Northwest Atlantic Fisheries Organization from bottom fishing in the international waters east of Newfoundland, Canada. That protection was stimulated through the United Nations General Assembly resolution 61/105 which calls for the protection of vulnerable marine ecosystems (FAO 2009), including sponge grounds. The closure of these areas may be the first created specifically to protect sponges. However, in general, suitable long-term management strategies are difficult to put in place due to knowledge gaps related to longevity, reproduction, and connectivity. In these areas, restoration plans are even more problematic due to this same knowledge deficiency. Modern technology is helping in some cases, where damaged grounds or dead reef mounds can be detected by examining sonograms that show obvious trawl marks on the seabed or through use of underwater cameras, ROVs, and manned submersibles.

With the advent of industrial underwater and coastal technologies, the ways habitats are affected by physical and chemical damage continue to increase and diversify, including increased exposure to sedimentation, suspended sediment plumes, and waste chemical discharges (including undesirably frequent shallow-water and deep-sea oil spills). In addition, there is also increasing exposure of sponges to episodic environmental and biological stressors. These include sudden temperature stress events, increased influx of organic carbon (e.g., as a function of sea ice retreating in high latitudes or man-driven nutrient discharges in coastal areas), and frequent incidences of disease outbreaks as a function of climate change and ocean acidification. Irrespective of their exact causes, diseases are becoming a serious threat to many shallow-water temperate and tropical sponge communities.

10 Conclusions and Future Directions

Although the role of sponge aggregations as builders of complex three-dimensional habitats has often been discussed, sponge biomass has seldom been measured accurately and, fluxes of matter and energy through sponges have been quantified even less often. Functional information is fundamental if benthic ecologists are to fully acknowledge the importance of sponge aggregations in marine ecosystems and communities. It has been recently demonstrated that sponges fuel the food chains of oligotrophic reef systems. They feed on bacteria as a main C source, but they also incorporate the DOM available in the water column of oligotrophic reefs, a resource that is not assimilated by most other invertebrates. In turn, energy from DOM is converted to POM resulting from cell renewal, but also abundant metabolic wastes, that escapes from the sponges, providing assimilable C and N to fuel the food chains of oligotrophic reefs. Whether this mechanism also operates in oligotrophic food chains of deep-sea systems remain to be addressed.

It has often been assumed that sponge aggregations are not food limited, but some of the information reviewed herein suggests otherwise. Studies of several bathyal aggregations indicate that periodic inputs of food from the upper ocean trigger peaks of growth and reproductive activity, hinting that the aggregations may be food limited during most of the year or even across multiple years. Compelling evidence also comes from the melting of Antarctic ice that promotes primary production on the ice-free continental-shelf while triggering major reorganizations in the sponge communities, including astonishing peaks of growth and/or recruitment. The hypothesis of food limitation in dense, multispecific sponge communities on coral reefs was proposed in the 1970s, but never proven, and has therefore been disregarded by most scientists. Observations that carnivorous sponges typical of oligotrophic bathyal environments are able to arrest many of their physiological functions during long periods also support the idea that these sponges experience food limitation over long periods of the year. Therefore, the impact of sponge aggregations on local food chains, the possibility of food limitation, and the ecological consequences of both processes emerge as major topics for future investigation. The ecological impact of the fluxes of inorganic nutrients (Si and N compounds) derived from either the biological activity of the sponges themselves or their associated microbiomes also remain to be evaluated for most sponge communities. This topic may be particularly important in deep-water aggregations.

Very little is known about reproductive biology and its impact on population structure for most of the sponge aggregations dealt with in this chapter. This major gap in knowledge is particularly important for the conservation of these unique and vulnerable communities. Sexual reproduction by direct development (i.e., in absence of a larval stage) produces dispersing juveniles (Fig. 1b, c) that land near the parent, and it has been suggested that this limited dispersal favors aggregations of spirophorids in the Antarctic (Fig. 8d), Boreal North Atlantic, and elsewhere (Fig. 1a). Likewise, asexual reproduction by budding of nonmotile propagules may favor the aggregation of at least some hexactinellids in the Antarctic sponge communities. However, this pattern may not be the rule for other hexactinellid aggregations, as molecular genetic data on the population structure of glass sponge reefs indicate no cloning, even within clumps of individuals. Recent molecular data also show significant genetic exchange over large distances for deep-sea lithistid communities, coral reef sponges, and several other sponge aggregations. It is evident that unraveling the development and larval ecology of dominant species is crucial if we are to ever understand how those aggregations are formed and maintained. Evidence from Antarctic and coral reef aggregations indicates that predation is another important factor controlling the formation and persistence of the aggregations, but it remains unknown how this factor affects most of the other aggregation types reviewed herein.

In summary, the few functional studies available suggest that sponge aggregations in both shallow and deep waters are singular, vulnerable systems. Available evidence suggests that these aggregations influence the functioning of surrounding at the local and regional scales by participating in the benthic-pelagic coupling of pivotal inorganic nutrients and organic matter. Yet, despite their anticipated ecological and functional relevance, these sponge-dominated systems remain largely understudied and rarely fall under the protection of environmental legislation.

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11 Cross-References

- ▶ Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Conservation and Management of Vulnerable Marine Benthic Ecosystems
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Filter-Feeding Zoobenthos and Hydrodynamics

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Mesophotic Coral Ecosystems

6

Sam Kahng, Joshua M. Copus, and Daniel Wagner

Abstract

Coral reefs are among the most biodiverse and productive ecosystems on the planet. However, our understanding of these ecosystems and their inhabitants has primarily been gleaned from shallow-water studies (<40 m), while light-dependent corals and the ecosystems they support extend much deeper (e.g., 150 m in some locations). In recent decades, coral reef ecosystems have substantially declined globally due to direct and indirect anthropogenic activities that differentially impact shallow-water habitats. This decline has led to the suggestion that surface-oriented stressors and disturbances may be mediated by depth. The role of deeper coral reef ecosystems, called mesophotic coral ecosystems (MCEs), as refugia for shallow-water species has fueled new investigations into this realm facilitated in part by advances in diving technology and remote observation platforms. The increasing access to these poorly studied ecosystems is revealing new insights into the biodiversity of MCEs as well as that of shallow coral reefs. The upper mesophotic community is largely an extension of the shallow-water coral reef community, much of the flora and fauna are shared across these depths. However, there is a transition with increasing depth to a lower mesophotic community dominated by flora and fauna that are largely

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endemic to this zone. Investigations are also expanding depth and geographic ranges for many species, and new species are being discovered regularly in MCEs. However, caution must be taken when generalizing due to the geographically and numerically limited nature of these studies.

Keywords

Mesophotic coral ecosystems (MCEs) • Biodiversity • Deep coral reef • Community structure • Endemism • Depth refugia

Contents

1 Introduction

Mesophotic coral ecosystems (MCEs) are light-dependent coral reef communities starting at 30–40 m and extend to the bottom of the photic zone, which varies by location and may reach depths of over 150 m in some regions (reviewed in Baker et al. 2016). By virtue of the distribution of obligate zooxanthellate corals, these communities are restricted to warm-water habitat (Kleypas et al. 1999). While high-latitudinal MCE investigations are sparse, the latitudinal extent of MCEs (e.g., Kure Atoll, Lord Howe Island, Bermuda) appears to mirror much of the range of shallow-water coral reefs (reviewed in Linklater 2016; Linklater et al. 2016). MCEs represent a direct extension of shallow-water reef ecosystems, which support a diverse abundance of habitat-building taxa including corals, crustose coralline algae, macroalgae, and sponges (reviewed in Kahng et al. 2010, 2014). The upper depth limit attributed to MCEs (30–40 m) corresponds to the depth limit of conventional scuba diving and a vast majority of coral reef research but does not represent a static physiological boundary for marine organisms. Due to the logistical and safety constraints of conducting research at these depths, MCE studies have lagged far behind shallow-water reef studies (e.g., Pyle 1996).

The lower depth limit of MCEs varies by location primarily due to site-specific attenuation of light and in some cases temperature regime (Kahng et al. 2010, 2014). While MCEs remain largely unexplored in many regions, especially in many parts of the Indo-Pacific, mesophotic investigations have accelerated in recent years (Loya et al. 2016), thereby providing new insights into the biodiversity of this largely understudied marine habitat. The recent growth in mesophotic studies has been aided in part by advances in technology and by a growing interest in the potential role of MCEs as refugia for shallow-water reef fauna (i.e., the deep reef refugia hypothesis) which are increasingly being subject to habitat degradation (Glynn 1996; Bellwood et al. 2004; Bongaerts et al. 2010a).

This chapter provides an overview of the known patterns of MCE biodiversity to date. Caution against premature generalizations is advised due to the uneven nature of available studies across locations. Historically, the Caribbean region has been more thoroughly surveyed and studied than other regions. In recent years, a growing number of studies from Hawaii, the Great Barrier Reef, the Red Sea, and Brazil are adding fresh insights into this understudied realm. For purposes of this chapter, the terms upper and lower mesophotic refer to depth zones bordering shallow-water coral reef ecosystems and the depth zone bordering lower limit of light-dependent coral communities, respectively. The depth gradient of transition between these two communities varies by location without a uniform boundary between the two.

2 Habitat-Forming Megabenthos

2.1 Phototrophic Taxa

The habitat-forming megabenthic fauna of the upper mesophotic is largely a continuation of the shallow-water coral reef community. Many of the coral species that dominate the substrate in shallow waters can also be observed at mesophotic depths (>40 m), albeit at lower relative abundance (e.g., Van den Hoek et al. 1978; Kahng and Kelley 2007; Wagner et al. 2014; Muir et al. 2015). With increasing depth, downwelling, light irradiance, and wave energy attenuate. This vertical gradient leads to changes in coral morphology within species and vertical zonation of the dominant coral taxa (reviewed in Kahng et al. 2010). For species found across a wide depth gradient, a flattening of colony morphology occurs at greater depths. In branching and foliose corals, branches become thinner and more widely spaced, thereby reducing self-shading and facilitating ventilation in hydrodynamic conditions with lower energy (Mass et al. 2007; Hoogenboom et al. 2008). In general, dominant shallow-water species with branching, massive, and other robust morphologies are eventually replaced by more delicate, foliose, and platelike species at deeper depths (e.g., Kühlmann 1983; Fricke and Schumacher 1983); however, branching corals do extend well into the mesophotic zone (e.g., Muir et al. 2015).

The following zooxanthellate anthozoan taxa have been reported as abundant or dominant at mesophotic depths in some locations (Kinzie 1973; Zlatarski and Estalella 1982; Sanchez 1999; Zlatarski 2007; Kahng et al. 2010, 2014, and references therein; Bridge et al. 2012a; Friedlander et al. 2014; Magalhães et al. 2015; Eyal et al. 2016; Eyal-Shaham et al. 2016). To date, mutualistic endosymbiosis with

Symbiodinium has only been reported for a single antipatharian species from Indonesia (*Cirrhipathes* sp., Bo et al. 2011).

Indo-Pacific

- Scleractinia: Acroporidae (*Acropora*, *Alveopora*, *Montipora*), Agariciidae (*Leptoseris*, *Pavona, Pachyseris*), Euphylliidae (*Euphyllia*), Fungiidae (*Cycloseris*, *Ctenactis*), Lobphylliidae (*Echinophyllia*, *Oxypora*), Merculinidae (*Dipsastrea, Favites, Mycedium*), Oculinidae (*Galaxea*), Pocilloporidae (*Pocillopora*, *Stylophora, Seriatopora*), Poritidae (*Porites*, *Goniopora*), Psammorcoride (*Psammocora*)
- Antipatharia: *Cirrhipathes*
- Hydrozoa: Milleporidae (*Millepora*), Stylasteridae (*Distichopora*)
- Octocorallia: Alcyoniidae (*Sarcophyton*), Xeniidae (*Cespitularia*)
- Zoantharia: *Palythoa*
- Actiniaria: *Entacmaea*

Western Atlantic

- Scleractinia: Agariciidae (*Agaricia*, *Helioseris*), Astrocoeniidae (*Madracis*, *Stephanocoenia*), Faviidae (*Solenastrea*), Meandrinidae (*Dichocoenia*), Montastreaidae (*Montastrea*), Mussidae (*Mycetophyllia*, *Scolymia*, *Colpophyllia, Manicina*), Poritidae (*Porites*),
- Octocorallia: Gorgoniidae (*Pseudopterogorgia*), Plexauridae (*Eunicea*, *Muricea, Plexaura, Plexaurella*)
- Hydrozoa: Milleporidae (*Millepora*)

At the deepest depths in the lower mesophotic, the coral community bears little resemblance to shallow-water coral reefs. Obligate zooxanthellate octocorals appear to be absent in the lower mesophotic due to higher sensitivity to light limitation and less efficient light harvesting than their scleractinian counterparts (Kinzie 1973; Enriquez et al. 2005). In both the Indo-Pacific and Western Atlantic, species in the family Agariciidae have been reported as depth specialists dominating the coral community, presumably due to superior adaptations to the environment at depth (Zlatarski and Estalella 1982; Kahng et al. 2010, 2014; Hoeksema et al. 2016). The Indo-Pacific coral species capable of inhabiting the deepest depths (e.g., *Leptoseris hawaiiensis, L. fragilis, L. scabra*) appear to be depth specialists and are typically not observed in shallow water (Fricke et al. 1987; Luck et al. 2013; Pochon et al. 2015). However, in the Caribbean, a few coral species (e.g., *Montastraea cavernosa, Madracis pharensis*, *M. senaria*) appear to be depth generalists, able to inhabit both shallow water (<5 m) and the lower mesophotic zone (60–90 m) (Frade et al. 2008a; Lesser et al. 2010; Bongaerts et al. 2015a). The depth range of obligate zooxanthellate corals extends significantly deeper in the Indo-Pacific compared to the Western Atlantic, likely due in part to superior optical water quality associated with more oligotrophic conditions (Kahng et al. 2010; Baker et al. 2016).

To date, the deepest in situ observations of obligate zooxanthellate corals are small colonies of *Leptoseris hawaiiensis* growing widely spaced on barren fossil reef at

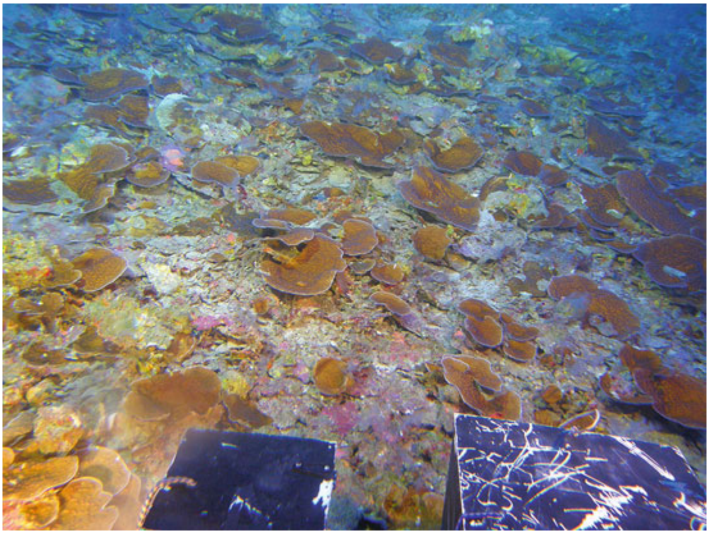

Fig. 1 Photo of monospecific aggregation of *Leptoseris scabra* from 90 m at Keyhole Pinnacle in the Au'au Channel. Shot was taken from the HURL Pisces IV (dive # P4–221) (Photo by Sam Kahng)

165 m at Johnston Atoll and at 153 m off the southwest coast of the Big Island of Hawaii (Maragos and Jokiel 1986; Kahng and Maragos 2006) (Fig. 1). These observations suggest stunted growth consistent with marginal habitat and light limitation of obligate photosynthetic organisms. Although more extreme depth ranges have been reported in the literature, caution must be applied when interpreting early records that are based solely on dredge hauls, as the exact depth that specimens were collected by dredges is often unknown (Kahng and Maragos 2006).

Obligate zooxanthellate octocorals and other anthozoan taxa do not appear to extend as deep as their scleractinian counterparts, nor do they appear to be as abundant in the lower mesophotic (reviewed in Kahng et al. 2010; Kinzie 1970; Bridge et al. 2012a,b). In contrast, phototrophic sponges have been reported as abundant at mesophotic depths (e.g., *Carteriospongia*) in the Indo-Pacific (Bridge and Guinotte 2013). While less studied than their anthozoan counterparts, phototrophic sponges are potentially widely distributed at mesophotic depths in the Indo-Pacific (Kahng et al. 2014 and references therein) with varying levels of contribution from their cyanobacterial symbionts (Keesing et al. 2012). However, phototrophic sponges are much less prevalent in the Caribbean and have not been reported as common at mesophotic depths (e.g., Wilkinson and Cheshire 1990). Given the more oligotrophic conditions associated with many Indo-Pacific reefs, food limitation is likely responsible for the greater prevalence of phototrophic sponges and lower biomass of heterotrophic sponges compared to Caribbean reefs, where food may not be limiting (reviewed in Pawlik et al. 2015a,b; Slattery and Lesser 2015).

2.2 Symbiont Biodiversity

For *Symbiodinium* found in MCEs, there are both depth-generalist subclades with broad depth distributions and depth-specialist subclades which may be adapted to the deep-reef environment (Frade et al. 2008a,b; Chan et al. 2009; Lesser et al. 2010; Bongaerts et al. 2011a; Pochon et al. 2015). Since biogeographic and habitat-specific host-symbiont associations have been reported for several coral species (Iglesias-Prieto et al. 2004; Bongaerts et al. 2010a,b, 2013; Thornhill et al. 2014), the discovery of depth-specialist *Symbiodinium* types is not unexpected. Given the energetic dependence of corals on autotrophy and the photo-physiological differences associated with *Symbiodinium* genotypes, the vertical zonation of *Symbiodinium* with depth could contribute adaptive value to the coral host (Iglesias-Prieto and Trench 1994; Hennige et al. 2010). For corals with conserved, vertical symbiont acquisition, these patterns may also reflect coevolutionary processes of both symbionts and hosts (Bongaerts et al. 2013).

In addition to depth-specialist subclades not found in shallow water, depth-related partitioning of *Symbiodinium* types has been reported within several depth-generalist coral species spanning across mesophotic depths (Lesser et al. 2010; Cooper et al. 2011; Schizas et al. 2012; Bongaerts et al. 2013). This partitioning includes depth-associated changes in host-symbiont associations in terms of subclades and their relative frequencies (Bongaerts et al. 2015b). Most depth-generalist coral species host distinct endosymbionts at different ends of their depth spectrums (Rowan and Knowlton 1995; Toller et al. 2001; Frade et al. 2008c; Bongaerts et al. 2015b). In Curacao, depth-generalist coral species with symbiont zonation exhibit significantly broader depth distributions than those without, highlighting the potential role of symbiont zonation in shaping the vertical distributions of the coral host (Bongaerts et al. 2015b). However, in some cases the depth-related partitioning of *Symbiodinium* types is only localized within a host species, as *Symbiodinium* types found at the lower end of one coral species' depth distribution may be found in shallow water in another coral species (Bongaerts et al. 2015a,b).

Depth-generalist *Symbiodinium* types are also common in MCEs (Bongaerts et al. 2011a). In some cases, depth-specialist coral species (e.g., *Leptoseris* spp.) host *Symbiodinium* types which are also commonly found in shallow water in other coral species (Chan et al. 2009; Bongaerts et al. 2011b; Pochon et al. 2015). For several depth-generalist coral species, the same *Symbiodinium* types can be maintained across a large depth range (Bongaerts et al. 2011a; Cooper et al. 2011; Nir et al. 2011; Bongaerts et al. 2015b; Ziegler et al. 2015).

In general, most reef-building corals host a single *Symbiodinium* type which does not appear to change over time (Goulet 2006). In the Great Barrier Reef, reciprocal transplants of *Seriatopora hystrix* colonies (which vertically transmit symbionts) between depth-partitioned host and symbiont genotypes did not result in novel host-symbiont recombinations after 14 months (Bongaerts et al. 2011c). Whether depth-related *Symbiodinium* partitioning within a species with horizontal transmission would be maintained after analogous reciprocal transplants is not yet known.

The substantial overlap in *Symbiodinium* community between shallow-water reefs and MCEs reinforces the idea of the upper mesophotic as a transition zone between the shallow and lower mesophotic reef (Kahng et al. 2010, 2014). However, in the lower mesophotic zone, there is growing evidence for specialized host-endosymbiont associations including *Symbiodinium* types either not observed or rarely observed in shallow water (Bongaerts et al. 2015b). Additional sampling of MCEs' *Symbiodinium* types will likely uncover additional, depth-specialist *Symbiodinium* types, novel host-symbiont associations, polygamy in previously reported host-specialists, and bathymetric range extensions (Bongaerts et al. 2011a, 2015b).

2.3 *Benthic Macroalgae*

Benthic macroalgae are important components of MCEs and provide critical ecological functions to coral reef communities including primary productivity, substrate stabilization, carbonate sand production, and nutrient recycling and retention (Fong and Paul 2011). Benthic marine macroalgae are a highly diverse functional group comprised of members from at least four major Phyla including Cyanophyta (blue-green algae), Chlorophyta (green algae), Heterokontophyta (includes brown algae), and Rhodophyta (red algae) (Lee 2008). Most marine macroalgae require some form of hard substrata to settle, but some macroalgae, predominantly siphonaceous green algae (e.g., *Halimeda*, *Caulerpa*, *Pennella*, and *Udotea*), are able to establish in soft sediment using specialized rhizomes (Fong and Paul 2011). While exhibiting less habitat complexity than coral aggregations, rhodolith beds and algal meadows on soft substrate can provide habitat and trophic support for fishes and invertebrates (Foster et al. 2013). While less thoroughly studied than their coral counterparts, the following taxa of benthic macroalgae have been reported as abundant at mesophotic depths (reviewed in Kahng et al. 2010, 2014; Van den Hoek et al. 1978; Hillis-Colinvaux 1986a,b; Littler et al. 1986; Aponte and Ballantine 2001; Parrish and Bolland 2004; Culter et al. 2006; Peyton 2009; Bongaerts et al. 2011b; Littler and Littler 2012; Spalding 2012; Friedlander et al. 2014; Magalhães et al. 2015; Pyle et al. 2016a; Spalding et al. 2016):

Indo-Pacific

- Brown algae: *Dictyota, Dictyopteris, Distromium, Padina*
- Noncalcareous green algae: *Avrainvillea, Codium, Caulerpa, Microdictyon, Neomeris, Ulva, Umbraulva*
- Calcareous green algae: *Halimeda, Udotea*
- Noncalcareous red algae: *Asparagopsis, Dasya, Veleroa*
- Coralline red algae: *Peyssonnelia, Mesophyllum*, unspecified crustose coralline red algae

Western Atlantic

- Brown algae: *Dictyota, Lobophora, Sargassum*

- Noncalcareous green algae: *Anadyomene, Avrainvillea*, *Cladophora, Microdictyon, Ostreobium*, *Plectonema*, *Verdigellas*, unspecified filamentous algae, unspecified endolithic green algae
- Calcareous green algae: *Halimeda, Pennella*, *Udotea*
- Coralline red algae: *Hydrolithon, Lithothamnion*, *Peyssonnelia*, *Sporolithon*, unspecified crustose coralline red algae

Distinct depth zonation of dominant floral taxa has been reported from locations in both the Caribbean and the Indo-Pacific (Kahng et al. 2010 and references therein). In many locations, the mesophotic algal communities include species with wide bathymetric ranges which also extent to shallow waters (Agegian and Abbott 1985; Hillis-Colinvaux 1986b; Drew and Abel 1988; Hanisak and Blair 1988). However, in some locations, the mesophotic floras are dominated by depth-specialized species that are presumably adapted to deep-water environmental conditions (Agegian and Abbott 1985; Aponte and Ballantine 2001; Ballantine et al. 2015). In Hawaii, 80 m is associated with a peak in macroalgae diversity and change in community composition (Spalding 2012). In at least some Caribbean locations, the peak in algal diversity, abundance, and shifts in dominant floras occur at shallower depths in the upper mesophotic (Hanisak and Blair 1988; Ballantine et al. 2008; Leichter et al. 2008). Unlike slower-growing and longer-lived corals, mesophotic algal abundance and diversity can vary seasonally at the same location, as many species exhibit bloom dynamics (Cheney and Dyer 1974).

In general, the lower depth distributions of benthic macroalgal taxa in oligotrophic waters follow a pattern from brown (phaeophytes) to green (chlorophytes) to red (rhodophytes), suggesting phylogenetic chromatic adaptation to low light of a particular spectral character (Dring 1981; Kirk 2011). The lower depth limits for foliose macroalgae and encrusting coralline algae correspond to a light level of 0.10% and ~0.01% of surface irradiance, respectively (Markager and Sand-Jensen 1992; Runcie et al. 2008). In many locations, rhodolith beds (aggregations of unattached, nongeniculate coralline red algae) can dominate level substrate in the lower photic zone where water motion is sufficient to prevent burial from sedimentation (Foster 2001; Foster et al. 2013). The deepest in situ observations of benthic macroalgae is a crustose coralline alga at 312 m in the Pitcairn Islands (Friedlander et al. 2014).

While chromatic adaptation arguably plays a significant adaptive role in the lower photic zone, other factors affecting efficiency of light harvesting and energetic demands may also be significant. Various calcifying algal taxa (green and red) are commonly abundant at mesophotic depths (reviewed in Kahng et al. 2010; Kirk 2011). The predominance of calcareous and coralline algae in the lower photic zone suggests that the reflective properties of calcium carbonate may play a supporting role in enhancing light-harvesting efficiency in the lower photic zone (Kahng et al. 2012). In particular, crustose coralline algae is commonly reported as the dominant phototrophic taxa at the deepest depths (e.g., > 200 m) (Agegian and Abbott 1985; Littler et al. 1986; Markager and Sand-Jensen 1992; Aponte and Ballantine 2001; Runcie et al. 2008; Friedlander et al. 2014). The superior reflectance of calcite versus aragonite particularly of short wavelength light (i.e., UVA, blue) (Gaffey 1986) may play a role in the relative depth zonation of calcareous green algae (aragonitic) and coralline red algae (calcitic). Although non-calcifying, endolithic green algae (*Ostreobium*) have also been reported as abundant below 200 m (Aponte and Ballantine 2001). This group inhabits calcium carbonate substrate possibly benefiting from its reflective properties and exhibits very low metabolic activity rates in extremely low-light habitats (Shashar and Stambler 1992).

2.4 Azooxanthellate Benthic Taxa

In addition to phototrophic organisms, several obligate heterotrophic taxa create habitat for a myriad of associated species and are notably abundant at mesophotic depths including azooxanthellate octocorals, antipatharians, and sponges. In general, the relative abundance of obligate heterotrophic benthic fauna increases with depth, due in part to decreased space competition with phototrophic taxa which become light limited with depth (Kahng and Kelley 2007; Bridge et al. 2012a). In several locations around the world, azooxanthellate octocorals, antipatharians, and sponges have been seen to replace obligate photosynthetics at depths below ~50 m (Grigg 1965; Sanchez et al. 1998; Sanchez 1999; Wagner et al. 2012). While less thoroughly surveyed and reported than zooxanthellate corals, abundant heterotrophic megabenthic taxa have been reported from select mesophotic locations around the globe (reviewed in Kinzie 1973; Sanchez et al. 1998; Sanchez 1999; Kahng et al. 2010 an references therein; Rivero-Calle 2010; Bridge et al. 2012a; Magalhães et al. 2015; Wagner 2015).

Indo-Pacific

- Porifera: *Dragmacidon*, *Prosuberites*, *Chondrosia*, *Batzella*, Niphatidae
- Octocorallia: *Annella*, *Carijoa, Dendronephthya*, *Junceella*, other nephtheids
- Antipatharia: *Antipathes, Cirrhipathes, Stichopathes, Myriopathes, Aphanipathes*

Western Atlantic

- Porifera: *Amphimedon, Aiolochroia, Agelas, Aplysina, Ceratoporella, Xestospongia*
- Octocorallia: Anthothelidae (*Diodogorgia*), Ellisellidae (*Ellisella, Nicella, Ctenocella*), Plexauridae (*Hypnogorgia*)
- Antipatharia: *Antipathes, Stichopathes, Cirrhipathes, Aphanipathes, Plumapathes*
- Bryozoa: *Margaretta*

In the Caribbean, the abundance of heterotrophic sponges increases with depth and constitutes a major component of the MCE community (reviewed in Kahng et al. 2010). Despite their non-phototrophic nature, the species composition of the sponge community exhibits vertical zonation including many depth-specialist species restricted to either shallow water (<40 m) or deep water (>40 m) (Lehnert and

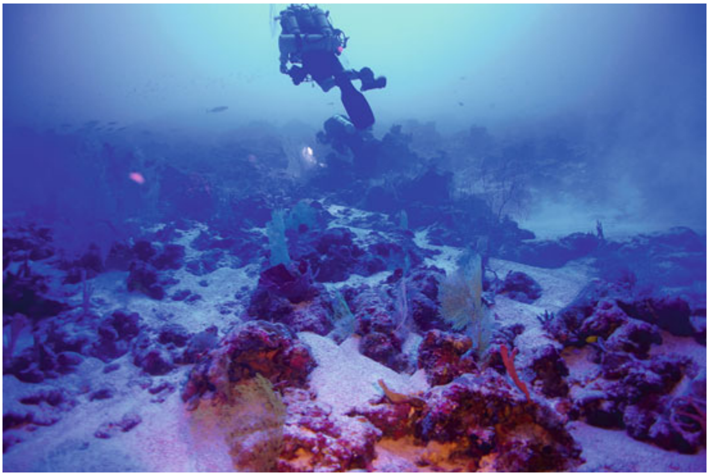

Fig. 2 Photo of diver on a sponge and gorgonian-dominated MCE at 100 m depth at Ant Atoll, located off of the west cost of Pohnpei, Federated States of Micronesia (Photo by Sonia J. Rowley)

Fischer 1999) (Fig. 2). Sponge communities are particularly diverse on the deep fore-reef escarpments at depths of 60–150 m, which are common to many Caribbean island reefs and include coralline sponges (formerly called sclerosponges) which secrete aragonite and contribute to reef formation at depth (Goreau and Land 1974; Ohlhorst and Liddell 1988).

In both the Indo-Pacific and Caribbean, antipatharians are a common component of MCEs (Sanchez et al. 1998; Sanchez 1999; Wagner et al. 2012; Wagner 2015). Similar to some deep-water gorgonians, the upper depth limit of arborescent antipatharians can be limited by strong turbulence and smothering by epiphytes, as well as being outcompeted by faster-growing photosynthetic species (Grigg 1965; Kinzie 1973). While low densities of endosymbiotic *Symbiodinium* have been found in several deep-water antipatharians, they are not considered phototrophic (Wagner et al. 2011). Concomitant with the transition from phototrophic to heterotrophic dominance with increasing depth, the abundance of antipatharians increases below 40 m, and antipatharian abundance typically peaks deeper than their gorgonian counterparts (Kahng and Kelly 2007; Ballantine et al. 2008; Rivero-Calle 2010; Magalhães et al. 2015).

3 Coral Reef Fishes

Growing evidence from both the Indo-Pacific and Western Atlantic suggests that the upper mesophotic fish community is largely an extension of the shallow-water coral reef fish community. At Johnston Atoll, 76% of species recorded in the upper mesophotic (30–60 m) also occur in shallow water (Wagner et al. 2014). A similar pattern has been observed in the Hawaiian Archipelago, the Mariana Islands, and Puerto Rico (Parrish and Boland 2004; Garcia-Sais 2010; Bejarano et al. 2014; Kane et al. 2014; Lindfield et al. 2016; Pyle et al. 2016a, Fukunaga et al. 2016), although the depths at which these faunal breaks occur fluctuate by location (Pyle et al. 2016a and references herein).

In contrast, the available quantitative data to date suggests that lower mesophotic zones (~60–150 m) harbor fish assemblages which are largely unique (e.g., Thresher and Colin 1986; Bejarano et al. 2014; Pinheiro et al. 2016; Rosa et al. 2015). In the Bahamas, Porter (1973) first reported the lower mesophotic zone as a unique zone, set apart from both the shallower water and abyssal communities and only occasionally visited by opportunistic species from above. In La Parguera, Puerto Rico, the abundance and frequency of most shallow fish decrease rapidly with depth, disappearing below 60 m (Bejarano et al. 2014). In mesophotic surveys of Bermuda and Curacao, 71% of fish species were restricted to depths <60 m, 8% were exclusive to the lower mesophotic, and only 21% were found in both upper and lower mesophotic zones (Pinheiro et al. 2016). At Enewetak, Marshall Islands, the lower mesophotic fish community (> 60 m) is composed of a higher proportion of non-shallow-water species than the fish community in both the upper mesophotic (30–60 m) and the subphotic (>150 m) (Thresher and Colin 1986). These findings imply that numerous species are restricted to the lower mesophotic depth zone, presumably due to its unique environmental conditions.

Given the largely unexplored nature of many MCEs, a high rate of discovery of new fish species has been reported across a variety of locations (e.g., Pyle et al. 2008, 2016b; Baldwin and Robertson 2014, 2015; Copus et al. 2015a,b; Baldwin et al. 2016; Pyle and Kosaki 2016; Tornabene et al. 2016; Easton et al. 2016), and there is an estimated potential for thousands of species to yet be discovered from these deep coral reef habitats (Pyle et al. 2016a). Early studies in Jamaica and Belize reported 33% of fishes between 60 and 150 m represented undescribed species (Colin 1974). During a 25 min exploratory dive in American Samoa to 113 m, over a dozen new fish species were observed (R.L. Pyle, pers. com.). Similarly, in Palau, Papua New Guinea, and the Cook Islands, 50 new fish species were reported from mesophotic dives between 60 and 126 m depth consisting of 9.9 h of bottom time (Pyle 2000). Of 144 species collected on a single dive site in Fiji, 40 were found to be undescribed (Baker et al. 2016).

As mesophotic surveys and exploration of new habitats continue, depth range extensions and new location records will continue to expand our knowledge of the distributions of many species. For example, initial mesophotic surveys of Johnston Atoll added new location records for 24 fish species (Wagner et al. 2014). Surveys of Vitória-Trindade Seamount Chain in Brazil revealed that 93% of fishes recorded on the seamounts and 11% of species at the two islands were new records for those locations, and most were found at mesophotic depths (Pinheiro et al. 2015). Depth range extensions were also recorded for 49 species along with two new species discovered. Similarly, one new record for the southwestern Atlantic and six new location records were discovered on the Abrolhos Shelf in the Western Atlantic (Simon et al. 2016).

Further exploration of mesophotic depths will likely expand the known biodiversity and biogeography of coral reef species worldwide (Wagner et al. 2014).

To date, MCE surveys have been primarily limited to upper mesophotic depths due to the obvious logistical challenges of operating deeper, and quantitative mesophotic fish data are largely lacking. Despite these limitations, several taxa from the following genera have been reported as dominant on mesophotic reefs (Pyle 2000; Feitoza et al. 2005; Brokovich et al. 2008; Garcia-Sais 2010; Lesser and Slattery 2011; Bejarano et al. 2014; Wagner et al. 2014; Pinheiro et al. 2015; Rosa et al. 2015; Fukunaga et al. 2016).

Indo-West Pacific

- Apogonidae: *Pristiapogon*
- *Chaetodontidae: Chaetodon*
- Gobiidae: *Trimma*
- Labridae: *Anampses, Bodianus, Cheilinus, Cirrhilabrus, Coris, Gomphosus, Hologymnosus, Larabicus, Labroides, Oxycirrhites, Paracheilinus, Pseudocheilinus, Pseudojuloides, Thalassoma*
- *Pinguipedidae: Parapercis*
- Pomacentridae: *Apolemichthys, Chromis, Dascyllus*
- *Pomacanthidae: Genicanthus*
- Serranidae: *Caprodon, Luzonichthys, Pseudanthias, Cephalopholis, Epinephelus, Variola*

Western Atlantic

- Balistidae: *Melichthys*
- Carangidae: *Carangoides, Caranx, Decapterus, Elagatis, Selar, Selene, Seriola, Trachinotus*
- Chaetodontidae: *Prognathodes*
- Grammatidae: *Gramma*
- Gobiidae: *Coryphopterus, Elacatinus, Gnatholepis, Lythrypnus, Prioleps, Psilotris, Risor*
- Haemulidae: *Anisotremus, Haemulon*
- Labridae: *Bodianus, Clepticus, Halichoeres, Thalassoma, Xyrichtys*
- Lutjanidae: *Lutjanus, Ocyurus, Rhomboplites*
- Pomacentridae: *Stegastes, Chromis*
- Scaridae: *Cryptotomus, Scarus, Sparisoma*
- Scorpaenidae: *Pterois* (alien species introduced from Indo-Pacific)
- Serranidae: *Cephalopholis, Epinephelus, Liopropoma, Mycteroperca, Paranthias, Rypticus, Serranus*

In general, fish species richness and abundance tend to decrease with increasing depth (reviewed in Kahng et al. 2010; Pearson and Stevens 2015; Andradi-Brown et al. 2016; Pyle et al. 2016a). In the Western Atlantic, mesophotic species richness generally correlates with live coral cover; the abundance of crevices and ledges promotes a comparatively high abundance of cryptic species (e.g., basslets, squirrelfishes, gobies, etc.) and large demersal fishes (reviewed in Kahng et al.

2010). In Florida and Brazil, low-relief habitats are primarily inhabited by unique communities of small fishes as compared to more complex habitats (Feitoza et al. 2005; Bryan et al. 2013). At the Vitória-Trindade Seamount Chain in Brazil, mesophotic fish habitats with the highest species richness were reefs, followed by rhodolith beds, the water column, and sandy substrate (Pinheiro et al. 2015).

Across several Indo-Pacific and Western Atlantic locations, a shift in trophic guild with increasing depth has been reported, away from abundant herbivores in shallow waters toward a zooplanktivore-dominated community at mesophotic depths (Kahng et al. 2010, 2014; Bejarano et al. 2014; Pearson and Stevens 2015; Pinheiro et al. 2016; Rosa et al. 2015; Pyle et al. 2016a; Fukunaga et al. 2016). However, mechanisms that drive trophic shifts likely vary by location as contrasting patterns have been reported. In Bermuda, a high biomass of herbivores at mesophotic depths suggests that unique oceanographic conditions may apply there (Pinheiro et al. 2016). At Enewetak in the Marshall Islands, piscivore abundance peaks at 60–75 m, whereas in the Red Sea it reaches minimum abundance at the same depth (Thresher and Colin 1986; Brokovich et al. 2008, 2010). In Honduras, with increasing depth, herbivore biomass declines and piscivore biomass increases, but zooplanktivore biomass appears to remain constant (Andradi-Brown et al. 2016).

In the Pacific, there are proportionately higher rates of endemism for fish communities on mesophotic reefs versus shallow reefs (Pyle 2000; Pyle and Kosaki 2016; Kane et al. 2014; Wagner et al. 2014; Kosaki et al. 2016). In the Northwestern Hawaiian Archipelago, 46% of fishes on mesophotic reefs are endemic to the archipelago, while only 21% of fishes found on shallow reefs are endemic (Kane et al. 2014) (Fig. 3). A comparison of fish communities between Fiji, Papua New Guinea, and Palau reveals higher rates of endemism and more restricted depth ranges for MCE

Fig. 3 Photo of aggregation of no fewer than 11 endemic fish species at Kure Atoll, Northwest Hawaiian Archipelago, at 100 m depth (Photo by Richard L. Pyle)

fishes compared to adjacent shallow-reef fishes (e.g., 50–60% overlap in shallow fish species and only 6–10% overlap in MCE fish species) (Pyle 2000; Baker et al. 2016).

In the Hawaiian Archipelago, endemism appears to increase both with depth and with latitude. For fishes found exclusively in MCEs, 43% endemism is reported for fishes found below 30 m and increases to 51% for fishes found below 70 m (Pyle et al. 2016a). At Nihoa (23°N, 162°W), endemism in MCEs is less than 20% and progressively increases to near 100% at Kure Atoll (28°N, 178°W) (Kane et al. 2014; Kosaki et al. 2016). Given that much of the Indo-Pacific MCEs have been unexplored, contemporary rates and patterns of endemism should be interpreted with appropriate caution since these rates and patterns may change as additional MCEs are investigated.

The marked differences in deep- and shallow-reef fish populations may be caused by glacio-eustatic sea-level fluctuations that periodically eliminate extensive areas of shallow coral reef habitat (i.e., gently sloping insular island and continental shelves) in many locations (Kosaki et al. 1991). Periods of low sea level would cause higher extinction rates for shallow-water fish communities that require these shallow habitats but would have less impact on deeper-water fishes that are accustomed to the vertical walls and drop-offs common to MCEs as these habitats are more likely to shift vertically and be retained during periods of low sea level.

While the available data to date is limited due to logistical challenges, the potential role of MCEs as refugia for shallow-reef fish (i.e., the DRRH) has been supported in recent MCE investigations (Kahng et al. 2010, 2014; Loya et al. 2016; and references therein). Many MCEs are isolated from anthropogenic and natural stressors common to shallow reefs due to factors such as geographic isolation, wave attenuation with depth, and reduced fishing pressure (Baker et al. 2016). Biophysical models in the northeast Caribbean show that larvae of the damselfish *Stegastes partitus* spawned at 80 m can sporadically disperse to shallow reefs (Vaz et al. 2016). In fact, there is a growing list of fish species known to exhibit ontogenetic depth migrations with larvae initially recruiting to shallow habitats (i.e., seagrass beds, back-reefs, and mangroves) and then migrating as they mature to deeper reef crests and slopes (Andradi-Brown et al. 2016, and references therein). In the Hawaiian Archipelago, the damselfish *Chromis verater* exhibits high genetic connectivity between MCEs and adjacent shallow reefs suggesting that the species may maintain one continuous population throughout their depth distribution (Tenggardjaja et al. 2014). These studies highlight the potential for MCEs to act as a depth refuge from which shallow reefs can be repopulated following extirpation.

For targeted species facing overfishing pressure on shallow coral reefs, such connectivity can have stock management implications. For locations studied to date, the abundance of fisheries-targeted species is higher in MCEs than on adjacent shallow reefs at locations exposed to higher fishing pressure. In Bermuda and the Marianas Islands, the abundance and biomass of macro-carnivores increased with depth and distance from the coast (Lindfield et al. 2016; Pinheiro et al. 2016) suggesting that MCEs may act as refugia for fishery-targeted coral reef fish. However, large and highly mobile predatory fishes (e.g., Galapagos shark and giant trevally) can readily migrate (daily and seasonally) between MCEs and shallower depths, thereby reducing the effectiveness of the MCE to act as refugia from shallow-water fishing (Papastamatiou et al. 2015).

When assessing the utility of the DRRH, the role of MCEs is both location and species specific and related to the nature and scope of the disturbance in question (e.g., overfishing, mass coral bleaching, etc.). Although the upper mesophotic may serve as a depth refuge for several fishes, the lower mesophotic may not as there appears to be little overlap in fish communities between these depths. Recent evidence shows that diet and morphology may play a role in shaping the community structure between deep and shallow reefs (Bridge et al. 2016), thereby reducing the overlap in fish communities and increasing the likelihood of depth endemism.

4 Ongoing MCE Exploration and Implications for Biodiversity

Given the limited exploration at mesophotic depths to date, particularly in many Indo-Pacific locations, new MCE investigations are substantially expanding our understanding of coral reef biodiversity (reviewed in Kahng et al. 2014; Lane and Hoeksema 2016). Aided by advancements in technology, contemporary MCE studies are discovering many new species and cryptic diversity, as well as new taxonomic records for species that were previously unknown to many biogeographic regions (e.g., Muir et al. 2015; Magalhaes et al. 2015; Spalding et al. 2016). Some species previously reported as rare or restricted to shallow water are also being reported deeper and in greater abundance at mesophotic depths (e.g., Blyth-Skyrme et al. 2013; Englebert et al. 2014; Muir et al. 2015; Eyal et al. 2016; Eyal-Shaham et al. 2016). Therefore, inferred lower depth limits for many organisms must be interpreted cautiously until more MCEs are comprehensively surveyed (Kahng et al. 2014). Recent investigations have also identified the introduction and proliferation of alien species (e.g., *Carijoa* sp., *Avrainvillea* sp., *Pterois* spp.) altering mesophotic community structure at the expense of native species biodiversity (reviewed in Baker et al. 2016). The contributions from new MCE surveys along with vertical connectivity studies are steadily advancing our understanding of the effectiveness and limitations of MCEs in buffering populations from natural and anthropogenic disturbances associated with shallow-water habitat.

5 Cross-References

- ▶ Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters
- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests of the World: an overview

- ▶ Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems
- ▶ Caribbean Coral Reefs: Past, Present, and Insights into the Future
- ▶ Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest
- ▶ Evolution of the Marine Animal Forest: EvoDevo of Corals, Sea Anemones, and Jellyfishes
- ▶ Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management
- ▶ Octocoral Diseases in a Changing Ocean
- ▶ Symbiotic Versus Nonsymbiotic Octocorals: Physiological and Ecological Implications
- ▶ The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep
- ▶ Trophic Ecology and Habitat Provision in Cold-water Coral Ecosystems

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Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea

7

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Abstract

Several studies using Remotely Operated Vehicles and manned submersibles have recently provided quantitative information on animal forests dominated by gorgonians, black corals, and sponges dwelling at 40–200 m depth in the Mediterranean Sea. These assemblages have received relatively little attention during the last decades due to the fact that they are found below scuba diving depths, and most submersible-based research has been traditionally conducted below 200 m depth. However, these communities are among the most threatened by the impact of fishing pressure, since the larger proportion of fishing activities, especially bottom trawling on soft bottoms and passive gears on hard grounds, concentrate between 50 and 200 m depth. This chapter reviews the recent advances in the study of the spatial and bathymetric distribution patterns of these animal forests, their species composition, ecology, and conservation status.

Keywords

Gorgonian • Black corals • Sponges • ROV • Manned submersibles • Mediterranean Sea

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Contents

1 Exploration of Hard Bottoms at Intermediate Depths in the Mediterranean Sea

Knowledge about coastal benthic communities has greatly increased during the last decades mainly thanks to the wide diffusion of scuba diving, allowing observation and sampling of rocky bottoms located from the shoreline down to around 40 m depth or deeper in the case of technical diving. Similarly, deep areas located under 200 m depth have been explored in the last decades by means of Remotely Operated Vehicles (ROVs) and manned submersibles. However, marine communities located on hard-bottom substrates at intermediate depths (40–200 m depth) have received relatively little attention (Sink et al. 2006).

In the Mediterranean Sea, the first scientific observations of the hard-bottom communities located at 40–200 m depth can be dated back to the 1950s, performed as marginal target of the first manned submersible explorations mainly focused on the exploration of much deeper areas. The bathyscaphs *FNRS III* and *Trieste*, developed by the visionary Swiss engineer Auguste Piccard, performed several dives in the western Mediterranean Sea (e.g., Gulf of Lions, Gulf of Naples, the Ponza Archipelago) at depths ranging from 100 to 2,800 m (Martin 1960). Although these early explorations were mainly focused on plankton studies, a major descriptive effort was also made on the benthic communities, and the amount of collected data was such that the results still represent the main reference for the bionomic zonation of the Mediterranean Sea (Pérès and Picard 1964). The development, in 1959, by the French explorer Jacques Cousteau of the manned submersible *soucoupe* *plongeante*, together with the great improvement of photographic equipment thanks to Cousteau and Harold Edgerton (Laban et al. 1963), made possible throughout the 1960s and 1970s detailed descriptions of the explored sea bottoms accompanied by a rich collection of black and white pictures. Numerous localities of the Mediterranean Sea were in this way explored between 70 and 400 m depth, mostly in the northwestern basin (e.g., Vaissière and Carpine 1964; Reyss and Soyer 1965). The photographic footage of these habitats clearly reported for the first time the occurrence of dense animal forests made of gorgonians, corals, and black corals accompanied by numerous sponges, crinoids, brachiopods, and bryozoans, which could dominate both the soft and hard bottoms over the continental shelf (Laban et al. 1963; Vaissière and Carpine 1964).

However, it was not until the last decade that the development of ROVs, manned submersibles, and technical diving equipment at more affordable operational costs increased their accessibility for marine ecologists. This has made possible a wide series of investigations, especially focused on the benthic communities dwelling in deep coastal bottoms and continental shelves of the Mediterranean Sea. Deep sublittoral coastal bottoms from 40 to 80 m depth were recently explored by ROVs and technical divers along the Catalan (Rossi et al. 2008; Gori et al. 2011a; Ambroso et al. 2014; Coppari et al. 2016) and the Liguro-Provençal coasts (Cerrano et al. 2010; Di Camillo et al. 2013; Fabri et al. 2014). ROVs and manned submersibles (Fig. 1) were also used to explore and characterize the hard-bottom communities located at 80–200 m depth on several areas of the continental shelf and shelf edge of the Catalan coast (Orejas et al. 2009; Gili et al. 2011; Gori et al. 2013; Dominguez-Carrió 2017), the Balearic Islands (Requena and Gili 2014; Grinyó et al. 2016a), as well as the Sicily Channel and the Ligurian, Tyrrhenian, and Ionian seas (Bo et al. 2009, 2011a, 2011b, 2012, 2014a, b, 2015; Angiolillo et al. 2012, 2015; Giusti et al. 2012; Priori et al. 2013; Cau et al. 2015). Deep coastal areas and rocky shoals and soft bottoms located at intermediate depths were also recently explored in the eastern Mediterranean Sea (Salomidi et al. 2009; Orejas et al. 2017) also by the analysis of the benthic fishery bycatch (Deidun et al. 2010; Mytilineou et al. 2014).

2 Animal Forests at 40–200 m Depth in the Mediterranean Sea

Gorgonians and black corals are among the main structuring species in the Mediterranean animal forests located in deep coastal areas and on the continental shelf. Gorgonians are the best-represented megabenthic species (more than 20 species), inhabiting a wide range of environments in the Mediterranean Sea (Carpine and Grasshoff 1975). Morphology and dimension vary widely from one species to another, from a few centimeters to more than 1.5 m high. Gorgonians form dense monospecific or multispecific assemblages that can extend over large areas (Gori et al. 2011a; Grinyó et al. 2016a). Black corals are less diverse than gorgonians in the Mediterranean Sea, where five species have been reported (Bo et al. 2009). Some

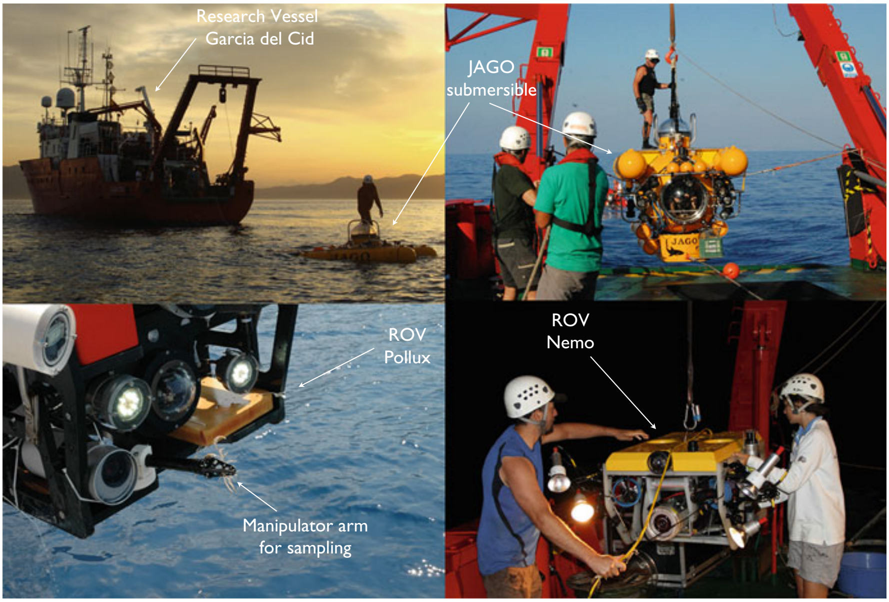

Fig. 1 ROVs and a manned submersible recently used to explore gorgonian and black coral assemblages at 80–200 m depth in the Mediterranean Sea; (*up left*) surveys in Cap de Creus and (*up and down right*) Menorca Channel using the submersible JAGO (IFM-GEOMAR) and the ROV Nemo (Gavin Newman) (*photos by Andrea Gori*); (*down left*) the ROV Pollux (ISPRA) (*photo by Federico Betti*)

species are often found associated to deep gorgonian assemblages, but more often they are the dominant species in multispecific assemblages (Bo et al. 2014a, 2015) with an overall deeper bathymetric distribution than most of the large, structuring gorgonian species (Bo et al. 2009). Black corals are extremely longevous and slow-growing organisms; therefore, presence of large colonies is an indicative of well-preserved environments (Bo et al. 2015). Finally, *Errina aspera* is the only hydrocoral species (stylasterid) in the Mediterranean Sea, reaching dimensions up to ~20 cm under strong hydrodynamic conditions in the Messina and Gibraltar straits (Salvati et al. 2010).

2.1 Deep Coastal Assemblages

Mediterranean shallow coastal gorgonians and other coral species have been recently shown to have a wider bathymetric distribution than previously thought, and to form dense assemblages in deep coastal rocky bottoms located below 40 m depth. Indeed, the highest abundances of the gorgonians *Eunicella singularis* and *Paramuricea clavata* in the Cap de Creus area, along the Catalan coast (NW Mediterranean) (Figs. 2 and 3), were observed at 15–70 m and 25–50 m depth, respectively

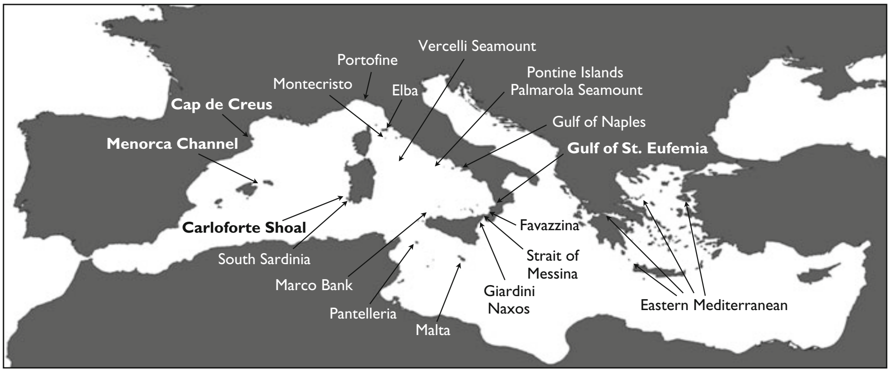

Fig. 2 Map of the Mediterranean Sea with the position of the explored gorgonian and black coral assemblages at 40–200 m depth (*in bold are the case studies highlighted in the text*)

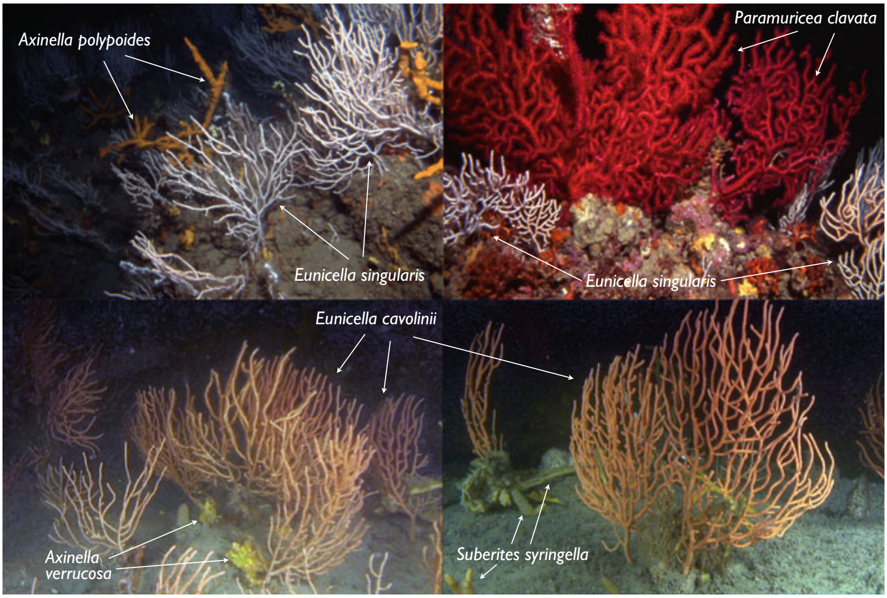

Fig. 3 Cap de Creus. Surveys “Coral Rojo” and “Life Indemares” in Catalonia supported, respectively, by Generalitat de Catalunya and European Union, 2003–2012 (60–100 m depth)

(Gori et al. 2011a). Deep coastal rocky bottoms are also characterized by high densities of the soft coral *Alcyonium acaule* (Ambroso et al. 2014) and the treelike sponge *Axinella polypoides* (Coppari et al. 2016) as typical component of the coralligenous community (Gili et al. 1989; Ballesteros 2006) (Table 1). Similarly, the gorgonians *P. clavata*, *Eunicella cavolinii*, and *Corallium rubrum* have been shown to dominate the coastal coralligenous bottoms at 55–120 m depth in the Gulf of Naples (Fig. 2) in the Tyrrhenian Sea (Angiolillo et al. 2015), as well as the coastal rocky bottoms up to 80 m depth at Pantelleria Island in the Sicily Channel (Fig. 2), together with some sparse colonies of the gold coral *Savalia savaglia* (Angiolillo et al. 2012) (Table 1). A dense population of this gold coral was observed together with *P. clavata*, *E. cavolinii*, and *Eunicella verrucosa* at ~70 m depth near the base of the cliff of the Portofino Promontory (Fig. 2) in the Ligurian Sea (Cerrano et al. 2010), where, in surrounding mud bottom, a dense population of the large-sized hydrozoan *Lytocarpia myriophyllum* was also observed (Cerrano et al. 2015) (Table 1). The black coral *Antipathella subpinnata* has been often found associated with *P. clavata* and *E. cavolinii* in coastal rocky bottoms at ~50–100 m depth in several localities in the Ligurian and Tyrrhenian Sea (Bo et al. 2008). Gorgonian assemblages were recently also reported in the deeper part of the volcanic island of Pantelleria (Fig. 2), which is the emergent summit of a large submarine edifice elevating over an oceanic crust. Sparse colonies of the gorgonian *Ellisella paraplexauroides* were observed on the hard substrate at 80–94 m depth, below the distribution limit of *P. clavata* and *E. cavolinii* (Angiolillo et al. 2012) (Table 1). Finally, in the eastern Mediterranean basin (Fig. 2), coastal gorgonian assemblages are rarely observed shallower than 40 m depth, and the mean distribution depth is ~60 m for *P. clavata* and *E. cavolinii*, which are the most widespread species on coralligenous, together with several sponges, bryozoans, and the gold coral *S. savaglia* (Salomidi et al. 2009) (Table 1).

2.2 Continental Shelf Assemblages

Deeper, coralligenous bottoms at 50–80 m depth on the continental shelf have been observed to host populations of the precious red coral *C. rubrum* together with *P. clavata* and *E. cavolinii* in the Elba Island (Fig. 2) (Priori et al. 2013; Angiolillo et al. 2015) with the common presence of the soft corals *A. acaule*, *Paralcyonium spinulosum*, and *Alcyonium coralloides* overgrowing dead gorgonians and some colonies of the black coral *A. subpinnata* (Angiolillo et al. 2015) (Table 1). Similarly, in the Menorca Channel (Figs. 2 and 4) coralligenous banks at 40–70 m depth host populations of *P. clavata* and *E. singularis*, with lower densities than in shallower waters, but with a dominance of large colonies; deeper banks host instead high densities of *E. cavolinii*. In this area, the maërl bottoms are characterized by extensive high-density assemblages of the gorgonian *Paramuricea macrospina* (Grinyó et al. 2016a) (Table 1).

At similar depths, but under lower light conditions due to higher turbidity, hard bottoms on the continental shelf support high densities of the gorgonian *E. cavolinii* together with several sponges (e.g., *Suberites syringella*) in the Cap de Creus area (Figs. 2 and 3) (Dominguez-Carrió 2017). Likewise, the same treelike gorgonians *E. cavolinii*, *P. clavata*, *C. rubrum*, *P. macrospina*, *Callogorgia verticillata* (Bo et al. 2012), the black

Table 1 Bathymetric distribution of the main megabenthic species of marine animal forests in (2.1) deep coastal areas, (2.2) continental shelf, (2.3) shelf edge and upper slope, and (2.4) offshore banks and seamounts in the Mediterranean Sea (data from the literature quoted in the text)

Species	Deep coastal areas	Depth (m)	Continental shelf	Depth (m)	Shelf edge and upper slope	Depth (m)	Offshore banks and seamounts	Depth (m)
Ellisella paraplexauroides (gorgonian)	Pantelleria	80–94						
Eunicella verrucosa (gorgonian)	Portofino	~70	Mantice Shoal	70–150				
Eunicella singularis (gorgonian)	Cap de Creus, Eastern Mediterranean	6–67 45–50	Menorca Channel	52–88				
Eunicella cavolini (gorgonian)	Eastern Mediterranean, Gulf of Naples, Portofino, Pantelleria	30–120 55–120 ~70 ~80	Favazzina, Elba, Cap de Creus, Gulf of St. Eufemia, Mantice Shoals	55–80 50–80 70–120 70–130 70–150	Menorca Channel, Montecristo Shoals, South Sardinia, Carloforte Shoal, Cap de Creus	94–200 100–200 120–170 186–200 87–280	Vercelli Seamount, St. Lucia Bank	70–100 140–180
Corallium rubrum (gorgonian)	Cap de Creus, Phlegraean islands, Amalfi coast, Eastern Mediterranean, Pantelleria, Gulf of Naples	45–85 50–130 50–120 60–65 ~80 110–140	Elba, Menorca Channel, Gulf of St. Eufemia	50–80 80–120 70–130	Montecristo Shoals, Cap de Creus, South Sardinia	100–200 125–225 120–170	Vercelli Seamount	70–100
Paramuricea clavata (gorgonian)	Cap de Creus, Eastern Mediterranean, Portofino, Pantelleria	15–62 30–120 ~70 ~80	Favazzina, Elba, Menorca Channel, Gulf of St. Eufemia, Mantice Shoal	55–80 50–80 67–92 70–130 70–150	Menorca Channel, Montecristo Shoals	109–120 100–200	Vercelli Seamount	70–100
Paramuricea macrospina (gorgonian)			Menorca Channel, Gulf of St. Eufemia	65–100 70–130	Menorca Channel	100–160	Vercelli Seamount	70–100
Callogorgia verticillata (gorgonian)			Gulf of St. Eufemia	70–130	Menorca Channel, South Sardinia, Carloforte Shoal, Montecristo Shoals	112–348 120–170 186–200 100–200	Vercelli Seamount, Palmarola Seamount, Marco Bank, Malta	70–100 194–220 200–280 300–400
Bebryce mollis (gorgonian)			Gulf of St. Eufemia	130	Montecristo Shoals, Menorca Channel, South Sardinia, Carloforte Shoal	100–200 112–347 120–170 186–200	St. Lucia Bank, Malta	140–210 250–400

(*continued*)

Table 1 (continued)

Species	Deep coastal areas	Depth (m)	Continental shelf	Depth (m)	Shelf edge and upper slope	Depth (m)	Offshore banks and seamounts	Depth (m)
Viminella flagellum (gorgonian)					Montecristo Shoals, Menorca Channel, South Sardinia, Pantelleria	100–200 124–225 120–130 156–242	Marco Bank, Malta	200–250 150–400
Acanthogorgia hirsuta (gorgonian)					South Sardinia, Menorca Channel, Carloforte Shoal	120–145 149–176 186–200	Marco Bank	200–250
Swiftia pallida (gorgonian)					Menorca Channel, Pantelleria	102–347 156–242	Malta	150–240
Villogorgia bebrycoides (gorgonian)					South Sardinia	120–170	St. Lucia Bank	140–210
Isidella elongata (bamboo coral)					Carloforte Shoal	~210		
Antipathella subpinnata (black coral)	Pantelleria	70–100	Elba, Capo Comino, Stromboli, S. Flavia, Favazzina, Bordighera, Capraia, Capo Mele, Portofino, Gulf of St. Eufemia	50–80 54 52–58 55–65 55–100 64–75 75–90 80 100 70–130	Mantice Shoal, South Sardinia, Menorca Channel, Montecristo Shoals	70–150 120–170 133–181 100–200	Vercelli Seamount, St. Lucia Bank, Malta	70–100 180–210 100–400
Antipathes dichotoma (black coral)			Gulf of St. Eufemia	70–130	Menorca Channel, Montecristo Shoals, South Sardinia, Pontine Islands, Carloforte Shoal	92–187 100–200 120–170 145–155 186–200	St. Lucia Bank, Marco Bank	140–210 200–250
Parantipathes larix (black coral)			Gulf of St. Eufemia	70–130	South Sardinia, Pontine Islands, Montecristo Shoals, Carloforte Shoal	120–170 130–155 100–200 186–200	St. Lucia Bank, Palmarola Seamount	140–210 194–220
Leiopathes glaberrima (black coral)					Montecristo Shoals, South Sardinia, Pontine Islands, Vedove Shoal,	100–200 120–130 145–155 160–200	St. Lucia Bank, Palmarola Seamount, Marco Bank, Malta	180–210 194–220 200–280 250–400

(*continued*)

Table 1 (continued)

Species	Deep coastal areas	Depth (m)	Continental shelf	Depth (m)	Shelf edge and upper slope	Depth (m)	Offshore banks and seamounts	Depth (m)
					Carloforte Shoal, Menorca Channel	186–200 180–290		
Alcyonium acaule (soft coral)	Cap de Creus	16–67	Elba	50–80				
Alcyonium palmatum (soft coral)	Cap de Creus	28–60	Elba, Gulf of St. Eufemia, Cap de Creus	60–90 70–130 85–140	Menorca Channel, Cap de Creus	99–130 140–187	Vercelli Seamount	70–100
Paralcyonium spinulosum (soft coral)			Elba	50–80	Cap de Creus, Menorca Channel	85–280 100–176	Vercelli Seamount, Marco Bank	70–100 200–250
Veretillum cynomorium (sea pen)			Elba, Gulf of St. Eufemia, Cap de Creus	60–90 70–130 80–120				
Pteroeides spinosum (sea pen)			Giardini Naxos, Cap de Creus	30–160 85–160				
Funiculina quadrangularis (sea pen)			Gulf of St. Eufemia, Cap de Creus	70–130 80–100	Menorca Channel	112–267		
Virgularia mirabilis (sea pen)			Gulf of St. Eufemia, Cap de Creus	70–130 95–120	Menorca Channel	97–140	Malta	250–300
Kophobelemnon stelliferum (sea pen)			Gulf of St. Eufemia	70–130				
Axinella polypoides (sponge)	Cap de Creus	10–70	Gulf of St. Eufemia, Cap de Creus	65–130 95–130			Vercelli Seamount	70–100
Suberites syringella (sponge)			Gulf of St. Eufemia	90–125	Cap de Creus	85–190		
Haliclona magna (sponge)			Gulf of St. Eufemia	90–120	Menorca Channel	100–297		
Haliclona implexa (sponge)			Gulf of St. Eufemia	80–130				
Poecillastra compressa (sponge)				116–225	Cap de Creus, Menorca Channel, Montecristo Shoals	115–225 94–245 100–200	Marco Bank	200–250
Savalia savaglia (gold coral)	Portofino, Pantelleria	~70 ~80						
Errina aspera (hydrocoral)			Strait of Messina	83–105				

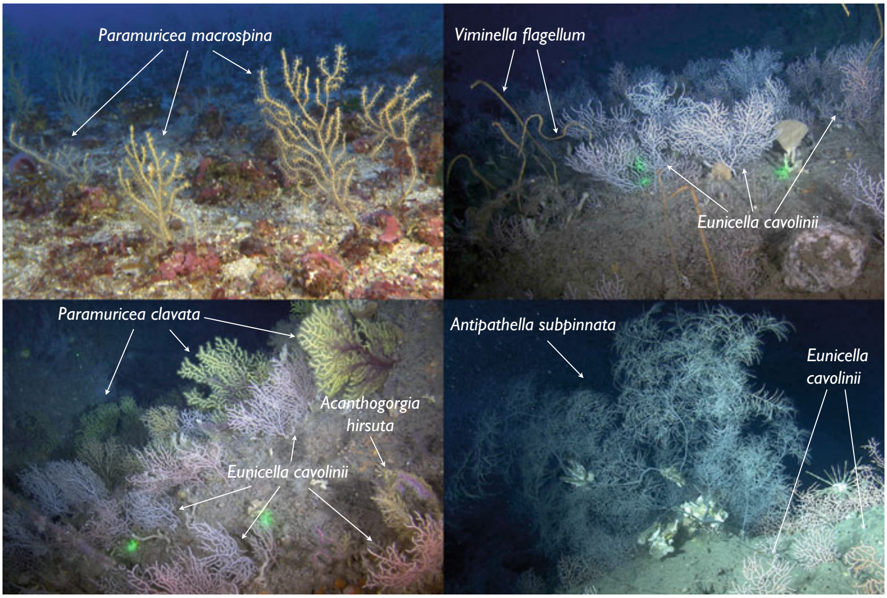

Fig. 4 Menorca Channel. Surveys "Life Indemares" in Balearic Islands supported by European Union, 2010–2012 (70–200 m depth)

coral *Antipathes dichotoma* (Bo et al. 2011b), and a rich sponge fauna (Bertolino et al. 2015) are characteristic of the "*roche du large*" community located at 70–130 m depth in the Gulf of St. Eufemia (Figs. 3 and 5, and Table 1). The black coral *A. subpinnata* forms dense assemblages together with *P. clavata* and sparse colonies of *E. cavolinii* on the top (50–70 m depth) of two rocky pinnacles that arise from the continental shelf at 50–100 m depth near Favazzina (Fig. 2, and Table 1). *A. subpinnata* extends deeper to 90 m, while gorgonians reduce with increasing depth and are completely absent at 90 m depth (Bo et al. 2009). Finally, dense assemblages of the hydrocoral *E. aspera*, with colonies up to 15–30 cm high, have been observed to develop on rocky shoals and coralligenous bottoms under the strong current conditions characteristics of the Strait of Messina (Fig. 2) (Giacobbe et al. 2007; Salvati et al. 2010) (Table 1).

Soft corals and sea pens are the main megabenthic species in soft bottoms of the continental shelf, where they can form high-density assemblages. *Veretillum cynomorium* and *Alcyonium palmatum* dominate the soft bottoms surrounding coralligenous banks and boulders at 60–90 m depth on the continental shelf near the Elba Island (Fig. 2 and Table 1) (Angiolillo et al. 2015). The sea pen *Pteroeides spinosum* occurs at 30–160 m depth on the sandy-muddy bottoms of the Giardini Naxos Gulf (Fig. 2) with the higher densities concentrated at 50–90 m depth, where they probably find optimal conditions and food availability (Porporato et al. 2014) (Table 1).

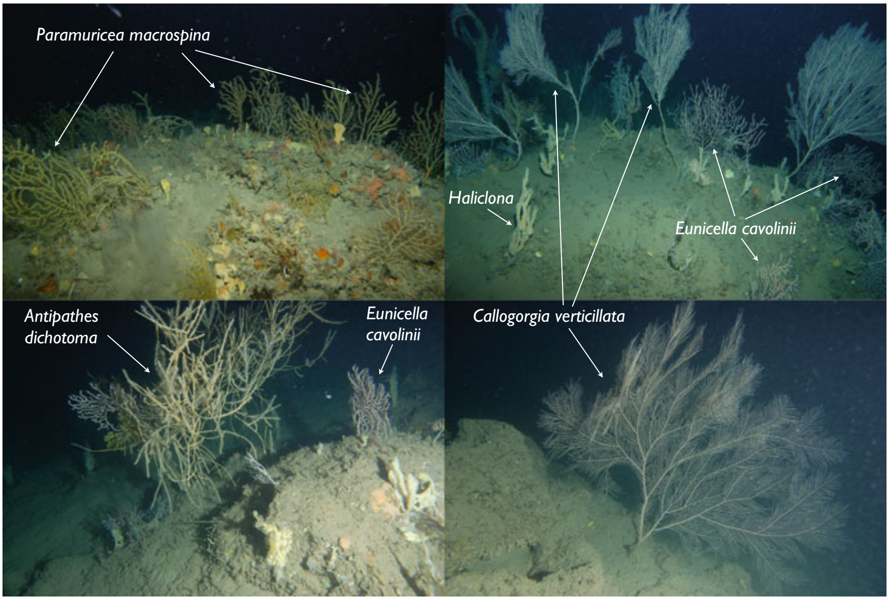

Fig. 5 Gulf of St. Eufemia. Survey "Biodiversity of Calabria" in Calabria supported by Regione Calabria and Ministero dell'Ambiente, 2008 (80–120 m depth)

2.3 Shelf Edge and Upper Slope Assemblages

The shelf edge is the transition zone between the continental shelf and the continental slope (at 110–200 m depth in the Mediterranean Sea, depending on the area). Gorgonian, black corals, and sponges colonize the infrequent and highly localized rocky outcrops that occur on the shelf edge (Bo et al. 2015; Cau et al. 2015; Grinyó et al. 2016a). Gorgonian diversity is much higher on the shelf edge than in coastal areas or on the continental shelf, with several species commonly occurring in multispecific assemblages. In the Menorca Channel (Figs. 2 and 4), these assemblages are dominated by the gorgonian *E. cavolinii*, *Swiftia pallida*, *Viminella flagellum*, and *C. verticillata*, together with lower densities of *P. macrospina*, *Acanthogorgia hirsuta*, *Bebryce mollis*, and *C. rubrum* (Grinyó et al. 2016a). The black corals *A. subpinnata*, *A. dichotoma*, and *L. glaberrima* occur at low density within these assemblages, and vertical rocky cliffs are largely covered by encrusting sponges of the genus *Haliclona* together with fanlike sponges such as *Poecillastra compressa* (Requena and Gili 2014). Among gorgonians, only *B. mollis*, *S. pallida*, *V. flagellum*, and *C. verticillata* were observed to extend their distribution below 200 m depth, in mainly monospecific assemblages with low densities (Grinyó et al. 2016a) (Table 1).

Rich gorgonian and black coral assemblages were also recently reported on pinnacles at 120–170 m depth (Cau et al. 2015) along the South Sardinia continental margin (Fig. 2). The gorgonian *C. verticillata* generally dominates on gently sloping silted rocky bottoms, and *C. rubrum* dominates on the highly sloping rocky walls without sediments with densities up to 64 col. m^{-2}. When the bottom morphological complexity increases and the silt coverage is highly variable, the gorgonian *E. cavolinii*, *A. hirsuta*, and *V. flagellum* accompanied *C. verticillata* (Cau et al. 2015). Similarly to the Menorca Channel (Grinyó et al. 2016a), black corals were less abundant than gorgonians in these assemblages, with *Paranthipates larix*, *A. subpinnata*, *A. dichotoma*, and *L. glaberrima* occurring at low density in the areas more covered by silt (Cau et al. 2015) (Table 1). Conversely, black corals mainly dominate the assemblages occurring on the deeper rocky shoals located on the upper continental slope. Dense forests of the black coral *L. glaberrima* were recently reported at 180–200 m depth in the Carloforte Shoal (Bo et al. 2015), where numerous rocky elevations emerge from a flat muddy bottoms at about 200 m depth on the southwest continental margin of Sardinia (Figs. 2 and 6). The black corals *A. dichotoma*, *P. larix*, and the gorgonians *C. verticillata*, *A. hirsuta*, *E. cavolinii*, and *B. mollis* were also present with low abundances (Bo et al. 2015) (Table 1). Large colonies (~1 m in average height) of the bottle-brush black coral *P. larix* occur in small patches (~4 colonies m^{-2}) on the rocky outcrops of two rocky shoals located southeast of the island of Montecristo (Tuscan Archipelago, Tyrrhenian Sea) between 100 and 200 m depth (Bo et al. 2014a), as well as on the rocky boulders interspersed within the soft sediments of the continental slope of the Pontine Islands (Fig. 2) together with *L. glaberrima* and *A. dichotoma* (Ingrassia et al. 2016) (Table 1).

The muddy bottoms at ~200 m depth surrounding the rocky terraces of the Carloforte Shoal (Figs. 2 and 6) hosted a dense meadow of large colonies of the bamboo coral *Isidella elongata* (Bo et al. 2015) (Table 1), which is the main treelike species in deep bathyal muds (Cartes et al. 2013).

2.4 Assemblages in Offshore Banks and Seamounts

The few Mediterranean banks and seamounts that have been so far explored regarding the benthic communities showed similar dense gorgonian and black coral assemblages in their shallower areas. The Vercelli seamount (Fig. 2) arises from the muddy sea bottom at about 2,000 m, with steep walls characterized by isolated rocky concretions. At 200–250 m depth, walls turn into sand flat bottoms gently sloping up to about 100 m depth, where a rocky peak rises reaching its maximal elevation at ~60 m depth hosting dense coralligenous assemblages dominated by the gorgonians *P. clavata* and *E. cavolinii* (Bo et al. 2011a). Rocky bottoms close to the detritic bottom of this peak (90–100 m depth) present dense assemblages of the gorgonian *E. cavolinii* together with few colonies of *P. clavata*, the sponges *Axinella verrucosa* and *Axinella damicornis*, scattered colonies of the gorgonians *C. verticillata* and *C. rubrum*, the scleractinian *Dendrophyllia cornigera*, and the black coral *A. subpinnata*. In the shallower area (70–90 m depth), the density of *P. clavata* progressively increases toward the surface, whereas that of *E. cavolinii* decreases, and the soft coral *P. spinulosum* was frequently observed (Bo et al. 2011a)

(Table 1). Similarly, the Marco Bank, situated off the northwestern coast of Sicily (Fig. 2), is a rocky shoal arising from a flat bottom around 500 m depth, whether its top remains deeper (~200 m depth) than that of the Vercelli seamount. Elevated rocky bottoms on the upper part of this bank host dense meadows of the black coral *L. glaberrima*, together with scattered colonies of the gorgonians *A. hirsuta* and *V. flagellum*. Conversely, the gently sloping silted rocky bottom of the Marco Bank is dominated by the gorgonian *C. verticillata* with the associated presence of sparse colonies of *V. flagellum*, *A. hirsuta*, and the black coral *A. dichotoma* (Bo et al. 2014b) (Table 1). The black corals *P. larix* and *L. glaberrima* and a few colonies of the gorgonian *C. verticillata* have also been recently reported on the rocky outcrop on the top of the Palmarola seamount (Ingrassia et al. 2016) (Fig. 2). Finally, in the deep waters of the Malta archipelago (Fig. 2), colonies of the black coral *A. subpinnata* were observed at ~100 m depth, and a community mainly composed of a mixed assemblage of *V. flagellum* and *S. pallida* was observed at 150–240 m depth (Giusti et al. 2012). An extended coral forest constituted by the treelike black coral *L. glaberrima* was observed together with colonies of *A. subpinnata*, *V. flagellum*, and *B. mollis* at 250–400 m depth (Deidun et al. 2015) (Table 1).

3 Case Studies in the Mediterranean Sea

3.1 Cap de Creus

The marine area of Cap de Creus is located in the southernmost part of the Gulf of Lions continental margin (Fig. 2). The position of a terrestrial promontory in proximity of a submarine canyon, together with severe atmospheric conditions and the presence of the Northern Current running close to the shelf edge, generate a complex environmental setting, responsible for the distribution of the benthic fauna along the deep sublittoral bottoms and the narrow continental shelf. The prevailing strong bottom currents, produced by the funneling of shelf water through the submarine canyon toward the deep basin, generate areas of low sediment deposition where coarse-grained deposits with a significant gravel fraction are dominant (Gili et al. 2011). The combination of such strong bottom currents, outcropping rocks, and coarse-grained sediments along with nutrient-rich waters derived from river runoff in the gulf, create suitable conditions for gorgonian-dominated assemblages to fully develop. The distribution of gorgonian species is somehow irregular along the coastline, since the northern side accumulates the highest frequency of occurrence of most species, as well as the highest recorded densities (Rossi et al. 2008; Gori et al. 2011). The white gorgonian *E. singularis* is present throughout the whole deep sublittoral area of the cape, but the patches developing on the northern side are not only more frequent but also hold higher number of colonies, reaching local densities of 30 colonies m^{-2} at 50–70 m depth (Fig. 3 and Table 1) (Gori et al. 2011a). The same pattern is observed for the red gorgonian *P. clavata*, although patches of this species are more scatter and with fewer number of colonies, with maximum densities ~7 colonies m^{-2} below 50 m depth (Fig. 3 and Table 1) (Gori et al. 2011a). The case of the soft-bottom gorgonian *Leptogorgia sarmentosa* is thoroughly different, since most colonies are generally found isolated and profoundly scattered along the entire cape, and very rarely it can be found forming high-density spots (Gori et al. 2011a). *C. rubrum* is present in the entire coastal zone, with significant larger colonies at 50–85 m than in shallower areas at 10–50 m depth (Rossi et al. 2008). Below 80 m depth, *E. cavolinii* replaces the sublittoral gorgonian assemblages, becoming the only gorgonian species that develops well-structured communities on the continental shelf (Fig. 3 and Table 1). Its presence is strongly related to outcropping and suboutcropping rocks, as well as coarse-grained sediments, such as large shells. The distribution of *E. cavolinii* is not exclusively restricted to the northern part of the cape, but well-developed patches reaching densities of 25 colonies m^{-2} have only been found on this side (Gili et al. 2011; Dominguez-Carrió 2017). The presence of this species in the flat habitats of the continental shelf produces an imbricate of tridimensional structures that promote the diversity of other benthic species, being of key importance to sustain the structure of this benthic assemblage, since the diversity of the associated fauna depends largely on the gorgonian abundance (Gili et al. 2011; Dominguez-Carrió 2017).

3.2 Menorca Channel

The Menorca Channel, located between the islands of Mallorca and Menorca (Fig. 2), is formed by a shallow (40–110 m depth) continental shelf mostly covered by extensive maërl beds alternated with detritic sediments and scattered coralligenous banks. In this area, both maërl and coralligenous banks can develop down to ~110 m depth thanks to the high light penetration as a consequence of the extreme clearness of the water (Ballesteros 2006). Shallow maërl beds (40–80 m depth) are mainly covered by dense assemblages of the gorgonian *P. macrospina* (Fig. 4 and Table 1) extending over widespread areas of the channel (Grinyó et al. 2016a). Conversely, in deeper maërl beds (80–120 m depth) gorgonian presence is scarce and mainly replaced by massive sponges like *Haliclona elegans* and *Aplysina cavernicola* (Grinyó et al. 2016a). Shallow coralligenous banks (40–70 m depth) resemble those reported in other coastal areas of the western Mediterranean Sea (Ballesteros 2006), being mostly covered by the coastal gorgonian *P. clavata* and *E. singularis* and erect sponges such as *A. polypoides* (Table 1). Conversely deeper coralligenous banks (70–120 m depth) present a wide abundance and diversity of massive sponges, being *Haliclona pachastrelloides, Hamacantha* sp., and *A. cavernicola* among the most abundant. In these deeper banks the erect part of the animal forest is composed by the gorgonian *E. cavolinii* (Grinyó et al. 2016a) (Table 1). However, it is on the rocky substrates on the continental margins (120–150 m depth) that animal forests reach their higher richness in the Menorca Channel. This environment is dominated by multispecific gorgonian assemblages with high densities (Fig. 4 and Table 1). The black coral *A. subpinnata* is also common in this depth range mostly occurring together with *E. cavolinii* and *P. clavata* (Fig. 4), as it has also been seen in other areas of the Mediterranean (Bo et al. 2009). Isolated colonies of the black corals *A. dichotoma* and

L. glaberrima are occasionally seen within these gorgonian assemblages. Several soft coral species are associated to these assemblages erect, together with massive or fanlike sponges such us *Haliclona magna*, *P. compressa*, or *Pachastrella monilifera* (Requena and Gili 2014). The well-preserved status of the animal forests in the Menorca Channel is probably related with the low bottom trawling pressure in the area (Requena and Gili 2014; Grinyó et al. 2016a). This area could indeed represent an example of how Mediterranean continental shelves and margins were before the impacts of decades of fishing activities.

3.3 Gulf of St. Eufemia

The Gulf of St. Eufemia, situated along the Calabrian continental shelf (Fig. 2), is a wide plain where the muddy bottoms, enriched by the continental river flows, gently slope down to 130 m depth just a few miles offshore. The area is also spotted by numerous small rocky elevations and sparse boulders emerging from the soft bottom and is lashed by only a slightly turbulent hydrodynamic regime that enhances the silt deposition on the hard grounds (Bo et al. 2012). These rocky shoals in the middle of the continental shelf host rich animal forests dominated by treelike gorgonians and black corals together with an impressive diversity of massive sponges (Fig. 5) (Bo et al. 2012; Bertolino et al. 2015). Due to the high silting conditions and relatively low hydrodynamic regime, bryozoans, ascidians, and encrusting sponges are, on the contrary, present with a relative low abundance. One of the most striking characteristics of the St. Eufemia Gulf deep shoals system is the high diversity of the dominant species on each shoal. The gorgonians *P. macrospina*, *P. clavata*, *E. cavolinii*, and *C. verticillata* dominate the high canopy part of the forests and may reach very large abundance and size (Fig. 5). The small gorgonian *P. macrospina* probably behaves as an opportunistic species, able to colonize various types of either natural or artificial substrates, whereas the black corals *A. subpinnata*, *A. dichotoma*, and *P. larix* are generally present with lower densities and occasionally very large colonies (Fig. 5) (Bo et al. 2012). The animal forests that develop on these shoals behave like small oases of biodiversity characterized by dense aggregations of organisms concentrated in relatively limited rocky habitats, surrounded by otherwise homogeneous soft bottoms (Bo et al. 2012). The susceptibility of these coral communities to the impacts of local fisheries suggests that the coral oases of the Gulf of St. Eufemia are highly vulnerable habitats.

3.4 Carloforte Shoal

The Carloforte Shoal is located within a complex topographic region of the southwest continental slope of Sardinia (Fig. 2) in which numerous rocky elevations emerge from flat muddy bottoms at about 200 m depth. The shoal is characterized by a series of steep bench terraces continuing into a rocky plateau and surrounded at their base by a belt of mud. This area hosts not only a rich animal forest dominated

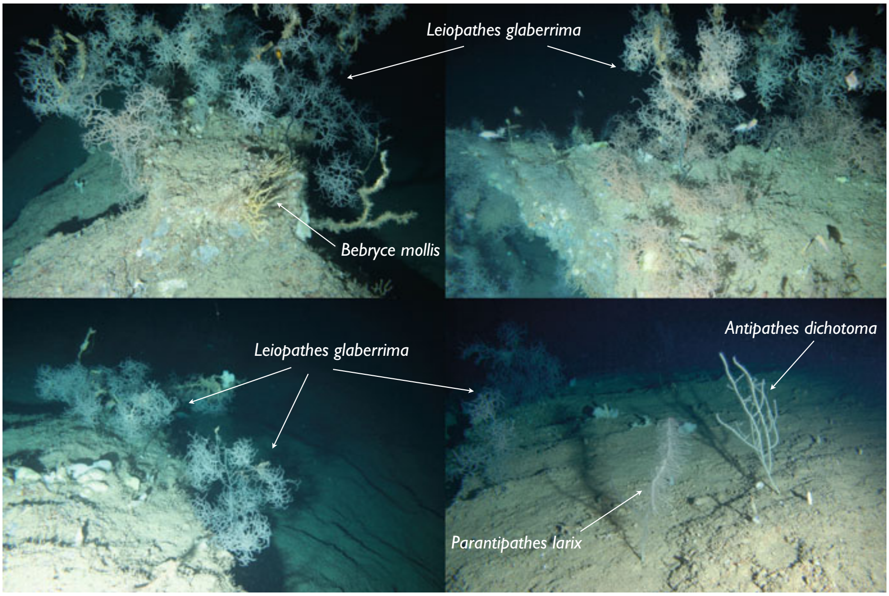

Fig. 6 Carloforte Shoal. Survey "Red Coral" in Sardinia supported by Regione Sardegna, 2013 (200 m depth)

by the black coral *L. glaberrima* with colonies as large as 2 m high (Fig. 6), but also numerous other black coral and gorgonian species occupying the high canopy layer of the forest and the undergrowth between the larger colonies (Bo et al. 2015). The high longevity of *L. glaberrima* (up to 2,000 years old, Bo et al. 2015) suggests a millennial stability of these deep communities in a heavily exploited basin as the Mediterranean Sea. This is also supported by the presence, on the surrounding enclosed muddy bottoms, of large meadows of the bamboo coral *I. elongata*, a long-lived species subjected to a heavy decline due to trawling fishing (Cartes et al. 2013; Bo et al. 2014c, 2015). The rough topography of the region with rocky elevations sufficiently high to avoid trawling and limiting longline fishing may represent a crucial factor in the persistence of the Carloforte Shoal animal forests (Bo et al. 2015). As for the animal forests recently observed in the Menorca Channel, those of Carloforte probably represent pristine communities that survived to hundreds of years of fishing impacts.

4 What Do We Know About the Ecology of These Animal Forests?

The dense assemblages of gorgonians and corals recently described in deep sublittoral areas as well as on the continental shelf and shelf edge of the Mediterranean Sea are marine animal forests with high complexity and diversity (Rossi 2013;

Bo et al. 2015). From a structural point of view, large treelike cnidarians and sponges act as ecosystem engineers by forming complex three-dimensional frameworks that enhance the spatial heterogeneity in the main environmental factors and represent substrates to colonize or temporary refugees for numerous associated species. From a functional point of view, these species determine a significant flow of matter and energy from the pelagic to the benthic system by capturing plankton and particulate organic matter suspended in the water (Gili and Coma 1998). Finally, the presence of these animal forests increases the organic matter and lipid content in the sediments, thus enhancing meiofaunal biodiversity and biomass (Cerrano et al. 2010, 2015).

4.1 Population Structure

In the coastal area of Cap de Creus, most of the deep *E. singularis* populations at 50–60 m depth present population structures dominated by medium-sized colonies and a high presence of large colonies, which contrast with dominance of small colonies in the shallower populations (Fig. 7) (Linares et al. 2008; Gori et al. 2011b). Similarly, larger *C. rubrum* colonies are present in deep sublittoral bottoms at 60–90 m depth in Cap de Creus (Rossi et al. 2008) as well as at 50–130 m depth in the Tuscany Archipelago (Priori et al. 2013) than in shallow populations. Due to the active harvesting of *C. rubrum*, these differences have been mainly related to a differential fishing pressure in shallow and deep habitat. Conversely, in the case of the non-harvested gorgonians, depth-related differences in their population structure have been linked to the dampened variability in environmental conditions and reduction in hydrodynamic forces with increasing depth in the Mediterranean Sea (Garrabou and Harmelin 2002), since strong water movements cause detachment or toppling of large gorgonian colonies (Weinbauer and Velimirov 1996). Indeed, medium-sized colonies also dominate the deep *P. clavata* populations at 70–130 m depth on the continental shelf of the St. Eufemia Gulf (Bo et al. 2012), as well as *V. flagellum* and especially *S. pallida* at 100–190 m depth on the shelf edge of the Menorca Channel (Grinyó et al. 2016a). Deep *E. cavolinii* populations are mainly dominated by medium-sized colonies in the St. Eufemia Gulf (Bo et al. 2012) as well as in Cap de Creus and the Menorca Channel, whereas in these last two areas the presence of some populations dominated by small colonies (Fig. 7) also highlights active recruitment and high suitability of the habitat for the species (Grinyó et al. 2016a; Dominguez-Carrió 2017). In a similar way, small colonies of *C. verticillata* are much more abundant in the Menorca Channel than in the rocky shoals of the St. Eufemia Gulf (Bo et al. 2012; Grinyó et al. 2016a). The dominance of small colonies in the *P. macrospina* populations on the maërl beds on the continental shelf of the Menorca Channel has been related to the structural instability of this substrate, which prevent the colonies to grow larger, as they can conversely do on the rocky bottom of the shelf edge (Grinyó et al. 2016a). The black corals

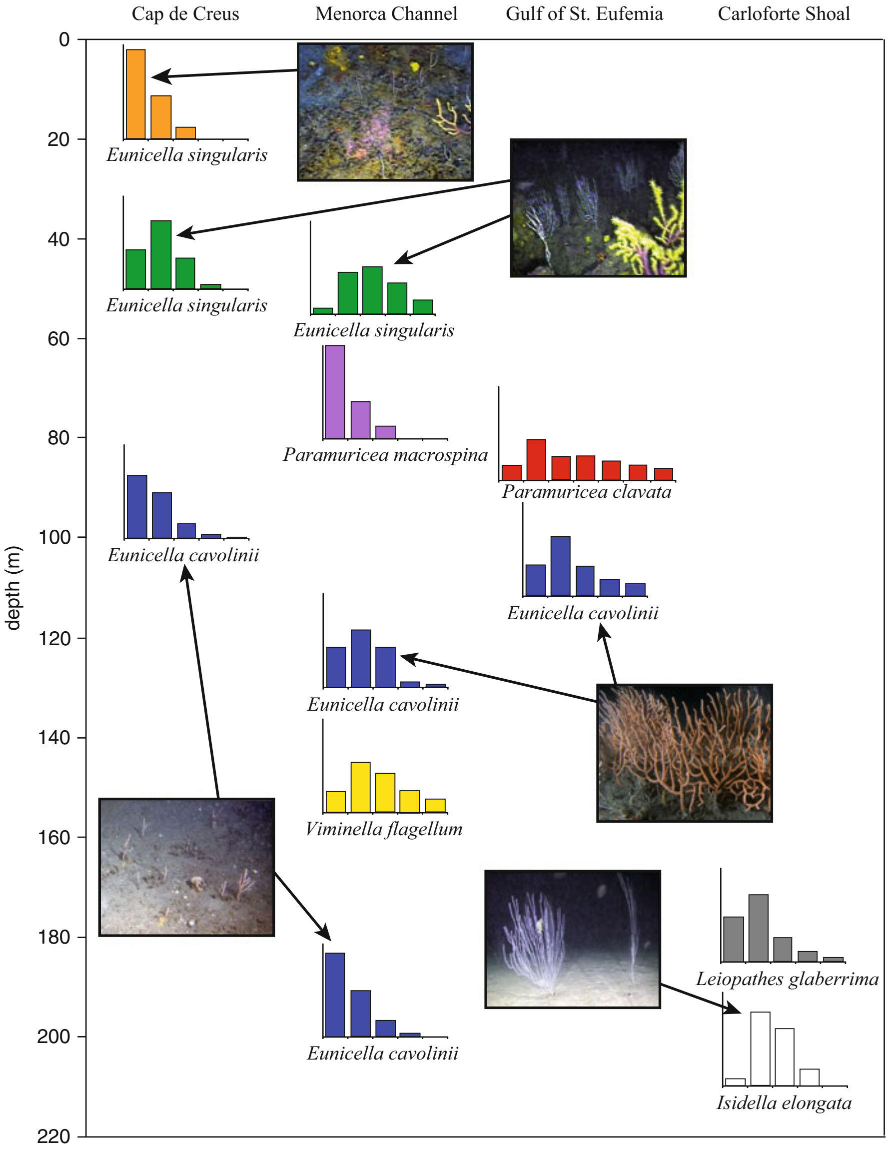

Fig. 7 Size structure of gorgonian and black coral populations in the case study locations; histograms represent the % distribution of colony size in increasing size-classes; photos show specific dominance of small- or medium-sized colonies (data from Gori et al. 2012*;* Bo et al. 2012, 2015; Grinyó et al. 2016a; Dominguez-Carrió unpublished data)

L. glaberrima in the Carloforte Shoal and *P. larix* in the Montecristo shoals also present populations dominated by medium-sized colonies (Bo et al. 2014a, 2015), as well as the bamboo coral *I. elongata* in the pristine population of the Carloforte Shoal (Fig. 7) (Bo et al. 2015).

4.2 Trophic Ecology

Increasing stability of environmental conditions with depth is also reflected in a more constant food supply for deep sublittoral colonies of the gorgonian *E. singularis* at 60 m depth (Gori et al. 2012), as well as for *P. macrospina* and *E. cavolinii* colonies on the continental shelf (Grinyó et al. 2016b; Dominguez-Carrió and Gori unpublished data). Indeed, deep coral and gorgonian populations are not affected by the reduced food availability induced in shallow waters by the water column stratification during the Mediterranean summer (Coma et al. 2000). At the same time, stable hydrodynamic conditions dominated by unidirectional currents at deeper depth may sustain a more continuous source of food particles sinking from the surface layer or resuspended from the bottom. Lipid content and C/N composition of tissue are more constant all along the year in *E. singularis* colonies at 60 m depth, whereas a clear seasonality occurs in colonies at 20 m depth (Gori et al. 2012). Similarly, lipid content in gorgonian tissue showed no significant seasonality in *P. macrospina* and *E. cavolinii* on the continental shelf (Grinyó et al. 2016b; Dominguez-Carrió unpublished data). Stable isotope composition shows a summer contribution of symbiotic algae for the C input in the shallow colonies of *E. singularis* (Fig. 8). Even if this contribution is relatively small compared to shallower Mediterranean coral species (Ferrier-Pagès et al. 2011), it clearly differentiates the δ^{13}C isotopic signature between shallow and deeper sublittoral colonies (Gori et al. 2012). On the continental shelf, the δ^{13}C signature reflects a similar heterotrophic diet in *P. macrospina* at 70 m depth on the Menorca Channel (Grinyó et al. 2016b) and an even more negative signature in the *E. cavolinii* from the Cap de Creus continental shelf (Fig. 8) (Gori unpublished data). A constant δ^{15}N isotopic signature, characteristic of suspension feeders feeding on zooplankton and

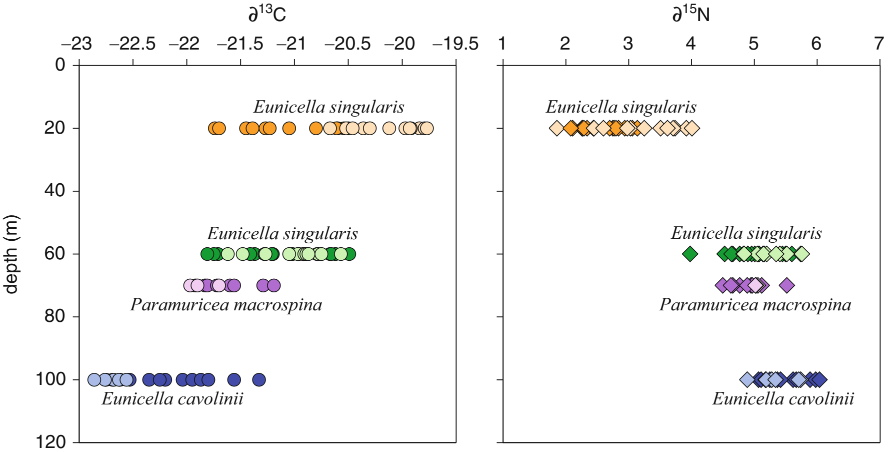

Fig. 8 Stable isotope (δ^{13}C and δ^{15}N) composition of gorgonian tissue in the Cap de Creus according to depth (data from Gori et al. 2012 and unpublished data; Grinyó et al. 2016b)

particulate organic matter, is basically shared by the deep colonies of the three gorgonian species (Grinyó et al. 2016b; Gori et al. 2012 and unpublished data), contrasting with the uptake of inorganic N mediated by the symbiotic algae in the shallow *E. singularis* colonies (Fig. 8).

4.3 Sexual Reproduction

Deep Mediterranean gorgonian species studied so far showed a single reproductive season during summer, similarly to shallow species. The deep sublittoral colonies of *E. singularis* at 60 m depth in Cap de Creus were found to reproduce almost simultaneously with the shallower ones at 20 m depth. However, the release of larvae from the female colonies was more prolonged in the shallow (June and July) than in the deep colonies (June) (Gori et al. 2012). Deeper on the continental shelf at 100 m depth, *E. cavolinii* was also observed to release larvae in July in Cap de Creus (Dominguez-Carrió unpublished data), whereas *P. macrospina* spawn gametes between August and September at 70 m depth in the Menorca Channel (Grinyó et al. 2016b). Total volume of oocytes produced per polyp in *E. singularis* at 60 m depth was slightly minor than at 20 m depth (Gori et al. 2012). Conversely, total volume of oocytes significantly increased in *P. macrospina* and *E. cavolinii* on the continental shelf. This increase was due to the production of a larger number of oocytes in *P. macrospina* (Grinyó et al. 2016b), whereas few but very large oocytes were produced by *E. cavolinii* (Dominguez-Carrió unpublished data).

4.4 Associated Fauna

The spatial heterogeneity generated by the complex three-dimensional framework formed by gorgonians, black corals, and sponges provides suitable habitat for hundreds of associated species. The main environmental features, such as current flow, food availability, and sediment resuspension, vary widely within these complex structures, and this heterogeneity increases the abundance and functional diversity of both the nektonic and benthonic associated fauna.

Species associated with living portions of corals are relatively uncommon due to the fact that corals have nematocysts or produce great quantities of mucus (in the case of black corals) that discourages potential stable associations (Bo et al. 2015). Among the most interesting associations, those with hydroids are especially remarkable, for instance, *Sertularella crassicaulis* on *E. cavolinii* or the recently described *Ectopleura* sp., a solitary hydroid living in apparently neutral association with numerous deep gorgonian species as well as with the black coral *A. subpinnata* (Bo et al. 2011c). This hydroid settles on the branches of the coral and allows the host's coenenchyme to envelope its perisarc resulting perfectly mimicked within the coral. Close associations are reported also for ophiuroids and crabs (as *Anamathia rissoana*) living on the ramifications of gorgonians and black corals (Bo et al. 2014a, 2015). Specialized predators such as ovulid gastropods are often found in almost exclusive association with the corals they prey, such as *Neosimnia* spp. on *E. cavolinii* and *C. rubrum* or the recently described association of *Aperiovula juanjosensii* with several deep gorgonian species (Bo et al. 2012). Similarly, the stylasterid coral *E. aspera* shows a peculiar association with the gastropod *Pedicularia sicula* (Salvati et al. 2010). The carbonate, gorgonin, and chitin skeletons of corals and gorgonians represent a suitable substrate for several organisms, in particular hydroids, sponges, bryozoans, anemones, zoanthids, soft corals, scleractinians, stalked barnacles, bivalves, ascidians, and polychaetes living on the dead portions of the colonies (Bo et al. 2009, 2012, 2015; Deidun et al. 2015). Occasionally, ophiuroids, crinoids, gastropods, bivalves, and small anthozoans also colonize the naked branchlets (Bo et al. 2015). Many fish species find a temporary refuge among coral branches of the deep Mediterranean animal forests, being the most common *Anthias anthias*, *Callanthias ruber*, *Macroramphosus scolopax*, *Zeus faber*, *Lappanella fasciata*, *Helicolenus dactylopterus*, *Trachurus* sp., and *Benthocometes robustus*; the latter being one of the most characteristic fish species in black coral forests. Also the catshark *Scyliorhinus canicula* is commonly observed moving around in both shallow and deepwater gorgonian and coral assemblages (Bo et al. 2015). The coral assemblages developing on hard bottoms typically show a strong relationship with the presence of fish (Mytilineou et al. 2014). Conversely, the relationship among the presence of fish and the occurrence of soft bottom coral assemblages seems to be more occasional (Cartes et al. 2013). The coral treelike canopy represents an optimal substrate to lay eggs for catshark and ray species. This can occur only occasionally or, as in the case of the Carloforte Shoal, be widely extended to the entire coral assemblage such that the site may turn into a nursery area. It therefore becomes evident the fragile but crucial relationship among the persistence of the coral assemblages and the survivorship of local populations of catsharks (Bo et al. 2015).

5 Treats

5.1 Fishing Impact

The gorgonians and corals forming the Mediterranean animal forests from deep coastal areas, continental shelf, shelf edge, and slope are among the most abundant and frequent species in fishing bycatch (Cartes et al. 2013; Mytilineou et al. 2014; Deidun et al. 2015). This is not surprising considering that many fish of commercial interest are often associated to these animal forests, which are consequently largely exploited by professional and recreational fishermen. All fishing activities operated with demersal gears impact the megabenthic communities and particularly the large treelike corals and sponges which are particularly vulnerable due to their shape and size, as they remain easily entangled in nets and longlines (Fig. 9). The catchability of a coral depends also on the type of gear, the nature of the coral skeleton, and its mechanical properties as well as on its type of aggregation on the sea bottom (Mytilineou et al. 2014; Bo et al. 2014c). Fishing impacts can directly remove the

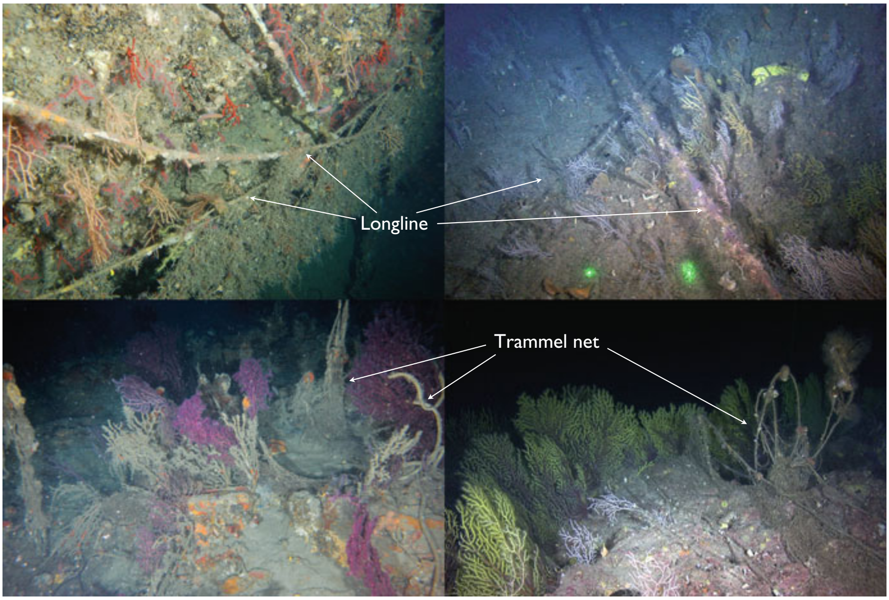

Fig. 9 Fishing impacts on gorgonian assemblages; (*up left*) longlines on *Corallium rubrum* and *Eunicella cavolini* (survey “Red Coral” financed by Ministero dell’Ambiente, 2010–2012, Ischia 80 m depth) and (*up right*) *Paramuricea clavata* and *E. cavolinii* (surveys “Life Indemares” financed by European Union, 2010–2012, Cap de Formentor 120 m depth); (*down left*) trammel net on *Paramuricea clavata* (survey “Marine Strategy” financed by ARPA Liguria, 2015, Vado Ligure 60 m depth) and (*down right*) *Paramuricea clavata* and *E. cavolinii* (surveys “Life Indemares” financed by European Union, 2010–2012, Cap de Formentor 120 m depth)

organisms (especially bottom trawling), cause partial damage (especially trammel net and longline fishing) (Fig. 9), as well as induce indirect consequence, such as epibionts overgrowing or chocking and burial caused by the resuspension of nearby sediments (due to bottom trawling) (Bo et al. 2014c). These impacts can have far-reaching and long-lasting effects for deep-sea ecosystems dominated by longevous, slow-growing species with low recovery ability due to the natural fragmentation of the populations and the limited larval dispersion and population connectivity (Bo et al. 2015).

5.2 Deep Mass Mortalities

Mediterranean mass mortalities of shallow gorgonians and sponges have severely increased in frequency and intensity over the past 30–40 years (Garrabou et al. 2009). These episodes are considered related to summer thermal anomalies in shallow waters (from the surface to 40–50 m depth) associated to global warming, sometimes enhancing bacterial infections. Conversely, very few data are available for deep gorgonian, coral, and sponge populations. Rivoire (1991) described a gorgonian and red coral mortality occurred off the Provence coastline at 80–160 m depth, tentatively attributed to polluted waters driven by dominant currents. Recently, an extensive mass mortality of *C. rubrum* at 90 m depth in an area not subjected to strong urban pollution was described in the Gulf of Salerno (Bavestrello et al. 2014). The occurrence of entire dead colonies without evident ruptures of branches excludes mechanical injuries, such as those produced by fishing activities. Neither can the mortality simply be attributed to pollution or thermal anomalies related to global changes nor due to the offshore location and depth of the site. One of the suggested hypotheses is that costal debris flows could produce gravity flows and submarine landslides with a consequent unusual drop of the summer thermocline. However, an alternative hypothesis takes in consideration sudden warmwater emissions, in an area characterized by important volcanic activities. Similar events are probably at the origin of the huge subfossil Sciacca red coral banks discovered in 1875 in the Sicily Channel. The typical orange color of the Sciacca coral would indeed be a consequence of prolonged exposure of the buried skeletons to hydrothermal emissions. Mass mortalities of the red coral populations probably occurred periodically for thousands of years giving rise to the accumulation of skeletal structures on the sea bottoms (Bavestrello et al. 2014).

5.3 Other Sources of Impact

Beside fishing activities and natural catastrophic events, it is possible to identify other sources of impact, mainly man driven, for the animal forests thriving on deep coastal areas and the continental shelf. As already suggested, there are some evidences that support the occurrence of deep mass mortalities potentially related to pollution (Rivoire 1991). No specific studies have been carried out on the effects of sewage discharges and river outflows, whether it is plausible that they may act on the most coastal assemblages. Moreover, seafloor drilling activities for oil exploration or mining are greatly threatening the integrity of several deep benthic communities (Aguilar 2004).

6 Future Research and Actions

Coral aggregations, internationally recognized as “coral gardens,” are considered as vulnerable marine ecosystems (VMEs), a term coined by UN which identifies species, communities, or habitats vulnerable to fishing activity. Based on the video footage gathered by means of ROV studies performed in the recent years in the Mediterranean Sea, there is indeed a growing concern that completely pristine deep animal forests are nowadays an exception due to fortuitous environmental constraints or local low industrial fishing efforts and that many of them are becoming extinct in the areas strongly exploited by fishermen (Bo et al. 2014c, 2015; Grinyó et al. 2016a). Studies are providing evidence that these deep animal forests are probably a small portion of the original natural ones (Bo et al. 2014c). The information supplied by recent studies focused on these assemblages has conducted to the inclusion of several gorgonian and coral species in the Mediterranean IUCN Red List and the Barcelona Convention list. Further efforts should be targeted on the identification of the occurrence and distribution of deep animal forests, and conservation and management measures should be adopted to preserve these assemblages, including offshore areas. An ecosystem-based fishery management of deep-sea ecosystems based on fishing restrictions, as recently carried out in the Gulf of Lions (Fabri et al. 2014), is fundamental for the conservation of deep animal forests. Self-regulations of the fishing grounds, as operated in the Menorca Channel by a small artisanal fishing fleet (Requena and Gili 2014), may also be useful tools to preserve these ecosystems. This approach must take into account the complex sociocultural background of the recreational and professional Mediterranean fishermen and the economical and physical constraints in monitoring and controlling offshore areas often localized in international waters (Bo et al. 2014c).

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Global Biodiversity in Cold-Water Coral Reef Ecosystems

8

Lea-Anne Henry and J. Murray Roberts

Abstract

Over half of all scleractinian coral species inhabit ocean depths greater than 50 m, some of which are capable of constructing reefs tens of kilometers long and hundreds of meters high. The biodiversity of life found on these cold-water coral reefs is astounding yet remarkable since, in contrast to the photic and mesophotic zones, so few coral species actually create a framework matrix at these depths. In light of rapid climate change and unprecedented rates of anthropogenic disturbance, it is urgent we understand how biodiversity in the depths of our oceans is coupled to the persistence of these habitats. We provide a synthetic overview of animal biodiversity associated with major reef framework-forming species, discussing this with respect to global trends in species diversity, composition, and regional species pools, large knowledge gaps, and also the frontiers in technology that cold-water coral science is adopting to help address these gaps.

Keywords

Cold-water coral reefs • Sharks • Fauna • Species diversity • Community assembly • Biogeography • Taxonomy • Landers • Underwater observatories • Robotics • Genomics

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Contents

1 Global Distribution of Cold-Water Coral Reefs

1.1 Introduction

Earth's vast deep oceans covering over two thirds of the planet are home to aphotic cold-water coral (CWC) reef ecosystems. Although less familiar to the public than shallow warm-water corals, CWC reefs are not only more globally distributed across wider latitudinal ranges than their tropical counterparts but they also harbor an equally remarkable level of biological diversity as that found in tropical reefs (see ► Chap. 2, "Caribbean Coral Reefs: Past, Present, and Insights into the Future" by Jordán-Dahlgren and Reyes-Bonilla in this volume). For example, 35 species of benthic Hydrozoa (hydroids) were recorded from CWC reefs in the southeastern USA, compared to 43 from tropical reefs off Belize and only 11 from Bermuda coral reefs (Henry et al. 2008). From bacteria to fungi, single-celled animals to large vertebrates such as sharks, this remarkable variety of life is the product of the sheer physical complexity of CWC reefs, their underlying seafloor topography, and interactions with water currents. These physical mechanisms supply high quality food to reef organisms, fuel the food chain, and promote species interactions, all of which contribute to the globally rich diversity harbored by these deep ecosystems.

At last count, there are overall 711 known recent azooxanthellate scleractinian species but only six major reef framework-building species (Roberts et al. 2009;

Roberts and Cairns 2014). These include: *Oculina varicosa*, *Madrepora oculata*, *Lophelia pertusa*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia profunda,* and *Bathelia candida. Enallopsammia rostrata* can also occur in very high densities. Although most of these reef builders are globally cosmopolitan, each occurs within its own particular environmental niche defined by the coral's biological, physical, and geochemical requirements (Flögel et al. 2014).

Over several millennia, coral colonization, recruitment, and growth processes are shaped by successional geochemical cycles of cementing, sediment baffling, and erosion. These processes can engineer giant coral carbonate mounds hundreds of meters high, structures which have in some cases persisted for over three million years (Raddatz et al. 2011).

Their habitat heterogeneity and associated high biological diversity, including valuable fish stocks, have attracted large-scale exploration and mapping initiatives, primarily by petroleum and fishing industries, governments, and academia, to characterize coral carbonate mound geology and biology. This has led to many new insights into how CWC reefs create and maintain species (α) and community (β) diversity, but also how they contribute to the wider regional biodiversity (γ) in our seas. Several paradigms of CWC reef biodiversity emerge from studies around the globe but many more knowledge gaps remain. While the most serious gaps can be addressed simply by continued exploration, technological frontiers can overcome some limitations to help acknowledge what stands to be gained by halting the global degradation of CWC reefs and conserving these fragile ecosystems.

2 Biodiversity Associated with CWC Reefs

Beyond the primary producers of the photic zone, the richness and functional diversity of species that inhabit CWC reefs clearly demonstrate that these ecosystems, and the complex substrata they provide, support a great diversity of trophic levels in the benthic food web (see ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems" by Buhl-Mortensen et al. this volume) with important roles in regional biogeochemical cycles (van Oevelen et al. 2009; Cathalot et al. 2015; Rovelli et al. 2015). Based on the ways in which this fauna use the coral habitat to live and feed, this functional diversity can be separated into categories that may overlap in the types of species they attract. The smaller, almost microscopic, biofilm organisms (see Sect. 2.1) are attracted to the bacterial and fungal mats along with particles that have encrusted coral surfaces. Fauna also include grazers, deposit feeders, and small benthic predators that find niches among reef polyps, branches, and other microhabitats (see Sect. 2.2). Hard larger coral surfaces are colonized by a diverse range of larger sessile suspension and filter-feeding epifauna (see Sect. 2.3). Benthopelagic and benthic demersal fish communities (see Sect. 2.4) also visit the reefs to forage, find refuge, and breed.

2.1 Fauna Associated with Coral Biofilm, Including Meiofauna

Small sponges, calcareous tube-building polychaetes, hydroids, and bryozoans encrust areas between coral branches and polyps and host a mixed assemblage of meiofaunal and smaller macrobenthic fauna including harpacticoid copepods, epifaunal nematodes, polychaetes, and platyhelminthes. The fauna associated with coral biofilm forms a very mixed and diverse animal community. In areas where CWC reef meiofauna and macrofaunal studies have been particularly intense such as in the northeast Atlantic and Mediterranean, species richness and changes in species composition over space (species turnover) at bathyal depths are in large part due to sediment accumulation around the corals themselves or just between coral polyps and branches that attracts a diverse mixture of both epifaunal and infaunal taxa including meiofauna (Raes and Vanreusel 2006; Bongiorni et al. 2010; Gheerardyn et al. 2010). Coral biofilm associated communities go on to support other CWC reef organisms, principally as food sources for brachyuran crabs, gastropods, polychaetes, urchins and seastars, and a variety of omnivores and predators (van Oevelen et al. 2009) including those that shelter amongst the biofilm-associated community (Fig. 1a).

2.2 Macrobenthic Grazers, Deposit Feeders, and Predators

The sediment-filled interstitial cavities found between coral polyps and branches also provide niches for a variety of larger sessile and mobile macrofauna that graze, settle between, or hunt for prey. These include bioeroding encrusting fauna such as bryozoans and sponges that excavate large cavities in the skeletons of live and recently dead coral in both deep-sea and coastal inshore CWC reefs (Beuck et al. 2007; van Soest and Beglinger 2009). The sponge family Clionaidae is particularly well known for the bioeroding capabilities of its constituent species on CWC reefs. Most of these species are endolithic living almost entirely within the coral skeleton, or grow to some extent outside the skeleton as well. The roles that CWC reef bioeroders play in these ecosystems cannot be underestimated, with growing concerns about ocean acidification increasing chemical bioerosion resulting in the coral reef framework essentially being dissolved before it has chance to build up into a geologically persistent reef (Wisshak et al. 2014). Deposit-feeders are most diverse in the coral rubble zone (Mortensen and Fosså 2006) or in adjacent noncoral areas (Henry and Roberts 2007). However, deposit-feeding nematodes can inhabit sediments in living coral habitat, with predominantly selective deposit feeders being present such as bacterivorous nematodes, but also with some nonselective deposit-feeding taxa (Bongiorni et al. 2010).

The abundance and biologically rich variety of small mobile prey among coral framework and rubble also make these habitats an excellent hunting ground for benthic predators such as carnivorous solenogaster molluscs, polychaetes (Fig. 1b), crustaceans, and echinoids, which themselves play hosts for other fauna such as

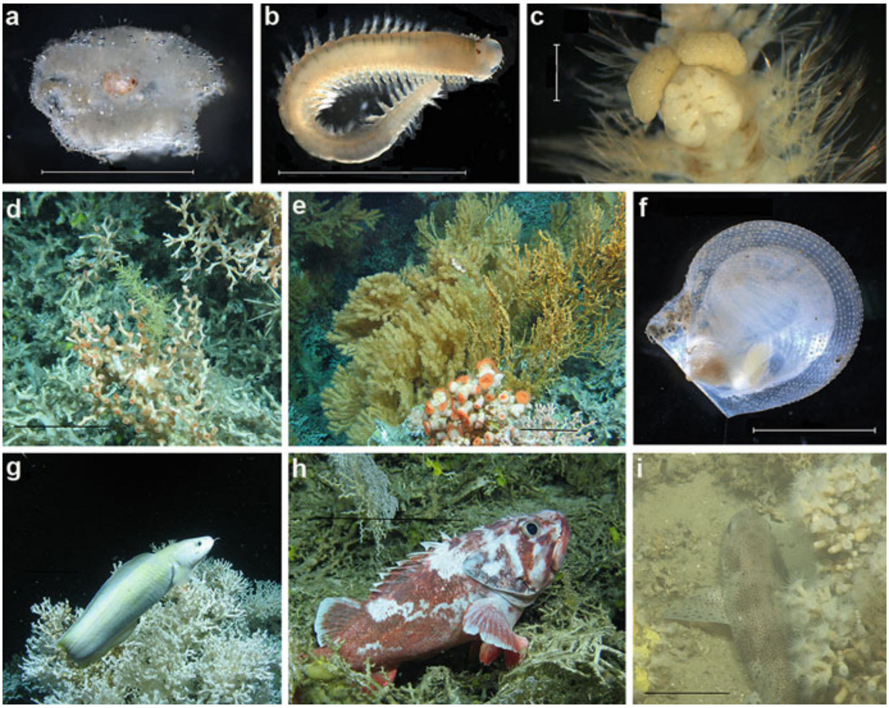

Fig. 1 Animal biodiversity associated with cold-water coral reefs is very high, as demonstrated by these images from northeast Atlantic *Lophelia pertusa* and *Madrepora oculata* reefs. The fauna associated with coral biofilm includes encrusting sponges in which the isopod *Caecognathia abyssorum* seeks refuge (**a**, scale bar 5 mm, water depth 857 m). Small carnivorous invertebrates like the polychaete *Nereimyra punctata* hunt among the coral biofilm and reef frameworks (**b**, scale bar 5 mm, water depth 857 m), while parasitic copepods find a host on a polynoid polychaete (**c**, scale bar 500 μm, water depth 857). Sessile suspension and filter-feeding epifauna like hydroids (**d**, scale bar 10 cm), gorgonian octocorals, and zoanthids (**e**, scale bar 10 cm, water depth approximately 700 m) and the bivalve *Delectopecten vitreus* (**f**, scale bar 5 mm, water depth 857 m) densely colonize the reef framework. Demersal fish such as the tusk *Brosme brosme* (**g**, scale bar 10 cm, water depth approximately 700 m) and the blackbelly rosefish *Helicolenus dactylopterus* (**h**, scale bar 10 cm, water depth approximately 700 m) hunt and rest among living and dead reef framework, as does the catshark *Scyliorhinus canicula* (**i**, scale bar 10 cm, water depth approximately 140 m) (All images taken by the authors; images **d**, **e**, **g**, **h**, and **i** were taken during the 2012 Changing Ocean Expedition (RRS *James Cook* cruise 073)

parasitic copepods (Fig. 1c). Urchins are known to aggregate in large numbers on CWC reefs to ingest live corals and coral skeleton and even shift their habitat use to the interior or base of coral skeletons in the presence of predators such as fish and decapods (Stevenson et al. 2014). Interestingly, CWC reefs in the southwest Atlantic have also been found to support a highly specialized group of carnivorous cladorhizid sponges (Lopes and Hajdu 2014). Their "sit and wait" approach to predation is associated with an entire loss of the classic sponge body plan of an aquiferous system or choanocyte chamber, and instead these sponges feed on crustacean prey.

2.3 Suspension and Filter Feeders

Some of the most biologically diverse components of the CWC reef ecosystem to colonize the stable reef framework are the suspension and filter-feeding fauna (Henry and Roberts 2007), typically comprised of sponges, cnidarians (hydroids and hydrocorals as in Fig. 1d, scleractinians, antipatharians, octocorals, and zoanthids as in Fig. 1e, anemones, benthic scyphozoans), bivalves (Fig. 1f), brachiopods, polychaetes, bivalves, bryozoans, crinoids, and tunicates.

The occurrence of these taxa in CWC reefs is directly related to the quality, availability, and retention capacity of food particles delivered to the reef by local hydrodynamics, without which, these sessile benthic animals could not survive. Local hydrodynamics are modified by seabed topography, an interaction that helps determine how suspension and filter-feeding communities are distributed over the coral reef, depending on which species can inhabit, e.g., stronger currents near the top of a mound versus slower currents in a seabed depression (Henry et al. 2013a).

2.4 Demersal Fish Communities

Demersal fishes most commonly observed on CWC reefs can be broadly divided into those with a very close association with the seafloor (benthic demersal) and those that swim more freely over the ocean floor (benthopelagic). Associations between CWC reefs and demersal fish are highly dependent on the spatial scale of the habitat, as well as fish species' niches and ontogeny (Biber et al. 2013; Kutti et al. 2014). This has made it difficult to discern clear patterns, but there is evidence that many teleosts and elasmobranchs appear to associate with reef habitats in different capacities such as foraging, finding refuge, and reproducing, and there is evidence for strong temporal, possibly seasonal, aspects to CWC reef habitat use by fish (Lavaleye et al. 2015; Ross et al. 2015). The overall result is that a number of fish species and increased fish densities tend to co-occur in areas with higher coverage of corals and biogenic substrata (Purser et al. 2013b). However, there may be local and regional differences in the ways in which fish make these associations. For example, although fish abundance was higher in coral areas than noncoral areas in the Arctic, Atlantic, and in the Mediterranean Sea, trends in fish diversity differed across areas, with only specific fish species being associated with corals in the Mediterranean and Arctic as opposed to the Atlantic where overall fish diversity was higher (Linley et al. 2015).

For example, commercially important demersal stocks of ling, tusk, and redfish (*Molva molva*, *Brosme brosme* seen in Fig. 1g, and *Sebastes marinus*, respectively) in the northeast Atlantic are all found in greater abundance in CWC reef habitats, with ling and tusk likely foraging on enhanced densities of benthopelagic fish and benthic crustaceans attracted to these structurally complex habitats (Husebø et al. 2002). For example, the average catch of redfish (*Sebastes marinus*) off southwestern Norway was 5.7 fish per long-line in coral habitats versus 0.8 fish in areas without corals (Husebø et al. 2002). Similarly, commercially important demersal blackspot seabream (*Pagellus bogaraveo*) and wreckfish (*Polyprion americanus*) in the Mediterranean Sea, as well as bycatch species such as conger eel (*Conger conger*) and blackbelly rosefish (*Helicolenus dactylopterus*, Fig. 1h), are all found in more abundance in CWC habitats. For example, the average number of blackbelly rosefish found in coral megahabitats of the Santa Maria di Leuca province in the Mediterranean Sea was 23.11 versus only 10.44 in noncoral habitats (D'Onghia et al. 2012). These positive associations with CWC reef habitats seemed to relate to enhanced foraging opportunities associated with the reefs (D'Onghia et al. 2010, 2012).

Juvenile size classes of many fish are also more abundant on CWC reefs than they are elsewhere, including the blackmouth catshark (*Galeus melastomus*) and the velvetbelly lantern shark *Etmopterus spinax* (D'Onghia et al. 2010, 2012). Increased numbers of conger eels (*Conger conger* and *Conger oceanicus*) that can be observed burrowing near the bases of coral reef framework in these habitats suggest a role for the coral ecosystems as refuges or resting areas as observed in the lesser-spotted catshark (*Scyliorhinus canicula*) among the reefs as seen in Fig. 1i (Henry et al. 2013b).

It is also emerging that globally, CWC reefs provide spawning habitat for oviparous (egg-laying) fish including deep-sea demersal elasmobranchs such as the blackmouth catshark (*Galeus melastomus*) and the Pluto skate (Quattrini et al. 2009; Henry et al. 2013b), among others being reported during exploratory ROV surveys (Henry et al. 2014b).

3 Emerging Ecological Paradigms

CWC reefs create and maintain very high levels of biodiversity compared to the surrounding seafloor (Henry and Roberts 2007). The occurrence of the CWCs themselves is a product of the right combination of oceanography (broadly referring to water mass structure and properties), hydrography (broadly referring to ocean mixing/stratification processes, ocean fronts, and hydrographic features such as internal tides, Taylor columns, and domes), geology (sedimentology and geomorphic features such as ridges, canyons, seamounts), and bathymetry that provide ideal conditions for the major framework-forming species.

These interactions and the sheer physical complexity of reef framework-forming corals allow CWC reefs to support the broad range of animals outlined in Section 2, as well as very high numbers of species per unit volume. Additionally, the life cycle of the coral structure itself from the very first colonizing polyp through to coral colony death actually creates a distinct zonation of CWC macrohabitats, similar to the vertical zonation patterns observed in other habitats such as intertidal rocky shores and shallow-water coral reefs in the photic zone. CWC macrohabitats typically grade from a background of primarily small coral sediments and fragments to larger pieces of coral rubble, followed by thick sediment-clogged dead coral matrix to a mixture of dead and live corals, which are then topped at the surface by living corals provided that recruitment of new corals continues.

Clear zonation patterns in the numbers of species and how these are equitably distributed (α diversity) across the different macrohabitat types are frequently evident, as are trends in the species composition (β diversity). The concepts of CWC reefs as biodiversity as well as nutrient cycling hotpots are rapidly emerging, effects that will have larger scale implications for regional (γ diversity) patterns in the deep sea.

3.1 Species (α) Diversity

A main driver of species diversity on CWC reefs is simply the physical zonation and stability of the different reef macrohabitats. This typically results in enhanced species richness on CWC reefs than off, a paradigm observed on the *Solenosmilia variabilis* reefs of the southwest Pacific (Thresher et al. 2014) and the *Lophelia pertusa*/*Madrepora oculata* reefs northeast Atlantic (Henry and Roberts 2007). Larger pieces of dead coral that no longer contain any live polyp-clearing parts are likely to offer reef fauna, particularly smaller ones, a high variety of niches with high physical stability. In fact, one of the most speciose CWC macrohabitats is the coral degradation zone, where larger fragments of dead coral and rubble are most abundant and living coral cover is sparse (Mortensen and Fosså 2006; Raes and Vanreusel 2006). This is in contrast to large but living sections of reef framework, which tend to be colonized (if at all) by specialists such as the excavating foraminifera *Hyrrokin sarcophaga* and the predatory polychaete *Eunice norvegica* (Mortensen and Fosså 2006) in the case of Norwegian *Lophelia* reefs, and the possible obligate specialist snail *Coralliophila* sp. in the case of *Lophelia* reefs in the Gulf of Mexico (Cordes et al. 2008). Smaller, finer-grained pieces of coral rubble and background sediments tend to have lowest species diversity (Mortensen and Fosså 2006). These observations suggest that substratum stability and low risk of mortality from coral polyps offer reef fauna the best chances at species coexistence.

Another main driver of α diversity in CWC reefs is the combined effects of oceanography and hydrography. Although not as well studied as effects of macrohabitat, CWC reef biodiversity appears to be higher in zones where two water masses interface (Henry et al. 2014b). This could occur either because fauna from two biogeographically distinct regions can now coexist, and/or because there may be enhanced tidal mixing associated with this stratification and internal tides, a biophysical effect that would result in increased particle delivery to reef fauna (Henry et al. 2014b).

3.2 Community (β) Diversity

Each CWC reef macrohabitat supports its own biological community, which in some cases, substantially differs from other macrohabitats and the adjacent surrounding seafloor habitats (Henry and Roberts 2007). This zonation is a product of gradients in substrata ranging from the surfaces of living and dead corals to the flatter aprons of smaller finer-grained pieces of dead coral rubble and underlying sediments. Zonation in these habitats is also a product of the fine and local scale differences in the hydrography. When the depth gradient is large enough, it can also be due to differences in the chemical oceanography of the waters bathing the corals (Thresher et al. 2014; Henry et al. 2014b), which can even produce zonation in the reef-building coral species themselves (Thresher et al. 2014). Importantly and less often considered are the effects of species ecology (Henry and Roberts 2007; Henry et al. 2013a), including life history traits, dispersal potential, environmental niches, and interspecific interactions including predation and competition.

Zonation also occurs across different CWC reef-building species in the same area. For example, the CWC reef megafaunal communities off southern Tasmania differed between live *Enallopsammia* corals (high megafaunal species richness, but low abundance), the live *Solenosmilia* corals (high richness, and high abundance), and the dead *Solenosmilia* and rock/rubble zone (low richness, with scattered megabenthos and encrusting fauna).

CWC reef zonation across macrohabitats is well documented. Globally, there are fewer species associated with macrohabitats having 100% live coral cover, with the exception of large mobile decapods, some echinoids, crinoids, and demersal fish, a relationship that is often seen in shallow water coral reefs of the photic zone. This probably relates to the fact that these kinds of large stable habitat offer these specific animals opportunities to rest, forage, find refuge, and hunt.

The most biologically diverse part of the CWC reef is actually the coral degradation zone, which grades from the dead/live coral framework (Fig. 2) to the coral rubble apron, a transition that can be quite distinct (Fig. 3). Here, many sessile epifaunal species that need strong currents and stable substratum may coexist, and often their reproductive and dispersal habits are such that very dense aggregations of these animals form extensive patches of, e.g., some sponges, zoanthids, cup corals, hydroids, brachiopods, bryozoans, and large sabellid and serpulid polychaetes (Henry et al. 2013a). Living amongst these will be specialist predators such as nudibranchs, hesionid polychaetes, caprellid amphipods, and carnivorous sponges, capable of feeding on the rich sessile epifauna and benthopelagic zooplankton. Mobile megafauna also inhabit this zone, such as the decapod crabs *Munidopsis* spp. and *Eumida picta* in the case of *Lophelia* reefs in the Gulf of Mexico (Lessard-Pilon et al. 2010). There is also a rich endofauna living inside dead coral skeletons including excavating macroboring fauna such as sponges, bivalves, polychaetes, and sipunculids. Smaller finer-grained pieces of coral rubble are typically colonized by only the most opportunistic and ephemeral species of groups like hydroids, bryozoans, and

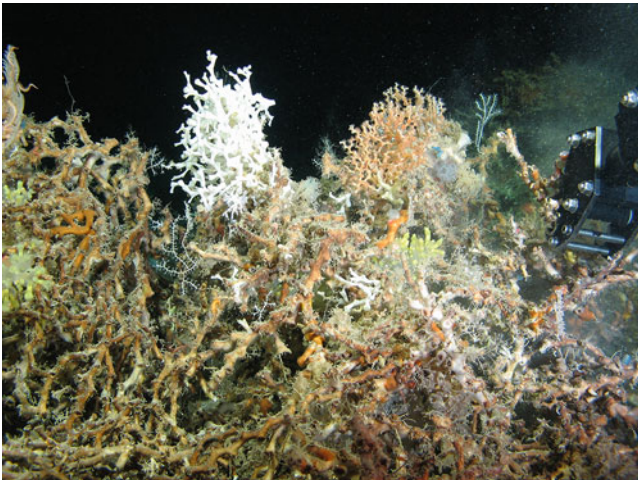

Fig. 2 ROV images showing part of a mixed *Enallopsammia rostrata*/*Lophelia pertusa* reef on the western slope of the Great Bahamas Bank. Dense and highly diverse epifaunal assemblages are seen inhabiting the mixture of live and dead coral framework in waters approximately 600–700 m deep (Images copyright MARUM, University of Bremen/Germany)

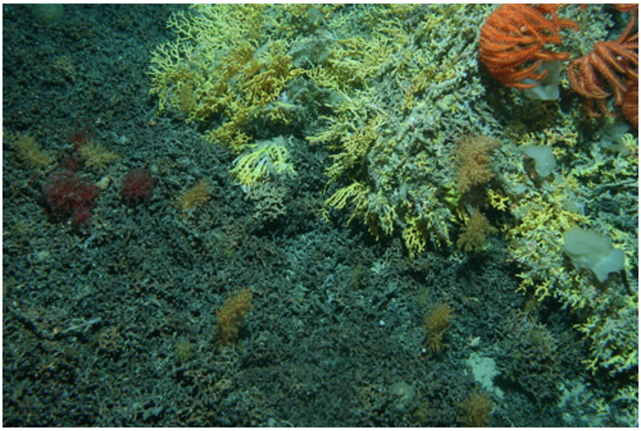

Fig. 3 The biologically rich live/dead coral degradation zone may include sharp transitions into dead coral fragments, as exhibited by these thickets of live reef-forming branching stony coral *Enallopsammia rostrata* (*yellow* color morph) at a depth of 912 m on the seamount Diabolical in the Graveyard Knoll area, Chatham Rise, southeast New Zealand. Overlaying the dead portion of the coral matrix are a small group of *Anthomastus* (soft corals), gorgonian *Thouarella* spp. octocorals, hexactinellid sponges, and brisingid sea stars (Image captured by National Institute of Water and Atmospheric Research (*NIWA*), New Zealand, and captured by NIWAs Deep Towed Imaging System (*DTIS*). Credited to NIWA)

serpulid polychaetes or are often entirely devoid of associated fauna. The result is that associated species composition on CWC reefs can strongly vary both horizontally and vertically across the CWC reef ecosystem, but also seasonally.

3.3 Regional (γ) Diversity

The strong evidence for increased numbers of species and sharp zonation patterns in the assemblages of species at CWC reefs underpins the concept of CWC reefs as global biodiversity hotspots (Cathalot et al. 2015). The regional and global species pool (γ diversity) of deep-sea fauna is in large part maintained and enhanced by the distribution of these ecosystems, particularly in the bathyal (200–2,000 m water depth) zone where the majority of CWC reefs occur and where there is a large body of evidence that these ecosystems significantly enhance biodiversity relative to noncoral areas (Henry and Roberts 2007). The huge amount of cryptic diversity revealed by genetics also suggests that endemic morphologically cryptic species could also substantially contribute to γ diversity patterns in the deep sea (Reveillaud et al. 2011), as outlined by Orejas and Jiménez , ▶ Chap. 23, “The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep” in this volume.

Regional CWC reef distribution patterns are critical, because increasing habitat fragmentation by commercial bottom trawling and dredging make it less likely that species and populations can be maintained unless these taxa can overcome the challenges of increasing geographic distance barriers. This makes the role of ocean transport and reef species dispersal capacity supremely important. For example, over the past 25,000 years, maintenance of CWC reefs and their biodiversity in the North Atlantic have directly relied on the supply of coral larvae from adjacent source seas such as the Mediterranean and possibly the Caribbean and South Atlantic Ocean (Henry et al. 2014a and references therein). Both the cold-water reef framework-forming corals themselves and some associated fauna such as sponges exhibit genetic signals that verify a “stepping-stone” phenomena whereby species are connected to adjacent habitat and disperse from there to habitats further away (Henry et al. 2014a). Thus, not only is the enhanced biodiversity and distribution typography of CWC reefs important to the regional seascape but so are the oceanic pathways that connect and maintain species and populations across vast distances (see also ▶ Chap. 38, “Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals” by Costantini and Abbiati in this volume).

It is also becoming well known that CWC reefs are hotspots of global biogeochemical cycling (van Oevelen et al. 2009; Cathalot et al. 2015; Rovelli et al. 2015). For example, CWC reefs of the Træna coral field in Norway had respiration, carbon and oxygen consumption rates, over an order of magnitude higher than in noncoral areas. Thus, another possible way in which CWC reefs may augment γ diversity is by their enhanced capacity to topographically focus or concentrate particles of food to the corals and associated reef fauna over a smaller area. This capacity to baffle sediments and augment currents at the surfaces of all the living coral polyps means that CWCs are potentially capable of drawing significant amounts of organic matter away from adjacent noncoral and soft sediment communities, which may strongly impact not only peripheral α and β diversity in other deep-sea ecosystems but also the overall γ diversity (Cathalot et al. 2015).

4 Knowledge Gaps and Technical Limitations

Core knowledge gaps and limitations of a current synthesis global CWC reef biodiversity include baseline information from areas outside the North Atlantic, habitat use by transient or migratory species, regional biogeography, and cryptic diversity. All are underpinned by a requirement to directly sample habitats and fauna, archive them correctly with accompanying metadata, and by the need to work with standardized protocols, internationally and collaboratively, to ensure the most accurate and robust data are generated.

4.1 Baseline Information in Key Regions

Deep-sea fishing grounds frequently overlap with CWC reefs (see Hinz, ▶ Chap. 37, "Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management" this volume), with some fisheries capable of fishing as deep as 2,000 m water depth. Both fish stocks and CWC reefs benefit from the drawdown of primary production from the sea surface to the seafloor, which interacts with complex topography of CWC reef habitats on the seabed. However, in several cases, both stocks and reefs are in decline as a result of historically unsustainable fisheries effort. The case of orange roughy (*Hoplostethus atlanticus*) is a well-studied example. Globally, the species exhibits a very close association with CWC reefs, and in New Zealand, but paradoxically, there continues to be stock declines in some areas but recovery in others (Doonan et al. 2015). Despite this clear example of habitat destruction and fisheries overexploitation, baseline information on the occurrence, taxonomic identity, species composition, and trophic structure of communities living on most CWC reefs is still lacking. This is particularly true for CWC reefs in the Indian Ocean, Southwest Pacific, and South Atlantic Ocean where studies of CWC reef biodiversity only began in 2013 in contrast to areas like the North Atlantic and Mediterranean (Fig. 4). The lack of information makes it difficult to ascertain what the natural or desired state of a CWC reef should be in order to develop appropriate management and conservation measures. Some CWC reefs are afforded a special status at the highest international level through the Food and Agriculture Organization of the United Nations (FAO) definition as a vulnerable marine ecosystem (VME) because of this fisheries overlap and the coral habitat's limited capacity to recover: yet there is a limited scientific evidence base in each of these regions as to

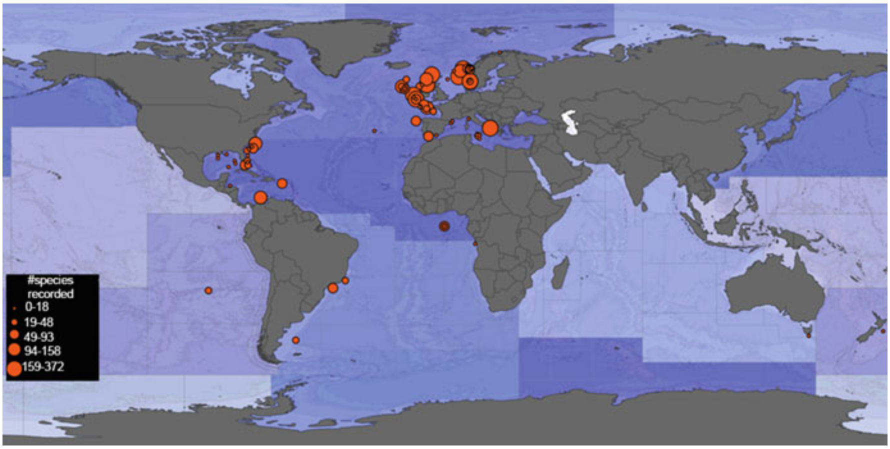

Fig. 4 Review of the literature on CWC reef biodiversity showing numbers of associated animal species found (as of early 2013). FAO major fisheries regions are shown by different shades of *blue*, with FAO subareas delineated within each major region. Note the lack of studies (as of 2013) in FAO major fisheries regions including the western and eastern Indian Ocean, southwest Pacific Ocean, and the southwestern and southeastern Atlantic Ocean, despite the known occurrences of the six major reef-building azooxanthellate species (Fig. 1)

what species are characteristic of these reefs and the potential for these reefs to act as hotspots of biodiversity and biogeochemical cycling.

4.2 Habitat Use by Migratory Animals

The lack of studies on transient or wide-ranging migratory animals using CWC reef habitat means that biodiversity studies in these ecosystems may have underestimated biodiversity and importance of these habitats to these animals, and possibly this has led to an oversimplification of CWC reef food webs. There have been no studies as to whether marine cetaceans interact with CWC reefs, and most studies of the reef fish fauna provide only a snapshot of the communities at any one time. Sustained sampling campaigns are needed, but these must be conducted so as to minimize environmental damage.

Complementary approaches could include investigation of longer-term migratory animal habitat use through the use of nonlethal techniques such as multitissue stable isotopes obtained from blood or tissues to elucidate trophic structure and partitioning and whether the animal derives most of its energetic resources from CWC reefs or elsewhere. Telemetry is also a rapidly evolving tool involving tagging and tracking migrating animal populations over short and long time periods, with transmitters now capable of archiving significant amounts of environmental metadata to link the time spent in a particular habitat as well as the drivers keeping them there or triggering them to move away. Evidence for fish aggregations, spawning sites and nurseries in CWC reefs (D'Onghia et al. 2012), year after year at similar sites (Henry et al. 2013b), suggests that telemetry has the potential to help elucidate habitat specificity and residency in migratory and transient animals and thus contribute to significantly improving our understanding of how CWC reefs support ocean biodiversity.

4.3 Regional Biogeography

A greater understanding of how species are distributed in the deep sea allows stakeholders to prioritize management decisions such as selecting representative marine protected areas (MPAs) and ensuring that an MPA network allow for the connectivity of marine genetic resources (Rice et al. 2011; see also ▶ Chap. 34, "Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest" by Rice and Smith; ▶ Chap. 38, "Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals" by Costantini and Abbiati; ▶ Chap. 35, "The Impact of Anthropogenic Activity on Cold-Water Corals" by Grehan et al. in this volume). The lack of standardized, systematic surveys in deep-sea ecosystems across the globe makes it difficult to synthesize data at spatial scales relevant to management. In the case of CWC reefs, there is sometimes very detailed knowledge of particular local systems. However, scaling up observations to other areas into a broader regional or global synthesis must be carefully undertaken, especially as sampling effort, gear, taxonomic expertise, and resolution may vary widely across studies. Some intraregional biogeographic analyses from CWC reefs have been made for associated sponge (Van Soest and de Voogd 2013) and hydroid (Henry et al. 2008) fauna across scales of 100s to 1,000s of kms, which refuted (in the case of sponges) and supported (in the case of hydroids) existing deep-sea biogeographic classifications based simply on direction of prevailing ocean currents.

Another confounding factor in tackling the challenge of species biogeography in the deep sea is that the ocean circulation and its properties constantly change on annual to millennial time scales. Oceans are also currently undergoing unprecedented rates of changes in temperature and carbonate chemistry regimes, with the expansion of oxygen minimum zones around the globe also expected to profoundly affect deep-sea processes and the distribution of life forms, e.g., by compressing available habitat for pelagic fish (Stramma et al. 2012). Thus, biogeographic classifications using historic collections obtained decades to over a century ago will very likely be inaccurate. Deep-sea species biogeographic boundaries are dynamic and very likely have transitional or unclear borders (Rice et al. 2011); thus, any attempt at rectifying the regional or global biogeography of CWC reefs must consider the oceanic regime in which the basic units of the biogeographic classification (species, environmental parameters) were collected. Essentially, any robust marine biogeographic classification should strive for four-dimensionality (latitude, longitude, depth, and time) to capture this dynamic nature.

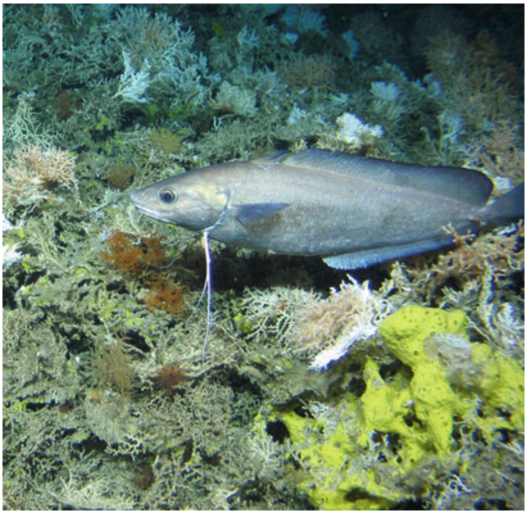

Fig. 5 Cryptic diversity on CWC reefs is hidden all around. The bright *yellow* sponge in the foreground, *Hexadella* cf *dendritifera* (aprox. 684 m) can densely colonize the mixed live/dead coral zone in the northeast Atlantic but molecular analyses revealed hidden diversity in morphologically similar sponges from the Ionian Sea in the Mediterranean to the Greenland Sea (Reveillaud et al. 2010) (Image credited to Heriot-Watt University and NERC)

4.4 Cryptic Diversity

Morphologically similar species may also exhibit varying levels of genetic differentiation, which has led to the vast underestimation of species diversity on CWC reefs and probably β and γ diversity as well. Cryptic species are becoming especially well-documented in the sponges associated with CWC reefs (Reveillaud et al. 2010, 2011), for example, in the genera *Hexadella* and *Plocamionida* (Fig. 5) which suggests there is far greater hidden species diversity than previously thought in these ecosystems.

5 Frontiers in Technology

Technological developments in deep-sea exploration continue to advance, driven mainly by the military applications and the need for increased understanding and exploitation potential of deep-sea resources. Deep-sea investments by traditional sectors including the petroleum industry and subsea telecommunications continue to grow particularly in deepwater oil and gas extraction but also from rapidly emerging industries such as blue biotechnology and deep-sea mineral mining businesses. Other sectors such as human health and agriculture have also enabled translational genomic technologies to open up new frontiers in the science of CWC reefs across the globe.

At the frontier of these technology developments are multisensory lander platforms, observatories, robotics, and genomics, all of which have been in service on land for many years, but which now offer extremely powerful tools with which a deeper understanding of CWC reef and deep-sea biodiversity can be obtained.

5.1 Landers and Observatories

Seafloor lander platforms offer the potential to obtain longer-term (several hours to years) in situ observations of the CWC reef environment and associated biodiversity. Landers became more routinely deployed in CWC reefs since the early twenty-first century (Roberts et al. 2005) and were typically equipped with standard instrumentation such as stills or video cameras, sediment traps, and acoustic Doppler current profilers (ADCPs) allowing for variations in current strength, temperature, and salinity to be measured. Frontiers in lander technology include significant enhancements in sensor modalities including carbonate chemistry and eddy covariance measures that use delicate probes and sensors to obtain very high resolution measurements of oxygen to understand how CWC reef biodiversity is linked to ecosystem functioning (Rovelli et al. 2015).

Cabled seafloor observatories in CWC reefs offer yet another tool to obtain novel observational data on environmental dynamics and species habitat use in relation to these properties. Since 2013, the petroleum company Statoil has maintained the LoVe Ocean Observatory at a CWC reef in approximately 255 m water depth off the Norwegian coast. LoVe offers free, near real-time camera stills, timelapse video, hydrophone, and fisheries acoustic data. Also included are packages for temperature, salinity, pressure, conductivity, turbidity, chlorophyll, organic, and suspended matter. Observatories such as these could help greatly advance the understanding of temporal dynamics in CWC reef biodiversity, especially with respect to camera-shy fish that may avoid large remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUVs) navigating the reef, but also the transient or migratory species that are not captured by snapshots during a cruise.

5.2 Robotics and Engineering

Surveys of CWC reef biodiversity are often conducted by means of specially engineered grabs, cores, stills, and video cameras mounted on landers, dropped systems, or as part of an ROV package or cabled seafloor crawler. It is vital that these surveys obtain actual samples of reef fauna to validate species identification and offer the potential for genetic studies to further refine species' boundaries. Sometimes this is not possible, and all that exists are images or videos of megafauna. Improvements and bespoke design of all types of sampling gear, such as videograbs specialized for collecting and retaining coral framework and smaller mobile and sessile epifauna, continue to be made. Off the shelf and specialized ROVs are now smaller, more manoeuvrable, have longer battery-lives, and in many cases are now capable of remote manipulation by means of dextrous arms or claws. Many vehicles also provide ample storage and additional sensor packages to obtain accompanying environmental metadata in deep-sea habitats and can return excellent quality images from the seafloor, a significant advancement beyond the very first low-resolution monochrome images. Internet-operated and cabled deep-sea crawlers are also emerging technologies for this frontier (Purser et al. 2013a).

Unlike ROVs that must remain tethered and powered to a surface vessel, AUVs are yet another significant and possibly more cost-effective advancement in the technology used to study CWC reefs. Tetherless platforms are especially good candidates to consider when implementing research and monitoring programmes in complex fragile environments such as coral reefs. AUVs have already proved vital to locating and mapping CWC mounds in the North Atlantic off Florida and in the northern Rockall Trough (Wynn et al. 2014). Some AUVs are hover-capable and ensure very precise station keeping. Autonomous manipulation is still very much an engineering frontier, but these tasks are also proving possible in trials at sea, which would open the possibility of autonomous sampling of target organisms. Some AUVs are also capable of tracking chemical plumes such as those simulated in carbon capture carbon storage facilities leaks and pollution outfalls. Other AUVs can even track migratory species like sharks and other fish in deep waters better than shipboard methods (Eiler et al. 2013), a capacity that should be explored in more detail for CWC reef habitats where there is little information on habitat use by these species.

The vast volumes of image, video, and acoustic data collected during modern CWC reef surveys is a challenge to studying biodiversity in these ecosystems, with much research effort, expertise, and cost attributed to annotating, mapping, and interpreting data. Computer-aided technology such as machine-learning algorithms is now being implemented on CWC reef datasets. These automated detection methods can potentially offer far more cost-effective, and even more accurate, solutions than those provided by experts who undertake classic point annotations (Purser et al. 2009). The ultimate goal is to be able to undertake accurate, reliable, and completely unsupervised segmentation and classification in real-time on board an autonomous system during each CWC reef mission.

5.3 Genomics

Recent advances in next-generation sequencing techniques such as restriction site-associated DNA sequencing (RADSeq) of single nucleotide polymorphisms (SNPs) now make rapid economic screening of marine genetic resources in the deep sea possible, even for organisms without reference genomes (Herrera Monroy 2015). These advances greatly facilitate obtaining answers to knowledge gaps in population genetics, species boundaries, and evolutionary genetics, especially as it pertains to adaptive potential under different scenarios of climate change (Herrera Monroy 2015). The potential to screen and monitor deep-sea biodiversity with samples of environmental deoxyribonucleic acids (eDNA) is also being validated in deep-sea systems such as canyons (Guardiola et al. 2015), an approach that could also be applied in the context of CWC reef ecosystems as part of a management toolkit.

6 Conclusion and Future Directions

Cold-water coral reefs are global biodiversity and biogeochemical cycling hotspots and play host to thousands of animal species throughout the ocean food web. CWC reefs not only enhance species diversity and harbor distinct assemblages across the reef structure but these ecosystems also enhance regional and global diversity.

Large gaps in the knowledge of global CWC reef biodiversity still exist. The overwhelming majority of biodiversity studies come from the North Atlantic, yet major azooxanthellate reef-building scleractinians are globally distributed. Particular knowledge gaps are in the Southwest Pacific, South Atlantic, and Indian Ocean, and like the North Atlantic and Mediterranean, very likely overlap socioeconomically important fishing grounds. Generally, there are still too few studies on habitat use by migratory species like sharks; certainly, the more undersea images from CWC reefs that are examined in close detail, the more that gains to be discovered in these habitats such as possible shark spawning grounds (Fig. 6). It is also not known to what extent deep-diving marine mammals may use CWC reefs. The lack of standardized, systematic surveys of the biodiversity on CWC reefs prevents regional and global syntheses in most cases; where they have been possible, such analyses provide new insight into biogeographic boundaries and their possible environmental drivers. Molecular genetics are revealing substantial levels of cryptic or hidden diversity among the sponges associated with CWC reefs and suggest that the global biodiversity of CWC reefs has been vastly underestimated.

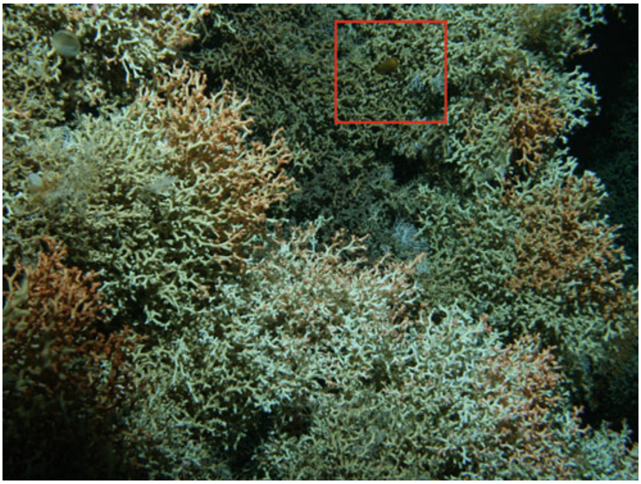

Fig. 6 A shark egg (bounded by *red box*) deposited amongst the dense thickets of the live reef-forming branching stony coral *Solenosmilia variabilis* at a depth of 996 m on the seamount Gothic in the Graveyard Knoll area, Chatham Rise, southeast New Zealand. Some dead coral matrix is also visible along with delicate lacy stylasterid hydrocorals and small hexactinellid sponges (Image provided by the National Institute of Water and Atmospheric Research (*NIWA*), New Zealand, and captured by NIWAs Deep Towed Imaging System (*DTIS*). Credited to NIWA)

The future of CWC reef biodiversity science will still rely on the fundamentals of direct sampling of habitats and fauna, which are then properly archived along with any accompanying metadata. This means that institutional links with private industries such as fisheries, oil and gas, deep-sea mining, and the public sector including governments and museums and sustained funding streams for archival work must be more firmly established. The science will also still rely on the need for standardized protocols developed internationally and collaboratively across disciplines.

Frontier technology has a huge role to play in advancing CWC reef biodiversity science across the globe. Landers and observatories provide much-needed long-term environmental time series with which biodiversity data can be matched to understand environmental drivers of species diversity and community change. These platforms also provide new insights into camera shy or transient visitors to the reefs. ROVs, AUVs, and further automation offer CWC reef biodiversity science opportunities to significantly advance how these ecosystems are studied at every step, from conducting mission across the reef, to in situ sample manipulation, to species annotations. Next-generation genomics provide the necessary genetic validation of species boundaries and will allow for a far deeper understanding of the evolutionary adaptations of species and lineages in a deep undersea world heralding great changes in the ocean.

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Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes

9

César A. Cárdenas and Américo Montiel

Abstract

Coexistence between species plays an important role in structuring marine benthic communities but is often underestimated in current ecological studies. In the cold-water ecosystem, such as Chilean fjord/channels and Antarctic areas, animal forests are dominant on rocky substrates and exist among dense macroalgal forests as well as encrusting coralline algae. The distribution patterns of both animal and macro-algal forests are influenced by the topography of the rocky wall, where animal forests formed by trees- and mound-like growth forms become dominant with an increasing degree of inclination. The macroalgal forest tends to decrease from the inclined toward the overhanging profile. Along a latitudinal gradient, very abundant gregarious animal forests (e.g., mytilids) on the subantarctic shallow rocky substrate tend to decrease in their abundance and distribution toward the rocky substrate of the Antarctic shallow areas. A contrasting pattern emerges regarding clonal animal forests (e.g., sponges), where dense assemblages of clonal growth forms are dominant in the Antarctic rocky substrate and tend to decrease toward the southern tip of South America. In both the Chilean fjord and channels and Antarctic ecosystems, the animal forests are key elements in the seascape as they have great potential as a tourist attraction and also provide important ecosystem services.

Keywords

Clonal • Gregarious • Climate change • Magellan • Antarctica • Rocky reef • Cold-waters ecosystem • Macroalgae • Seascape ecology

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Contents

1 Introduction

1.1 Animal Forest in Cold-Water Ecosystems

Animal forests (AFs; Rossi 2013) encompass sessile heterotrophic organisms, which build their three-dimensional (3D) living structures based on either modules growth (Jackson 1985) or by mean population growth. In this regard, two subgroups are considered: first, clonal organisms, which have the ability to grow and reproduce asexually in potentially unlimited quantities and thereby, build their 3D structures (Wood 1999). This subgroup includes organisms like sponges, hard and soft corals, bryozoans, and hydroids (Fig. 1a, b). A second subgroup consists of solitary organisms of AFs with gregarious capacities, which build their 3D structures forming clusters of individuals. Within this subgroup are the bivalves, brachiopods, and tubeworms (polychaetes) (Fig. 1c, d).

Following this definition it has been shown that AFs are widely distributed throughout the globe at all depths from the southeast continental shelf of the Weddell Sea (Antarctic), mainly represented by large sponge fields (see Gutt et al. 2016), to the tropical continental shelves where coral reefs dominate the seafloor (Adjeroud et al. 2015). They are also present from the intertidal zone, represented by blue mussel beds (Gutiérrez et al. 2003) or oyster beds, to the deep-sea plain, where Alvinelid polychaetes are a common feature of hydrothermal vents (Kiel and Tyler 2010) or with aggregations of *Calyptogena* spp. bivalves on cold seeps (Vrijenhoek 2010).

Rossi (2013) shows that AFs are highly important at ecosystem level, as they organize and structure the functionality of the ecosystems. The AFs act as autogenic ecosystem bioengineers (Jones et al. 1994; Hastings et al. 2007), influencing the abiotic habitat and facilitating the presence of other organisms within their 3D structures. These relationships that are characterized by the AFs and supporting

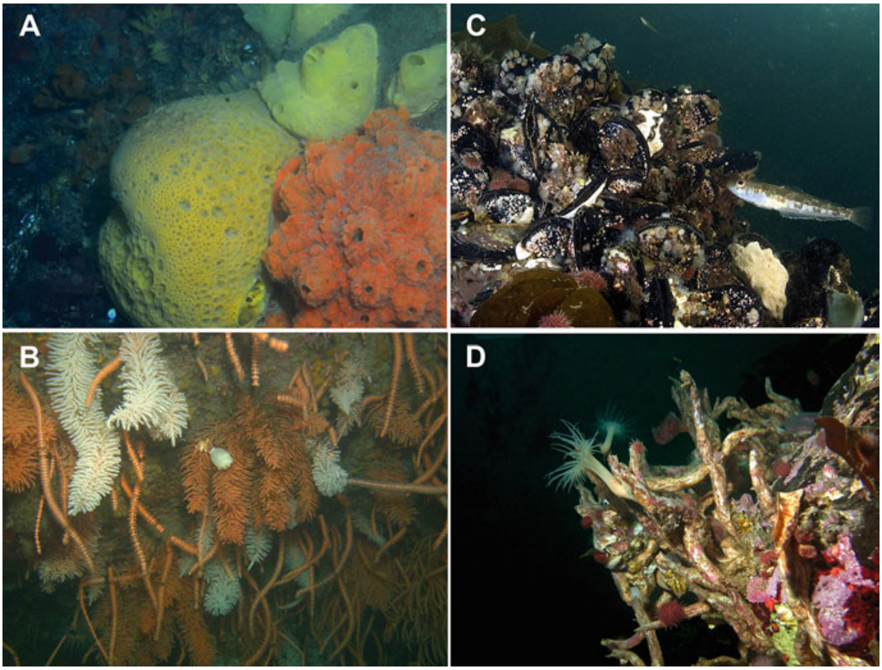

Fig. 1 Examples of clonal organisms of AFs (**a, b**) and solitary organisms with gregarious capacity of AFs (**c, b**). Vertical wall dominated by diverse sponge assemblages (15 m) from Maxwell Bay, King George Island (**a**). Overhanging wall with high abundance of gorgonaceans (35 m) from Admiralty Bay, King George Island (**b**). Mytilids assemblage (app. 10 m water depth) from fjord coast off South Patagonia Ice Fields, Chile (**c**). Vertical wall showing a diverse community associated with *Chaetopterus variopedatus* (20 m) from Isla Santa Ines, Strait of Magellan (**d**)

other species result in increasing alpha and beta diversity. For this reason, local extinction of AFs may cause a loss of resilience and consequently the loss of the capacity to recover after disturbance or resistance (Pimm 1979).

Cold-water ecosystems, defined as marine ecosystems with an average temperature of ≤ 10 °C, are highly vulnerable to increased temperature and acidification. This vulnerability is explained by the adaptation of most of the cold-water organisms living in a narrow and cold thermal range. Hence an increase of water temperature in 1 or 2° C will put most of the organisms very close to their critical temperature limit (Sokolova et al. 2012).

Two chapters presented in this book provide evidence of the importance of the AFs in the cold-water ecosystems of the southern hemisphere; AFs as dominant features of benthic communities in the Southern Ocean (see Gutt et al. 2016) and also on the seafloor of the Chilean fjord and channel ecosystem (see Försterra et al., ▶ Chap. 10, "Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters" in this volume) provide good examples.

However, quantitative benthic data on the rocky shore of the Chilean fjord and channel ecosystem is still scarce, and much more research is needed for improving our knowledge about the distribution and functional roles of AFs.

1.2 Theoretical Gaps and Challenges in the Framework of AFs

There are three ecological aspects of AFs that have not yet been thoroughly analyzed. One of the research gaps addressed in this chapter is the plant-animal relationships. For decades, the relationships between plant and animals have caused intense scientific debates (John et al. 1992; Cárdenas et al. 2016a). Despite this considerable debate, many questions remain open, because both negative (competition, predation, and parasitism) and positive (symbiosis, facilitation, and mutualism) relationships are mechanisms that can simultaneously or independently influence the way in which organisms coexist in a geographic area. In this chapter, the coexistence between organisms will be operationally defined as the distribution pattern resulting from the ecological interactions between species that compete for a common resource (Worm and Karez 2002).

On rocky substrates, AFs coexist among many macroalgae species (for comparative purposes, the term macroalgae forest (MFs) will be used), and this coexistence occurs only in a narrow area of the seafloor (see Boudouresque et al. 2016). MFs, like AFs, build 3D structures in the rocky marine ecosystem (Steneck and Dethier 1994) and are extremely dominant in both the intertidal and sublittoral zone. Given that MFs mainly depend on sunlight, its fundamental niche is not as eurybathic as the niche of AFs.

Another research gap addresses the question of how the concept of AFs fits within the emerging discipline of ecosystem functioning. In fact, AFs show very diverse amounts of ecophenotypes (e.g., trees, bushes, plates, and mounds), which are defined as the array of growth morphologies with a potential to adapt to local environmental conditions. Jackson (1979) introduced for the first time a functional categorization for benthic sessile invertebrates, which until then had existed only for terrestrial plants. Jackson's characterization has been widely accepted and has been further adapted and used to study processes of competition and ecological succession for both hard and soft substrates (Buss and Jackson 1979; Greene et al. 1983; Connell and Keough 1985; Teixidó et al. 2007). The present chapter investigates the concept of AFs using a modification of the categorizing system as introduced by Jackson, including invertebrate and macroalgal taxa.

A third research gap that has not been addressed so far regards the change of abundance in AFs along a latitudinal gradient. This question becomes even more relevant when considering this distribution within the framework of evolutionary and ecological relationships between the South American and Antarctic continents (Arntz and Ríos 1999; Arntz et al. 2005).

The present chapter reviews the empirical evidence of the coexistence between AFs and MFs in rocky habitats under cold-water conditions. In addition, we analyze how the growth forms of both AFs and MFs coexist along rocky seascape topography and how the AFs are distributed along the latitudinal gradient.

2 Coexistence of Animal and Macroalgal Forests

Subtidal rocky reefs have been subject of intense studies from the ancient naturalists to the current macroecologists (Siegfried et al. 1994). All of them have been fascinated with the great diversity and high productivity of these ecosystems. Within these epilithic ecosystems, one or a few dominant species monopolize the available space. Nonetheless, high densities of AFs exist among the dominant MFs (Cárdenas and Montiel 2015).

The coexistence between species in the benthic zone is a result of competition for common resources along an environmental gradient (Worm and Karez 2002) if the available space is the only limiting resource. While AFs require food, MFs depend upon sunlight, carbon, and nutrients (Worm and Karez op. cit.). Coexistence can be the result of predation, facilitation, mutualism, or a combination of both (Bulleri 2009). Most of the research on relationships between animal and algae focuses on the interactions between mobile fauna (grazers) and sessile macroalgae (John et al. 1992). In this regard, the role that sea urchins play in structuring MFs as well as affecting the complex interactions between MFs and AFs has been widely documented for different latitudes in the literature (Norderhaug and Christie 2009; Newcombe et al. 2012). Palumbi (1985) described the existence of complex interactions between erect corallines, herbivorous fauna (chitons), and sessile organisms (sponges). This author experimentally demonstrated a complex commensal relationship between the erect coralline alga *Corallina vancouveriensis*, the sponge *Halichondria panicea*, and a common chiton since the removal of the latter resulted in the sponge being outcompeted by the coralline alga.

Since the vast majority of research on relationships between AFs and MFs has focused on negative interactions between both, it is relatively well known that MFs (mainly canopy-forming algae) negatively affect the understory due to scouring from fronds, preventing settlement and survival of different organisms (Fowler-Walker et al. 2005). In contrast, only a few studies have described the existence of positive interactions between AFs and MFs. In recent research, positive interactions between AFs and MFs have suggested that canopy-forming algae facilitate the occurrence of sponges (Ávila et al. 2010; Cárdenas et al. 2016a, b). Other examples of positive mechanistic effects produced by canopy include abrasion caused by kelp fronds that can prevent sponge *Halichondria panicea* from being outcompeted by turf algae (Smale et al. 2013). Other positive effects produced by the fronds of MFs include provision of shelter (Wright et al. 1997; Ávila et al. 2010), protection from waves, and light reduction (Cárdenas et al. 2016a). In addition, it has been suggested that AFs may enhance nutrient supply (Duggins and Eckman 1997). A recent study reported a high level of coexistence between sponges and Antarctic canopy-forming algae

(*Himantothallus grandifolius* and *Desmarestia* spp.) in sites around the South Shetland Islands and the Western Antarctic Peninsula (Cárdenas et al. 2016b). Their findings suggest that "canopy formers" may help maintain sponge richness in highly disturbed areas (ice scouring) in the Western Antarctic Peninsula. In contrast, a different positive role is suggested in Magellan region, where "canopy formers" may provide protection from waves and high irradiance, especially in the sublittoral areas.

2.1 Animal and Macroalgal Forests Under a Morpho-Functional Approach

The study of ecosystem functioning has become a prominent discipline in ecology and studies the processes and properties of the flux of energy between biotic and abiotic components of ecosystems (Jax 2005). Nowadays, the use of functional groups has become more common, which is a useful technique to avoid highly complex taxonomic analyses and species identification. This decrease in complexity is achieved by considering biological characteristics of the studied organisms and subsequently defines them by a small number of their features. One of the ways to study functional groups is to characterize species according to their trophic guild. For example, sponges, bryozoans, and bivalves are often grouped in the trophic guild of filter feeders. Other categorizations combine more than one feature, linking, for example, trophic guild, mobility of the organism, and feeding strategy (Barnes et al. 2009; Jumars et al. 2015). Other examples of categorizations combine internal or external skeletal structures and chemical composition of the organismic structure (Jackson 1977). The acceptance of each categorization by the scientific community depends on how well the categorizations explain ecological patterns and if they lead to new hypotheses.

For example, Jackson (1979) developed his classification based on the morpho-functional traits of species of benthic invertebrates. This classification aims to understand how organisms with clonal growth compete with gregarious organisms for physical space. This categorization has been widely used in studies of ecological succession on both artificial and hard substrates (Buss and Jackson 1979; Greene et al. 1983) as well as in the soft bottom benthic communities in the Weddell Sea (Teixidó et al. 2004). It was also applied and improved by Connell and Keough (1985), who investigated how forms of clonal growth behave under disturbance in tropical areas. A decade after Steneck and Dethier (1994) describe a classification based on the anatomical structures of algae, which is relatively similar to the ones described by Jackson for benthic invertebrates. However, a united categorization for both sessile invertebrates and macroalgae has not yet been outlined. Recently, Cárdenas and Montiel (2015), using the criteria originally proposed by Jackson (1977) and Teixidó et al. (2004), proposed a classification that unifies the growth forms of sessile invertebrates and macroalgae to study the distribution and diversity pattern in the rocky reefs from Punta Santa Ana (Strait of Magellan).

Table 1 shows the five growth forms for sessile invertebrates and macroalgae. Due to their 3D structures, four of these growth forms (trees, bushes, plates, and

Table 1 Growth forms recorded at Punta Santa Ana, Strait of Magellan (Modified from Jackson 1979)

Growth forms	Main characteristics	Sessile invertebrates (examples in Figs. 1 and 3)	Macroalgae (examples in Fig. 4)
Trees	Upright growth on the substrate, with a main shaft, which gradually branches to a height forming a three-dimensional structure	*Primnoella chilensis*^{3F}	*Macrocystis pyrifera*^{4A}
Bushes	Upright growth, branching nearly from the base substrate close to reaching a three-dimensional shape	Hydrozoa, Bryozoa^{3D}	*Callophyllis* sp.^{4B}
Mounds	Individual growth mass, several individuals as stacked grouping thus giving rise to a three-dimensional structure or one individual growth form with extensive vertical and horizontal growth	*Mytilus chilensis* ^{1C}, *Aplidium fuegiense*^{3H}	*Adenocystis utricularis*^{4C}
Plates	Upright growth, adheres to the substrate by means of a central short axis and at the top is continued with a concave blade resembling an umbrella	Coral[a] (*Agaricia* sp.)	*Gigartina skottsbergii*^{4D}
Sheets	Encrusting growth on the substrate or on other organisms	*Phorbas* sp.^{3B}	*Lithothamnion rugosum*^{4A}

[a] Not mentioned in this chapter

mounds) were grouped within the AFs and analog growth forms of macroalgae within the MFs, whereas sheet growth forms of sessile invertebrates and macroalgae were not included as AFs or MFs, because they are encrusting species and build bidimensional structures.

2.2 Epilithic Animal Forests Among Macroalgal Forests in Punta Santa Ana: A Case Study in the Strait of Magellan Coast

Punta Santa Ana is located in the Strait of Magellan (53° 37′ 34″S, 70° 55′ 13″ W), 20 km south from the city of Punta Arenas (Fig. 2a, b). This area is characterized by the presence of a rocky platform dating from the Cretaceous (Brambati et al. 1991; Setti and Veniale 1991). The coast is moderately exposed to wave and wind action. The water column in this area generally shows cold water (≈6–9° C) and low salinity (≈ 30–31 psu) (Brambati et al. 1991). The underwater rocky walls show significant variations in the tilt profile, which can be classified into three categories: an inclined surface ranging from 45 to 80°, a vertical surface app. 90°, and finally an overhanging surface which ranges from 100 to 135° (Cárdenas and Montiel 2015).

Macroalgae and bivalves are the dominant organisms of hard substrate communities in Punta Santa Ana. The seascape is dominated by a forest of *Macrocystis pyrifera* (Fig. 2c, d), in which the kelp's canopy reaches a coverage of about 2.1 ha

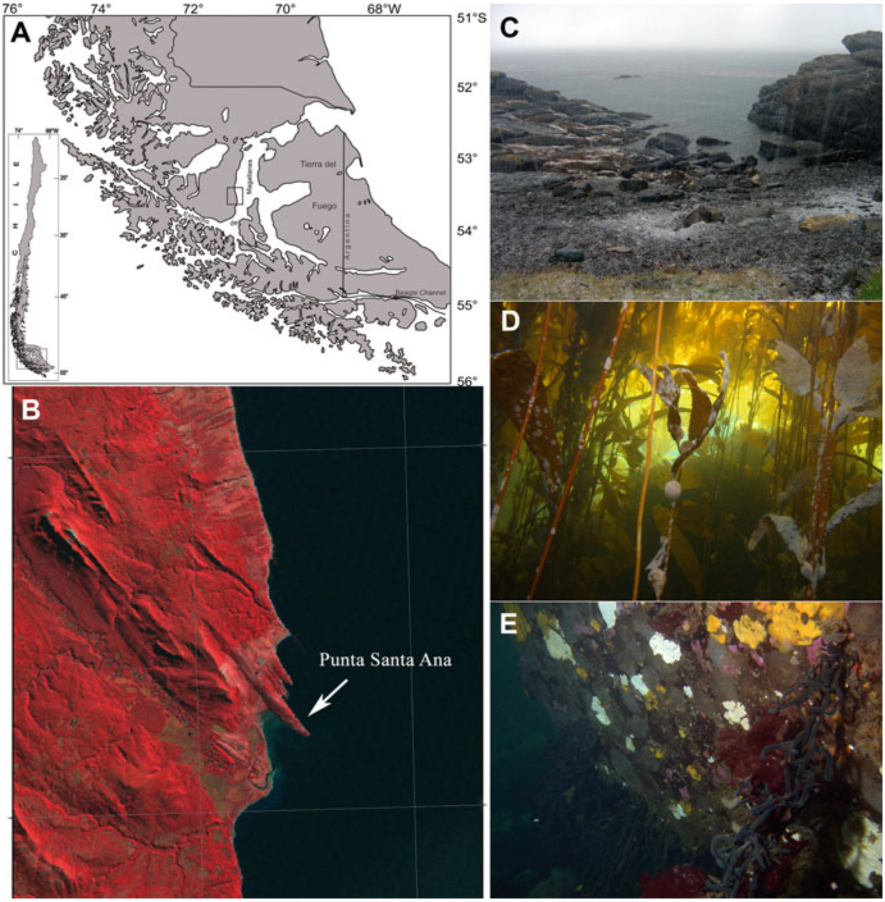

Fig. 2 Location of Punta Santa Ana, Strait of Magellan (**a**, **b**). Rocky shore at Punta Santa Ana, mainly composed by bedrock, a common feature of the Chilean fjord and channel ecosystem (**c**). Dense *Macrocystis pyrifera* forests dominate the shallow-water rocky reefs (10 m) in the Strait of Magellan (**d**). Overhanging wall with conspicuous presence of the bryozoan *Alcyonidium australe* and ascidians colonies (Didemnidae and *Aplidium* sp.; 25 m; **e**)

and an average of 0.25 individuals per m^{-2} (Ríos et al. 2007). Newcombe et al. (2012) investigated the sea urchin *Arbacia dufresnii* among the assemblages of macroalgae on rocky substrates, where the sea urchin controlled their distribution and abundance. Recently, Andrade et al. (2016) described the trophic structure of benthic communities, identifying three heterotrophic levels, with macroalgae and organic suspended matter being the main food sources. Cárdenas and Montiel (2015) recorded a total of 37 species of sessile invertebrates and 31 species of macroalgae on rock walls. In terms of coverage, corallinaceous species were dominant. Some of these species of invertebrates and macroalgae are illustrated in Figs. 3 and 4.

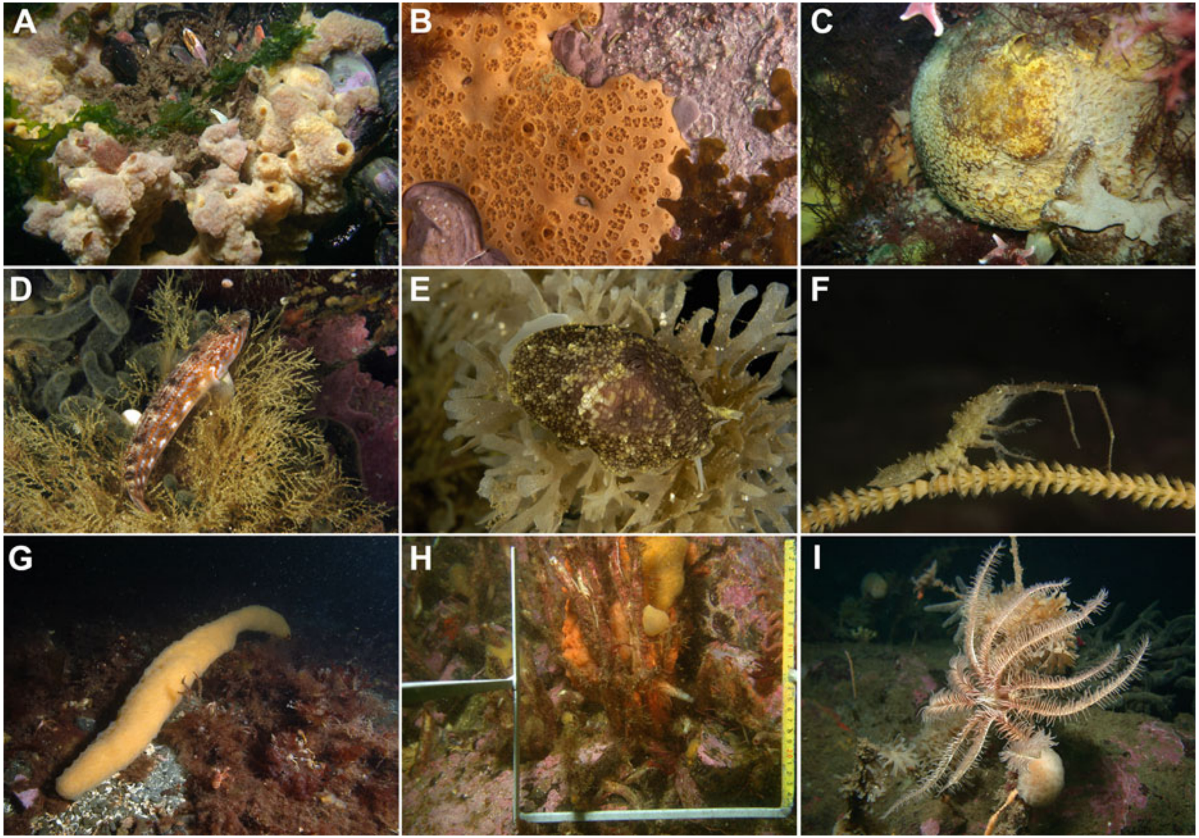

Fig. 3 Selected species as example of animal forests: the sponge *Mycale (Aegogropila) magellanica* and bivalve *Mytilus* spp. dominating the bedrock in a shallow embayment Strait of Magellan (**a**). The encrusting sponge *Phorbas* sp. competing for space with brown algae and the coralline algae *Lithothamnion*

2.2.1 Distribution of Animal and Macroalgal Forests Influenced by the Topography of the Rocky Reef from Punta Santa Ana

The topography of the wall and the interaction between depth and light availability are forces that influence the organization of the benthic communities (Bell and Barnes 2000; Miller and Etter 2011; Cárdenas et al. 2012). Therefore, all these parameters may also affect the coexistence between AFs and MFs on the rocky walls off Punta Santa Ana (Fig 2e). In this example, the AFs and MFs were subcategorized following the criteria of the morpho-functional classification given in Table 1.

Figures 5 and 6 summarize the results obtained from 275 underwater photographs taken on two sublittoral rocky walls off Punta Santa Ana, during four sampling seasons (see details in Cárdenas and Montiel 2015). These radar charts describe the distribution pattern of the five growth forms of invertebrates and macroalgae. Four of them are considered AFs and MFs, excluding the sheet growth form. Each radar chart is based on the frequency of occurrence (expressed as percentage) for each growth form among three categories of inclination (inclined, vertical, and overhanging), which are described below.

Inclined Surfaces

The inclined surfaces were characterized by the occurrence of three growth forms of AFs (trees, bushes, and mounds). Similarly, the same three growth forms of MFs were found (Fig. 5). Additionally, MFs with plate growth forms were also present (Fig. 5g). However, MFs comprising trees, bushes, and mounds growth showed a higher percentage frequency of occurrence (Fig. 5d–f) than each of the three forms of AFs with similar growth (Fig. 5a–c). A similar trend was observed when comparing sheet-like macroalgae with the same invertebrate growth form (Fig. 6a, b).

Vertical Surfaces

Similar to the inclined surfaces, the vertical surfaces were characterized by the occurrence of AFs showing three forms of growth and MFs exhibiting all four

Fig. 3 (continued) sp. (**b**). The sponge *Hemimycale* sp. and other massive sponges dominating inclined rock surfaces from Maxwell Bay, King George Island (**c**). Bushy hydroids (e.g., *Symplectoscyphus subdichotomus*) and bryozoans such as *Alcyonidium australe* provide important tridimensional substrate for fishes (*Patagonotothen longipes*) and many invertebrates in zones dominated by encrusting corallines (**d**). *Llamellaria* sp. on the bryozoan *Carbasea ovoidea,* Magellan Strait (**e**). The isopod *Neastacilla magellanica* on the sea whip *Primnoella chilensis,* Punta Santa Ana, Strait of Magellan (**f**). The colonial ascidian *Distaplia cylindrica* can grow up to 8 m depth forming abundant forests below 25–30 m depth in the Magellan region and the Western Antarctica Peninsula (**g**). Tubes of the polychaete *Chaetopterus variopedatus* provide habitats for different species of ascidians such as *Aplidium fuegiense* and *Distaplia* sp. Murray Channel, Magellan region (**h**). Several species such as the crinoid *Florometra magellanica,* the ascidian *Aplidium* sp., bryozoans, and hydroids can be found associated with dead and of the sea whip *Primnoella chilensis,* Magellan Strait (**i**)

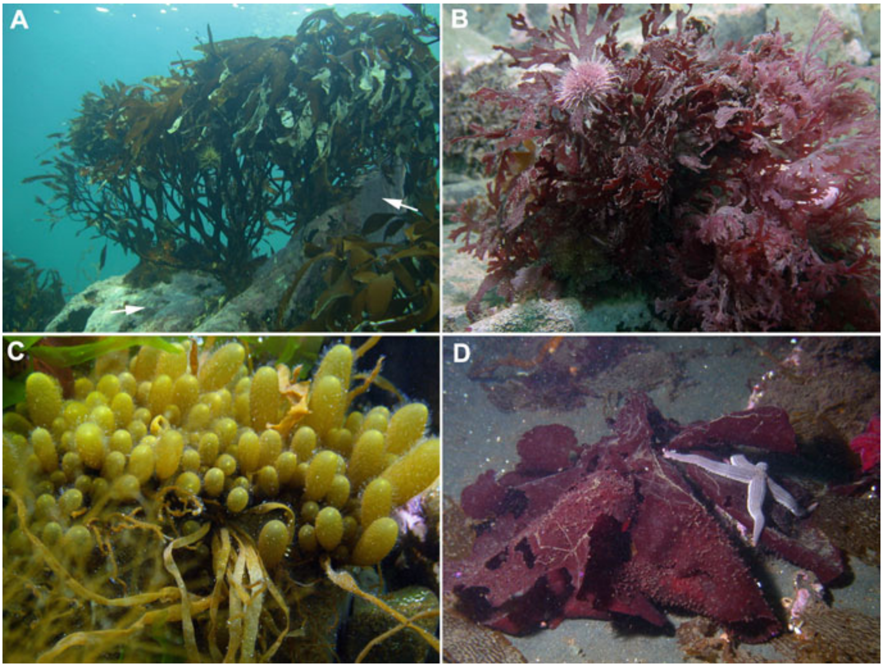

Fig. 4 Examples of five growth forms of macroalgal forests: trees *Lessonia* spp. (**a**), bushes *Callophyllis* spp. (**b**), mounds *Adenocystis utricularis* (**c**), plates *Gigartina skottsbergii*, (**d**) and sheets *Lithothamnion* sp. (*white arrow*)

forms of growth (Fig. 5). However, the three growth forms of AFs occurred more often (Fig. 5a–c) than their analog growth forms of MFs (Fig. 5d–f), with the opposite trend visible on inclined surfaces. In contrast, MFs sheet growth forms were more frequent than their analog invertebrate growth form (Fig. 6a, b).

Overhanging Surfaces

Unlike the previous two inclination surfaces, the MFs plate and tree growth forms were absent on the overhanging surface (Fig. 5f, g). In terms of frequency of occurrence, the AFs were exceptionally dominant over the MFs throughout all forms of growth (Fig. 4a–c). Invertebrates with sheet growth showed the same trend as described for the AFs of overhanging surfaces (Fig. 6a, b).

In summary, tree, bush, and mound growth forms of AFs coexist with the four forms of 3D growth exhibited by MFs in all the three categories of inclination. There are two exceptions, the first referring to the form of plate growth forms that has no analog form in the group of AFs on rocky walls off Punta Santa Ana. The second exception refers to tree MFs that were absent from overhanging surfaces.

Notwithstanding the exceptions described above, certain trends can be distinguished along the topographic profile of the rocky wall. For example, bush and mound growth forms of AFs tend to become more frequent with increasing steepness

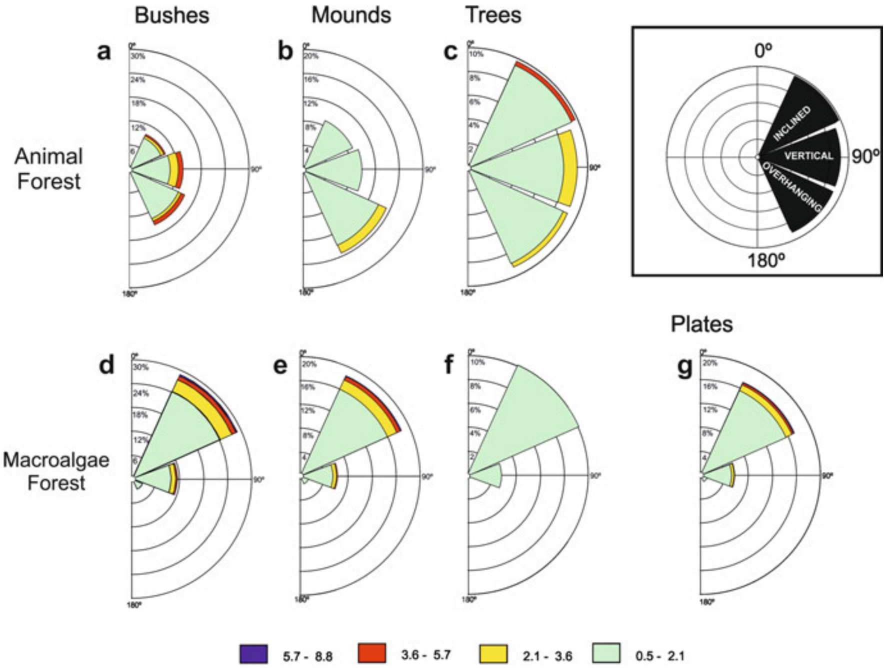

Fig. 5 Radial chart shows the distribution patterns of four AFs and MFs growth forms from each surface inclination (inclined, vertical, and overhanging; see *inset* chart). *Colors* indicate the percentage frequency of occurrence

of the overhanging surface. In contrast, tree-shaped AFs show a relatively constant frequency and are, apparently, independent of the degree of inclinations, while the frequency of MFs tends to decrease with an increasing degree of inclination. This may be due to the inclined surfaces getting more sunlight. Therefore, MFs compete for space successfully and displace AFs on this surface. In contrast, on vertical surfaces the increased light decreases and grazing by the sea urchin *Arbacia dufresnii* increases. Hence, MFs tend to stop competing for space with AFs. Finally, the lack of sunlight in the overhanging surfaces makes it a very inhospitable habitat for MFs. Coexistence tends to decrease to a minimum or is not existent at all. Concomitantly, the AFs tend to take advantage of all available space, and MFs with trees growth disappear on this surface.

3 Ecological Patterns of Animal Forests on the Southern Tip of South America and Antarctic Continental Shelves

In the last two decades, the evolutionary, biogeographical, and ecological relationships between the tip of South America and Antarctica have been undoubtedly one of the issues that caused vigorous scientific controversy. In fact, 89 papers

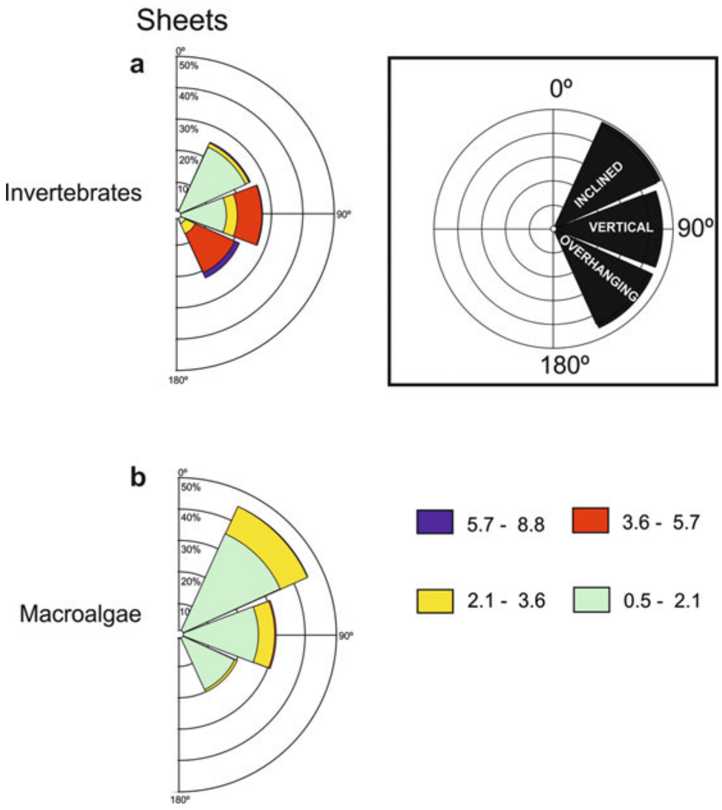

Fig. 6 Radial chart shows the distribution patterns of invertebrates and macroalgae with sheets growth forms from each surface inclinations (expressed as degree of inclination, see *inset* chart). *Colors* indicate the percentage frequency of occurrence

were published under the umbrella of the interactions between the Magellan region and the Antarctic (IBMANT) congress (Arntz and Ríos 1999; Arntz et al. 2005).

On the one hand, this happened because the study of the distribution of benthic species along a latitudinal gradient is a subject of ongoing discussion (Roy et al. 2000; Gray 2001; Berke et al. 2014). In this context, the concept of AFs cannot be absent from this important debate. On the other hand, while the competition between clonal growth form and solitary (= aclonal) organisms with gregarious growth form (*sensu*, Jackson 1977) has been continuously investigated locally, it is poorly understood how this local competence influences the distribution patterns on a larger geographical scale (Barnes and Neutel 2016). The competition among clonal and gregarious AFs between the tip of South America and the Antarctic continent may result in an emergent distribution pattern.

3.1 Abundance Patterns of Gregarious and Clonal Animal Forests

Mollusk bivalve species such as *Mytilus chilensis*, *Aulacomya atra*, and *Perumytilus purpuratus* are some of the most conspicuous members of the gregarious AFs on hard substrates in the Chilean fjords and channels ecosystem, as they are extremely abundant and normally can monopolize the physical space in the intertidal zone (Ríos and Gerdes 1997). In the sublittoral, gregarious AFs such as mytilids are so productive that annually more than 160 million tons are extracted (Carranza et al. 2009). Gregarious AFs are not only composed of mollusk bivalves but also of other bivalve-like organisms such as the brachiopod *Magellania venosa* (Försterra et al. 2008). Another gregarious group, which is very important in subtidal rocky reefs in several areas of the Chilean fjords and channel ecosystem, are tubeworm polychaetes (Fig. 1d) such as *Chaetopterus variopedatus* (Försterra et al., ▶ Chap. 10, “Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters” in this volume).

In contrast, south of the Antarctic Polar Front, AFs with clonal growth forms are the most dominant bioengineers on both hard and soft substrates. Hexactinellid and demosponges are the dominant groups on the Weddell and Ross Sea continental shelves and also on the Bransfield Strait and other sites around the West Antartic Peninsula (Gerdes et al. 1992; Ragua-Gil et al. 2004; Gutt et al. 2010, 2016; Cárdenas et al. 2016b). In a second place, cold-water soft corals (octocorals) are also a dominant group of clonal AFs in the Antarctic seabed (Orejas et al. 2000; Gili et al. 2002). Hard cold-water corals such as *Errina* sp. (Gutt et al. 2010) are also present in the Antarctic seafloor but less abundant than the former groups of clonal AFs.

3.2 Distribution Pattern of Gregarious and Clonal Animal Forests: Is There a Pattern Along a Latitudinal Gradient Between Magellan and Antarctic Areas?

Figure 7 summarizes the proposed conceptual model based on previously described empirical evidence from available literature. This distribution pattern shows a shift in the dominance of AFs groups between gregarious and clonal

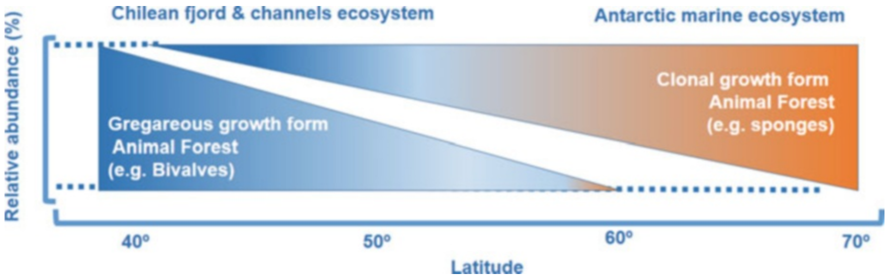

Fig. 7 Conceptual scheme of the distribution pattern, which shows a shift in the dominance of AFs groups between gregarious and clonal organisms along a latitudinal gradient

organisms along a hypothetical north-south latitudinal gradient. When dissecting the latitudinal distribution pattern between Magellan and Antarctic areas, some empirical evidence shows that the clonal growth forms diminish with decreasing latitude. At low latitudes, represented by the Chilean fjords and channels, most of the clonal AFs are mainly formed by sponges with encrusting growth forms (see Willenz et al. 2009), whereas massive sponges are very evident and dominant on the Antarctic shelves. In contrast, gregarious AFs growth forms show abrupt decline with increasing latitude, where large mollusks bivalve beds are virtually absent on the continental Antarctic shelf, and they are not replaced significantly by any other group sessile invertebrate that reach similar abundances.

3.2.1 A Hypothesis

The proposed distribution pattern of clonal and gregarious AFs may be explained by the influence of the extremely low temperatures, to which the Antarctic marine ecosystem has been subjected for over 30 million years. Low temperatures in Antarctica have resulted in the low abundance of calcified organisms, explained by the increased cost of calcification due to decreased solubility of calcium carbonate at these temperatures. This has also been cited to explain the absence of durophagous and the prevalence of weak-shelled organisms in Antarctic waters (Aronson et al. 2007; McClintock et al. 2009; Gazeau et al. 2013). On the other hand, it is possible that abiotic factors inside the Antarctic marine ecosystem, such as the weak relationship between land and ocean, inherited from the last maximum glaciation (Gili et al. 2006), may have favored the most primitive growth forms represented by clonal growth. In contrast, the last glacial maximum drastically changed the coastline along the southern tip of South America (Hulton et al. 2002; Thomson et al. 2010), with the consequent retreat of ice and the increase of the ocean level generating the current geomorphology and oceanography conditions of the Chilean fjords and channels. Therefore, this marine ecosystem has been described as an ecosystem geologically recently (<8k years, Montiel et al. 2005). As a result, benthic organisms that have colonized this marine ecosystem are relatively modern. In addition, abiotic conditions in the Chilean fjords and channels are highly influenced by the land-ocean relationship (Silva et al. 2011) that is characterized by a significant discharge of sediment from rivers and cold freshwaters from glacial (Salcedo-Castro et al. 2015). These extreme oceanographic conditions are not conducive to the establishment and growth of AFs with primitive clonal growth forms such as mounds sponges. Further empirical studies are needed to confirm the proposed pattern.

4 Highlights and Outlook

One of the great challenges of science is to explain successfully the complexity of biological ecosystems to society nonspecialist. In this context, the concept of AFs is an easy, intuitive, and didactic way to transmit in simplified form how important these forms are for marine ecosystems. Marine ecosystem services have been useful to raise awareness among decision-makers for the importance and value of marine organism to the humankind. For instance, the epilithic AFs and MFs can provide an important ecosystem service, specifically for the future development of future underwater tourism in cold-waters ecosystem.

Along a latitudinal gradient, very abundant gregarious AFs (e.g., mytilids) on the subantarctic shallow rocky substrate tend to decrease in their abundance and distribution toward the rocky substrate of the Antarctic shallow areas. A contrasting pattern emerges regarding clonal AFs (e.g., sponges), where dense assemblages of clonal growth forms are dominant in the Antarctic rocky substrate and tend to decrease toward the southern tip of South America.

Despite that AFs distribute worldwide, the coexistence between AFs and MFs only occurs in a narrow spatial range on rocky substrate. Consequently, these mixed ecosystems are highly vulnerable to increased ocean temperature and acidification. Hence, global warming not only caused dramatic changes in the distributions of AFs or MFs but can also break the coexistence between them. This disruption in ecological relationships caused the collapse of ecosystems (Keith et al. 2013). All of these effects and consequences highlight the importance of the conservation of the unique AFs and MFs (and their interactions) that occurs in southern cold-water ecosystems.

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5 Cross-References

- ▶ Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters
- ▶ Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems
- ▶ Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems
- ▶ Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages
- ▶ Where Seaweed Forests Meet Animal Forests: The Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem

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Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters

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Günter Försterra, Verena Häussermann, and Jürgen Laudien

Abstract

The Chilean fjord region, situated between 42 and 56° S, forms one of the most ragged shorelines and belongs to the ecologically and biogeographically least understood marine regions of the world. A labyrinth of fjords, channels, and islands extends over 240,000 km^2 and creates a coastline of more than 80,000 km. Due to strong abiotic gradients, numerous habitats are created, which are further diversified by temporal dynamics (tidal cycle, seasonal changes in precipitation, temperature, radiation, etc.). The region is a biodiversity hotspot hosting unique and fragile ecosystems. Among the species living here, several are species forming habitats in the ecosystem. These organisms can reach high densities conforming the so-called marine animal forests. Examples are marine animal forests dominated by cold-water stony corals, gorgonians, hydrocorals, brachiopods, polychaetes, giant

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barnacles, sponges, and ascidians. Many of these communities have been discovered only recently. There is also a singular characteristic in this area: exceptionally low pH levels of the waters of Patagonian fjords provide the opportunity to study calcifying organisms in an environment with pH conditions in the same range as the ones predicted by the IPCC for the world oceans in 2100. Despite the scarce ecological and biogeographical knowledge of this area, it encounters an unparalleled economic development including high-impact industry-scale salmonid farming, ambitious infrastructure and industrialization projects, and increasing extractive activities. Baseline research on the abiotic and biotic environment of the region is needed to reach sustainability in the use of the marine resources. Management plans including the establishment of marine protected areas to preserve benthic diversity and ecosystem services are urgently needed.

Keywords
Cold-water scleractinian coral bank • Hydrocoral reef • Mytilid bank • Brachiopod bank • Gorgonian forest • Polychaete forest • Giant barnacle forest • Deep-water emergence • Low pH • Aquaculture • Marine protected areas

Contents

1 Introduction

The coastline of Chilean Patagonia extends along 1,500 km from 42 to 56° S (Fig. 1). A labyrinth of channels, islands, and fjords covering an area of 240,000 km^2 multiplies the coastline to more than 80,000 km (e.g., Pantoja et al. 2011) yielding the largest and most ragged fjord region of the world (Försterra 2009). Here, pronounced

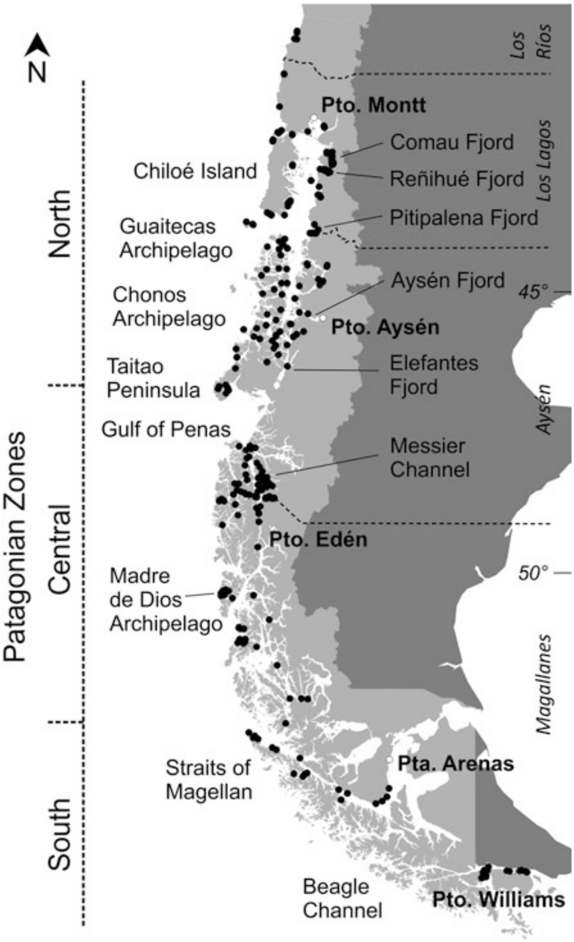

Fig. 1 Map of Chilean Patagonia (light grey) indicating the separation of the Magellanic Province into the North, Central, and South Patagonian Zone and the separation into political regions (Los Lagos, Aysén, and Magallanes Region). The study sites visited between 1998 and 2016 are indicated with black circles

physical and chemical gradients overlap (e.g., salinity and wave exposure have a pronounced east-west gradient), forming a complex pattern with multiple combinations, which can be stable or can fluctuate in time and space on different scales (e.g., considerable seasonal and spatial variation in depth of the low-salinity surface layer). Marked differences often occur within short spatial distance, e.g., the salinity or sedimentation rate may vary strongly due to river runoff. These overlaying sets of different factors shape many unique habitats and niches for marine organisms, resulting in elevated species richness when compared to the coast north of 42° S.

In the fjords, a pronounced low-salinity layer (LSL) (Iriarte et al. 2014) is responsible for a reduced diversity in the upper few meters (down to 15 m water depth in the inner fjords). Below the LSL, many new species of different taxa have been reported (Häussermann and Försterra 2009), e.g., south of 42° S, the number of anthozoan species doubles (Häussermann 2006).

In Chilean fjords, the benthic species, including calcifying organisms, thrive in waters with pH values, which may locally be as low as 7.4 (Jantzen et al. 2013). These are similar conditions as predicted for the world oceans for the end of this century due to ongoing ocean acidification (Caldeira and Wickett 2003; Orr et al. 2005). This allows to study in situ the effects of low pH on benthic organisms and to test hypotheses if they can develop mechanisms to cope with these conditions.

Another interesting phenomenon of Chilean fjords is that the benthic fauna in the littoral zone includes many species commonly known from greater water depth, a phenomenon called deepwater emergence (Försterra 2009). The depth ranges of the respective species are enlarged; they occur from deep to shallow water. An example is the cold-water stony coral *Desmophyllum dianthus* (depth range 7–2,500 m). Deepwater emergence is also known from other fjord regions, e.g., from antipatharians in New Zealand (depth range 1–2,000 m) (Grange et al. 1981) and reefs of the stony coral *Lophelia pertusa* (depth range 39–3,000 m) from Norway (Fosså et al. 2002).

Chilean Patagonia hosts one of the least studied marine regions of the world (Arntz 1999; Schwabe et al. 2006). Not only the enormous extension and complexity contribute to this lack of knowledge, but there are also technical reasons. For example, the most important taxonomic inventory studies, such as the Challenger Expedition 1872–1876 (Murray 1895; Rice 1999) and the Lund University Chile Expedition 1948–1949 (Brattström and Johanssen 1983), were carried out by research vessels in the late nineteenth and early twentieth century. Since 1994, the Chilean National Oceanographic Committee (CONA) carries out the CIMAR Fiordos research program to study the oceanography of Chilean Patagonia (Silva and Palma 2006). In the poorly mapped channels and fjords, these vessels had to keep a safe distance from shore. Thus they were restricted to take samples of the seafloor in the center of the U-shaped fjords and channels, which is characterized by soft sediment, and to take samples in the LSL-influenced intertidal zones, respectively. With nearly 1,300 m, the deepest spot of Chilean Patagonia is situated in Messier Channel. Today it is known that an important portion of the benthic biomass and most of the benthic diversity is restricted to the rocky slopes in the upper subtidal zone (Försterra 2009), habitats that can only be studied by scuba diving or with remotely operated vehicles (ROV) equipped with a manipulator for sampling. Both approaches have only recently been applied systematically for benthic studies in the area. However, the largest part of Chilean Patagonian maritime environments is very remote, and due to harsh weather conditions and the difficult and costly access to suitable research vessels, huge portions of the ecosystem are virtually unknown.

Therefore, it is not surprising that the biogeographic subunits of the Chilean fjord region are still being discussed, and several different classifications were proposed. Most authors agree on the existence of the warm-temperate or Peruvian Province from the Peninsula Illescas to Chiloé Island (6–42° S) and the cold-temperate or Magellanic Province from Chiloé Island to Cape Horn (~42–56° S) (Häussermann and Försterra 2005). Based on oceanographic characteristics, Pickard (1973) subdivided the Magellanic Province into three zones. Viviani (1979) and Stuardo and Valdovinos (1992) agreed to this subdivision and called these three zones North (42° S–46° 30′ S), Central (46° 30′ S–53° S), and South Patagonian Zone (53–56° S) (Fig. 1). Camus (2001) reviewed 27 different zoogeographic studies and proposed a Peruvian and a Magellanic Province with an extended intermediate area in the middle (30–42° S) and transition areas in between. Lancellotti and Vásquez (1999) neglect the widely assumed faunal break at 42° S and suggest a transitional temperate region between 35 and 48° S. Montiel et al. (2005) confirmed a separation of the Magellan region into Pacific and Atlantic subregions.

The Chilean fjord region is recognized as a unique, highly fragile and vulnerable ecosystem (Iriarte et al. 2010; Pantoja et al. 2011) and a biodiversity hotspot (Fernández et al. 2000; Häussermann and Försterra 2009). Within the benthic fauna, there is still a huge fraction of organisms that has not been described yet. Recent species inventories of the shallow rocky subtidal zone (0–30 m water depth) yielded an average of >10% of new species, with proportions as high as 66% in taxa such as sponges, gorgonians, and corals, even in the relatively easy-to-access parts of the area (Häussermann and Försterra 2009). Despite the scarce biological and ecological knowledge of the marine life of Chilean Patagonia, the anthropogenic activities in this region significantly increase including high-impact aquaculture industry, mainly large-scale salmonid farming, ambitious infrastructure and industrialization projects (e.g., hydroelectricity, road works, building of wharfs and ports), and increasing extractive activities (fisheries, shellfish harvesting) (Pantoja et al. 2011).

Although 18% of Chile's land is currently protected, few marine protected areas (MPAs) existed; until recently only 0.03% of the Chilean sea was protected before 2010 (Thiel et al. 2007). With the new large MPA around the offshore islands of Sala and Gómez, the percentage rose to 4.41% in the year 2010. In 2014, the Patagonian MPA Piti Palena-Añihue was added. Including the large Nazca-Desventuradas MPA, approximately 12.3% of Chile's exclusive economic zone (approximately 3,681,989 km^2) was protected in 2016. There are still few coastal MPAs, especially in southern Chile. Currently, Chilean Patagonia hosts six MPAs (Table 1), which only cover approximately 0.7% of its exclusive economic zone. A main problem of these MPAs is that control and surveillance in this remote region is poor or lacking at all. Hence a precautionary approach, creating enough and sufficiently large MPAs including extended no-take zones in each biogeographical subunit (the aim of the Chilean government was to save at least 10% of each relevant habitat), is necessary to prevent major losses of species, entire communities, and ecosystem services. However, lower-impact human activities within MPAs are encouraged by the government, and the highly favored multiple-use MPAs even allow for extractive activities (Thiel et al. 2007).

Table 1 Marine protected areas of Chilean Patagonia

Name	Category	Approx. coordinates	Area (ha)	Main aim
Pullinque Marine Reserve	Marine reserve (genetic reserve)	41°50′ S; 73°59′ W (Golfo de Quetalmahue)	243.56	Preserve genetic diversity of the oyster *Ostrea chilensis*
Putemún Marine Reserve	Marine reserve (genetic reserve)	42°27′ S; 73°44′ W (Estero de Castro)	753.1	Preserve genetic diversity of the mussel *Choromytilus chorus*
San Ignacio del Huinay Coastal Marine Protected Area	Coastal marine protected area[a]	Approx. 42°23′ S; 72°25′ W (Comau fjord)	414.55	Facilitating research
Piti Palena-Añihue MU Marine and Coastal Protected Area	Multiple-use marine and coastal protected area	Approx. 43°46′ S, 72°57′ W (Piti Palena Fjord, Añihué Bay)	23.862	Protecting coast and islands of the Aysén region
Francisco Coloane MU Marine and Coastal Protected Area	Multiple-use marine and coastal protected area	Approx. 53°38′ S, 72°20′ W (Straights of Magellan)	65.350	Protection of the feeding area of the humpback whale *Megaptera novaeangliae*, Magellan penguin *Spheniscus magellanicus* and the sea lion *Otaria flavescens*
Isla Carlos Tercero Marine Park (part of Francisco Coloane)	Marine park	Approx. 53°38′ S; 72°20′ W (Straights of Magellan)	6,562.17	See above

[a] Several aquaculture concessions which had been given before designation of MPA are still present

2 Animal Forests of Chilean Patagonia: Latitudinal, Longitudinal, and Bathymetric Distribution

During the biodiversity surveys, conducted between 1998 and 2016 by two of the authors of this chapter (G. Försterra and V. Häussermann), 11 benthic assemblages have been found along the Chilean Patagonian shore, which are structured by habitat-forming species, creating the so-called animal forests (Figs. 2 and 3). The respective ecosystem engineering species (sensu Jones et al. 1994) modulate the abiotic and biotic environment and maintain a distinct self-organizing habitat used by a diverse associated fauna. All recorded habitat-forming species of Chilean Patagonian animal forests are heterotrophic suspension feeders and thus enhance

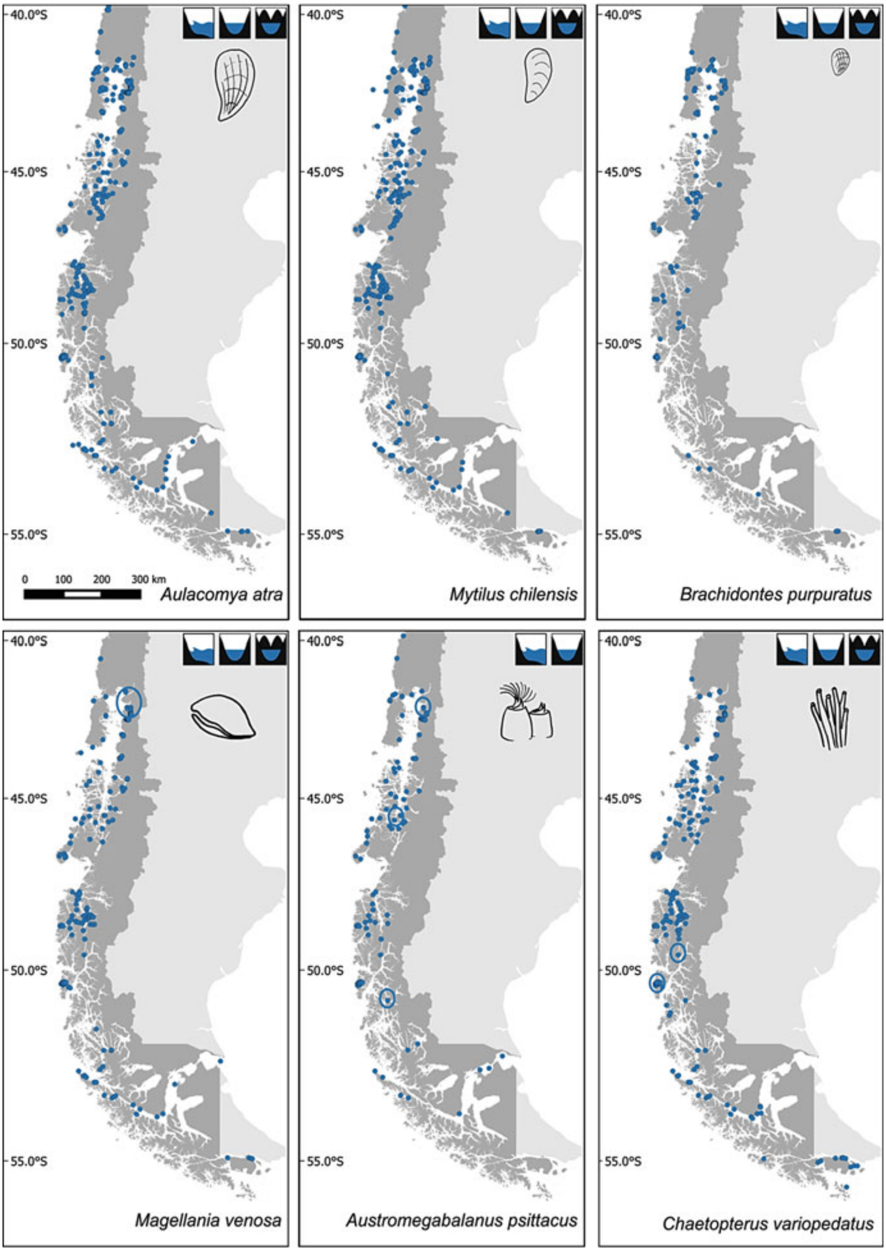

Fig. 2 Distribution records of *Aulacomya atra*, *Mytilus chilensis*, *Brachidontes purpuratus* (all Bivalvia), *Magellania venosa* (Brachiopoda), *Austromegabalanus psittacus* (Cirripedia), and *Chaetopterus variepedatus* (Polychaeta) in Chilean Patagonia. *Circle*: area where species forms habitats. The mytilids are habitat-forming throughout their distribution ranges. Little pictograms above species symbols represent habitat types in which species can be found: in *top left* map from *left* to *right* exposed coast, channels, and fjords

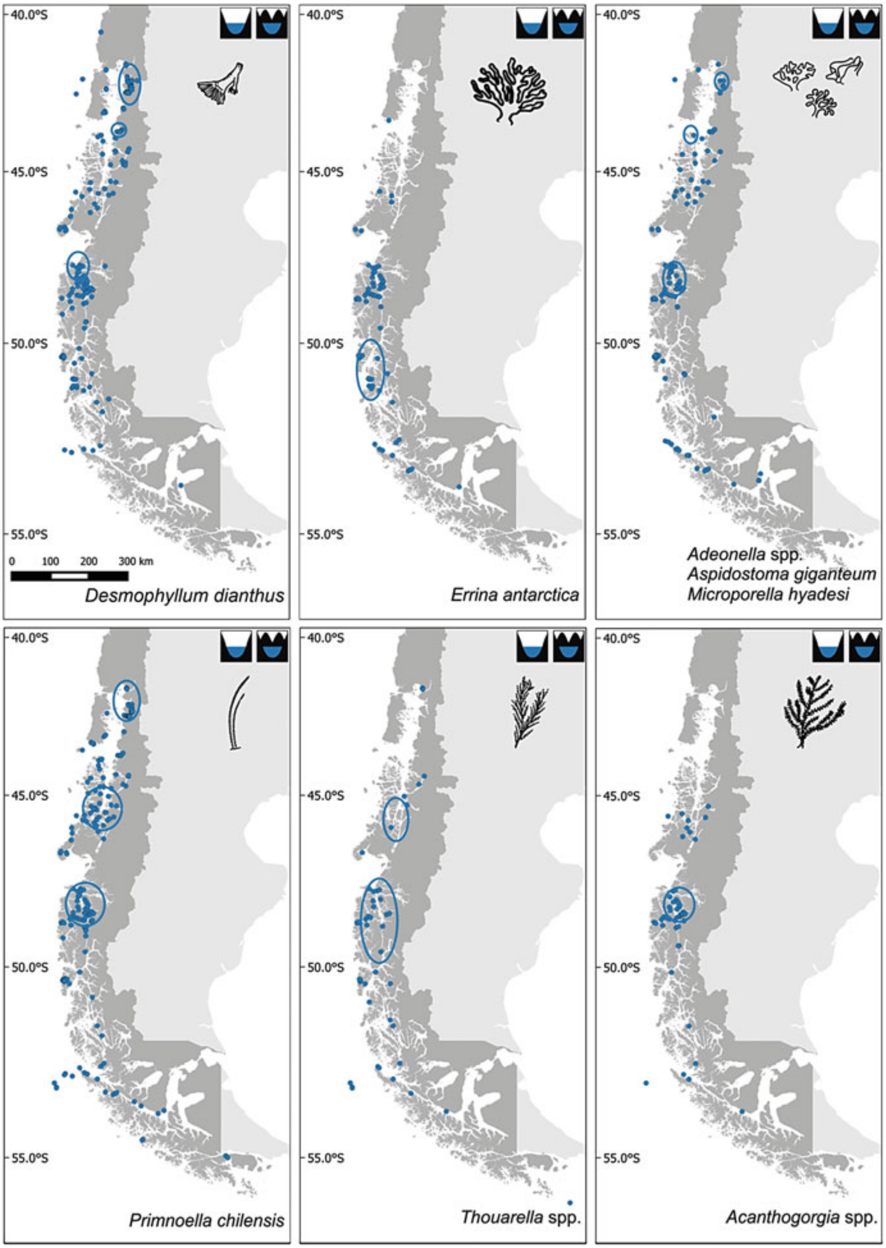

Fig. 3 Distribution records of *Desmophyllum dianthus* (Scleractinia), *Errina antarctica* (Hydrozoa, Stylasteridae), *Adeonella* spp./*Aspidostoma giganteum*/*Microporella hyadesi* (all Ectoprocta), and *Primnoella chilensis*/*Thouarella* spp./*Acanthogorgia* spp. (all Alcyonacea) in Chilean Patagonia. *Circles*: areas where species form habitats. Little pictograms above species symbols represent habitat types in which species can be found: in *top left* map from *left* to *right* channels and fjords

the pelago-benthic coupling through carbon and nutrient fluxes between the pelagic and the benthic realm. By colonizing bare (up to nearly vertical) rock faces, these animals form complex ecosystems maintaining high biodiversity. Although the respective habitat-forming species have wider latitudinal, longitudinal, and sometimes bathymetric distributions, animal forests recorded so far were only discovered in distinct areas. The matrix organisms of Chilean Patagonian animal forests may be subdivided into three main categories, presented below:

1. Marine animals with massive calcified skeletons separated in the subcategories:
    (i) Bioengineers presenting a massive exoskeleton (mussels, brachiopods, and barnacles)
    (ii) Bioengineers presenting a massive endoskeleton (cold-water scleractinians, hydrocorals, and ectoprocts)
2. Bioengineers with scattered calcified structures (spiculae) (gorgonians, sponges) and
3. Marine noncalcifying animals (Table 2) following the classification system by Jackson (1977).

The categories including massive exo- and endoskeletons frequently provide the ecosystem-structuring elements even after the animal died. Thereafter the structures may even be modified creating additional habitats (e.g., cold-water coral rubble or shell gravel habitats).

2.1 Marine Animal Forests Conformed by Animals with Massive Calcified Skeletons

2.1.1 Animal Forests Conformed by Calcifying Bioengineers Presenting a Massive Exoskeleton

Mussel Banks

In the upper 10 m, mytilid banks dominate the rocky substrate (Fig. 4). *Mytilus chilensis* (highly abundant in fjords and channels, 20–56° S) and *Brachidontes purpuratus* (abundant at the exposed coast, scarce in fjords and channels, 18–56° S) dominate the intertidal zone (*B. purpuratus* is only described from the intertidal zone, and *M. chilensis* can be found down to 37 m water depth), while *Aulacomya atra* (18–56° S) thrives from the shallow subtidal zone down to 30 m water depth (high abundances in fjords and channels), although individuals can be found as deep as 50 m (Fig. 2). The upper depth limit for mussel communities is controlled by abiotic factors (mainly air exposure and temperature differences due to a tidal range of more than 7 m), whereas biotic interactions limit the expansion at the lower depth limit. Mussel predators, such as abundant sea stars (e.g., *Cosmasterias lurida*) and carnivorous gastropods, are restricted to depths below the LSL. Thus, the LSL may act as a refuge for *A. atra* in its upper distribution range (Baumgarten et al. 2013). Old mussel banks with a thickness of up to 30 cm present a balanced population with juvenile, mature,

Table 2 Hard bottom marine animal forests of Chilean Patagonia (see Figs. 2 and 3) Northern Patagonian Zone = NPZ, Central Patagonian Zone = CPZ, Southern Patagonian Zone = SPZ

Name	Ecosystem engineering specimen	Category of ecosystem engineering specimen	Bathymetric distribution of the species	Geographical distribution of the species	Main habitat of the animal forest
Mussel banks	*Mytilus chilensis*	Bioengineer presenting a massive exoskeleton	Intertidal to 37 m	20–56° S	Fjords, channels, exposed coast
	Brachidontes purpuratus		Intertidal	18–56° S	Fjords, channels
	Aulacomya atra		Lower intertidal to 30 m	18–56° S	
Brachiopod banks	*Magellania venosa*	Bioengineer presenting a massive exoskeleton	2–1,362 m depth	30–54° S	Northernmost fjords Reloncaví, Comau, Reñihué, and Pitipalena; steep rocky substrates
Barnacle aggregations	*Austromegabalanus psittacus*	Bioengineer presenting a massive exoskeleton	Intertidal to 35 m	18–56° S	More abundant toward the exposed coast
Cold-water stony coral forests	*Desmophyllum dianthus*	Bioengineer presenting a massive endoskeleton	7–2,460 m	Cosmopolitan, in Chile: 42–56° S	Forms banks from shallow to deep waters of northernmost fjords Reloncaví, Comau, Reñihué; and in depth below 40 m in Piti palena Fjord; larger accumulations around the northern end of Messier Channel below 30 m
	Caryophyllia huinayensis		11–800 m	37–54° S	Mainly near vertical to overhanging rocky substrates
	Tethocyathus endesa		11–200 m	37°S–54° S	Substrates with angels of 71 to 145° (Diercks 2015)
Cold-water hydrocoral forests	*Errina antarctica*	Bioengineer presenting a massive endoskeleton	10–500 m	43° S to the Antarctic	Channels with strong currents in the CPZ, horizontal to vertical rocky substrate

Ectoprocta aggregations	*Adeonella* ssp.	Bioengineer presenting a massive endoskeleton	10–33 m	42–56° S	Fjords, channels with strong currents; horizontal to vertical rocky substrate
	Microporella hyadesi		14–27 m	43–56° S	
	Aspidostoma giganteum		4–45 m	42–56° S	
Gorgonian gardens	*Primnoella chilensis*	Bioengineers presenting scattered calcified structures	Down to 320 m	41–54° S	Fjords, channels; mainly NPZ
	Thouarella spp.		Down to 1,500 m	41–51° S	Fjords, channels; mainly CPZ
	Acanthogorgia ssp.		20–28 m	48–51° S	Fjords, channels; CPZ
	Muriceides ssp.		18–32 m	48–49° S	Fjords, channels; CPZ
Sponge fields	Demospongiae and Calcarea	Bioengineers presenting scattered calcified structures			Exposed areas
Polychaete fields	*Chaetopterus variopedatus*	Bioengineer without calcifying structures	1–485 m	Cosmopolitan, in Chile: 27–56° S	Channels
Ascidian aggregations	*Sycozoa sigillinoides*	Bioengineer without calcifying structures	10–548 m	44–54° S	SPZ (Beagle Channel)

Fig. 4 Subtidal mussel forest (*Aulacomya atra*) at Lilihuapi Island, Comau Fjord (42°09′32.0″ S, 72°35′41.1″ W); ~10 m. Epizoic species visible on main photo: *Incrustatus comauensis* (encrusting soft coral), *Crepidula* sp. (slipper snail), *Loxechinus alba* (sea urchin), *Austromegabalanus psittacus* (barnacle); largest mussels in foreground approx. 12 cm in length; on detail: *Halcurias pilatus* (orange sea anemone), *Halisarca magellanica* (pink sponge); scale bar 10 mm

and old individuals and provide habitat for many invertebrates. Associated invertebrates colonize the surface of the mussel shells or inhabit the spaces between the mussels, e.g., sea anemones (in the Northern Patagonian Zone (NPZ) *Anthothoe chilensis* and/or *Halcurias pilatus*, further south *Metridium senile lobatum*, which often densely cover the mytilids; other species such as two unidentified acontiarian anemones and *Anthopleura hermaphroditica* are less common), barnacles (in the fjords, mytilid banks in the upper 10 m can be completely covered by *Elminius kingii*), sponges (e.g., *Haliclona* spp.), echinoderms (sea cucumbers, mainly *Heterocucumis godeffroyi*; sea urchins of the species *Arbacia dufresneij*, *Pseudechinus magellanicus*, and *Loxechinus alba*; starfish such as *Henricia* sp.), hydrozoans, ectoprocts, soft corals (*Alcyonium* sp.), mollusks (gastropods mainly *Crepidula* sp., nudibranchs, and chitons), crustaceans, ascidians (e.g., *Didemnum studeri*, *Pyura chilensis*), and polychaetes (e.g., Spirorbidae). Some associated invertebrate species settle on the shells (encrusting soft corals, e.g., *Incrustatus comauensis*; ectoprocts, e.g., *Beania magellanica*; and sponges, e.g., *Hymenancora* sp.); others, such as polychaetes (e.g., Nereididae), ophiuroids, and little amphipods live between the byssus filaments of the mussels and are only detected when the mussels are removed from the natural

Fig. 5 Brachiopod forest (*Magellania venosa*) at entrance of Cahuelmó Fjord, a lateral fjord of Comau Fjord (42°15′46.8″ S, 72°26′21.9″ W), ~25 m. Epizoic species visible on main photo: various hydrozoans, ectoprocts (the most eye-catching is *Cellaria malvinensis*), and sponges; largest specimens approx. 6 cm in diameter; on detail: *Clavularia magelhaenica* (soft coral), *Beania magellanica* (encrusting ectoproct); scale bar 10 mm

environment. Small fish species such as *Calliclinus geniguttatus* are also abundant in this habitat.

Brachiopod Banks

The largest currently living brachiopod species *Magellania venosa* (30–54° S, down to 1,362 m depth), which may reach sizes up to 7.5 cm in diameter, is the only known brachiopod species forming *forests* in the Patagonian fjord region. These communities are reported from the northernmost fjords Comau, Reñihué, and Piti Palena, in the Northern Patagonian Zone (Figs. 2 and 5; Försterra et al. 2008). In this area, these terebratellid brachiopods occur in clusters (several up to approx. 20 individuals of different sizes with smaller growing on larger individuals) (Försterra et al. 2008) or banks (extension up to 10,000 m^2) with a population abundance of up to 416 individuals per square meter (Baumgarten et al. 2013). The exceptionally high growth rates of *M. venosa*, together with the high overall growth performance (OGP index = 5.1, the highest recorded for a rynchonelliform brachiopod; Baumgarten et al. 2013), may explain the locally high population abundance. When occurring in dense groups, the shell morphology of single brachiopods may be influenced by shape, size, and orientation of neighboring individuals resulting in irregular shell shape (Försterra et al. 2008). Despite its large lophophore, rynchonelliform brachiopods are considered to have a low metabolism, at least in Antarctic waters (Peck et al. 1997), and low filter-feeding ratios compared to associated bivalves (Rhodes and Thompson 1993). Although no information is available for lower latitudes, we suppose *M. venosa* may not play a major role in the food web, at least outside of the areas where it forms extended banks. However, it is considered ecologically important as habitat-structuring species. Epizoic organisms predominantly settle along the front edges of both valves; invertebrates growing on the shells are sponges (e.g., *Clathrina* sp.), cnidarians (*Clavularia magelhaenica*, *Gonactinia prolifera*, *M. senile lobatum*, *Corynactis* sp., including the benthic polyps of *Aurelia* aff. *aurita* and several species of hydrozoans), ectoprocts (*Cellaria malvinensis*, *Cellaria tenuicollis*, *B. magellanica*), ascidians (*D. studeri*), gastropods (*Crepidula* sp.), polychaetes (*Spiochaetopterus patagonicus*), and the less-abundant brachiopod *Terebratella dorsata*. Further benthic organisms are regularly recorded on brachiopods, e.g., gastropods (*Calliostoma consimilis*, *Nassarius gayi*) and echinoderms (the sea urchins *A. dufresneij* and *P. magellanicus*). Other organisms thriving in the same habitat as *M. venosa* are cnidarians (*D. dianthus*, *Primnoella chilensis*, *Parazoanthus elongates*, *Actinostola chilensis*, and *Corynactis sp.*), polychaetes (*Chaetopterus* sp.), echinoderms (*C. lurida*), and bivalves (*A. atra*). The coexistence of brachiopods and bivalves suggests that brachiopod survival is affected neither by the presence of potential predators nor by space and feeding resource competitors (i.e., mytilids). It is noteworthy that in Chile the geographic distribution of the most dense populations of *M. venosa* coincides with aggregations of the scleractinian cold-water coral *D. dianthus*. Both species are known from the entire fjord region but occur in forest-like structures only in the northernmost fjords (Figs. 2 and 3).

Barnacle Aggregations

The giant barnacle (*Austromegabalanus psittacus*), which can reach 30 cm in length, thrives between 18 and 56° S down to 35 m (Fig. 2), often as small (up to 10 cm) solitary individuals or in small clusters. This species becomes more abundant toward the exposed coast apparently due to more stable and higher salinity values. Here, individuals can reach their maximum size, forming large clusters with younger individuals settling on the plates of older conspecifics. These clusters can largely exceed the length of single individuals (Fig. 6). At sites with moderate wave exposure, large rocky walls can be covered with *A. psittacus* individuals and/or clusters forming a highly structured hard substratum. Especially the cavities originated by the skeletons of dead barnacles are popular refuges or nursing sites for small fishes (*Hypsoblennius sordidus*), decapods (*Pilumnoides perlatus*), and all kind of sessile or cryptically living invertebrates, such as the sea anemone *H. pilatus*. We found large accumulations at three sites: Lilihuapi Island (Fig. 6), Canal Pitt Chico (50°50′6″ S 74°8′20″ W) and Roca Gloria (45°39′26.47″ S; 73°51′57.30″ W) (Since these are single sites, they are not encircled in Fig. 2). Other invertebrates use the barnacles as substrate to settle;

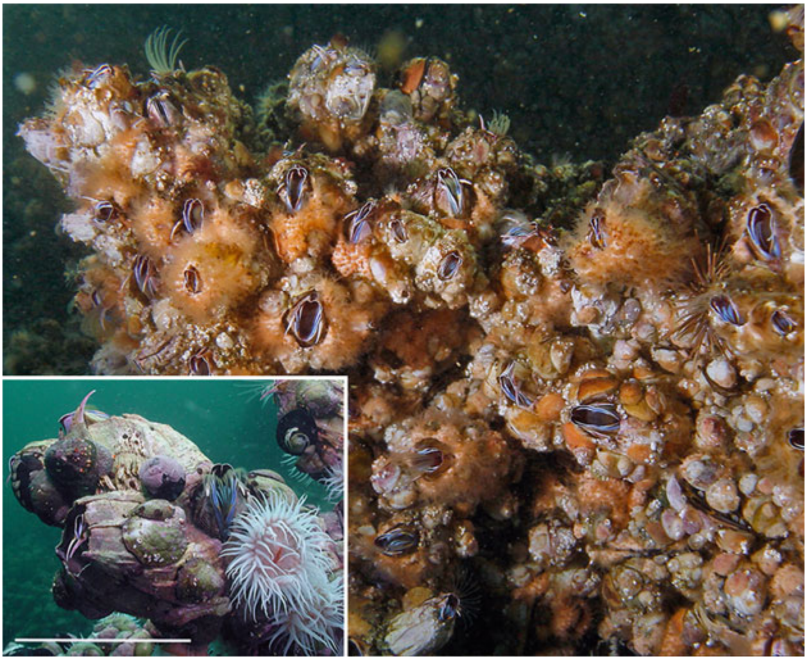

Fig. 6 Barnacle forest (*Austromegabalanus psittacus*) at Lilihuapi Island, Comau Fjord (42°09′32.0″ S, 72°35′41.1″ W); ~15 m. Epizoic species visible on main photo: *Incrustatus comauensis* (orange encrusting soft coral); largest barnacles up to 5 cm diameter; on detail: *Anthothoe chilensis* (white sea anemone), *Crepidula* sp. (slipper snail), *Tegula atra* (black gastropod), *Fissurella* sp. (limpet), *Tonicia atrata* (chiton); scale bar 10 cm

this is the case for some anthozoans: soft corals (*I. comauensis* and *Alcyonium* sp.), zoanthids (*Parazoanthus elongatus*) and anemones (e.g., *A. chilensis* and *Corynactis* sp.), hydrozoans (including the hydrocoral *Errina antarctica*), gastropods (*Crepidula* sp., *Tegula atra* as well as chitons and limpets), bivalves (*A. atra*), and echinoderms (e.g., the sea urchins *A. dufresneij* and *Loxechinus albus* and sea cucumbers). Furthermore, some invertebrates live encrusted on the plates of the barnacles such as sponges, ectoprocts, and ascidians (mainly *D. studeri*).

2.1.2 Animal Forests Conformed by Calcifying Bioengineers Presenting a Massive Endoskeleton

Cold-Water Stony Coral Forests

Dense scleractinian coral banks are well-structured habitats. The cosmopolitan scleractinian cold-water coral *D. dianthus* can be found in continental Chile between 42 and 56° S. It grows on overhanging rock faces and on steep rocky walls (Cairns et al. 2005) with a slope of more than 80° (Försterra et al. 2005) and with its calyx oriented downward presumably to prevent effects of sedimentation, which is high in the area (0.14 ± 0.03 cm year^{-1}; Rebolledo et al. 2011). These corals may anastomose their skeletons; up to 20 individuals grow on each other forming pseudo-colonies. In Chilean fjords, stony corals live already below the LSL starting in approx. 15 m depth; single individuals around islands have been found as shallow as 7 m. *D. dianthus* is supposed to be cosmopolitan; in Chile, specimens are distributed between 42 and 56° S and may be found down to 2,460 m water depth (Häussermann and Försterra 2007a). *D. dianthus* is the most abundant and dominant framework species of cold-water coral forests. It forms three-dimensional habitats from approximately 20 m to at least 280 m water depth (Fillinger and Richter 2013) in the three northernmost fjords of the Northern Patagonian Zone (Figs. 3 and 7) but also at least in some areas at depths below 40 m in the Piti Palena Fjord (43° S). *D. dianthus* grows up to at least 40 cm in length, with a specimen of 25 cm length estimated to be more than 60 years old (McCulloch et al. 2005). The coral banks in the fjords of the Los Lagos Region attain abundances of up to 1,500 coral individuals per square meter (Häussermann and Försterra 2009). The two smaller scleractinian species *Caryophyllia huinayensis* and *Tethocyathus endesa*, associated with *D. dianthus* in the three fjords of the Los Lagos Region, may reach 1,280 individuals per square meter and 1,000 individuals per square meter, respectively, in Comau Fjord but numerically dominate (2,200 ind. m^2) the coral community in the Piti Palena Fjord (43° S) at approximately 20 m water depth (Wurz 2014).

Phototrophic endoliths (e.g., the green alga *Ostreobium queckettii* and the cyanobacterium *Plectonema terebrans*) live on the surface and bore into the uppermost layer of the corallites of individuals of *D. dianthus* and *C. huinayensis* from the euphotic zone (Försterra and Häussermann 2008). Furthermore bioeroding sponges such as *Cliona chilensis* are commonly boring in coral skeletons and may cause the break-off providing new settlement substrate.

In shallow water, the basal portion of the *D. dianthus* skeleton that is not covered by polyp tissue any more is eagerly colonized by sponges (mainly encrusting) such as *Geodia magellani*, *Mycale thielei*, *Iophon* sp., *Clathrina* sp., *Tethya* sp., and ectoprocts (*C. malvinensis*, *Adeonella* aff. *patagonica*); a variety of hydrozoans (e.g., *Obelia dichotoma*); brachiopods (*M. venosa*); tube-forming polychaetes (e.g., *Apomatus* sp., *Hypsicomus phaeotaenia*); the two other stony corals (*C. huinayensis*, *T. endesa*; both approx. 1 cm calyx diameter); and barnacles such as *A. psittacus*. Further associated fauna with *D. dianthus* consists of other anthozoans, such as actinarians (e.g., *Halcurias pilatus*, *A. chilensis*, *Bolocera* aff. *occidua*, and *Hormathia* aff. *pectinata*), stoloniferans, and zoanthids; corallinaceans and gastropods (e.g., *Crepidula* sp.); mytilids (*Aulacomya atra* and *Acesta patagonica*, the latter in Comau Fjord mainly below 60 m depth); and echinoderms (mainly starfish such as *Henricia* sp. and *Poraniopsis echinaster*). Stony coral forests also provide shelter for fish such as *Congiopodus peruvianus* (Fig. 7) and the Cape redfish *Sebastes capensis*, which commonly live between the stony corals (Häussermann and Försterra 2007a). A recent coral mass mortality was observed in Comau Fjord, and it was apparently followed by a decline in Cape redfish abundance at the affected site (pers. observ.). This might indicate a close and long-term

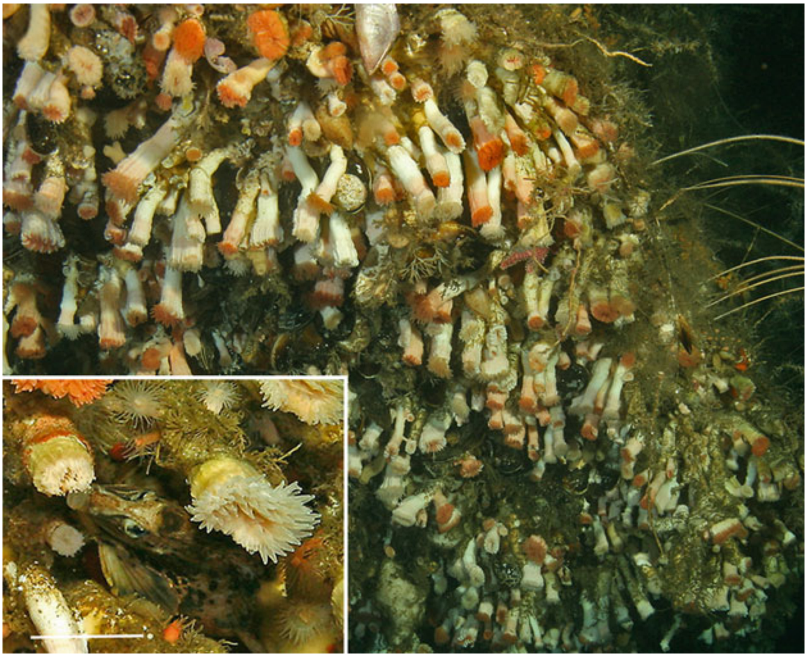

Fig. 7 Cold-water stony coral forest (*Desmophyllum dianthus*); Punta Llonco, Comau Fjord (42°20′38.0″ S, 72°27′25.7″ W); ~25 m. Species visible between and on corals on main photo: *Poraniopsis echinaster* (reddish-violet starfish), *Aulacomya atra* (mussel), various hydrozoans and ectoprocts (the most eye-catching is *Cellaria malvinensis*; see center of photo); calyx diameter of largest corals approx. 4–5 cm; on detail: *Congiopodus peruvianus* (fish), *Halcurias pilatus* (orange and white anemones); scale bar 50 mm

interaction (facultative mutual symbiosis) between the fish *S. capensis* and the coral *D. dianthus*. The fish, especially juvenile individuals, may benefit from the three-dimensional structure, which provides shelter from predators. Furthermore, the coral-associated faunal community provides food to the fish. In turn the coral may benefit from the fin movement of the fish preventing sediment to settle on the coral tissue, which otherwise may affect the corals.

South of 43° S, *D. dianthus* does not seem to form banks, at least not as shallow as 30 m, and rather small and scattered individuals of up to 10 cm length occur. In contrast, certain accumulations of these individuals were also recorded at some sites, especially in the Piti Palena Fjord and around the northern limit of the Messier Channel located in the Central Patagonian Zone (Figs. 1 and 3), where it reaches its greatest depth (1,300 m). In the rest of Chilean Patagonia, the species seems to be very rare in the upper 30 m.

Cold-Water Hydrocoral Forests

The hydrocoral *E. antarctica* can be found from the waters around the southern tip of Chiloé Island (43° S), North Patagonian Zone, to the Antarctic at depths from 10 to

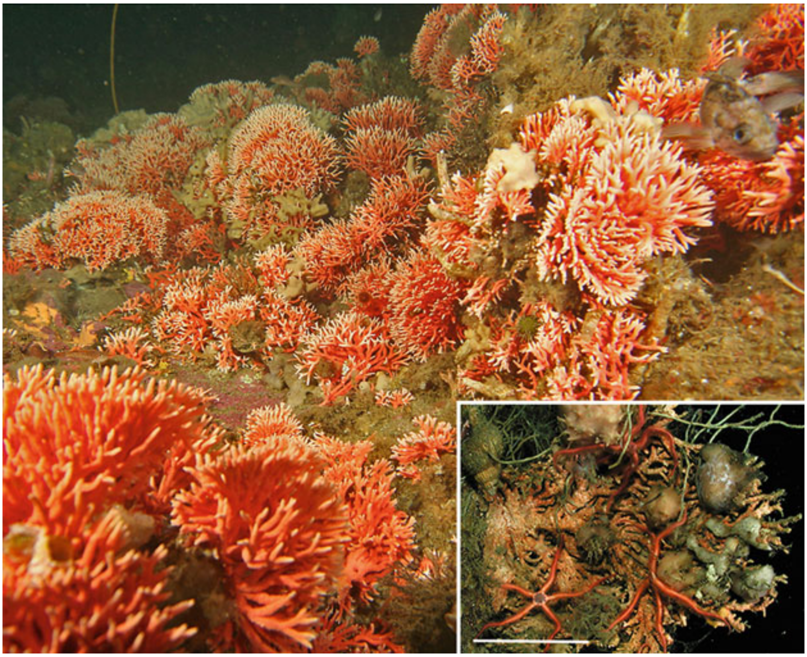

Fig. 8 Cold-water hydrocoral forest (*Errina antarctica*), Copihué Channel, Madre de Dios Archipelago (50°20′23.1″ S, 75°22′39.2″ W), ~25 m. Associated species visible on main photo: various hydrozoans and sponges, *Sebastes capensis* (Cape redfish, *top right*), *Arbacia dufresneij* (green sea urchin); largest colonies approx. 40 cm in diameter; on detail: *Ophiacantha rosea* (crinoid), *Fusitriton cancellatus* (gastropod), various sponges and hydrozoans; scale bar 10 cm

500 m (exceptional 771 m). Colonies are rare and small in diving depths in the North Patagonian Zone (Figs. 1 and 3). Fan-shaped colonies can regularly be seen at sites exposed to currents in channels of the Central Patagonian Zone. Reef-like formations were recorded from the Copihué Channel, Madre de Dios Archipelago, where the bottom was densely covered by three-dimensional colonies up to 40 cm in diameter (Häussermann and Försterra 2007b; Fig. 8). Here, the species was found to dominate the benthos on a surface of at least 10,000 m^2. Autoecological information from this stylasterid species is still lacking; however, colonies of *Errina novaezelandiae Hickson*, 1912 from New Zealand fjords are known to present a linear growth between only 1 and 7 mm per year; it was also observed that in some years, colonies were diminishing in size through partial mortality (Stratford et al. 2001; Miller et al. 2004). The hydrocoral reef provides habitat for many species. Living parts of the colonies are used as substrate or shelter by many sedentary and mobile species such as the filter-feeding crinoid *Florometra magellanica* and the ophiuroids *Gorgonocephalus chilensis* and *Ophiacantha rosea*, the sea anemone *M. senile lobatum*, the hermit crab *Pagurus comptus*, and the gastropod *C. consimilis*. At many sites, the colonies grow intermingled with large sponges and giant barnacles (*A. psittacus*). Several fish species such as *Patagonotothen longipes*, *Sebastes oculatus* (Fig. 8), and *C. peruvianus* live between

the hydrocoral colonies. Dead parts of the colonies are colonized by a multitude of sessile, sedentary, mobile, and boring organisms such as sponges, cnidarians (sea anemones, soft corals, hydrozoans), polychaetes, mollusks (mainly gastropods), and echinoderms (starfish, ophiuroids, sea urchins) (detail of Fig. 8). Among these, the polychaete *C. variopedatus*, the crustacean *Paralomis* aff. *granulosa*, the sea urchin *Arbacia dufresneij*, and the starfish *Lophaster stellans* as well as several not-yet-identified sponges and ectoprocts belong to the most conspicuous representatives.

Ectoprocta Aggregations

Other habitat-building filter feeders are the calcifying ectoprocts *Adeonella* ssp. (42–56° S; 10–33 m), *Microporella hyadesi* (43–56° S; 14–27 m), and *Aspidostoma giganteum* (42–56° S; 4–45 m) (Fig. 3). The latter is abundant on the sill of a lateral fjord of Comau Fjord at 45 m water depth (Northern Patagonian Zone); large aggregations were observed colonizing a steep rocky wall below 25 m water depth in the northern part of the Messier Channel (Central Patagonian Zone) (Figs. 1 and 3); here *M. hyadesi* (detail of Fig. 9) co-occurs. High densities of ectoprocta colonies have also been found below 15–20 m depth around exposed islands of the Guaitecas

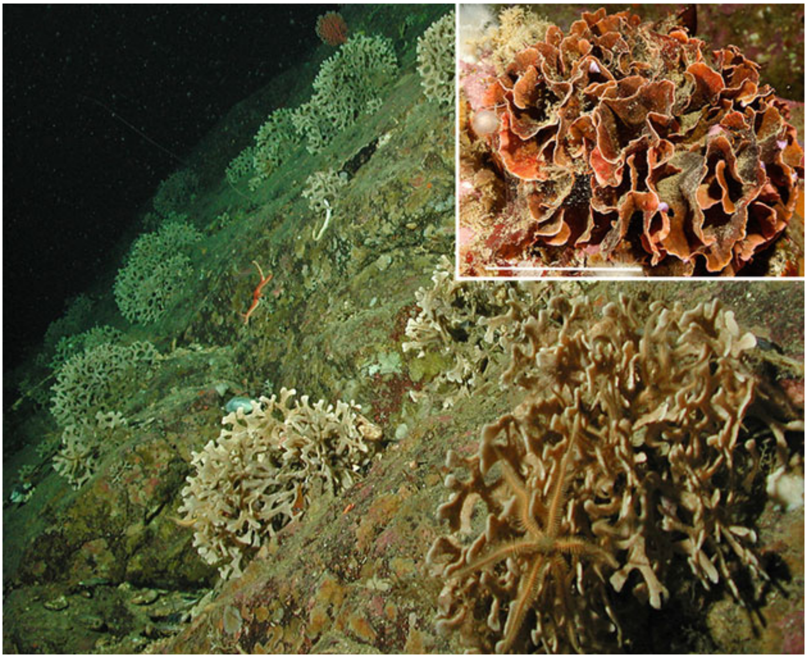

Fig. 9 Ectoprocta forest, Messier Channel (48°58′29″ S, 74°25′16.9″ W); ~30 m. Epizoic species visible on main photo on the ectoproct *A. giganteum*: *Ophiacantha vivipara* (ophiuroid), ectoproct colony in foreground approx. 20–25 cm in diameter; on detail: On the ectoproct *M. hyadesi*: *Calliostoma consimilis* (pink snail), *Pagurus comptus* (hermit crab), *Metridium senile lobatum* (white lobed anemone), *Sycozoa sigillinoides* (stalked ascidian), *Calliostoma consimilis* (pink snails); scale bar 10 cm

Archipelago (Northern Patagonian Zone; 43°53′S, 73°43′W) (pers. observ. 2005). All these sites are characterized by an environment with strong currents (pers. observ.). Individual colonies may reach diameters of 30 cm and are finely branched creating a highly structured substrate for semi-sessile organisms and shelter for mobile ones such as the hermit crab *P. comptus*, the gastropod *C. consimilis*, ophiuroids (e.g., *O. rosea*), starfish (e.g., *Lophaster stellans* and juvenile specimens of *Labidiaster radiosus*), sea urchins (e.g., *A. dufresneij*), anemones (*M. senile lobatum*, *G. prolifera*), bivalves (e.g., *Zygochlamys patagonica*), polychaetes (e.g., *H. phaeotaenia* and *C. variopedatus*), and hydrozoans. Due to the brittle consistency of these ectoprocta colonies, they are eroded comparably fast (e.g., faster than the robust stony coral *D. dianthus*) after the zooids have died. Before dead colonies are completely eroded, a large number of semi-sessile and mainly short living, sessile benthic organisms (such as hydrozoans, other ectoprocts, sea anemones, ascidians, and sponges) eagerly colonized the colony surface.

2.2 Animal Forests Consisting of Calcifying Bioengineers Presenting Scattered Calcified Structures

Gorgonian Gardens

In most gorgonian families, the three-dimensional erect structure of the specimens is mainly supported by a noncalcified gorgonian endoskeleton. Considering these characteristics of gorgonian skeletons and the kind of communities they conform, the habitats created by gorgonians are not reefs and ecologically rather belong to the noncalcifying-animal forests. But due to the fact that the spiculae of gorgonians are built of carbonate material, we classify these communities under the marine calcifying-animal forests.

Below the influence of the LSL (15 m depth), gorgonian gardens dominate the moderately steep rocky substrates of many channels and fjords. While the sea whip *P. chilensis* (41–54° S) dominates in the North Patagonian Zone (Figs. 3 and 10) down to 320 m, being only locally common in the Central and South Patagonian Zone, bottlebrush gorgonians *Thouarella* spp. (41–51° S) (*Thouarella koellikeri* and two undescribed species of *Thouarella*) are the dominant gorgonians in the channels of the Central Patagonian Zone and occur down to 1,500 m (Figs. 2, 3 and 11). In some sediment-influenced channels of the Central Patagonian Zone, ramified gorgonians of the genus *Acanthogorgia* (48–51° S; 20–28 m) and *Muriceides* (48–49° S; 18–32 m) dominate the otherwise rather poor benthic community at least down to 32 m water depth (Figs. 3 and 12). The Straits of Magellan and the Beagle Channel (Southern Patagonian Zone) seem to be inhabited only by few gorgonian species. Gorgonians provide habitat for small species such as the hermit crab *P. comptus*, the sea cucumber *Cladodactyla crocea croceoides*, the gastropod *C. consimilis*, and a still unidentified anemone (exclusively found on gorgonian stems). Gorgonians constitute a substrate for large filter-feeding animals such as ophiuroids (*G. chilensis, Astrotoma agassizii, Ophiactis asperula*) and crinoids (*F. magellanica*). Other organisms are species-specific predators, such

Fig. 10 Gorgonian forests: *Primnoella* forests (*Primnoella chilensis*), Lenca, Seno Reloncaví (41°37′58.9″ S, 72°40′07.0″ W); ~25 m. Thickness of sea whips approx. 1 cm. Epizoic species visible on detail: *Dactylanthus antarcticus* (gorgonian-feeding anemone), *Calliostoma consimilis* (pink snail); scale bar 10 mm

as the sea anemone *D. antarcticus*, which feeds obligatory on primnoid gorgonians (Dayton et al. 1995). These sea anemones are especially abundant in the channels of the Central and South Patagonian Zone, where high-velocity currents characterize the area. When the abundance of *D. antarcticus* is high, they can leave extended areas of dead gorgonians behind. The large nudibranch *Tritonia odhneri* also preys on gorgonians. Dead parts of the gorgonian stems and dead colonies are readily colonized by a multitude of organisms such as alcyonaceans (*C. magelhaenica*, *I. comauensis*, *Alcyonium* sp.), sea anemones (*M. senile lobatum*, *G. prolifera*), zoanthids (*Mesozoanthus fossii*), mytilids, crustaceans (barnacles and an unidentified giant decapod), small ascidians (*D. studeri*, *Paramolgula gregaria*), and a diversity of hydrozoans, ectoprocts (e.g., *C. malvinensis*, *Osthimosia* sp., *Fenestrulina* aff. *vivianii*), and sponges. Other organisms live on the epifauna of the gorgonians (e.g., *Trophon* sp. and pycnogonids). Furthermore, species such as *Chaetopterus* sp. (Polychaeta), *A. chilensis* (Actiniaria), *M. venosa* (Brachiopoda), *E. antarctica* (Hydrozoa), and *A. giganteum* (Ectoprocta) often live in gorgonian forests.

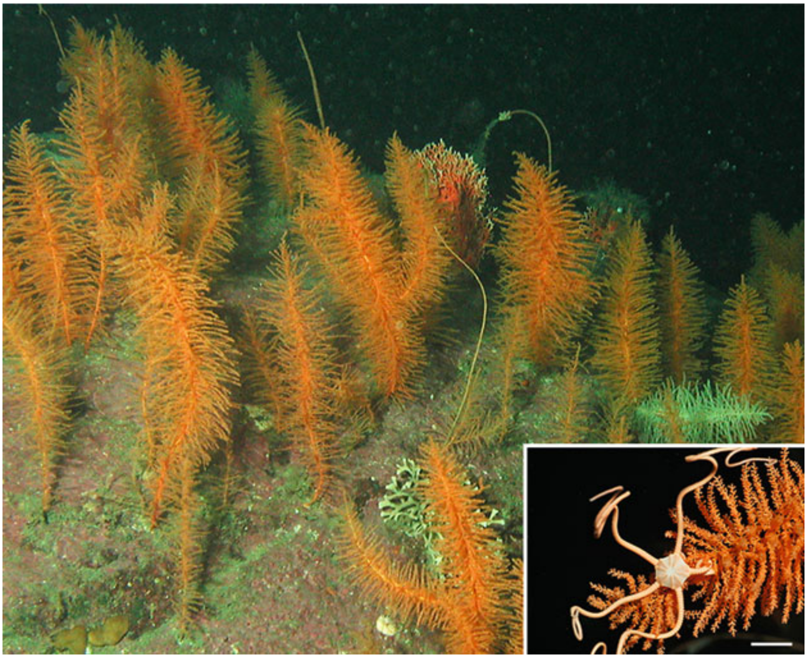

Fig. 11 *Thouarella* forests (*Thouarella* n. sp.), Canal Cochrane, Isla Wellington (48°49′33.5″ S, 75°03′06.5″ W); ~25 m. Associated species visible on main photo: *Errina antarctica* (hydrocoral), *Aspidostoma giganteum* (calcified ectoproct); height of tallest colonies approx. 50 cm; epizoic species visible on detail: *Astrotoma agassizii* (ophiuroid); scale bar 50 mm

Sponge Fields

Species belonging to the classes Demospongiae and Calcarea have calcified spicules. The three-dimensional structures built by these organisms are mainly supported by a noncalcified spongin skeleton, and consequently, the habitats they form are rather related to the noncalcifying-animal forests, as they do not have the capacity to construct reefs. Sponges are very abundant in some places in the Chilean fjord region. Especially erected species, which create colorful "sponge fields," offer places to hide and substrate for other organisms. Sponge communities are not frequent but can be regularly found throughout the Chilean fjord region, mainly in the more exposed locations of the region that are difficult to access. Consequently there is very little information on the structure and associated fauna. Since most of the sponge species have soft bodies and a porous surface, as well as bioactive compounds, which avoid the settlement of epifauna and thus act as a very efficient antifouling mechanism (e.g., Krug 2006), there are only few sessile organisms that can grow directly on sponges. Nevertheless, benthic mobile organisms such as ophiuroids and hermit crabs (*P. comptus*), the small gastropod *C. consimilis*, and amphipods can climb the higher structures of some sponge species, which provide them with a

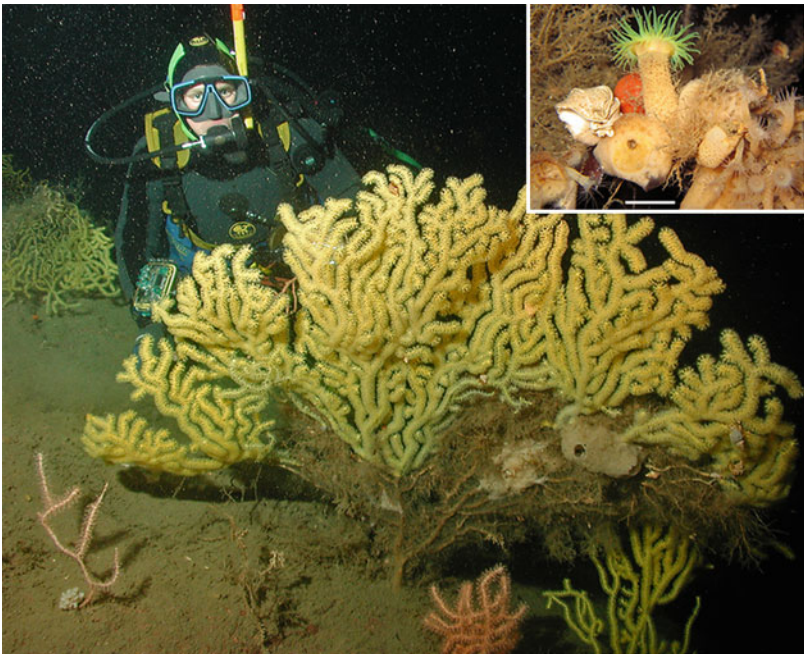

Fig. 12 *Acanthogorgia*/*Muriceides* forests (*Acanthogorgia* spp., yellow gorgonians, *Muriceides* sp., rose-colored gorgonians), Isla Caldcleugh (48°21′37″ S, 74°26′13″ W); 30 m. Epizoic species visible on main photo: *Pagurus edwardsii* (hermit crab), various sponges and hydrozoans; epizoic species visible on detail: *Phellia exlex* (yellow anemone), *Mesozoanthus fossii* (gray zoanthid), *Trophon* sp. (gastropod), *Alcyonium* sp. (red soft coral), various sponges and hydrozoans; scale bar 10 mm

better, elevated position for capturing plankton and other food particles from the water column. Sponges are also a food resource for some organisms, as it is the case for some sea stars such as *P. echinaster* and gastropods (e.g., *Fissurellidea* sp., *Buchanania onchidioides*).

2.3 Marine Non-Calcifying Animal Forests

Polychaete Fields

In some channels and fjords, at least in the Central Patagonian Zone, *C. variopedatus* (27–56° S; 1–485 m) (Figs. 2 and 13) form very dense polychaete fields in the depth range between 10 and 20 m. Individual worm tubes can protrude up to 50 cm from the substratum, and a patch of worm tubes can cover a surface of more than 100 m^2 (pers. observ.) (larger accumulations were found at Cono Guarello (Fig. 13) and Paso del Abismo (49°34′39″ S 74°26′49″ W)). The tubes themselves are habitat for several sessile and semi-sessile organisms such as echinoderms (the sea urchin *A. dufresneij*, the sea cucumber *H. godeffroyi*), nudibranchs (e.g., *Tritonia*

Fig. 13 Polychaete forest (*Chaetopterus variopedatus*), Cono Guarello, Madre de Dios Archipelago (50°23′04″ S, 75°21′05″ W), ~15 m. Epizoic species visible on main photo: *Halisarca magellanica* (pink sponge), *Actinostola chilensis* (sea anemone), various species of hydrozoans, pedal disk diameter of sea anemone approx. 9 cm; on detail: *Campylonothus vagans* (rock shrimp); scale bar 10 mm

challengeriana), decapods (e.g., *Pisoides edwardsii*, *Campylonothus vagans*), ascidians (e.g., *D. studeri*, *P. gregaria*, *Cnemidocarpa verrucosa*), and a variety of ectoprocts (e.g., *C. malvinensis*) and hydrozoans. Other organisms overgrow the tubes of the polychaetes, e.g., sponges (e.g., *H. magellanica*) and soft corals (*C. magelhaenica*). The space between the tubes is a shelter for all kinds of mobile organisms such as sea stars (e.g., *C. lurida*), crustaceans, and fish.

Ascidian Aggregations

Ascidians, in particular the stalked forms, can form aggregations in some areas of the Beagle Channel (Southern Patagonian Zone) that meet the criteria which define an "animal forest" (e.g., three-dimensional structures providing habitat for other species) with short canopy. Colonies of the species *Sycozoa sigillinoides* (44–54° S; 10–548 m) can protrude up to 15 cm from the substratum, and patches can cover dozens of square meters (Fig. 14). Nevertheless, there is very little data on the associated fauna, but some thick bushes of hydrozoans, polychaetes (*Chaetopterus* sp.), and sea whips (*P. chilensis*) have been observed associated to the ascidian forest (pers. observ.).

Fig. 14 Ascidian forest, Angostura Murray, Beagle Channel (54°58′56.6″ S, 68°20′10.7″ W); (*Sycozoa sigillinoides*); 20 m. Accompanying species: *Primnoella chilensis* (sea whips), *Chaetopterus variopedatus* (tube worm), encrusted by *Incrustatus comauensis* (soft coral), various species of hydrozoans; diameter of heads of larger colonies 2–2.5 cm

3 Threats and Observed Impacts

3.1 Indirect Anthropogenic Impacts on Animal Forests of the Chilean Patagonian Fjord Region

Of the three main impacts of climate change on animal forests, i.e., warming, increase of sea level rise, and ocean acidification (see ▶ Chap. 1, "Animal Forests of the World: An Overview" of this volume), the latter may become most relevant for calcified animals of the Chilean Patagonian fjord region. Since they occur in cold subtidal waters with a high tidal range, warming and rising sea level may be less-prominent threats to these communities. Coral skeletons are composed of aragonite, while bivalve shells are composed of calcite; both are crystal forms of calcium carbonate (Constantz 1986). Aragonite is more soluble in cold and deep water than calcite. A reduced seawater pH shifts the carbonate chemistry equilibrium in a way that it gets more difficult for the corals to calcify. Therefore the acidification of the oceans will affect the ability of corals to build up skeletons in deeper waters by rising the so-called aragonite saturation horizon (Ω_{arg}), the benchmark below which calcification is not possible (e.g., Gattuso et al. 1999; Guinotte et al. 2006; Atkinson and Cuet 2008). The fjords of Chilean Patagonia are characterized by naturally pronounced pH gradients (from pH 8.1 to 7.4); the two values of the carbonate chemistry parameters from 50 m water depth measured in 2011 correspond to values predicted for the year 2100 (Jantzen et al. 2013). Changes of up to 0.5 pH units have been recorded both vertically (at some sites within 50 m depth not including the surface LSL; see Fig. 2 in Jantzen et al. 2013) and horizontally (from the head to the mouth of the fjord). Interestingly, all three scleractinians described from shallow water of Chilean Patagonia (*D. dianthus*, *C. huinayensis*, and *T. endesa*; see paragraph "cold-water stony coral forests") grow along the course of the entire pH range and may thrive close to the aragonite saturation horizon ($\Omega_{\mathrm{arg}} = 1$) and even at least sometimes in unsaturated waters ($\Omega_{\mathrm{arg}} = 0.78 \pm 0.13$) (Jantzen et al. 2013). This suggests a high capability of these organisms to adjust the calcification process (precipitation of aragonite) to environmental unfavorable conditions. Calcification in acidified waters may depend on the corals' ability to regulate the internal milieu. In vitro respiration rates of the scleractinian *C. huinayensis* indicate that oxygen consumption under acidified conditions (pH 7.4) is increased by 250% compared to that of the control group (pH 8.0) (pers. observ.). An increased energy demand under low pH conditions apparently indicates stress and a physiological adaptation (McCulloch et al. 2012): in coral skeletons, boron isotope variations provide a measure of the pH of the coral's internal calcifying fluid due to the pH-dependent and isotopically distinctive speciation reaction between the borate ion and boric acid. Several cold-water corals, including *D. dianthus*, have δ11B compositions substantially higher than the expected value of the pH-dependent inorganic seawater borate equilibrium curve. This indicates a strong up-regulation of the pH of the corals' internal calcifying fluid (McCulloch et al. 2012). Direct measurements are currently undertaken with microsensors. The abilities to withstand adverse conditions also depend on factors such as the nutrition level and the overall fitness of the specimens. However, combined effects (e.g., low pH and poor nutrition status) are likely to negatively influence coral physiology and thus may limit and shift cold-water scleractinian distribution (Guinotte et al. 2006; Jantzen et al. 2013). Some areas in the Central Patagonian Zone such as the Madre de Dios Archipelago (Fig. 1) however are characterized by high pH values: this archipelago is composed of limestone; the water surrounding this archipelago is buffered by the runoff and might thus be a refuge for calcifying organisms when the current seawater acidification continues elsewhere.

3.2 Direct Anthropogenic Impacts on Animal Forests of the Chilean Patagonian Fjord Region

Most of the direct impacts mentioned for animal forests (bottom trawling, harvesting, mining, impacts by tourism; see ▶ Chap. 1, "Animal Forests of the

World: An Overview") are not – or at least not yet – of major importance for the benthic communities of Chilean Patagonia. The complex structure and uneven, often rocky bottom of the channels and fjords restrict bottom trawling. In the southern part of Chile, mining is a minor issue so far. Harvesting of hydrocorals (which are sold as decorative elements) is carried out only at few sites (Häussermann and Försterra 2007b). Tourism still represents a minor income for the region and is concentrated on the mountains rather than on the ocean, but at least in the Los Lagos Region there are plans to increase small-scale ecotourism (Outeiro et al. 2015). Ecotourism in coastal areas (e.g., diving tourism) has to be strictly regulated; otherwise it could also negatively impact benthic communities. Further anthropogenic impacts due to waste discharges in to the sea can also locally be strong: since Puerto Montt has no wastewater treatment (only the major solid waste is retained), the water around the city is polluted (Galindo 2014).

Artisanal fisheries have been increasing significantly over the last two and a half decades (SERNAPESCA 2014). Today small-scale fishermen can reach even the most remote areas of Chilean Patagonia to harvest species such as the carnivorous gastropod *Concholepas concholepas*, mytilids, limpets, large decapods, the sea urchin *L. alba*, giant barnacles, and algae. They have more efficient equipment and satisfy a much larger market than in the past. In the easier accessible regions Mytilid banks have been decimated in both the intertidal and the subtidal areas during the last two decades (see, e.g., Häussermann et al. 2013). The intertidal mussel forests (see paragraph "Mussel forests") in Comau Fjord have not recovered significantly during the last decade since recolonization in the high to mid intertidal zones seems to be very difficult due to the harsh environment conditions (e.g., dehydration, huge temperature range, wave exposure, salinity range; Müller 2012) and slow due to extreme conditions (Häussermann et al. 2013). The giant barnacle *A. psittacus* is a sought-after seafood and populations reachable for seafood divers are heavily harvested. Due to progressively decreasing annual extractions, López et al. (2012) state that the stock is overexploited. The increasing harvesting reduces abundance and average size and in many cases destroys the three-dimensional structure created by the matrix species.

After the almost-complete eradication of the indigenous cultures, the Chilean Patagonia has been scarcely populated, and a significant recolonization by nonindigenous settlers started only during the second half of the twentieth century. These new settlers experienced the sea as an endless source of resources, where harvesting limits were only defined by the demand. Collapsing populations and the need of sustainable fishing and extractive techniques are not an elemental part of the culture yet. The main fishery resource in Chilean Patagonia, the southern hake *Merluccius australis*, is one of the nine fisheries that were declared as collapsed in early 2016; nine further are overexploited (SUBPESCA 2016). While some fishermen understand the need for sustainable management, based on the ecosystem carrying capacity, their efforts in the sustainable use of the natural resources are often sabotaged by other users who legally have the same access to those resources (e.g., some fishermen know that some old mussel banks should be maintained since they have a much better recruitment, but others go for these old mussels for short-term benefit). As Hardin (1968) already stated, the freedom of the common eventually leads to the ruin of all.

3.3 Aquaculture

Recently, large-scale salmonid farming was induced in most sections of Chilean Patagonia, highly impacting marine animal forest of the region. Since the mid-1980s, finfish farming grew to a yearly production of 1 million tons of salmonids in 2008, with yearly exports of US$ 2–2.5 billion. Due to the expansion of the infectious salmon anemia virus (ISAV), the production collapsed in 2009, when 60% of the farms had to cease production. The production has been recovering since then and reached a value of 59,219 t in 2012 (increase over the last 19 years by 3.395%; SERNAPESCA 2014) (Fig. 15). In 2013, 3,058 aquaculture (1,493 fish farms) concessions were registered for Chilean Patagonia, of which 95% are situated in the Los Lagos and the Aysén Region (SERNAPESCA 2014). Local densities of farms are much higher compared to Norway (e.g., in Norway there are up to 12, rarely 16–28 other concessions in a radius of 15 km around each concession, while in Chile there are 28, rarely up to 40 other concessions in this radius; Proctor et al. 2009). In Chile the defined minimum distance between finfish (e.g., salmonid) infrastructures is one nautical mile, 200 m between extensive (e.g., mussel) farms and 400 m between an intensive farm (e.g., finfish) and an extensive (e.g., mussel) farm (Buschmann et al. 2009). Distances can even be shorter if optical barriers are present. These high densities also produce sanitary problems. Besides the ISAV, the

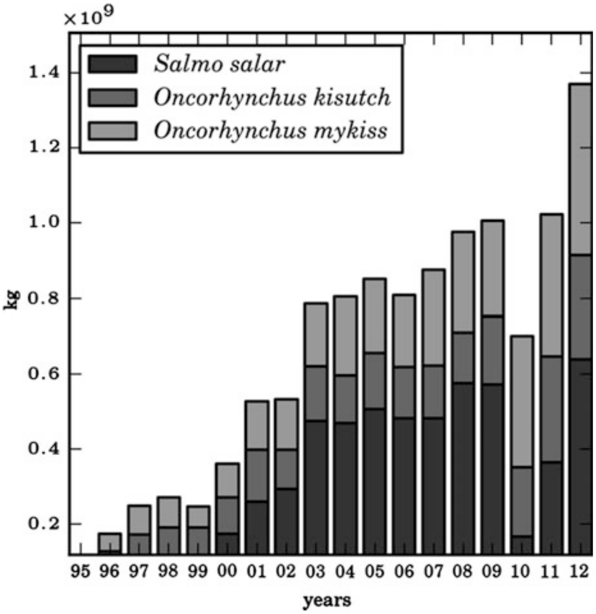

Fig. 15 Course of the production [kg × 10^9] of salmon species (*Salmo salar*, *Oncorhynchus kisutch*, *Oncorhynchus mykiss*) in the Chilean Patagonian fjord region between 1995 and 2012 (Source: SERNAPESCA)

parasitic “sea louse” *Caligus rogercresseyi* and the bacterium *Piscirickettsia salmonis* (SRS) today cause additional problems to the salmon industry. As a consequence, chemicals are used extensively; e.g., the amount of antibiotics used in 2007 was more than 1,400 times the amount used in Norway for the same amount of produced salmon, which in Chile is kept on a quarter of the concessionary area in comparison to Norway (Buschmann et al. 2006). Enforcement of the use of chemicals is insufficient, and rumors about the illegal use of banned products and the excessive use of legal products are controversially discussed; scientific information is scarce in relation to the production levels (Buschmann et al. 2009).

The salmonids are fed with fish meal, which is mainly produced from anchovies and jack mackerel populations from the central Chilean and Peruvian coast. Consequently large amounts of nutrients are dumped to the originally relatively poor-nutrient fjords (Niklitschek et al. 2013). Observed effects of salmon farming on marine animal forests are dead zones directly under the farms and changes in the species composition of benthic communities through increased sedimentation (Włodarska-Kowalczuk and Węsławski 2001) and through eutrophication (Mayr et al. 2014). Eutrophication is induced through nitrogen and phosphorus loading into the water; depending on volume and duration of this nutrient influx and on the assimilative capacity of the receiving waters, this can ultimately lead to a fundamental shift in the food web structure of an area. This change is commonly expressed in an ecological simplification (McClelland and Valiela 1998), where few species become more abundant and the total species number is reduced (for reviews of the effects of salmon farming on benthic communities, see Milewski 2001 and Buschmann et al. 2006).

Large infrastructure and industry projects are associated to the development of the aquaculture industry such as road building or the construction of harbors and other infrastructures. Where land topography prevents the implementation of land-based infrastructure, huge floating salmon farm complexes, including three-floor buildings, allow salmon production even in the most remote channels. This economic development significantly increases boat traffic and pollution. Mussel banks and beaches in areas with high numbers of farms are often heavily trash-strewn with lost buoys, ropes, nets, empty fish-feed bags, and chemical containers as well as domestic waste. Lost nets from farms have been found entangled in two cold-water coral forests in the Comau Fjord region (Lilihuapi Island and Punta Gruesa; Häussermann et al. 2013, pers. observ.) (Fig. 16). The effects of the increasing fish production have been raising national and international concern (Niklitschek et al. 2013); a Letter to Nature, calling Chile to cooperate in containing the damage from its salmon farms (Vester and Timme 2010), had no obvious effects. The environmental challenges and the risks for the unique Patagonian ecosystems are summarized in Niklitschek et al. (2013).

Mytilid aquaculture has also increased significantly. In 2013, SERNAPESCA (2014) registered 1,165 mollusk farm concessions for the Los Lagos Region. Effects are more local since no nutrients and chemicals are added into the water. Problems of neighboring marine animal forests arise from the local dead zones below the farms due to excessive accumulation of mytilid feces and pseudo-feces and the hypoxic conditions resulting from aerobe bacterial demineralization. As a side effect, some

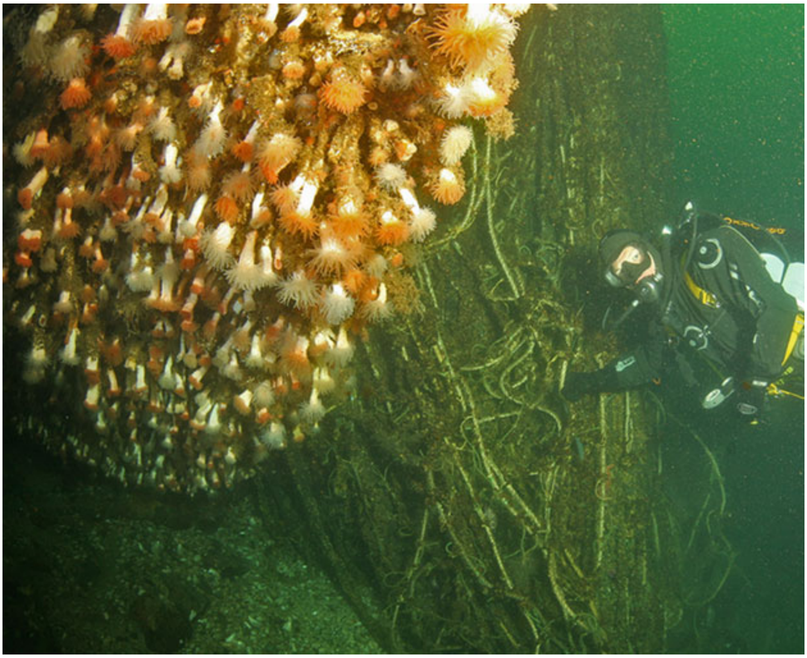

Fig. 16 Lost net entangled in cold-water scleractinian coral banks, matrix species *Desmophyllum dianthus*. Lilihuapi Island, Comau Fjord (42°09′32.0″ S, 72°35′41.1″ W), at 25 m depth

beaches are heavily polluted from ground up Styrofoam, which is widely used for flotation devices in mussel farms. Currently however, Styrofoam buoys are successively replaced by plastic buoys in some areas, but deficiencies in trash management remain.

3.4 Natural Hazards, Which Threaten Animal Forests of the Chilean Patagonian Fjord Region

A natural hazard affecting Chilean Patagonian animal forests is the high volcanic and seismic activity of the area. The eruption of the Chaitén volcano in 2008 was followed by a runoff of strongly ash-loaded waters into the Reñihue Fjord. The significantly increased sediment input through the river Vodudahue after the eruption covered the benthic communities. Corals were still observed covered by sediment in February 2009 (pers. observ.). Today however no significant long-term damages can be observed from this event.

Other natural hazards in Chilean Patagonia are tsunami waves. In 2012, a landslide caused a tsunami wave in the Aysén Fjord; consequences for the benthic communities have not been documented. The Comau Fjord is evaluated as high risk area concerning tsunamis (Sépulveda et al. 2011).

In 2012, the extension of submarine cold seeps in the Comau Fjord increased with an augmented output of methane and sulfide-loaded waters, which were together with hypoxia apparently responsible for a mass die-off of *D. dianthus* coral banks along 8.4 km of coastline (see Försterra et al. 2014).

3.5 Effects and Impacts of Anthropogenic Activities and Natural Hazards on the Animal Forests of the Chilean Patagonian Fjord Region

Effects on animal forests of the Chilean Patagonian fjord region observed during the development of anthropogenic activities (aquaculture, shellfish harvesting) over the last decade revealed a decline in biodiversity (see also Buschmann et al. 2006). We observed a strong depletion of mussel abundance due to overexploitation and reduction of densities of gorgonian populations of up to 75%; strong decline of populations of other long-living animals such as large deepwater sea anemones, calcified ectoprocts, and decapods, which probably was caused by eutrophication; and increased sedimentation and/or increase of chemical substances used during salmonid farming (Häussermann et al. 2013). Below the salmonid farms, the seafloor and the benthic animals appear frequently covered by white aerophobe chemotrophic bacteria; corals in the close neighborhood to salmon farms are often necrotic (Häussermann et al. 2013). The mechanisms behind these observed declines and degradations are not known in detail yet, but it can be expected that filter-feeding invertebrates will be probably impacted by increased sedimentation and eutrophication, while decapods may be affected by crustacean-specific pesticides that are widely applied to fight fish lice (Häussermann et al. 2013).

In April/May 2012 a mass die-off of cold-water stony coral forests along 8.4 km of coastline, reaching depths down to at least 70 m, was observed at the station Cross-Huinay in Comau Fjord (Försterra et al. 2014). Interestingly only individuals of *D. dianthus* were affected, whereas the two smaller associated scleractinian species *C. huinayensis* and *T. endesa* apparently were not impacted. The close to 100% mortality coincided with a phase of exceptionally high efflux of methane and sulfide-enriched water seeping out from cold vents located in the area and the typical time of the algal blooms in autumn. Due to the strong increase in salmon farming activity, algal blooms have significantly increased in frequency and intensity as a result of the amplified nutrient supply. There is evidence that a combination of elevated sulfide and methane output of the submarine cold seeps in combination with hypoxia following the decay of a strong algal bloom might have caused the mass mortality (Försterra et al. 2014). Indeed, in vitro respiration experiments indicated that *D. dianthus* (respiration, 23.71 ± 7.56 µmol O_2 cm^2 d^{-1} at a pH of 7.84 ± 0.08; Böhmer 2013) has a significantly higher oxygen demand compared to *C. huinayensis* (respiration, 3.69 ± 0.80 µmol O_2 cm^2 d^{-1} at pH 7.8; Wurz 2014) and *T. endesa* (respiration, 8.05 ± 2.93 µmol O_2 cm^2 d^{-1} at pH 7.87 ± 0.06; Diercks 2015). As *D. dianthus* is the main structure building species, hypoxic events may have huge impacts on the fjord ecosystem.

Populations of the rare gorgonian *Swiftia comauensis*, which is endemic to Comau Fjord, were reduced by approximately 75% and disappeared at one of the two sites, where it was originally discovered (Breedy et al. 2015). Gorgonians are generally long-living animals, which grow slowly and exhibit slow population dynamics; they are affected by an increase in sedimentation (Rogers 1990), and they are more sensitive toward diseases when they live in a nutrient-enriched environment (Bruno et al. 2003). The reduced abundance of *S. comauensis* in Comau Fjord between 2003 and 2013 might be due to elevated sediment stress and an increased nutrient input through elevated impact of aquaculture (Breedy et al. 2015). The salmonid production in the Hualaihué commune, Palena Province, to which Comau Fjord belongs, increased from 20,618 t year^{-1} in 2003 to 59,219 t year^{-1} in 2012; primary productivity increased by a factor of at least two during the last two decades (Mayr et al. 2014).

There are other cases of population decreases of marine animal forests, for instance, the hydrocoral reef, which was discovered in the Copihué Channel in 2006 and found wiped out in 2013. No clear reasons to explain this phenomenon have been documented (Häussermann and Försterra 2014), but an ongoing project investigates the cause of the mortality. The reduction and loss of habitat-forming species represent losses of ecosystem services (besides other biodiversity, nursery ground for fish species, wildlife, endangered and habitat-forming species, ecotourism, and recreation) to which authorities have not paid sufficient attention so far (Iriarte et al. 2010; Outeiro et al. 2015).

4 Conclusions and Future Directions

Marine animal forests are abundant throughout Chilean Patagonian waters. Many of them are dominated by fragile and long-living species such as calcified corals. Once the communities of these organisms decrease, due to the effect of natural hazards or anthropogenic activities, their recovery might take a long time and in some cases would probably not occur.

Suspension feeders such as corals and gorgonians are in most cases not able to fully cope with elevated sedimentation, eutrophication (Rogers 1990; Weber et al. 2012), and probably with chemicals in the water (see, e.g., Haya et al. 2005). The degree and velocity of degradation of marine biodiversity in Chilean Patagonia are alarming. These complex ecosystems face an imminent threat by a large-scale anthropogenic transformation of the region caused by the salmon farming industry, which is spreading southward into the more pristine areas (Niklitschek et al. 2013). Under the current practices of the salmon farming industry and the associated environmental damages, this industry does not meet any reasonable definition of sustainability (Buschmann et al. 2009). Patagonia is at high risk of losing several marine ecosystem services (biodiversity, habitat-forming and endangered species, ecotourism, and recreation) (Outeiro et al. 2015), at least in the Northern Patagonian Zone, where densities of aquaculture installations are very high. In addition, an increasing amount of small-scale fishermen nowadays reach even the most remote areas to harvest marine resources. Exploitation is regulated in management areas, generally for a single species, which are common along the central and northern Chilean coast (Castilla and Fernandez 1998). When exploitation is not regulated – as it is the case for most resources and in most remote areas – the caused damages are probably more local and not as long lasting. The destruction of the ecosystems is invisible to the broad public and to the authorities, and thus, the awareness of an actually existing problem is still low. Scientific information is deficient, regulations are lax and inadequate, and control and enforcement are insufficient. Precautionary- and science-based management approaches are scarcely practiced. A permanent monitoring system needs to be installed to detect unexpected changes in the ecosystem (Niklitschek et al. 2013). The authorities need to apply in their regulations the ecosystem approach considering the natural values of the area and the ecosystem services and taking into account the carrying capacity of the system and the synergic and additive effects. Using a precautionary approach, the creation of replicated MPAs in each zoogeographic zone of Chilean Patagonia (Northern, Central, and Southern Patagonian Zone) including the different habitats in the respective fjords and channels and along the exposed coast is urgently needed. A strong increase in public awareness, locally, nationally, and internationally, is required to promote political will and secure support for the creation of MPAs.

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Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems

11

Julian Gutt, Vonda Cummings, Paul K. Dayton, Enrique Isla, Anke Jentsch, and Stefano Schiaparelli

Abstract

Both Southern Ocean and terrestrial systems contain three-dimensional biotic components that are key in shaping and defining their respective ecosystems and communities. Antarctic suspension-feeding communities, which inhabit the shelf of the Southern Ocean, resemble “Terrestrial Vegetation Forests” (TVF) or shrublands and support the concept of “Antarctic Marine Animal Forests” (AMAF). They comprise mostly sessile animals, provide microniches for an associated mobile fauna, and are fragmented and regionally mixed with other

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communities. On land, only high mountains and very dry regions are unsuitable for TVF, analogous to the virtual absence of AMAF from the deep sea (>1000 m). Besides fundamental differences between these systems in energy flow and other ecological drivers such as light requirements and dispersal opportunities, both "forests" experience similar disturbances, which impact ecosystem dynamics and diversity in similar ways. While land use affects and reduces terrestrial forests, climate change and fishing impacts are the most serious threats to the Southern Ocean ecosystem. Research priorities for a better understanding of "Antarctic Marine Animal Forests" demand (1) mapping biotic communities and their structural and functional diversity, especially in terms of hot and cold spots; (2) understanding ecological function, including ecosystem productivity and dynamics; (3) cross-system comparison to identify generality or uniqueness in ecosystem structure and dynamics; and (4) implication of existing and new research approaches and conservation strategies.

Keywords
Limiting factors • Ecological drivers • Areal coverage • Three-dimensional structure • Interactions • Energy flow • Disturbance • Climate change • Conservation

Contents

1 Introduction

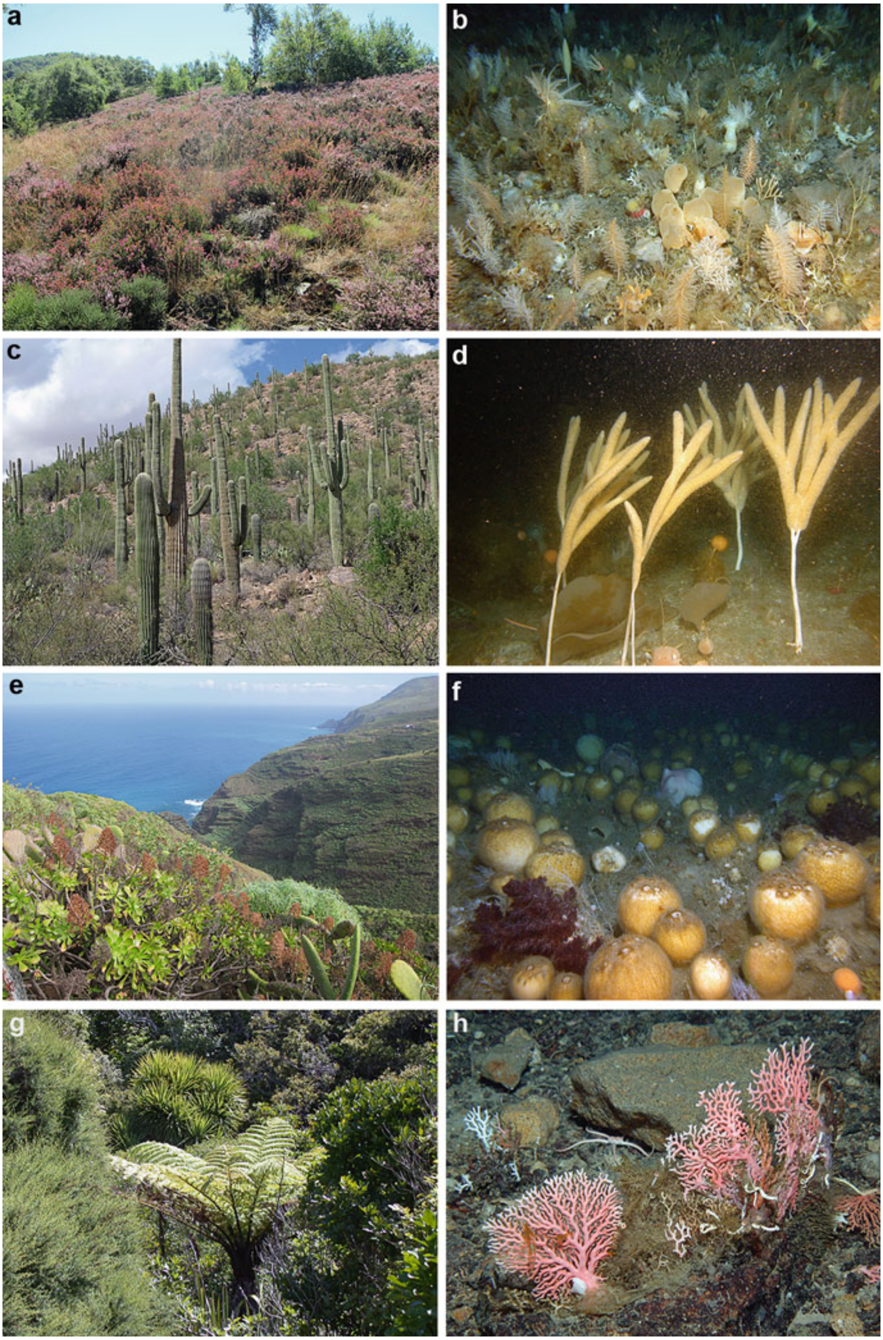
Both on land and in the sea, flora or fauna provide a three-dimensional structure important in shaping and defining their respective ecosystems and communities. In terrestrial systems, plants (trees, bushes) create forests (hereafter, "Terrestrial

Vegetation Forests" (TVF)), which support and sustain a wide variety of life. In Antarctic marine systems, sessile fauna, e.g., hydrocorals, gorgonians, sponges, and ascidians, are common on the seafloor in shelf depths, where they often reach high densities over large areas and form "Antarctic Marine Animal Forests" (AMAF) (for compilation, see Gutt et al. (2013); for data repository, see http://ipt.biodiversity.aq/resource.do?r=macrobenthos; for sponges, see Maldonado et al. (In press)). Despite fundamental differences between Southern Ocean and terrestrial ecosystems, both "forests" create and encompass a broad range of habitats (e.g., Groombridge and Jenkins, 2002) and influence the composition of their local ecosystems. Differences are icy, constant water temperatures vs. a range from cold to hot air, seasonal vs. diurnal light cycles, predominance of sessile vs. mobile fauna, and primary trophic levels comprised of floating microalgae vs. sessile rooted trees. In both realms, environmental constraints shape the establishment of speciose communities (Fig. 1).

The aim of this chapter is to provide a comparative view of the structural characteristics and dynamics in both systems and to place the AMAF in a macroecological context for wider readership. In particular, the possible analogies of, and fundamental differences between, TVF and AMAF are evaluated. An important reason for this assessment is that the poorly known origin and functional organization of generally vulnerable Antarctic three-dimensional macrobenthic communities may be better understood by applying a cross-system comparison. Such comparisons between marine and terrestrial systems have already been attempted (Cornell and Harrison 2013; Gray et al. 2006; Steele et al. 1993; Webb 2012) but not with a specific focus on the Antarctic benthos. In addition, Southern Ocean communities are unique; thus, our knowledge of the global biosphere wouldn't be complete without including them in the global picture. A general problem of such approaches is that if comparisons are carried out at the same trophic level, the vegetation of terrestrial systems must be compared to the planktonic realm in marine systems, and the three-dimensional marine benthos is ignored. If, however (as here), ecosystem structure is the focus, different trophic levels must be compared (e.g., plants and corals).

2 Definitions and Perspectives

On land, a forest is defined as >10% areal coverage by the canopy, following the Convention on Biological Diversity (CBD) and Food and Agriculture Organization of the United Nations (FAO 2001). Classical forest definitions even require canopy closure, which often occurs in more productive habitats but is less common in dry or cold TVF near the altitudinal or northern treeline (e.g., in the Arctic zone). While defining a "canopy" in the Antarctic benthos is difficult, an AMAF can similarly be considered as a seafloor ecosystem that consists of >10% areal coverage by sessile, erect organisms, or colonies of them, which form a three-dimensional habitat. As a consequence, AMAF are more comparable to shrubland vegetation types. In this



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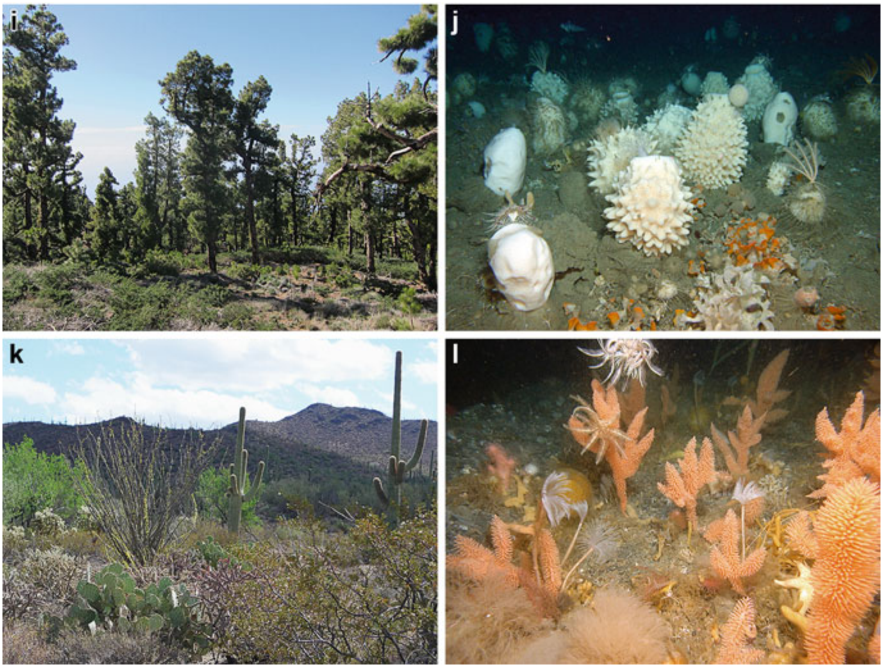

Fig. 1 Three-dimensional landscapes (*left*) and seascapes in the Southern Ocean on the shelf of the Weddell Sea at water depth between 150 and 300 m (*right*). Vague structural similarities assembled next to each other (Photographs **a**, **c**, **e**, **g**, **i**, **k**: A. Jentsch, University of Bayreuth; **b**, **d**, **f**, **h**, **j**, **l**: J. Gutt, © AWI/MARUM; University of Bremen, data repository of sea-bed photographs: www.PANGAEA.de. (**a**) *Calluna* heathland in France. (**b**) Diverse epibenthic community shaped mainly by compound ascidians and gorgonians ("bushes"). (**c**) Desert scrub with huge cacti in Arizona, North America. (**d**) Stalked and branched sponges. (**e**) Succulent scrub at La Palma, Canary Islands. (**f**) Benthic community with demosponges of the genus *Cinachyra* being dominant. (**g**) Tree fern forest in New Zealand. (**h**) Hydrocorals on hard substratum. (**i**) *Pinus canariensis* forest with open canopy. (**j**) Glass sponges (Hexactinellida: *Rossella* and *Anoxycalyx*) are the dominant three-dimensional organisms, and bryozoans form the understory. (**k**) Desert scrub with diverse vegetation in Arizona, North America. (**l**) Cnidarians (*Thouarella*/*Daystenella* and others) used as biotic substratum for occasionally swimming crinoids; smaller branched and spheric demosponges and polychaetes have also colonized the seafloor

chapter, AMAF are considered to be generally restricted to shelf depths, between 0 and 1000 m. However, most of the AMAF exist at <400 m (Figs. 2a, b and 3) and are less common on the adjacent slope and deep-sea habitats. Since AMAF are functionally and structurally indiscernible from associated and adjacent benthic communities and the overlying pelagic system, these are also occasionally considered in this analysis.

A very general level of difference in this cross-ecosystem comparison is the human perspective; humans can walk through TVF. They can observe single trees, multiple plant species, huge animals, and tiny organisms down to one millimeter in

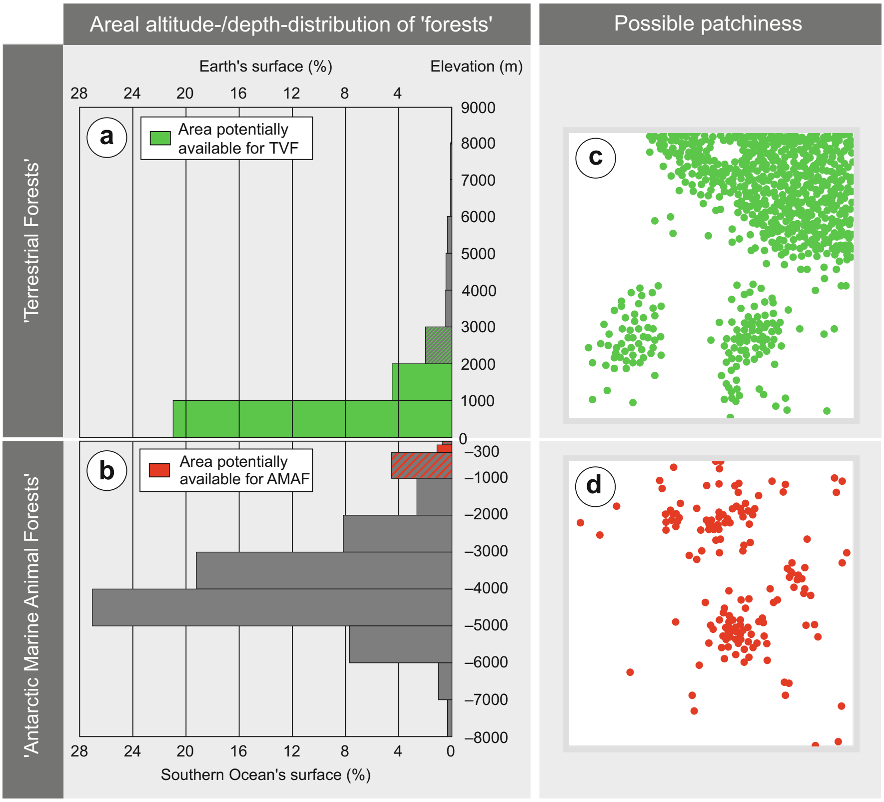

Fig. 2 Differences in spatial patterns (**a**) with respect to altitude of "Terrestrial Vegetation Forests" (*TVF*) and (**b**) with respect to water depth (=negative altitude) of "Antarctic Marine Animal Forests" (AMAF). Assumed patchiness of (**c**) TVF and (**d**) AMAF

size, including primary producers, pollinators, herbivores, predators, and symbiotic communities such as lichens and decomposers – all of which form a network of biotic interactions that shape the forest ecosystems as a whole. These organisms and their interactions can easily be studied at different temporal and spatial scales, including ecological processes such as response to discrete and extreme events (e.g., storms, forest fires, intensive herbivore grazing). Humans are also often part of this ecosystem, considerably shaping its functions (e.g., by resource exploitation, via logging), altering equilibrium, and thus affecting ecosystem services.

In contrast, surveys and studies of the Antarctic benthos are more logistically difficult, not only because of the aquatic environment, but also because of the regions' remoteness, low temperatures, sea-ice cover, seasonal darkness, and the great pressure of the water column. All these peculiarities make sampling in Antarctica a challenging activity that is often completely ruled by weather conditions. However, this drawback can also be considered an advantage: it obliges researchers to carefully prepare their scientific surveys, develop testable

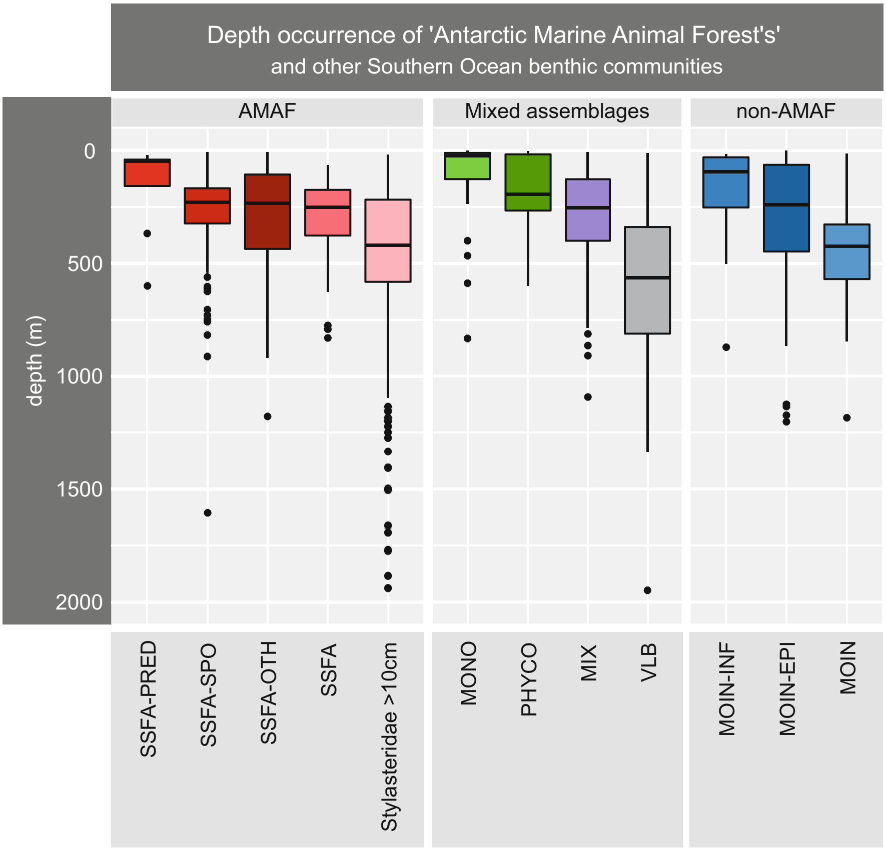

Fig. 3 Depth distribution of "Antarctic Marine Animal Forests" and other macrobenthic communities on the shelves and upper slopes of the Southern Ocean (only records shallower than 2000 m considered). Classification including color code according to Gutt et al. (2013). *SSFA* sessile suspension feeders and associated fauna, *PRED* predator driven, *SPO* sponge dominated, *OTH* non-sponge dominated, *MONO* monospecific, *PHYCO* physically controlled, *MIX* mixed assemblage, *VBL* very low biomass or absence of trophic guilds, *MOIN* mobile deposit feeders, *INF* infauna dominated, *EPI* epifauna dominated. Data published by De Broyer et al. (2014) and available at data network/repository ANTABIF (http://ipt.biodiversity.aq/resource.do?r=macrobenthos). "Stylasteridae >10 cm" refers to the occurrences of all Stylasteridae species (hydrocorals) taller than 10 cm also recorded in http://data.biodiversity.aq/: *Calyptopora reticulata*, *Conopora verrucosa*, *Errina antarctica*, *E. boschmai*, *E. fissurata*, *E. gracilis*, *E. kerguelensis*, *E. labiata*, *E. laterorifa*, *E. lowei*, *Errinopsis reticulum*, *Lepidopora granulosa*, *Sporadopora dichotoma*, *Stellapora echinata*, *Stylaster densicaulis*

hypotheses, and select appropriate a priori sampling strategies independent of subjective impressions, which are difficult to suppress in a more easily accessible ecosystem. Furthermore, the trophic level of the dominant elements of both "forests" differs, i.e., heterotrophic animals (consumers) in AMAF (with the exception of the large brown algae *Himantothallus grandifolius* and *Desmarestia antarctica*) and autotrophic trees (producers) in TVF. In the first case, primary production is performed mainly by microalgae growing and drifting in the euphotic zone, which is vertically more or less far apart from the AMAF. In TVF (sensu lato), biomass is primarily produced and accumulated by trees and shrubs, which form the dominant part of these woody, perennial ecosystems. A general compromise must be made for this comparative approach: TVF exist worldwide, while AMAF are restricted to the marine belt around one continent only.

3 Areal Coverage

Despite the fundamental differences mentioned above, a comparative analysis of TVF and AMAF with respect to their spatial distribution is motivating because large-scale patterns result either from similar or different ecosystem dynamics. Forests are complex ecological systems, in which trees are the dominant life forms. Forest definitions are reviewed in Schuck et al. (2002), and, according to the CBD, they cover 30% of global landmasses. For the Southern Ocean, an educated best guess for areal coverage of AMAF would include 20% of shallower regions ($\leq$250 m), <5% of deeper shelf areas (250–800 m), and <0.5% of the slopes and deep sea >800 m, with the latter comprising 87% of the entire Southern Ocean. In addition to the canopy aerial criterion mentioned above, TVF must have a minimum size of 5000 m^2. The largest, in Russia, covers 12×10^6 km^2 and is twice as large as the more famous Amazon tropical rain forest. A typical European forest, such as the German Black Forest (fragmented by human impact), is only 8000 km^2 and hence at the lower end of this size-based classification. Thus, forests cover a size range that spans through nine orders of magnitude. For AMAF, a precise two-dimensional mapping of benthic communities is generally lacking on spatial scales that would enable direct comparison with TVF. Deduced from one-dimensional transects using imaging methods, surveys with grabs or dredges, and interpolations from this information, AMAF size spans from the lower end of this range (i.e., 5000 m^2) over only two to three orders of magnitude and reach a one-dimensional extent of no more than tens of kilometers. If the narrower definition of a TVF with high canopy coverage is applied, distinct communities with >80% coverage, such as tropical rain forests or Siberian taiga forest, are many orders of magnitude larger than their Antarctic analogues because the latter rarely attain such high coverage over very small areas. As a result, AMAF have comparably very small core areas with high benthic coverage, surrounded by larger areas with a gradient of continuously decreasing coverage. In contrast, most TVF have large areas with homogeneous and often high canopy coverage in their centers and loosened ecotones (margins), being small compared to those of the AMAF (Fig. 2c, d). AMAF patterns sometimes appear to have a fractal nature: patches exist at all spatial scales, and when “zooming” in the patchiness persists. Such looser benthic aggregations resemble a steppe or grassland on land, with single trees, shrublands with cacti, or bushes shaping the environment locally (Breckle 2002).

4 Distribution, Limitations, and Species Richness

Natural limiting factors for TVF include pure bedrock, mobile ground, and climate conditions such as drought (mean annual precipitation <250 mm) and low temperature (annual average of around 0 °C). Climatic restrictions can be further exacerbated by inclination, exposure to precipitation and wind, and the lack of soil. As a result, if sufficient water is available, TVF can potentially exist on all continents except Antarctica. If, however, area proportions of elevation strata potentially suited for TVF and AMAF are compared, an inverse image appears (Fig. 2a, b). TVF occur in the large low- and upland areas between sea level and the treeline at 300–4400 m altitude. In contrast, AMAF do not exist in the Antarctic deep sea and are rare on the continental slopes (i.e., the marine "low- or upland" counterparts), which represent by far the largest area in the Southern Ocean. Most AMAF are found in a relatively narrow belt of "high mountains" around the Antarctic continent, in water depths <400 m (Fig. 3). This region accounts for <50% of the shelf not covered by ice shelves, but only <4.2% of the entire Southern Ocean area. At the shelf break between approximately 400 and 800 m water depth, AMAF face largely unknown but trophically limiting factors similar to those of TVF in the high mountains. They progressively disappear with decreasing depth below sea level. A notable exception is the occurrence of high densities of hydrocorals (e.g., *Errina fissurata*) on the shelf break and at slope depths, where their colonies form a hard network of calcified branches hosting a variety of invertebrates (Bullivant 1959; Bullivant and Dearborn 1967; Post et al. 2010; Fig. 3). The distribution of these and other species occurrences can be visualized through a search on the Antarctic biodiversity data portal ANTABIF (http://data.biodiversity.aq/, cited 08 February 2016).

While there is no clear evidence of the main ecological drivers supporting or limiting AMAF, the advective supply of phytodetritus serving as main primary food source likely plays an important role (e.g., Thrush et al. 2006). Temperature is obviously less relevant for AMAF as, at shelf depths, water temperature is very consistent year-round. Exposure to ice disturbance (mainly from sea ice and anchor ice) and to other physical disturbance (e.g., waves in ice-free areas) results in a coastal margin between 0 and approximately 40 m depth that is regionally devoid of three-dimensional communities, similar to the high mountains on land. This reduced biological richness and complexity ≲40 m water depth is mirrored along most rocky coasts on land: there is a general lack of vegetation at altitudes between 0 and 5 m above sea level due to a lack of soil caused by a variety of disturbances (e.g., high salinity, floods, wave action). With depth, a gradient of increasing complexity in seafloor communities is observed, and AMAF characteristics become more similar to those of true TVF (Dayton 1990). A fundamental difference between the main drivers in the very shallow Southern Ocean and on land is that the limiting climatic conditions in TVF act relatively homogenously and consistently at the regional scale, making the lack of trees above the treeline very predictable. Conversely, ice disturbance is quite variable in space and time in the

Southern Ocean. Thus, in areas naturally protected from this disturbance, exceptionally rich communities can locally develop in shallow waters.

Ecological and evolutionary histories are also key drivers of the present distributions of AMAF (Gutt et al. 2010). The ecologically based composition of AMAF is young relative to that of some TVF (i.e., 12,000 years old). Most shelf areas were covered by grounded ice shelves, becoming available as a habitat for recolonization only at the end of the last glacial maximum. In contrast, TVF such as the Amazon rain forest may have existed in places for 55 million years. The relative youth of most AMAF in terms of ecological development may also explain their patchy distribution over the continental shelf. The recolonization of the shelf after the last ice age from depths beyond the shelf break could have been limited by local physical conditions such as seafloor topography (e.g., glacial troughs, shape of the shelf break, presence of seamounts), sea ice (primary production in intermittent, restricted areas such as polynyas), and hydrodynamic patterns. Such constraints may have favored local settlement and growth of species in restricted areas with optimal combinations of each. Therefore, it is plausible that AMAF still persist in a status of high fragmentation.

A fundamental information characterizing the structure and affecting the functioning of ecosystems is their species richness (=number of species). However, life on land and in the oceans is due to the enormous richness to a large extent unknown; thus, cross-ecosystem comparisons are difficult. Nevertheless, a coarse impression is presented here. Seventeen thousand macrobenthos species were estimated for the Antarctic shelf of which the majority contributes to AMAF (Gutt 2004), 9058 of these are scientifically known for the SO. Of these less than 4% are pelagic and 79% benthic invertebrates and additional 17% are birds, mammals, and fish (DeBroyer et al. 2014). Approximately, 40% of the benthic species are assumed to be benthic sessile suspension feeders. Consequently, AMAF species richness of a few thousand species is closer to that of their terrestrial equivalent in Europe, comprising 11.000 (Winter et al. 2009), than compared to the >200,000 worldwide-occurring vascular plant species (Wilson et al. 2012). Forty thousand of the latter alone occur in the biodiversity hot spot of the Malesian floristic region (Kessler et al. 2005) comprising the rain forest in the Philippines, Malaysia, Indonesia, and Papua New Guinea, being not more than 1.5 million km^2 large, which is half as large as the Antarctic shelf and, thus, roughly of similar size as AMAF. Among the fauna associated to the sessile organisms, insects, with one million species and the richest terrestrial metazoan group, are by far richer than its Antarctic equivalent, the benthic mobile animals, e.g., amphipods, isopods, some echinoderms, and polychaetes, which comprise approximately 5400 species. When species richness of the large SO deep sea is considered and assumed to be of the same order of magnitude as that of the rest of the worldwide deep sea with approximately 1 million species (or more), this SO habitat is not much poorer than the rain forests assumed to comprise the majority of the worldwide-occurring terrestrial 6.5 million species (Mora et al. 2011). Coarse figures for this estimation are based on worldwide 2.2. million marine species (Mora et al. 2011) minus 830,000 species for the other hot spot in marine species richness, the coral reefs (Fisher et al. 2015). However, we do not consider herein the deep-sea habitat as a true AMAF.

5 System Architecture

It has been shown that, in terms of two-dimensional global coverage and large-scale vertical distribution, the Antarctic benthos can only be superficially compared with TVF. If the third dimension of the "vegetation" itself is considered, differences become more obvious. TVF must have, by definition, a height of ≥5 m. However, this height includes young forests; an average would be 20 m, and an extreme height is around 115 m (redwood forests). The vertical range of a three-dimensional Antarctic benthic community (AMAF) could be defined as between 0.1 and 2 m. The lower value is the lower limit of a three-dimensional shape with an assumed significant impact on the benthic system, while an example of the upper limit an occasionally beyond includes stands of the macroalgae *Himantothallus grandifolius* and *Desmarestia antarctica* which are restricted to a few (and shallow) Antarctic areas and of the compound ascidian *Distaplia cylindrica*. Thus, the difference in the average heights between AMAF and TVF is two orders of magnitude, which, while considerable, is much less than the difference of six to seven orders of magnitude in vertical extent observed within TVF. Another fundamental difference between these systems lies in the detail of their vertical form. By CBD definition, a TVF must have a canopy, which rests on comparably tiny stems. This umbrella-like form occurs in only a few Antarctic benthic stalked animals, e. g., the ascidian *Pyura bouvetensis*, the lollipop sponge *Stylocordyla chupachups*, or colonial cnidarians. However, even if the main body of the animal rests on a slim stalk or is tree like and branched (e.g., *Homaxinella* sponges, *Thouarella*/*Dasystenella* gorgonians), a true canopy never develops; such AMAF structures resemble a bush, a leafless tree, or a tulip-like flower rather than an umbrella. Also, other non-stalked but three-dimensional organisms in the Antarctic benthos resemble bushes or cacti rather than trees, such as bryozoans, corals, compound and solitary (non-stalked) ascidians, and some sponges (Fig. 1). As a consequence of the significantly lower profile and the lack of a closed canopy, AMAF are more comparable to low-growing shrublands, e.g., subtropical dry savannah with single trees, subtropical succulent scrub with cactuses, Mediterranean macchia, North American chaparral, or European Calluna heathlands.

As in plants, the branched shape of individual AMAF components has the function of outer surface-area amplification, especially in case of cnidarian colonies where a large surface provides more space for tiny individuals than would a more simple shape. In other animals, the principle of an inner surface-area amplification is also realized, for example, in sponges and ascidians with pharyngeal stigmata or choanocyte chambers. As a consequence, these organisms have a roundish body and, stalked or not, do not form a true canopy that specifically impacts ecosystem functioning. However, in both Antarctic marine and global terrestrial three-dimensional systems, a multistoried structure exists independently of their size and specific shape. Modifications of simplified schemes of forests with only stems and a canopy can include smaller annual vegetation, perennial bushes, and trees of different heights and shapes. Such a coexistence of organisms representing a structural diversity also exists in the Antarctic macrobenthos, maybe even with a higher variability due to the characteristics described above. One reason for the partially greater structural variability in AMAF might be that their less obvious (or nonexistent) canopy doesn't limit growth and the structural and functional diversity beneath it, as does a true dense forest.

6 Ecosystem Engineering, Associated Fauna, and Secondary Habitat Formation

Perhaps the strongest similarity between TVF and AMAF is the presence of "ecosystem engineers", defined as organisms that directly or indirectly alter resources of other organisms (Jones et al. 1994). The two ecosystems not only form a three-dimensional structure, but also provide microhabitat for a variety of other species that live within it, obtain food from it, or are just loosely associated with it (e.g., Gutt and Schickan 1998). In the oceans, three-dimensional systems that attract an associated fauna and flora are found globally, e.g., drifting seaweeds in the Sargasso Sea; kelp forests in shelf systems (rare in the Antarctic); natural or artificial three-dimensional seafloor substrates such as rocks, boulders, caves, escarpments, cobbles, and anthropogenic waste; or reefs. The latter have less obvious analogues in the Antarctic, where they are formed by sponges and cnidarians (for illustration and evolutionary background, see Gili et al. (2006)). In all of these cases, the interaction between structure-forming species and their associated fauna results in speciose communities with a high trophic and functional diversity. Relatively rich "associate" faunas are attracted by, or adapted to, the three-dimensional architecture because of the habitat as well as the protection (or shelter) and food this provides.

In both systems, almost all imaginable structural microniches are occupied, ranging from loose and facultative to obligatory relationships. These "symbioses" sensu lato are grouped here from the perspective of the AMAF in the classical way (De Broyer et al. 2014). Commensalism is one of the most obvious relationships, of which many may be regarded as specific cases of epibiosis, where rheophilic, i.e., "current-loving," organisms take advantage of an elevated position on their "host" to get access to particulate organic matter (POM) resuspended by near-bottom currents and activities of benthic organisms. Echinoderms, especially comatulid crinoids, dendrochirote sea cucumbers (e.g., *Heterocucumis steineni*), as well as suspension-feeding and copepod-capturing ophiuroids (e.g., *Astrotoma agassizii*), are the most abundant epibionts. The favorite "substrate" organisms are mainly sponges (especially, large hexactinellid glass sponges), gorgonians (among the cnidarians), and erect bryozoans, and occasionally also ascidians and hemichordates. Less obvious but more specific relationships of this type involve sea cucumbers, i.e., *Echinopsolus acanthocola*, which lives only on the spines of pencil sea urchins, together with encrusting sponges and bivalves (*Lissarca notorcadensis*). Suspension-feeding crustaceans of the family Antarcturidae also belong to this group and are abundant on sponge, gorgonian, and ascidian stalks. Due to the above-described fundamental differences between the trophic level of the structuring organisms of AMAF and TVF and, in turn, of their environmental demands, it is difficult to find analogues between these two situations. However, epiphytic ferns, lichens, orchids, and bromeliads may conceptually be considered, in their search for light, similar to the rheophilic species that seek optimal food conditions by climbing on an elevated substrate. In this respect, access to essential resources, i.e., light in TVF systems, and POM as a food source in AMAF could be considered analogues. On land, some epiphytic plants (e.g., mistletoes from the family Loranthaceae) obtain nutrients from their host, in a kind of parasitism for which parallels exist in AMAF. The gastropod family Capulidae, in fact, encompasses representatives of the genera *Capulus* and *Torellia* that exploit suspension-feeding tubicolous polychaetes, stealing their food in a kleptocommensal relationship.

There are obvious similarities in the way mobile fauna use TVF and AMAF. Amphipods and fish use the three-dimensional habitat on the Antarctic shelf in the same way as insects, birds, and bats use TVF. In both systems, many of the mobile fauna are specialists in their role as predators or are specific prey. In the marine realm, there are examples of nudibranchs, which feed on sponges and reside on a single sponge individual for more than a year. In some cases, such host associations can be regarded as the major driver of speciation. In TVF, some bird species, such as the lapwing, curlew, snipe, and redshank in the UK, build “nests” on the ground that they guard until their eggs hatch. Similarly, in AMAF, some ice fish species build a kind of “nest” – a sediment mound or simply a drop stone – where they lay eggs that are also guarded until hatching. In AMAF, *Trematomus* fish species or amphipods lay their eggs in the large osculum of glass sponges, similarly to those birds, which lay their nests in trees and bushes. These fishes also use the elevated position on the margin of a sponge osculum to observe their surroundings for food, as predatory birds do on land. Despite being mobile, other Antarctic fish species do not predominantly swim but remain on the ground (e.g., *Pogonophryne*) like partridges in forests. The holothurian *Sigmodota contorta* lives between the branches of bryozoan colonies and behaves like a tree snake in a TVF. Many epibionts not only occupy a broad variety of spatial niches but also may take advantage of food provided by their hosts. In AMAF, a very common example is that of the polychaete *Polyeunoa laevis*, which lives within the branch network of gorgonians from the widespread Antarctic genera *Thouarella* and *Dasystenella*. They spend all their lives on the same host, from which they gain food either by directly grazing tissues (i.e., the coenenchyme) or by stealing the food trapped by the hosts’ polyps. Another example of host fidelity in AMAF is the shrimp *Lebbeus kiae*, which is found only in proximity of large sea anemones, mainly *Bolocera kerguelensis*, where it finds partners to mate with (Schiaparelli et al. in press) and the gastropod *Margarella antarctica* feeding on the surface of glass sponges.

Besides behavior related to reproduction and feeding, another common reason why some of these animals use the biogenic three-dimensional structure is protection from visually hunting predators. As well as the above-described sit-and-observe strategy, other fishes perform an observe-and-hide strategy, for example, on glass sponges where they can hide in the osculum in case of danger, a situation that could be compared to small predatory vertebrates that are potentially threatened by their predators (e.g., birds). Mobile insects serving as an important food source for hunting birds or bats can be compared to the predominantly pelagic and only occasionally hyperbenthic krill being grazed by mobile predators on the Antarctic shelf. In both cases the prey organisms can only hardly escape.

Mutualism, such as found in many plant-insect interactions, is not a frequent biotic relationship in the Antarctic benthos as most "symbiotic" relationships seem to be shifted toward commensalism and parasitism (Schiaparelli 2014). This might be due to the great availability of deposit and suspension feeders as hosts in AMAF. Suspension feeders in particular may be so successful due to their feeding plasticity that allows them to feed on resuspended organic matter for most of the year, not only during the limited window of primary production in summer. On the contrary, in terrestrial ecosystems and TVF, thousands of examples of mutualism exist, above all, the mycorrhizal association between fungi or nitrogen-fixing bacteria, which colonize the host plant's roots and trade nitrogen fixed from the atmosphere for sugar produced by the plant. The myriads of insect species associated with plants and shrubs for pollination and herbivory services is too long to be listed here. Some of these associations appear so finely tuned that they can only be explained by hypothesizing a long-standing coevolutionary relationship. This is, for example, the case with ants belonging to the genus *Colobopsis*. They are specialized to live within the vines of carnivorous pitcher plants of the genus *Nepenthes*, from which they steal large insects that fall and drown in the pitchers. Another example is that of the arms race between gall wasps and their hyperparasites, where the shape and size of the induced gall is the result of a finely tuned adaptation aimed at escaping the injection of the hyperparasite egg in the gall wasp larva. In AMAF, specifically adapted amphipods live in oval pouches which they excavate in the surface of glass sponges and share with a variety of other amphipod species; a negative impact on the host can be assumed but has never been demonstrated. Similar interactions in terrestrial plants are the many epiphytes such as ferns, bromeliads, and orchids that dwell on subtropical and tropical forest trees. Likewise, in temperate and boreal forests, numerous bark beetles find habitat under the bark or in little hollows and crevices. A general conclusion can be drawn from the comparison of the biotic relationships occurring in the AMAF and in TVF ecosystems. If the strength of the positive effect for both partners and its uniqueness is considered as a measure of progress of the evolutionary development of an ecosystem (Odum 1973), then the AMAF represent a moderately advanced system due to dominance of nonobligatory relationships and the reduced number of obligatory mutualistic interactions. This corresponds, compared to other large ecosystems, with a moderately old evolutionary age of approximately 30 million years of the Southern Ocean as it exists today, a largely isolated ecosystem shaped at its southern margin by a mostly glaciated coast and a deep shelf.

For reasons of completeness, it must be mentioned that in both systems animals live without an obvious site fidelity, such as sessile species and their associated fauna. On land, migratory birds or butterflies have long-range dispersal capabilities, even crossing continents. Analogously, in AMAF, the Antarctic toothfish *Dissostichus mawsoni* migrates from coastal waters to the polar front for spawning. In land ecosystems, seeds of plants as well as smaller insects and spiders drift with the wind, in a similar way to large jellyfish, a variety of planktonic organisms (including larvae and offspring of sessile animals), and krill, which drift in local and circumpolar currents.

7 Interactions Between Soil/Sediment and Their Inhabitants

Land plants shape their substratum to their own benefit, for example, through humification. A somewhat similar marine phenomenon almost unique to the Southern Ocean is the formation of sponge spicule mats as a consequence of sponge mortality. Large hexactinellid sponges, and some demosponges, are rich in siliceous spicules. After their death, these spicules can accumulate in high concentrations on and in the seafloor sediments. Complete specimens are sometimes compressed by grounding icebergs, and when the organic matter is degraded, felt-like "spicule mats" remain. These might provide a special substratum for the next generation of the same sponges, for other macro-epibenthic animals and for macro-infauna and meiofauna. Analogously to these spiculae, leaves, branches, trunks, and roots of trees from TVF accumulate and change the structure of the soil. A main difference between both ecosystems lays in the fact that the trees are entirely recycled over time, while it is unknown whether inert spicule concentrations remain "forever" in the Southern Ocean's sediments, or if they slowly dissolve and act as an autochtone source of silicates from which newly growing sponges may take advantage.

8 Energy Flow and Other Ecological Processes

A fundamental difference between AMAF and TVF is the source of energy for marine animals and land plants. Marine animals at the lowest trophic level (i.e., grazers) living below the euphotic layer obtain energy from in the ambient water and also, in an unknown proportion, from dissolved organic matter (DOM). In contrast, plants forming the TVF are primary producers, as are all autotrophs. They get nutrients from the soil and rely on sunlight for the energy necessary to fix carbon. As a consequence, forests are shaped by the access of single trees or leaves to light in a similar way that three-dimensional benthic communities in the Southern Ocean are affected by characteristics or events occurring in the nepheloid layer, the water above and around them. For this reason, ocean currents, as the vector for food and nutrient transportation, may be considered important positive drivers. This is in contrast to mostly destructive intensive winds in terrestrial systems, where high wind energy can even limit forest occurrence and result in a treeline. In addition, the terrestrial vegetation is influenced more by spatial and temporal variations in soil, its quality, humidity, nutrients, and organic matter recycling by decomposers than are Antarctic macrobenthic three-dimensional communities, for which the substrate mainly acts only a growing platform. In this respect many sessile marine organisms, especially on the Antarctic shelves, seem to be adapted to a very broad grain size spectrum of the sediment.

The differences between AMAF and TVF in terms of structuring species and the available energy sources are, of course, also reflected in higher trophic levels. On land, autotrophs are grazed by herbivores, either big animals such as elephants, buffalo, deer, and antelopes or insects such as grasshoppers, caterpillars, and beetle larvae. In fact, insect herbivory is a major disturbance factor in tropical rain forests (Lowman and Rinker 2004). In AMAF, this trophic level is occupied by suspension-feeding organisms (i.e., sponges, cnidarians, ascidians, etc.) that are much smaller than the big herbivores on land, but have direct access to the microscopic primary producers in the water column (Shurin et al. 2006). When benthic animals benefit from phytodetritus or fecal pellets deposited on, and partly incorporated into the sediment through bioturbation by infauna, the high relevance of the soil in land ecosystems can also be applied to those Antarctic benthic habitats. This marine "soil" can act as a "food bank" (Smith et al. 2006) mainly for deposit feeders associated with AMAF. By removing organic matter from the seafloor, deposit feeders parallel terrestrial decomposers such as insects, worms, fungi, and bacteria that recycle the organic matter content of fallen leaf or tree trunks, producing the forest litter layer. Resuspension of deposited organic matter by water currents also makes this material available for suspension feeders (Isla et al. 2011), who also benefit from the energy available in the POM suspended in the nepheloid layer. In contrast to the long-term storage of energy in the refractory structure of cellulose that may require years to be completely mineralized by decomposers, the "food banks" in the oceans have only a midterm relevance of weeks to months before microbial degradation processes significantly reduce their nutrient value, a trophic process, which could be considered as a shorter bypass in a complete biological cycle. When organic matter is degraded to inorganic nutrients by benthic infauna, they are in turn released into the water column, particularly when sediment is reworked by biological and/or physical processes (e.g., bioturbation, iceberg scouring; Lohrer et al. 2013; Gutt and Piepenburg 2003). Another example of the high relevance of soil for TVF and of near-bottom physical oceanographic processes for AMAF is that both ecosystems can be fertilized through the "air." For example, the Amazon rain forest receives Sahara dust (Yu et al. 2015), and many temperate forests are influenced by deposition of anthropogenically enriched atmospheric nitrogen. In the Southern Ocean, where iron can be a limiting factor, this can be transported from near-shore and terrestrial areas to offshore ones. This affects primary production in particular and therefore ultimately the entire ecosystem, including the AMAF (Charette et al. 2013). The productivity of the Amazon rain forest is also affected by supply of nutrients, which are recycled in the area of the tree crowns, and not so much by the soil. This is comparable to cycling in shallow Antarctic habitats, especially those shaped by bedrock, where most energy transfer happens in the ambient water and not at all in the sediment.

In terrestrial systems, nutrients accumulate downslope, so that TVF richer in biomass often occur at lower elevations. In the Southern Ocean, in addition to the "normal" downward energy flux from the euphotic layer to the seafloor, this process can also be compared to diurnal migration of plankton and pelagic fish between the bottom-near nepheloid layer and the euphotic zone. This represents an upward flux of energy and links the consumers at the seafloor to the primarily light-dependent pelagic system. In TVF, there are cold air masses flowing downslopes every night, accumulating in the valleys, so that, for example, insect herbivory occurs in mid elevations (it becomes too cold at high and low elevations). Thus, mid slopes are usually specific and different from plateaus or valleys. With this respect, they are similar to slopes, sills, escarpments, and shelf breaks in the oceans, where primary producers and consumers, sessile and mobile animals benefit from the upwelling of nutrients and organic particles.

One factor shaping especially polar ecosystems is their marked seasonality, in case of marine systems not only by the light regime but also by the advancing and retreating sea-ice cover. Another main difference between TVF and AMAF especially in polar and subpolar latitudes is that such terrestrial forests are directly exposed to the seasonally changing day-night light regime, while most AMAF lay below the euphotic light-flooded upper zone of the ocean. Obvious differences in size of huge glass sponges between habitats in shallow and deeper Antarctic shelf areas are that those growing to a size of 2 m have access to fresh phytoplankton as a food source, while those on the deeper shelf rarely reach a size of 1 m, which, however, can be abundant but must live from degrading particulate organic matter. Nevertheless, all AMAF depend more or less on the pulse of the summerly phytoplankton bloom, and thus, different modes of adaptation evolutionarily developed. Suspension feeders are either able to starve for long periods and respond immediately when fresh food becomes available or they can benefit in terms of growth and reproduction from organic matter being available over longer periods in the nepheloid layer most likely through resuspension (Gutt et al. 1992; Barnes and Clarke 1995). Alternatives are various types of predators and scavengers, which are relatively uncoupled from the seasonality in the upper water column. Some anthozoans graze on gorgonians or nudibranchs, and gastropods nibble at sponges; gorgonocephalids and anthozoans catch copepods or asteroids krill from the near-bottom water column. Additional predator-prey relationships, e.g., asteroids controlling by predation populations of sponges and other asteroids (Dayton et al. 1974) and pycnogonids sucking polyps of hydrozoans, are not abundant but structure in some areas AMAF considerably.

9 Air and Water, the Surrounding Environments

On the one hand, the physical and trophic conditions of the environment, namely, water and air, shape both AMAF and TVF ecosystems directly and indirectly in similar ways, particularly in terms of dispersal. On the other hand, the two environments differ in density, which affects the temporal variability of ecological processes. Marine currents generally are relatively permanent features which act year-round as a vector for dispersal of food, offspring, and adult organisms, albeit with regional and temporal variations. As a consequence, pelagic organisms (including larvae of benthos) can generally disperse widely at any time within a large current system. On the Antarctic shelves, they can potentially reach any point ("global" dispersal), due to meanders, gyres, and tidal currents. Antarctic and sub-Antarctic islands are also reachable, and even dispersal into the Southern Ocean from adjacent oceans is possible (Clarke et al. 2005); nevertheless, there are still genetically distinct populations existing quite close to each other. The Southern Ocean component of the global thermohaline circulation also enables the reverse to occur: benthic species can disperse into adjacent oceans, even as far as the Northern hemisphere, where relatively similar environmental conditions exist in the deep sea (e.g., Clarke et al. 2005). Obvious barriers exist only in exceptional cases where two completely different water masses coexist close to each other, e.g., in the Ross Sea or in surface waters at the polar frontal system. This general environmental homogeneity does not exist on land. Most wind patterns (analogous to current regimes) are more variable in space and time and do not have the capacity as a long-range dispersal vector to the same extent as ocean currents. As a consequence, offspring on land disperse in a spatially less predictable way and may be much patchier ("local dispersal") than within the Southern Ocean. However, when propagules arrive in a certain area, many of them can survive in the soil for a long period (e.g., years) and "wait" for favorable conditions ("insurance in time"). This contrasts with their marine analogues, which only recruit and establish successfully where favorable conditions exist. These dispersal processes might cause patchy distribution patterns in sessile plants and animals on land and in the Southern Ocean, respectively, which are hard to explain, because complex processes responsible for a successful colonization differ considerably. Surprisingly, the difference in buoyancy of organisms in air and water does not cause obvious further differences. Where trees have developed a solid "skeleton" that can grow as high as 120 m, upward transportation of water might be the limiting factor for further vertical growth. Among land animals at different trophic levels, only dinosaurs reached their size limit. In the ocean, sessile animals should have no problem developing and maintaining an erect position, since most of their buoyancy is provided by the relatively high density of the water. However, it is not known why most of them do not exceed approximately 2 m in size (e.g., as reported for sponges, sea pens, and giant hydroids). Based on observations of masses of exceptionally long 7 m sessile ascidian colonies stranded on beaches or floating at the sea surface, it can be speculated that such erect benthic organisms are not well adapted to continued stress imposed by water currents and that they finally "break off" the seafloor. Highly mobile animals in both systems developed during their evolution an almost perfect morphology and physiology to swim or fly. Such animals include penguins, mammals, squid, and smaller invertebrates in the Southern Ocean and birds, bats, and insects in terrestrial ecosystems.

Biogeochemical processes are also affected by a combination of differences in buoyancy/gravity and dispersal of organic and inorganic material in the ocean or the air. In terms of remineralization processes, on land most recycling of organic material from plants is spatially limited, e.g., falling leaves can only drift over short distances before reaching the ground. In the ocean, however, nutrients and POM can be transported over long distances, with their consumption and remineralization happening along the way. For example, differential modification of organic (food) particles occurs depending on their sinking rates. The heaviest particles, e.g., krill feces, representing an attractive food source for some consumers and decomposers, quickly sink to the bottom, and their horizontal dispersal is limited. Consequently, only fine particles reach the remote areas beneath the ice shelves, which may be hundreds of kilometers from the open ocean (Gutt et al. 2011). Due to their short residence time in the water column, in open water the heavy particles are less grazed upon and thus provide an important food source for the deep benthic life, a phenomenon that is unimaginable far under ice shelves. In land ecosystems, the food source mainly comes from the vegetation itself, and remote fertilization happens only exceptionally (e.g., of the Amazon rain forest by Sahara dust; in riparian ecosystems during seasonal flooding).

10 Ecosystem Response to Disturbance

Both AMAF and TVF experience recurrent disturbances and extreme events, which may devastate major proportions of the ecosystems. A disturbance is defined by Pickett and White (1985) as “any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or physical environment.” Studying such events and processes allows advanced insights into ecosystem functioning and system dynamics, e.g., the relationship between diversity and disturbance, pace of colonization dynamics, role of early life history and offspring dispersal, recruitment success, degrees of functional resilience, and climate- or other human-induced events disrupting community dynamics. In the Antarctic benthos, such disturbances are relatively well known. In many places, the upper approximately 40 m of coastal habitats are regularly scraped by sea ice. As a consequence, vertical gradients in community composition develop and affect the distribution of mobile animals (e.g., fish, ophiuroids, and pycnogonids, which can immigrate and escape quickly), fast-growing opportunistic sessile animals (e.g., hydrozoans, alcyonarians, and ascidians), and, especially, of long-lived, sessile benthic species (e.g., large sponges) that can only thrive in areas with low-magnitude disturbance (Dayton 1990). In terrestrial systems, a clear zonation of typical disturbance regimes is found across altitudinal gradients in mountains, ranging from late frost to landslides and rock fall (Jentsch and Beierkuhnlein 2003). Moreover, each ecozone in the terrestrial world, and each ecosystem type, is prone to different disturbance regimes (Walker 2009; Schultz 2005) – from the Arctic and sub-Arctic (i.e., cryoturbation) via the boreal (i.e., fire), the temporal (i.e., seasonality), and the Mediterranean (i.e., fire) to the subtropical and tropical zone (i.e., insect herbivory).

In contrast to very shallow Antarctic waters which are regularly disturbed by sea ice, most of the shelf is undisturbed and experiences "normal" ecological dynamics with respect to reproduction, dispersal, recruitment, growth, species' interactions, and mortality. However, large areas of shelf are potentially exposed to iceberg disturbance down to 250 m and, in extreme cases, to 600 m. Sudden, but locally discrete, iceberg scouring events devastate entire benthic communities but also provide new space for a recolonization (Gutt and Piepenburg 2003). Studies show that some mobile immigrants are attracted to and show a higher abundance inside than outside these scours. First successional stages of sessile pioneer species can perform "explosive" growth, and their faunistic composition is not very predictable. These can recruit very fast but can also disappear just as quickly. Animals contributing to the three-dimensional structure can play an important role in any stage of recolonization, with the exception of the very early mobile immigrants. Ascidians are considered as pioneers; moss-shaped bryozoans and bush-like gorgonians also belong to an earlier stage of recolonization. A recent long-term study showed that long-living glass sponges can shape the habitat faster than previously thought (i.e., within a few decades post-disturbance if other driving forces are favorable). During recolonization of disturbed areas, diversity seems to increase constantly and does not follow the Intermediate Disturbance Hypothesis (Huston 1994). This hypothesis suggests that competitive displacement occurs at the end of this development stage, leading to reduced diversity. However, in AMAF, many additional species are attracted to the newly formed three-dimensional habitat. At larger spatial scales, which include the coexistence of different isochronic as well as successive stages of recolonization, species diversity is significantly higher in areas with iceberg disturbance than in those without. Models predict that climate-induced ice shelf disintegration will result in higher iceberg scouring rates. As a consequence, diversity will firstly increase to an unknown threshold, past which it will decrease or collapse. In terrestrial systems too, most disturbance regimes are patchy and heterogeneous in space, and the events occur more or less frequently with different degrees of predictability (White and Jentsch 2001). On land, highest levels of species diversity are commonly observed with intermediate frequencies and intensities of disturbances – as stated by the Intermediate Disturbance Hypothesis. Some species have developed traits and life histories which are concordant – in harmony – with a given disturbance regime and benefit from reduced competition, while less disturbance tolerant species usually decrease in abundance until recovery is possible. Moreover, evidence suggests that disturbance-dependent species exist, which profit from enhancing the local disturbance regime for their reproduction, such as pyrophytes in South African fynbos. In fact, in TVF, fire is considered one of the major drivers of change and is incorporated into vegetation models (Thonicke et al. 2001). Fire disturbance is also known to affect soil characteristics.

A local disturbance phenomenon in the Southern Ocean is the formation of anchor ice; ice crystals attach to the seafloor sediments, encompassing any flora or fauna at the surface. It eventually lifts off, transporting these trapped (mostly dead) organisms with it. Consequently, anchor ice affects the distribution of benthos, particularly that of sessile fauna (e.g., sponges, soft corals). Such events can leave areas several 10s of m^2 in size devoid of epifauna. Recolonization by an exceptionally fast-growing sponge of the genus *Homaxinella* has been observed in these areas (Dayton et al. 2013), as well as in places subject to other types of disturbance, e.g., where icebergs grounded and around glacier tongues.

While volcanic disturbance is not especially important for “forests” – except in cohort dynamics – it should be mentioned, along with recently discovered marine seeps and vents (Niemann et al. 2009; Rogers et al. 2012). The latter form three-dimensional structures that are primarily of mineral rather than biological nature and provide habitat for a variety of specifically adapted animals. Little is known about other extreme events, such as mass sinking of phytodetritus to the seafloor following storms (Isla et al. 2009). Similarly, local mortalities of sponges (e.g., in the South-eastern Weddell Sea) in areas obviously not physically affected by icebergs may also be due to storms. In the Ross Sea, high mortality of glass sponges was attributed to a variety of factors, including low food availability resulting from unusually high ice cover (Dayton et al. 2013). It can be assumed that additional events and processes, which, due to the specific constraints of a marine, ice-covered and remote environment could not be observed in the past 100–1000 years, might have significantly structured AMAF. Finally, physical impact of other, little-known ecological drivers (e.g., near-bottom currents, turbulence, and tides and their effects on food delivery, resuspension, and mortality) shapes the highly variable abundances, patchiness, and changing species composition of such benthic communities.

11 Climate Change and Direct Human Impacts

Anthropogenically induced climate change and human exploitation have both significantly affected AMAF and TVF and will continue to do so. While climate change, including natural processes, might be the most serious threat to the Southern Ocean (for review, see Turner et al. (2014). the “Antarctic Climate Change and the Environment” report, and literature cited therein), natural primary TVF are most seriously damaged by land use (Foley et al. 2005). In the Southern Ocean, changes in sea-ice concentration and duration seem to be the biggest problem at present, affecting ecosystem components that directly depend on the ice such as ice algae, krill, some fishes, penguins, and seals. However, these do not belong to the AMAF per se, although they partially rely on or generally shape them. Effects of climate change on the benthos are less obvious; however, there is speculation on the consequence of regime shifts resulting from reduced sea ice, for example, from a system with a strong seasonal peak in phytoplankton production to one with higher food input over a longer period in summer. This effect is analogous to climate-change-induced shifts in seasonally changing temperate forests, where energy from sunlight and winter temperatures shapes primary production and seasonal leaf shed. In specific marine habitats, food or energy is obviously a limiting factor in the establishment and sustenance of only an impoverished bottom fauna, e.g., in areas beneath ice shelves. These conditions can significantly change locally where the ice shelf has disintegrated. However, in an originally oligotrophic system, increased food availability would likely take years if not centuries to result in development of a richer benthos. Antarctic benthic organisms are assumed to be adapted to typical phytodetritus-poor polar conditions, i.e., the suspension feeders shaping the AMAF might suffer under high concentration of phytodetritus, which may in fact clog their feeding apparatus. Similarly, suspension-feeding species are also expected to be poorly adapted to high concentrations of suspended mineral particles washed into coastal regions following deglaciation on land. In essence, AMAF cannot be expected to generally benefit from increased food supply, even if impressive exceptions exist (including the unexpectedly fast growth of large hexactinellid sponges in McMurdo Sound due to a combination of factors including food quality). Analogously, coral reefs do not develop close to big estuaries due to high concentrations of suspended sediment in these areas. Potentially higher food levels (eutrophication) in AMAF due to future climate change might even result in a decrease in species diversity. However, in TVF, climate-induced "eutrophication" is not a serious issue. Forests are more likely to experience a shift in composition and functioning as a direct result of warming rather than secondary effects. Such changes are known from alpine treelines around the word, i.e., in the European Alps, the Himalaya mountain range, and the North and South American Cordillera mountain ranges, where low temperatures are a crucial growth-limiting factor. Potentially important secondary effects of warming in the Southern Ocean include species range shifts, e.g., of crushing predators such as king crabs to the west of the Antarctic Peninsula, which could devastate major components of AMAF.

Deforestation of an area 18 million km^2 has occurred on land since human settlement (FAO 2012). Today, this and other human impact has an associated conservatively estimated extinction rate of 100 species per million existing species per year, or $>$1000 times higher than natural evolutionary species turnover (Pimm et al. 2014). Assuming the existence of 10 million species on earth, this results in a net loss of 1000 species per year. In addition, deforestation has reduced atmospheric CO_2 sequestration which, when combined with the additional increase in CO_2 emissions through burning and decomposition, is larger than the emissions of all cars and trucks on earth. The degree to which this can be compensated by long-term physical absorption of CO_2 and biological production of O_2 by a "future" Southern Ocean following the shrinking of sea ice and consequent increased primary production is unknown. However, the calculated increase in CO_2 uptake by the Southern Ocean, the equivalent to CO_2 sequestration of $\leq$170 km^2 of a typical rain forest, is just a drop in the bucket.

Ocean acidification, a phenomenon caused by ocean absorption of this excess atmospheric CO_2, might become one of the most serious problems for marine ecosystems in the future. Polar oceans, which are especially sensitive to acidification due to their low water temperatures, are likely to feel the impacts sooner than other regions. While numerous studies have documented effects on various polar ecosystem components (including pelagic and benthic, calcifying and non-calcifying species), ecological thresholds and consequences for the benthos are not yet known. The AMAF at the seafloor will be especially modified if structure-forming calcifiers such as bryozoans and some cnidarians are seriously affected. Interestingly, forest diebacks due to acid rain became a serious problem in Europe and North America just a few decades before acidification in the oceans attracted the attention of scientists. About 20 years ago, huge forest stands began dying as a result of chemical pollution of their root systems by acid rain (including sulfur dioxide) and physiological stress, combined with recurrent drought events in consecutive years. Entire forest ecosystems disappeared, especially in Eastern and Northern Europe, before effective environmental protection measures were introduced.

On land, logging is one of the biggest anthropogenic threats to TVF. A form of logging, “bottom trawling” was also practiced in the Southern Ocean until it was banned for the entire continental shelf and is today only still allowed around two sub-Antarctic islands. Impacts to the AMAF happened especially west of the Antarctic Peninsula, mainly around Elephant Island where trawling occurred until 1985/1986. On the adjacent shelf of the Peninsula where less fishing occurred, the sessile epibenthos is much richer. It is unknown whether present-day communities in the intensively fished areas resemble an animal forest to a lesser degree due to past high fishing effort, or whether the formerly high (and now over exploited) fish stocks prefer naturally poorer epibenthic habitats. Ongoing and officially sanctioned fishing, plus illegal exploitation of natural fish resources of the Southern Ocean (e.g., Patagonian and Antarctic toothfish), alters important components of the food web. Toothfish have been caught since the 1980s by longlines at depths >550 m. This occurs mainly in the Ross Sea and adjacent waters and around South Georgia and Kerguelen/McDonald/Heard Islands, where benthic three-dimensional communities are not abundant, but where some very specific, coral-dominated AMAF do exist. Damage to such sessile fauna must be assumed, especially if the kilometers long longlines are towed sideways. In essence, AMAF have not yet suffered from direct anthropogenic impact to the same extent as TVF. The latter have already and are currently experiencing dramatic destruction driven by exploitation of natural resources, including logging and slash burning for agriculture (e.g., creation of palm oil plantations). However, it is difficult to predict how long the privileged, relatively “untouched” status of the Southern Ocean will last.

12 Conservation Issues

A major difference in nature conservation status between the AMAF and most TVF worldwide is the fact that – based on the “Protocol on Environmental Protection to the Antarctic Treaty” – the Southern Ocean as a whole is better protected than any other marine area or any land ecosystem of comparable size. However, the national implementation of international law is very variable, and, due to the international status of the Southern Ocean, it is much more difficult to establish specifically protected areas because national political and economic issues seem to have the final say. Protected areas are necessary to preserve ecological complexity and diversity hot spots for scientific (preferably noninvasive) studies. If hot spots and, additionally, interesting and unique cold spots (as opposed to sterile paper reserves that protect nothing of value) can be protected, they will offer valuable opportunities to evaluate ecosystem effects of future climate change. The Antarctic is unique because pristine areas undisturbed by humans still exist for study. Protection measures also are necessary to maintain major trophic interdependencies and thus entire food webs, which provide important ecosystem services. Pristine areas should also be carefully protected as critically important refugia, which is especially relevant in the Southern Ocean. In case of ongoing warming, the opportunity for species to migrate to more southern areas that are assumed to be less affected is very much reduced because of the position of the Antarctic continent around the South Pole.

It may be an ethical rather than a scientific question whether the possible extinction of charismatic wild animals, such as elephants, insects, parrots, eagles, or tigers on land, or the great baleen whales, colorful corals, bizarre deep-sea fish, or the impressive apex predators in the sea, e.g., Orcas, seals, penguins and the Antarctic is allowed to persist in a natural setting. However, it is the responsibility of scientists to speak up and stress the importance of undisturbed reference ecosystems, so that future scientists have the opportunity to study essential and fundamental parts of their living planet and that these unique ecosystems are preserved for the future of humankind.

13 Future Directions

To enhance scientific knowledge of AMAF, three interrelated research themes are here proposed, which are based on the “SCAR Antarctic and Southern Ocean Science Horizon Scan” (Kennicutt et al. 2014): (1) circumpolar mapping of biotic structure and function, (2) understanding ecological processes and ecosystem services by experimental community ecology and model-based future projections, and (3) cross-ecosystem studies.

13.1 Mapping Structural and Functional Diversity of Biotic Communities

For a quantitative assessment of AMAF (or indeed, any Antarctic benthic community), much better data on their spatial coverage are needed. Since surveys across the entire extent of Antarctic shelves are not logistically possible, this could be completed on smaller spatial scales by targeting selected areas considered to be representative of specific community types. In addition, there is a need for at least a coarse imaging of larger areas, for example, using a stratified random sampling across the broad shelf-area. In addition to numerous single species records (DeBroyer et al. 2014), a first circum-Antarctic attempt to collate existing information on macrobenthic communities has recently been published (Gutt et al. 2013). However, a survey with higher levels of precision is required and could be carried out using a standardized identification of communities based on quantitative composition of higher systematic groups. In selected target areas, detailed surveys could identify and, most importantly in this context, quantify the abundance (including absence) and biomass of all species. A relatively coarse identification level with a specific focus on higher taxa and on the most abundant and ecologically key species would also be possible. Our basic scientific knowledge on the existence of AMAF and other benthic communities would be considerably improved if structural complexity could be correlated with species diversity, biomass, and productivity. Important questions on functional diversity remain around the role of epibiotic relationships. For example, does the complex, three-dimensional architecture of AMAF really increase regional diversity or “only” attract species at the local level? How does this effect functional diversity? Or alternatively, do AMAF-specific characteristics suppress diversity (and eventually also biomass) as a result of competition? If grazing and other predation pressures are considered a “disturbance” to AMAF, they could have both a positive and negative effect on the diversity and functional resilience of these unique ecosystems.

13.2 Understanding Ecosystem Function

A second major knowledge gap with respect to AMAF is whether structurally rich hot spots are also hot spots in ecosystem dynamics. Before ecosystem structure and dynamics can be correlated with each other, processes contributing to ecosystem function must be defined and measured on appropriate spatial scales. In this context, improved knowledge of pelagic-benthic coupling is key. Information on the source, quality, and quantity of food available to suspension feeders would significantly advance our understanding of potential limiting factors for AMAF. Such data will not only help interpret existing patterns, but will improve our predictions of how the benthic system may respond to changes in other components of the Southern Ocean ecosystem. This approach also demands detailed knowledge of ecologically relevant physical and chemical factors – including temporal variability and extreme events – at a high spatial resolution. For example, experimental studies of successional dynamics following disturbance (e.g., iceberg scouring) could deliver basic information on age structure and system productivity as well as ecosystem functioning, e.g., on turnover rates between trophic levels and nutrient (re-)cycling in benthic systems, for which fundamental information is lacking in the Southern Ocean.

13.3 Research Strategies

The implementation of all these approaches demands considerable field work, processing, pattern analyses, and modeling. It requires traditional sampling using a question-driven design and remote sensing techniques (e.g., AUVs, ROVs, crawlers, and gliders) which are designed for spatially explicit sampling. Newly developed tools for in situ sampling and measurements (e.g., lander-based autonomous laboratories and crawlers) are very promising and can potentially advance our process-based understanding of these AMAF ecosystems. However, access to these tools is presently limited. New methods are also to be developed. For example, determination of biomass demands much physical and temporal effort. Before this can be determined by remote imaging, proxies must be developed or conversion factors determined to extrapolate from two-dimensional seafloor coverage to true biomass. Regardless, material sampling will still be necessary for precise species identification and for traditional as well as more advanced studies on life history traits. Imagery, however, provides additional important information on three-dimensional structure as well as on the spatial coexistence of species and can contribute significantly to the community mapping approach discussed above. Also, the old question of "whether communities can be determined using proxies from sediment backscatter" could be revisited across larger areas rather than using spatially limited imaging methods or punctual sampling (e.g., by grabs or corers). Some of these questions can be answered using biomolecular techniques ("omics"), which are under continual and rapid development. A fast and efficient species determination is possible if genetic libraries are established, methods are standardized, and equipment is widely available. Considerable effort is still required to use these new techniques, especially transcriptomics, in combination with traditional measurements to better understand various biological processes and ecosystem response, especially to environmental change. Especially SCAR's biology programs *Antarctic Thresholds – Ecosystem Resilience and Adaptation* (AnT-ERA) and *State of the Antarctic Ecosystem* (AntEco) facilitate international cooperation to answer such big scientific questions on ecosystem functioning and diversity patterns, respectively.

Only the combined results from structural and process-based studies can answer fundamental questions on the driving forces and limiting factors for AMAF (and other Antarctic macrobenthic communities). Investigating AMAF offers the opportunity to study an ecosystem free from human perturbations – as, for instance, studying European forests in the times of the Roman Empire, or the North American forests before European colonization. At first glance, this call to action seems challenging with regard to present research funding. However, instead of finding ways to allow destructive exploitation of the Southern Ocean, this is a promising opportunity for SCAR, the Commission on the Conservation of Antarctic Marine Living Resources (CCAMLR), and Committee for Environmental Protection (CEP) to provide unique opportunities for visionary scientists to orchestrate international cooperation necessary to provide the science basis for the conservation of a unique ecosystem.

13.4 Cross-System Comparisons

In addition to ecosystem-specific studies of AMAF and TVF, cross-system literature-based reviews, true comparative surveys, in situ experiments, and model applications have the greatest potential to answer questions around the generality and uniqueness of ecological processes and the diversity of these three-dimensional ecosystems in the oceans and on land.

14 Cross-References

- ▶ Animal Forests of the World: An Overview
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Evolution of the Marine Animal Forest: EvoDevo of Corals, Sea Anemones, and Jellyfishes
- ▶ Growth Patterns in Long-Lived Coral Species
- ▶ Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages
- ▶ Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998
- ▶ Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles
- ▶ Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns

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Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean

12

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Abstract

Vermetid mollusks form reefs that protect coasts from erosion, regulate sediment transport, serve as carbon sinks, and provide habitat for many fish and invertebrates. This biogenic habitat is found in tropical, sub-tropical, and warm-temperate coastal areas, such as Bermuda, oceanic islands in Brazil, and Hawaii, several locations within the Caribbean and the Mediterranean. These reefs are functionally similar to tropical coral fringing reefs but are built by gregarious vermetid gastropods cemented by a crustose coralline algal species, which probably triggers their settlement. Some descriptive studies in different regions worldwide and comparisons among tropical and Mediterranean reefs contributed to show their important role as engineered habitat and biodiversity hotspots. In recent years, a dramatic decrease in the vermetid live cover was recorded in the Eastern basin of the Mediterranean, with some documented local extinctions within a few decades. Pollution and the spread of invasive species are potential threats to this animal forest and to the biodiversity it supports. Yet, the response of the vermetid reef to climate change is almost unknown, although recent experiments demonstrated high sensitivity of this snail species to ocean acidification. Hence, the ongoing rapid environmental change and increasing anthropogenic use along the coast may have detrimental effects on the remaining reefs and therefore significant ramifications for coastal systems in the Mediterranean and subtropical and warm-temperate regions. This chapter aims at filling these knowledge gaps by presenting both a short literature-based study and a set of

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new research paths to explore and improve conservation and research activities given the range of ecosystem services pristine vermetid reefs may provide.

Keywords
Temperate reef • Encrusting coralline algae • Biogenic reef • Animal forest • Biodiversity hotspot • *Dendropoma petraeum* • *Dendropoma lebeche* • *Dendropoma anguliferum* • *Dendropoma cristatum* • *Dendropoma irregulare*

Contents

1 Introduction

1.1 A Reef Constructed by Gastropod Snails and Encrusting Coralline Algae: The Mediterranean Vermetid Reef

A reef is any construction made by a single or a group of living organisms able to progressively modify the environment at local scale (Fagerstrom 1987), generating physical structures and thus modifying the habitat and its structural complexity (Bell et al. 1991). Biogenic reefs have a complex structure according to both biotic (the reef-building species and their morphology) and abiotic factors (e.g., shore geomorphology, rock typology, water transparency, depth, and wave exposure). Reef-building species are typically calcium-carbonate secreting animal and algal taxa (i.e., coralline algae, corals, mollusks, bryozoans, and serpulid polychaetes) or those organisms forming dense aggregations able to secrete tubes with coarse sand particles, such as sabellariid worms (Cocito 2004).

What makes a reef system different from other shallow marine ecosystems is its capability to build wave-resistant structures that eventually can reach the sea surface and follow subsequent sea level changes. These characteristics make any bioconstructions highly resistant to disturbances and enhance the stability of coastal environments (Safriel and Ben-Eliahu 1991). Being less conspicuous, colorful, and speciose than tropical coral reefs, up to date it is still overlooked that bioconstructions of various types are present in the temperate seas. These habitats are those formations that the famous French marine biologists of the so-called *School of Marseille* (Roger Molinier, Jean-Marie Pérès, Jacques Picard) have distinguished under a rich nomenclature, whose most used terms were *encorbeillement*, *corniche*, *trottoir*, *plateforme*, and *récif* (Molinier and Picard 1953; Molinier 1955a, b; Pérès and Picard 1964; Laborel et al. 1994).

Specifically, serpulid worms, vermetid mollusks, and red coralline algae (along with bivalves, bryozoans, and corals) are all capable of building more than 22 different types of biogenic reefs along the Mediterranean coast (Laborel 1987; Relini 2009).

Vermetid reefs are generally found in warm-water temperate seas and subtropical areas, such as Bermuda (Stephenson and Stephenson 1954), oceanic islands in Brazil (Van Andel and Laborel 1964), and the Mediterranean, although they have also been recorded from several locations within the tropical Caribbean (Focke 1977; Jones and Hunter 1995). In the Southwestern and Eastern sectors of the Mediterranean basin, the vermetid reefs are constructed by the gregarious gastropods belonging to the genus *Dendropoma* and the coralline alga *Neogoniolithon brassica-florida* (Safriel 1966).

This intertidal vermetid-coralline algae aggregation was first described by the French naturalist Antoine de Quadrefages in 1848, along the coast of Isola delle Femmine, a small village near Palermo city (NW Sicily, Italy). The vermetid reef or “trottoir à vermets” (according to Molinier and Picard 1953) is a biogenic formation bordering the rocky coast at tide level and is of particular interest because of its broad horizontal extension (representing *de facto* an amplification of the intertidal zone, particularly in microtidal systems like the Mediterranean basin), its restriction to the warmest part of the Mediterranean Sea, and the many microhabitats and high levels of biodiversity it supports (e.g., Safriel and Ben-Eliahu 1991; Chemello et al. 2000; Chemello 2009).

Vermetid reefs along the Mediterranean rocky shores have very different morphologies (Antonioli et al. 1999; Fig. 1). The crust (a thin formation made by a single layer of *Dendropoma* spp. shells), the ledge (usually <1 m wide and 20–30 cm thick) (Laborel 1987), and three other forms resulting from differential erosive processes between the rock substrate not covered by the vermetids and the living bioconstruction: the mushroom-like pillar (appearing as a large vermetid rim on a thin stalk), the micro-atoll, and the island (Safriel 1966). In addition to this, on intertidal abrasion platforms the massive bioconcretion gives rise to the most complex structure: the intertidal terrace or vermetid platform.

Whatever the morphology of the vermetid-coralline aggregations, by creating a living three-dimensional structure and by altering the biotic or abiotic conditions to other associated benthic species, these vermetids rims represent a poorly known and often neglected animal forest (sensu Rossi 2013).

On vermetid reef platforms, it is easy to identify an outer and an inner margin more or less deeply excavated in response to abiotic factors (Antonioli et al. 1999).

Fig. 1 **How vermetid reefs look like**. Different vermetid reef structures (According to Safriel 1966): a vermetid platform in the bay of Makari (NW Sicily, Italy) (**a**), a reef ledge near Alicante (SE Spain) (**b**), a micro-atoll (**c**), a mushroom-like pillar in the Gulf of Cofano (NW Sicily, Italy) (**d**), and islands or macro-atolls in Sdot Yam (Israel) (**e**) ((Photo credits: R.C. (a,b,d), modified after Bayle-Sempere and Sánchez-Jerez, 2004 (c), M.F. (e))

The outer margin is generally composed by a thick (sometimes >50 cm), highly articulated, and crevices-rich layer of *Dendropoma* spp. shells and *Neogoniolithon brassica-florida* encrusting thalli, representing the most biologically active margin of the platform expanding seaward. The inner edge develops more vertically, is less thick and dense of *Dendropoma* individuals than the outer one, and is subjected to emersion during low tide, desiccation, and UV-irradiation stress. The two margins enclose a shallow depression – namely, the *cuvette* (Molinier and Picard 1953; Pérès and Picard 1952) – which usually holds water on the flat during period of low tide and calm sea and is covered by perennial canopy-forming brown algae and encrusting organisms of subtidal origin, particularly in more shaded areas and in submersed pools. Below the outer margin, the vermetid reef is fringed by a characteristic upper subtidal belt made by the canopy-forming alga *Cystoseira amentacea* var. *stricta*, which usually delimits a highly speciose overhang habitat represented by a submersed wave-cut notch. Often, the hard skeletons of other intertidal organisms, namely, the foraminiferan *Miniacina miniacea*, the coralline algae *Lithophyllum byssoides*, *L. incrustans,* and *Neogoniolithon mamillosum*, some encrusting bryozoans and the solitary vermetid *Vermetus triquetrus* may also support the *Dendropoma* snails and the *N. brassica-florida* encrustation in the process of bioconstruction (Safriel 1974). Counteracting the bioconstruction of these species is a rich group of boring organisms such as sponges, bivalves, and sipunculid worms, making the reef more breakable during strong winter storms (Bressan et al. 2001).

Together with a suite of other thermophilic species, *Dendropoma* ssp. is characteristic of the Southern sector of the Mediterranean Sea and seems to be quite a recent "invader" of this semi-enclosed basin, very likely entered in the latest interglacial warming of the basin (Antonioli et al. 1999). The earliest fossil records from the coast of Syria are dated about 6000 years Bp. Remnants of fossilized platforms on the island of Crete have been detected at about 7 m above the present sea level and date back to 2000 years Bp. In Southern Italy, records of fossil fragments washed ashore by storms are about 2600 years Bp old (Antonioli et al. 1999).

The largest Mediterranean vermetid formations have been described along the Israeli, the Lebanese, and the northern part of the Syrian coast, from Lattakia up to the Turkish border. Large reefs have also been reported in southern Turkey and Greece (Crete). In Malta, vermetids mainly develop as concretions and small reefs. In Italy, most of the vermetid reefs are distributed in Northern Sicily, between Milazzo Cape (NE Sicily) and the Egadi Islands (NW Sicily). Along the Mediterranean coast of Spain, vermetids are present from Castellòn de la Plana (Valencia) to Càdiz (Andalusia), including the Balearic Islands and the Alboran Sea. The most developed formations are reported from the southeastern regions of Alicante, Murcia, and Almeria. Along the southern rim of the Mediterranean, vermetid reefs have been recorded in Eastern Libya along the Cyrenaica coast. Few data are available for the Tunisian coast where vermetid reefs were recorded in Sidi Mechreg, Lakhouet Islets, Bizerta, Zembra, and Zembretta, while well-structured vermetid platforms are also present in Algeria and small formations have been found along Mediterranean Moroccan coast, particularly in the Chafarinas Islands and Sebta. Over the last three decades, *Dendropoma* concretions have progressively expanded in the northernmost sectors, crossing a long recognized biogeographical divide at 40 °N latitude and 14 °C winter SST, where they develop mainly as crusts and ledges in the upper subtidal.

1.2 The Peculiar Biology and Ecology of the Mediterranean Vermetid Reefs

Reef-building vermetids are known for their extreme plasticity and the Mediterranean *Dendropoma* species seem not to be an exception to this common trend. Their tubular shells present a rugged sculpture and grow partly embedded in the surface along its whole length (Fig. 2). During low tide, the shell opening is tightly sealed by

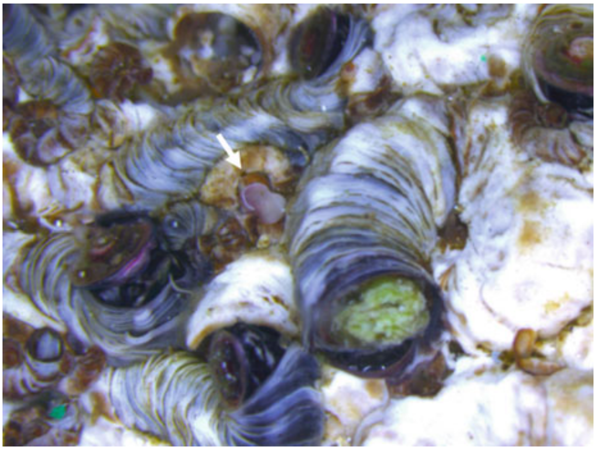


Fig. 2 A close up of the rugged tubular shells of *Dendropoma cristatum* adults, in some instances cemented by the coralline alga *Neogoniolithon brassica-florida* (on the *right*). The shell openings of *Dendropoma* are sealed by a chitinous operculum. A newly settled vermetid recruit can be also seen (*white arrow*) (Photo credit: M.F. and M.M)

an operculum when the animal withdraws. This operculum is multispiral, rather flat or slightly dome shaped, and serves also as protection from predators (Fig. 2).

Recently, genetic analyses revealed that the reef building species *Dendropoma petraeum* – originally described along the NW Sicilian coast and supposed to be widely distributed throughout the Mediterranean Sea – comprises a complex of four cryptic species (Calvo et al. 2009, 2015). Such a genetic difference has phenotypic correspondence and has led to distinguish up to date three *Dendropoma* species, all of which are reef building and inhabit similar habitats: *Dendropoma lebeche* (Western Mediterranean lineage), *Dendropoma cristatum* (Sicilian-Tyrrhenian lineage), and *Dendropoma anguliferum* (Levantine Sea lineage) (Templado et al. 2016). A fourth species from the Ionian-Aegean area lacks a detailed morphological description. *Dendropoma lebeche* and *D. cristatum* share similar morphological characteristics but differ in protoconch size and sculpture, and some developmental features (e.g., number and size of the egg capsules simultaneously brooded by females, the intracapsular larval development, or the presence absence of nurse eggs) (Templado et al. 2016).

Despite phylogenetic differences, *Dendropoma* species share a very peculiar reproductive and developmental biology and an extremely low larval dispersal and population connectivity that makes the recovery of vermetid reefs after local mortality unlikely. Males are aphallic and their sperm are encapsulated in spermatophores which are released to the water and trapped by females through feeding sticky filaments. Sperm is held in the female mantel cavity until gonads maturation and internal fertilization occurs when the seawater starts to warm. Females brood their fertilized eggs in capsules held in the mantle cavity and metamorphosed larvae hatch inside the maternal shell. After hatching, crawling juveniles typically spend a few hours finding a suitable place to settle (usually very close to the maternal shell) whereon they immediately calcify a flat base to firmly attach to the substratum and start a sessile life. It seems that settlement is triggered by the coralline algae (Spotorno-Oliveira et al. 2015).

Feeding strategies in *Dendropoma* may vary according to local environmental conditions and are related to reef morphology. The individuals forming intertidal platforms are mainly filter feeders, while those building "crusts" or "ledge" reefs in the upper subtidal are rather shifted to mucus feeding (Schiaparelli et al. 2006). Differential exposure to tides and waves, furthermore, can affect feeding rates and behaviors of *Dendropoma* species (Vizzini et al. 2012). Besides enhancing food inputs, water turbulence and wave-pumping of water through the bioconstructions may also aid cementation and lithification processes and most authors recognize that such reefs grow best under exposed conditions, thus benefiting from wave action (Chemello and Silenzi 2011). Also, grazing with the radula has been observed in *Dendropoma* species particularly in the larval stage (Calvo et al. 1998).

An indication of the ecological requirements of the main reef building species and of their optimal conditions to develop large reefs may be resumed from the snail capacity of colonizing and covering a stretch of rocky coast. In the intertidal zone, in addition to a warm winter SST (>14 °C) and a high salinity level (>37 ‰), the following abiotic factors seem to control the snail settlement and distribution: (a) the geological nature of the substratum, (b) the exposure to waves and storms, (c) the coastal slope (Chemello et al. 2000; Chemello and Silenzi 2011).

The rock typology and texture beneath these reefs are central factors for its build up at mean sea level and some authors recognize a strict relation between the geological nature of the rock substrate and the way the reef may develop best (Chemello et al. 2000). The more a rock substrate is subject to physical erosion, the higher is the width of a reef (i.e., the distance between the inner and the outer rim) (Fig. 2). The best conditions to develop were recorded on eolianitic and calcarenitic geological substrates (Chemello 2009) (Fig. 3). Less suitable rocky substrates seem to be in the series: dolomite, basaltic, granitic, and flysch (but see Schiaparelli et al. 2003). On these rock typologies, the outer and inner rims are always clustered in a single intertidal ledge (if present at all), and the formation of a true terrace is not possible (Chemello 2009).

The slope of the shoreline is the third physical factor affecting the size and shape of the reef. On flatter coasts (0–15°), these formations are less ample and appear as ledges or thin crusts. Underneath the upper intertidal notch of cliffs, vermetids progressively show reduced thickness and width at >40° slope, being completely absent on >50° slope of the shore. On Sicilian carbonate substrates, for instance, Chemello et al. (2000) observed that *D. cristatum* (as *D. petraeum*) larger reefs develop where the slope is between 15° and 40°, on the mean sea level. The synergistic effects of these abiotic factors, thus, may strongly affect the size and shape of a vermetid bioconstruction and the density of its main reef-building species.

The density of *Dendropoma* aggregations is generally higher on outer rims than inner ones of the reef structure (Di Franco et al. 2011) and is much lower where reefs develop as crust or ledge morphs despite the substrate mineralogy (Schiaparelli et al. 2003). Data available from descriptive surveys carried out along the Spanish, the Italian, and the Israeli coast revealed that in pristine conditions vermetid reefs usually show >50,000 individuals m^{-2} in the outer rims (Bayle-Sempere and Sánchez-Jerez 2004; Graziano et al. 2007; Di Franco et al. 2011; Usvyatsov and

Fig. 3 Pristine Mediterranean vermetid reefs at low tide in Capo Gallo, NW Sicily (Italy) and a detail of the outer rim of a vermetid reef (*top right*) (Photo credits: M.M.)

Galil 2012). However, since the vermetid reef persistence seems to be strongly affected by local factors such as pollution and sedimentation, densities may be much lower in disturbed areas (Graziano et al. 2007; Di Franco et al. 2011; but see also below).

2 Importance of Vermetid Reefs in Providing Valuable Ecosystem Services

Humans often neglect the relevance of the ecosystem goods and services provided by marine biogenic habitats worldwide, despite freely benefiting from them both directly and indirectly. By protecting the rocky shores from erosion, regulating sediment transport, serving as carbon sinks, and providing habitat for many fish and invertebrates, the vermetid reef has indeed a considerable role in the intertidal zone with consequent influences on the productivity and dynamics of the Mediterranean coastal area. Via secretion of carbonatic shells and thalli, the two reef-building species *Dendropoma* spp. and *Neogoniolithon brassica-florida* are indeed autogenic engineers. This causes physical state changes in biotic and abiotic materials, providing living space for other organisms and also modulating abiotic forcing, such as currents, sediment transport, and substratum features that, in turn, affect natural resources and their availability. Bioeroding species as well (grazers, micro- and macroborers), operating synergistically with physical and chemical erosion, may increase the reef habitat structure, if both the reef builders are able to maintain a higher reef accretion than the erosion rate. This confers these reefs a significant role in the functioning of Mediterranean coastal systems. Indeed their presence alters the habitat structure at different spatial scales. At low spatial scale, these biological encrustations modify the substratum and its characteristics, enhancing the presence of crevices, holes, and irregularities that locally ameliorate surface rugosity increasing space and generating microclimatic conditions which are different from the surroundings. Similarly, submerged vermetid reefs, which were formed along ancient coastlines when sea level was 30–100 m lower than the present, serve as hotspots of biodiversity in deeper water, long after the organisms that built them no longer live. Coastal habitats with high density of these structural organisms compared to those where they are absent are considered more complex and rich in microhabitats. A better understanding of the ecological functioning of this biogenic habitat may trigger its conservation and sustainable management in Mediterranean coastal systems.

2.1 Supporting High Biodiversity Levels

The three-dimensional framework offered by the vermetid reef formations is an important structuring feature of the Mediterranean coastal ecosystems, critical for their functioning and the high biodiversity levels they support (Safriel and Ben-Eliahu 1991). In areas with very low tidal range, which never exceeds 40–45 cm along most of the Mediterranean coastline, space is a limited resource for intertidal species. Vermetid reefs do contribute in different ways to widen the available ecological niches for a variety of benthic and fish assemblages, e.g., by limiting physical disturbances, by providing refuge from predation and critical nursery habitat, by affecting the strength of competitive interactions, or representing themselves important food resources (Goren and Galil 2001; Consoli et al. 2008; Chemello 2009).

Similarly to other intertidal biogenic habitats, such as oyster and mussel beds, the physical structure of vermetid reefs essentially reduces the energy of waves and milds their physical impact on the shore. This allows an increasing number of species to be able to colonizing such intertidal habitat. For instance, a high number of gastropods' shell morphologies with different foot shapes are present on rocky shores where this biogenic habitat is present (Fig. 4). Gastropod species richness is 1.6-fold higher in rocky shores with vermetid reef than those without, where only two shell morphs are present (Fig. 4).

Ecological theory predicts that limited resources can be effectively partitioned by ecologically similar species by reducing their spatial overlap (MacArthur and Levins 1967). Indeed for animals that can choose where to live, like intertidal crabs, spatial segregation becomes a viable solution to reduce potential competition and locally persist within a vermetid reef. Grapsids belonging to the genus *Pachygrapsus* are very common crab species in the Mediterranean rocky intertidal. On vermetid reefs, they actively feed on algal turfs in the cuvette, finding refuge from predators, and shelter from adverse environmental conditions (e.g., high irradiance and air temperature) in crevices both of the inner and the outer margins of the vermetid reef. A clear spatial segregation was detected for three congeneric and ecologically similar grapsid species: *Pachygrapsus marmoratus* (Fabricius 1787), *Pachygrapsus maurus*

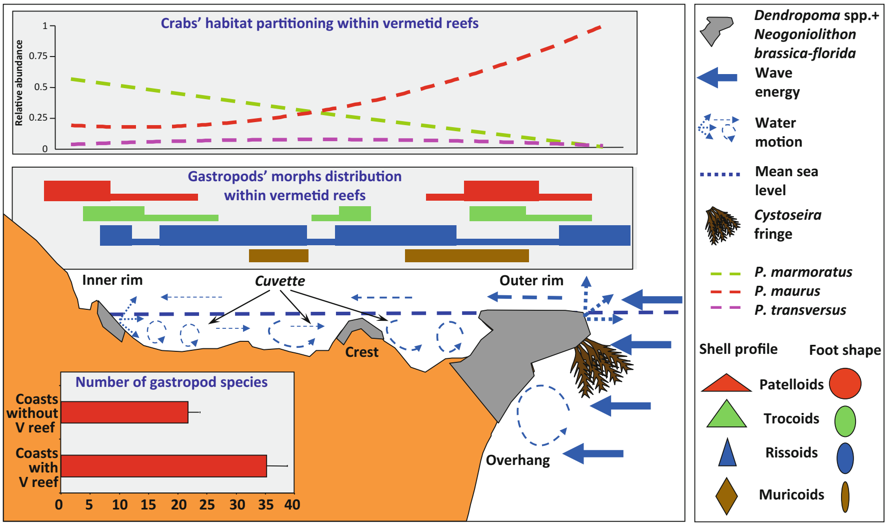


Fig. 4 Vermetid reefs contribute to widen the availability of space for a variety of benthic and fish assemblages, providing refuge from predation and affecting the strength of competitive interactions. Three congeneric and ecologically similar crab species partition spatial resources within vermetid reefs in NW Sicily. By absorbing the wave energy and modifying the water flow, the vermetid reef enhances the number of species morphologies inhabiting this biogenic habitat. Gastropod species richness is 1.6-fold higher in rocky shores with vermetid reef than those without vermetid reefs where only two shell morphs (e.g., patelloids and trocoids) are present

(Lucas 1846), and *Pachygrapsus transversus* (Gibbes 1850), indicating an opposite trend of habitat use for the two most abundant crab species, *P. marmoratus* and *P. maurus*, whereas the third species, recently entered into the Mediterranean from the Gibraltar Strait, exhibited low numbers (Fig. 4).

To date no studies have been addressed to exhaustively estimate the biodiversity levels the Mediterranean vermetid reefs may support. However, several descriptive studies in different locations, as well as comparisons among similar reefs in tropical and Mediterranean regions, have been contributing to show their important role as engineered habitats and biodiversity hotspots.

It has been long considered that algal growth is not lush when *Dendropoma* is healthy (Safriel 1975); however, algal assemblages associated with these reefs are composed by at least a hundred of macroalgal species distributed across the different parts of the reef (Mannino 1992). In addition to *Neogoniolithon brassica-florida*, whose central role is to cementing the *Dendropoma* shells, and *Lithophyllum byssoides* – often forming cushion-like structures in the two margins of the platform – the most characteristics algae are the *Laurencia* complex of species (a set of red algae belonging to Rhodomelaceae family), and the brown algae *Padina pavonica, Cystoseira,* and *Dyctiota* species, mainly present in the cuvette (Graziano et al. 2009). On reefs exposed to anthropogenic disturbances, these species are often substituted by Corallinales and Ulvales (Graziano et al. 2007). Encrusting red algae and sometimes *Halimeda tuna* are dominant in those reefs where the *cuvette* is deeper (sometimes 0.5 m deep at low tide), tidal pools are present, or underneath the *Cystoseira* and *Dictyota* canopy. Below the outer rim, the narrow upper infralittoral fringe is often characterized by *Cystoseira*-dominated assemblages. In this lower border of the reef formation, high-density belts *of Cystoseira compressa* and/or *Cystoseira amentacea* var. *stricta* are usually dominant, and their presence follow both natural (i.e., hydrodynamics, light exposure, and herbivorous pressure) and anthropogenic factors (habitat destruction, pollution, and human trampling).

The *Dendropoma-Neogolithon* aggregation itself and the macroalgal species associated with the vermetid reefs host highly diverse zoobenthic assemblages. Algal-dwelling and undercanopy species are mostly present in the reef flat (*cuvette*) and in the upper infralittoral *Cystoseira* fringe. The reef structure adds crevices and refuges to a set of interstitial species and *Dendropoma* empty shells are colonized by animals belonging to rich and diversified cryptofaunal groups. Vermetid tubes and reef crevices act as sediment and organic matter traps. Many molluscs, polychaetes, and crustaceans feed on these resources, continuously renewed according to tidal cycle and wave energy. Indeed mollusks and polychaetes are the most studied animal groups associated with vermetid reefs.

Past surveys outlined the importance of the molluskan component in the intertidal vermetid reefs (Orlando and Palazzi 1985; Chemello et al. 1990, 1997) and an estimate in defect of the reef malacofauna reports an assemblage composed of 46 species. In addition to *Dendropoma* spp., the most representative species are the chiton *Lepidochitona caprearum*, the bivalves *Mytilaster minimum* and *Cardita calyculata*, and the gastropods *Pisinna glabrata*, *Patella ulyssiponensis*, *Onchidella celtica, Eatonina cossurae,* and *Barleeia unifasciata*.

A comparison of the polychaete communities associated to vermetid rims in tropical and Mediterranean regions revealed that the Red Sea species pool was 1.6 times larger than the Mediterranean one, but the Red Sea vermetid reefs were only 1.3 richer (90 vs. 70 polychaete species) than the Mediterranean reefs (Safriel and Ben-Eliahu 1991). The observed higher polychaete diversity in the Red Sea than that of the Mediterranean reefs has been explained by the harsher and less predictable exposure to environmental disturbances (aerial exposure and storm events) combined with region-related differences in the size of the species pool and life-histories (Ben-Eliahu et al. 1988). Interestingly, worm assemblages were twofold denser in the Mediterranean (15.7 ind. cm^{-2}) than the tropical reefs (7.4 ind. cm^{-2}) (Safriel and Ben-Eliahu 1991). Provided populations recovery is relatively slow and competitive displacement is rare in tropical areas, this was again explained by the higher frequency of disturbance affecting the worm populations inhabiting the interstices of the Red Sea reefs than the Mediterranean ones (Ben-Eliahu et al. 1988).

As interesting as the between-regions comparisons proposed by Ben-Eliahu and colleagues (Ben-Eliahu and Safriel 1982; Ben-Eliahu et al. 1988; Safriel and Ben-Eliahu 1991), Badalamenti et al. (1998) showed that the Mediterranean polychaete community of the vermetid reefs was 1.3 times richer than that associated with mussel beds along the NW Sicilian coast. A total of 70 worm species were identified in two reef locations and these data were consistent with the findings from the Mediterranean Israeli coast (Ben-Eliahu and Safriel 1982). Qualitative comparisons with other areas of the Italian peninsula characterized by the absence of bioconcretions also point out a higher species richness on the vermetid reefs (Abbiati et al. 1987; Giangrande 1988; Lardicci et al. 1992).

Fish fauna of vermetid reefs has been investigated both along the Israeli and the Italian coasts. In Israel, a total of 36 fish species was recorded on intertidal vermetid reefs and represented the highest fish biodiversity reported in any habitat along the Mediterranean coast of Israel (Goren and Galil 2001). Four species were of Red Sea origin and entered in the Levantine region after the opening of the Suez Canal in 1869. The strictly benthic fish community was typical of the Mediterranean Sea and composed by 18 species. Gobids and blennids were the most abundant families with 4 and 9 identified species, respectively. The blennids *Parablennius zvonimiri* and *Scartella cristata*, both with cryptic habits finding refuges in the reef crevices were the two most abundant species. More recently, the comparison of the fish assemblages of three shallow Mediterranean rocky habitats, the vermetid reef, the rocky-algal reef, and the boulder field, revealed that, despite total number of species did not differ between habitats, the vermetid reefs showed the higher physical complexity supporting on average the highest values of fish density and species richness (Consoli et al. 2008). A total of 29 fish taxa were identified in the investigated vermetid reefs. Interestingly, the commercially important *Diplodus* species were more abundant on vermetid formations than the other two habitats, letting hypothesized that reefs provide additional resources for adults and juveniles of many fish species. However this assumption remains to be specifically investigated.

2.2 Preventing Coastal Erosion, Regulating Sediment Transport, and Providing Carbon Sequestration

Settlement of *Dendropoma* recruits is probably driven by physical, chemical, and biological cues which make the surface attractive for larvae. Once the bioconstruction is established, vermetid and coralline algae act as a biological crust that modifies and protects the underneath space. Likely to other shallow biogenic habitats, such as oyster and mussel beds, the vermetid reef does change the morphology of a given coast and well-developed external margins amplify often up to three times the coastal profile (Fig. 3). To date scant information is available about the role of the vermetid reef as a biogeomorphological agent able to shape rocky shores and to mediate earth-surface processes. However, whatever the geological and morphological characteristics of a given coastline, the vermetid reef locally increases the rock resistance to multiple detrimental factors, giving rise to bioprotection of the beneath substrata.

Bioprotection can be broadly defined as the active or passive, direct or indirect role of organisms in preventing or reducing the physical, chemical, and biological processes that cause substrate erosion. In general, the vermetid reef bioprotection might act at a variety of spatial scales. Firstly, vermetid reefs are biophysical structures which do interfere with marine water flow and affect wave energy. When in a pristine state, vermetid reefs act as a wave energy damper reducing coastal regression and littoral erosion. The amplitude and the microrelief of *Dendropoma* reef essentially modify water flow, absorbing wave force and reducing their impact on the shore. Therefore, reefs reduce coastline erosion phenomena. Although there is no robust research in this field for the vermetid reefs, it is likely they act as a buffer of coastal erosion, proportionally to their width. Preliminary experiments, accompanied by field observations, agree with this insight. Wave energy attenuation is also strengthened by the vegetation present on the reef, especially by canopy species whose density and structure can play an additional hydrodynamic control and mediate stressors on the covered substratum. Accordingly, using a simple replacement cost method (Spurgeon 1992), a first assessment of the ecosystem service made by the vermetid reef only regarding coastal erosion has assigned a value of 350–750 euro m^{-1} $year^{-1}$.

In addition to this, within the Mediterranean Sea vermetid reefs are not subjected to great tidal excursion and usually residual water is trapped between the reef rims. Under these circumstances, biological erosion should be the first cause of rock alteration. Chemical and physical weathering, instead, are mostly represented in the inner edge of the reef which is mostly subjected to emersion and desiccation stress, especially during warm months. Under these circumstances, substrates reach very high temperatures and experience consistent water evaporation. This allows salt-crystallization and temperature and humidity variations inside rocks and affects their microclimate. As demonstrated for other biogenic habitats, such as barnacles, seaweeds, or lichens and ivy for terrestrial environment, the presence of the vermetid encrustation would limit these processes reducing the potential for chemical and physical rock-breakdown to act where the bioconstruction is present.

Beach erosion, e.g., the removal of sand from a beach to deeper water offshore or alongshore, has become a common phenomenon around the world including the Mediterranean Sea. Beach erosion is a natural process where elements such as currents, waves, and sea level changes play a significant role, but this process may be exacerbated by human activities such as land hard defense, land reclamation, and vegetation clearing. The consequences are vast economic costs in repair (e.g., beach nourishment) and prevention (seawalls and breakwaters, submerged soft and hard installations). Vermetid reefs act in many areas as natural seawalls or breakwaters (when detached from the shore), and it is very common to see accumulation of sand at the lee side of the reef, forming a tombolo, especially where the longshore currents are dominant. As such, extensive vermetid reefs are a natural shore protection able to regulate sediment transport, as long as living *Dendropoma* and an active rim prevents erosion of the reef itself.

Another process in which vermetid reefs are involved is the carbon sequestration, which might play a relevant role in climate change mitigation. Carbon sequestration is not an explored field of study for vermetid bioconstruction, although both *Dendropoma* spp. and *Neogoniolithon brassica-florida* are able to use natural carbon sink as source to build their structures, thus reducing CO_2 quantity in the atmosphere. Likewise other marine habitats, such as *Posidonia oceanica* meadows, salt marshes, and mangroves, the vermetid reef develops accumulating carbon. At present, minimal data are available to quantify the carbon sequestration rate and to estimate the total stock of carbon stored in the vermetid reef. Therefore, the extent of this role has not received enough attention and to recognize the potential stability of natural carbon sink is a fundamental field of research which needs further attention.

3 Potential Threats to Vermetid Reefs' Persistence Within the Mediterranean Sea

Historically, vermetid reefs have been strongly affected by natural disturbances and shifts in environmental conditions. Shier (1969) suggested that hurricanes and sharp changes in local ecological conditions occurred in the last century off the Florida coast have affected the growth of some vermetid reefs. Similarly in the West Indies, the occurrence of dead vermetid reefs in low energy coastal environments was correlated to temperature changes and decreasing exposure of the coast occurred at the end of the Little Ice Age (1625–1740) (Jones and Hunter 1995).

No quantitative data on historical vermetid reef demise are presently available for the Mediterranean Sea, although a negative influence of Little Ice Age has been recorded in the Sicilian vermetid reefs (Silenzi et al. 2004; Chemello and Silenzi 2011). However, the destructive effects of earthquakes on vermetid reefs have been indirectly derived from many studies conducted in the eastern Mediterranean, where seismic events were able to displace or tilt the coast exposing the reef building species to unfavorable conditions. For instance, in western Crete, almost eight different emerged shorelines can be identified by algal-vermetid rims (Pirazzoli 1991). The results of seismic events on vermetid reefs were also used by Stiros et al. (1994) to describe the effects of the 1953 earthquake on the coasts of Cephalonia, in the southeastern Adriatic Sea.

In the last decades, an increasing number of studies are documenting local extirpations and detrimental responses of *Dendropoma* aggregations as a consequence of coastal habitat degradation, increasing human activities, pollution, invasive species, and projected ocean acidification.

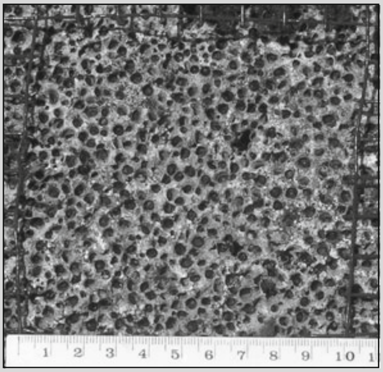
3.1 Biological and Chemical Pollution

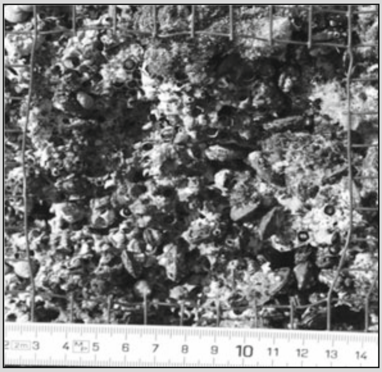
Along the Mediterranean rocky shores, significant habitat modifications occurred in the last centuries. Indeed, reefs in the Eastern Mediterranean Sea are presently showing the worst signs of degradations and troubles were firstly recorded in the 1990s. Causes are still unknown and several hypotheses have been proposed (Box 1). During the 1960s and 1970s, living *Dendropoma* covered 3% of the area of the raised rims (Lipkin and Safriel 1971); 15 years ago an estimate put it at 1% for most of the sites (Klerman et al. 2004). Much of the habitat degradation was supposed to result from anthropogenic activities related to urban development and high organic loads from industries' outfalls along the coast (Klerman et al. 2004).

Box 1 Biological Invasion Poses a Great Threat to Recovery of Mediterranean Vermetid Reefs

Most of the Israeli reefs where living rims were reduced by unknown causes are now dominated by an invasive Red Sea mussel *Brachidontes pharaonis* suggesting that the *Dendropoma* local extinction may have also facilitated this invasion and a significant reduction of the native *Mytilaster minimus* (Didham et al. 2007). *Brachidontes pharaonis* is an Eritrean mussel that has accessed in the Mediterranean Sea shortly after the opening of the Suez Canal in 1869. At the beginning it had a restrained distribution with small local populations along the Israeli intertidal coast. More than a hundred years later it spread westward as far as NW Sicily, colonizing some hyperaline and natural habitats. Field observations indicated that between 2005 and 2007 new *B. pharaonis* populations have patchy invaded vermetid reefs inside a marine protected area near Palermo, NW Sicily (Milazzo et al. 2010). Additional quantitative surveys, carried out before and after the *B. pharaonis* arrival in these locations, indicated great detrimental effects of this non-native mussel settlement and growth on the density of *D. cristatum* and the cover of *Neogoniolithon brassica-florida*. Often a coexistence between mussels and vermetid has been observed but it is likely that *B. pharaonis* shells have ultimately outcompeted the reef building species. No evident degradation in the receiving habitat and nearby areas was recorded before this mussel invasion, therefore suggesting that *B. pharaonis* may also represent a direct hazard to vermetid reefs, although at local scale (Milazzo et al. 2010).

Before the invasive mussel arrival





After the invasive mussel arrival

Coastal urbanization and the artificial sheltering of intertidal communities by the construction of jetties and marinas are themselves a great impact on vermetid reefs. Recently, Di Franco et al. (2011) demonstrated that the presence of a small marina in NW Sicily heavily affects the density of *D. cristatum* and the cover of *N. brassica-florida*, when compared with near control locations. The recorded drop in the density of *D. cristatum* (as *D. petraeum*) was from on average >50,000 individuals m^{-2} in control locations to ∼10,500 individuals m^{-2} in the reefs inside the marina (Di Franco et al. 2011). Although not causing local extirpation of the reef builder species, reductions in the gastropod density were specifically recorded in the outer rim of the vermetid reef and authors hypothesized that this was related to altered water flow regimes, increased water turbidity, along with nutrient enrichment, and the accumulation of toxic compounds inside the marina (Di Franco et al. 2011).

Fig. 5 Details of pristine (*top*) and eroded (*down*) outer rims of vermetid reefs in Israel (Photo credits: M.F)

Vermetids and corallines were the taxa mostly affected inside the marina, where the assemblages were mainly dominated by turfs and low-profile algae (Di Franco et al. 2011).

At present, in many locations along the Israeli coast, the outer rims of the vermetid reef themselves have been eroded considerably as a result of the local extinction of *Dendropoma anguliferum* (Galil 2013, as *Dendropoma petraeum*). Vast areas of vermetid reefs have recently died off in the Eastern Mediterranean which is thought to be due to widespread environmental changes in recent decades (Galil 2013). Further physicochemical erosion and bioerosion of the dead vermetid shells is now occurring, leading to the collapse of the entire structure and reducing the coastal complexity and topography with an abrupt change in biodiversity (Fig. 5).

3.2 Sea Level Rise, Ocean Warming and Acidification

Potential effects of sea level rise on vermetid reefs are presently largely unknown. To maintain a positive accretion, the synergistic growth rate of the gastropods and the coralline algae must be higher than the sea level rise rate. However, there is great concern that the slow growth rate of the reef-building *Dendropoma* will not likely allow present vermetid reefs to cope with projected sea level rise. In such a scenario, inundation of the reef flat by sea level rise would potentially cause an increased competitive strength by subtidal species and likely an overall decrease of biodiversity levels, as a result of vermetid demise. Further research should be directed on the vermetids responses to such kind of stressor. Certainly, sea level rise effects will be more detrimental if interacting with other ongoing stressors in the global ocean (e.g., ocean acidification and warming) affecting physiological performance and reproduction, calcification, and recruitment rates of the reef building species.

At present, changes in seawater carbonate chemistry due to rising atmospheric CO_2 levels and lowered ocean pH – a process known as ocean acidification – are occurring at an unprecedented rate and are predicted to further increase in the near future. Many marine organisms will not be equipped to cope with ocean warming and acidification in the near future and mollusks are likely the most sensitive taxon (Kroeker et al. 2013). The most evident effects on marine communities will be losses in those species having trouble in creating calcium carbonate structures in acidifying waters, namely, by calcification inhibition and in some cases by dissolution of their calcareous shells and skeletons. In addition to direct effects on calcifying species, a decrease in seawater pH may reduce the whole complexity of a biogenic habitat, as observed in coral reefs, by affecting their structural complexity and the many reef-associated macroinvertebrates they support. This can be further exacerbated by bioerosive processes that are occurring at higher rates in acidifying oceans. Recent work revealed that levels of ocean acidification predicted to occur this century and beyond impair the reef-building gastropod *D. cristatum* (as *D. petraeum*) recruitment success, cause dissolution of the recruits shells, and alter their shell mineralogy (Milazzo et al. 2014). Since the vermetid snails brood their young and the hatchlings crawl only a short distance before becoming a sessile individual, unless snails adaptation to ocean acidification does not occur, there are only slim chances for *Dendropoma* to form reefs in the near future with this having far-reaching consequences on the Mediterranean coastal zone. Like many other species of the intertidal zone, the vermetid snails are adapted to such conditions experiencing a wide range of temperature. However, at present it cannot be excluded that rising temperatures could affect *Dendropoma*'s recruitment and development processes. Research on effects of interacting ocean warming and acidification on vermetid reefs is presently underway.

3.3 Recreational Uses and Related Human Impacts

Increasing human use of rocky shoreline has long been deemed to have an impact on marine biogenic habitats (Liddle 1991). Indeed, the presence of the vermetid reef flat on rocky shores may enhance human frequentation and related “foot-traffic” on the shoreline. Reefs’ vulnerability to human trampling depends mainly on the nature and morphology of marine organisms and on the level of human use. Encrusting forms like the coralline algae and the vermetids aggregations are resistant to this kind of disturbance showing no direct effects on their density and cover (Graziano et al. 2007), although it is presently unclear if physical impacts of trampling may affect vermetid recruits survival and settlement success. In turn, the detrimental consequences of human trampling may be recorded on the macroalgae of the reef flat. Step on erect algae of *cuvette* may cause a rapid decrease in algal cover, canopy, and biomass, leading the community to a less structurally complex state dominated by low-profile and turfing-form algae (Milazzo et al. 2004). This may reduce the high levels of benthic and fish diversity associated with these reefs (Chemello et al. 2000). In some cases, these effects on rocky shallow communities have been reduced by positioning boardwalks, aimed at concentrating tourist access to the sea and thus reducing the trampling impact on nearby areas (Liddle 1991). However, it has been demonstrated that the presence of these artificial structures may exert negative consequences on the benthic species associated with the vermetid reef flat, with observed effects also on the reef building species (Dieli et al. 2003). In addition to this, anecdotal evidence also suggests that along the NW coast of Sicily these reefs are threatened by the use of copper sulfate $CuSO_4$. Copper sulphate is a nonselective toxic compound for aquatic invertebrates and has been long illegally used to harvest worm baits (e.g., the nereid *Perinereis cultrifera*) for recreational fishing. Collection of large portions of the outer rim as ornaments for the aquarium industry has also been observed along the Israeli coast.

4 Conclusion and Future Directions

Similarly to other types of biogenic reefs, vermetid reefs play a major functional role in intertidal areas, providing a range of goods and services which may be added to the overall coastal economic value (Costanza et al. 1997). Healthy vermetid reefs serve as important wave breaks, preventing coastal erosion and storm damage in the Mediterranean. Furthermore, they locally promote the spatial heterogeneity of the intertidal zone supplying shelter, food, and home to a very high number of different species, including fish and invertebrates of recreational and commercial interest, making them a key habitat in the Mediterranean intertidal zone. Unfortunately, up to date the contribution of temperate vermetid reefs in providing such services has been less investigated than that of other functionally similar systems, such as tropical reefs (e.g., Moberg and Rönnbäck 2003). Indeed, biological and chemical pollution, ongoing climate change and ocean acidification, and uncontrolled human activities along the coast may threaten the vermetid reef persistence and the biodiversity it supports.

Indeed, there are compelling reasons to be concerned about these impacts on vermetid reefs. The scarce resilience of the reef-building species and the reduced ability to recover from local depletion and habitat degradation do confirm that vermetid reefs are highly vulnerable to both direct and indirect human activities.

If CO_2 emission continues to rise unchecked and eventually, once CO_2 emissions are reduced, given the long time necessary to reverse these changes, further research is urgently required to assess the effects of ocean warming and acidification relevant to Mediterranean vermetid reefs and to quantify the effects of exposures to these factors using both field-based and laboratory assessments on vermetid population dynamics and the reef building species physiology. Regarding to this, we still need to understand the time required for a vermetid reef to transition from calcium carbonate net deposition to calcium carbonate net dissolution and eventually how this may have far-reaching consequences on the ecosystem services the vermetid reefs provide (e.g., wave breaks, carbon storage, coastal erosion prevention, and habitat provisioning). Importantly, future research paths should explore the synergistic effects between rising CO_2 emissions disturbances and other anthropogenic factors like pollution and habitat degradation. In doing so, an additional research effort should be also made to identify the ecological and economical costs of vermetid "local" demise, especially in those vast areas where vermetid reefs have recently died off in the Eastern Mediterranean.

Following a precautionary approach and recognizing their important role in the Mediterranean intertidal *Dendropoma petraeum* (all the laws are still using that old species name) and some of the algae accompanying it (as *Neogoniolithon brassica-florida*, *Lithophyllum byssoides* and *Cystoseira amentacea*) have been included in the annexes of the Berna Convention, and in the Annex II (Endangered or Threatened Species) of the Protocol for Specially Protected Areas in the Mediterranean (SPAMI Protocol of the Barcelona Convention). *Dendropoma* has been also proposed to be included in the annexes II and IV of the Habitat directive (Chemello 2009) and the reef structures have been listed as threatened bioconstructions in the European Red List of Habitats (Marine: Mediterranean Habitat). Despite this, only the 28.5% of vermetid reefs in the Mediterranean are apparently protected by means of MPAs or coastal reserves, as summarized by Chemello et al. (2014), and, officially, the Spanish National Catalogue on Threatened Species and the Maltese "the Flora, Fauna and Natural Habitats Protection Regulations" are the only acts suggesting protection of these reefs at national level. These facts strongly stress the need to extend action plans for vermetid reef protection and to improve its management at the Mediterranean level. However, accurate information on population connectivity is essential to optimize vermetid reef protection. Developing a conservation strategy at a basin scale and implementing monitoring of protected and not protected reefs are both essential actions to guarantee an effective protection of this neglected but relevant coastal habitat.

To respond to the ongoing decline of the reef ecosystems, in addition to creating marine protected areas (MPAs) or Sites of Community Importance (SCI), the promotion of rehabilitation plans is indeed a required best practice.

Where the MPAs are difficult to be created, habitat rehabilitation may be a valid approach in the attempt to face local declines of Mediterranean vermetid bioconstructions. This kind of approach has been widely applied to coral reefs, where restoration activities are developed through a strong ecological knowledge of the community and the use of a wide variety of different methodologies. At present, attempts of habitat restoration of *Dendropoma* reefs are still at an infancy stage. These strategies should include in situ transplantation of sexually mature individuals or the application of ecological engineering principles to improve the biological and physical substratum characteristics for larval settlement. Both epilithic biofilm and crustose coralline algae are known to have implications in the settlement of many marine invertebrates, including scleractinian corals, and Spotorno-Oliveira et al. (2015) have very recently shown a positive correlation among settlement rates of the southwestern-Atlantic *Dendropoma irregulare* and live cover of coralline algae. It is a matter of fact that along the Mediterranean coast, the two main reef builders *Dendropoma* spp. and *Neogonilithon brassica-florida* live in what is considered an obligatory association. In this context, promising findings belong to a set of ongoing laboratory experiments aimed at shedding light on the complex interplay between the rocky substrate, the epilithic biofilm, and the coralline algae in triggering the vermetid snail settlement. Preliminary evidence suggests that limestone rocks show the best physical properties for *Dendropoma* settlement and more importantly that the biofilm ageing (i.e., the higher biological complexity of the older biofilm, rich in diatoms, cyanobacteria, and protozoa embedded in a mucal web) plays a key role in the settlement preference of *D. cristatum* larvae. Further analyses at molecular level to identify which microorganisms and/or potential chemical cue (e.g., metabolites) effectively trigger *Dendropoma* settlement are strongly required to built up reliable protocols for facilitating and promoting vermetid reef restoration activities.

In summary, although synthesizing ecological information on Mediterranean vermetid reefs may have contributed to fill the knowledge gaps on this often neglected marine animal forest, given the range of ecosystem services pristine vermetid reefs may provide to Mediterranean coastal systems, major needs are (1) to increase impact assessment studies (e.g., biological and chemical pollution, climate change, and ocean acidification), (2) to explore novel research paths (e.g., habitat restoration techniques), and (3) to improve conservation activities at regional level.

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Where Seaweed Forests Meet Animal Forests: The Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem

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Abstract

The Mediterranean coralligenous and the intertropical coral reef ecosystems are similar in several aspects, such as their ability to thrive in nutrient-poor waters and the communities associated with them. For example, these ecosystems encompass communities ranging from bioconstructions by calcified blade-forming coralline macroalgae, bioconstructions by calcified hexacorallians, canopy-forming seaweed forests, canopy-forming gorgonian (animal) forests, to turfs of macroalgae. They depend mainly upon available light, temperature, and herbivore pressure. In spatial terms, these communities can constitute a complex mosaic. Over time, they can follow each other throughout ecological successions, i.e., a suite of shifts, or phase-shift events, as a consequence of natural or anthropogenic disturbances. Some of these communities, of which the autogenic ecosystem engineers are esthetically pleasing, large-sized, and long-lived, such as blade-forming corallines, gorgonians, and hexacorallians, are often explicitly or implicitly, but erroneously, regarded as the whole ecosystem, whereas they are in fact only part of it. Both coral reefs and the Mediterranean coralligenous ecosystems dwell in highly oligotrophic waters. Their success hinges upon mutualism with unicellular primary producers (dinobionts), the efficient recycling of nitrogen, and diazotrophy (coral reefs), and upon the input of allochthonous organic matter (coralligenous), rather than on the primary production of macroalgae alone (e.g., *Cystoseira*, *Sargassum*, *Turbinaria*, and turf-forming species). In addition, species diversity is high, which substantially helps to make these ecosystems

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species diversity hotspots. The close intertwining of the different communities (seaweed forests, heterotrophic animal forests, photosynthetic animal forests – via mutualism – and highly productive macroalgal turfs) within these two ecosystems, together with the massive precipitation of calcium carbonate, makes the structure and functioning of these ecosystems highly original, without counterpart in the terrestrial realm.

Keywords
Animal forests • Coralligenous • Coral reefs • *Cystoseira* • Disturbances • Mediterranean Sea • *Sargassum* • Scleractinians • Seaweed forests • *Turbinaria*

Contents

1 Introduction

The term “forest” is traditionally associated with tall, long-lived trees in the terrestrial realm. These trees are autogenic ecosystem engineers (as defined by Jones et al. 1994). They belong to Magnoliophyta (Embryophyta, Viridiplantae, kingdom Archaeplastida; see Fig. 1, Boudouresque 2015; Boudouresque et al. 2015). Subsequently, the term “forest” has been extended to marine habitats. At first, it only referred to large and perennial canopy-forming “seaweeds,” such as *Macrocystis pyrifera* and *Laminaria* spp. (“brown algae,” Phaeophyceae, Chromobionta, kingdom Stramenopiles; Fig. 1), algae reaching ~30–40 m and 5 m in height, respectively (Steneck et al. 2002). Then, it was also used for smaller, long-lived, canopy-forming seaweeds, such as *Cystoseira* spp. and *Sargassum* spp., a few tens of centimeters high in the Mediterranean Sea (e.g., Hereu et al. 2008). Finally, the term “forest” has also been applied to habitats structured by large long-lived sessile metazoans such as gorgonians, scleractinians, and sponges (Rossi 2013) (Metazoa, kingdom Opisthokonta; Fig. 1), which are the focus of the present volume.

The term “algae” has been traditionally applied to “lower plants,” characterized by a so-called primitive and simple pattern of organization. The vegetative apparatus, called “thallus,” was considered by nineteenth- and early twentieth-century authors as devoid of specialized tissues organized into specialized organs, e.g., stems, leaves, and vascular tissues which distribute resources, such as products of

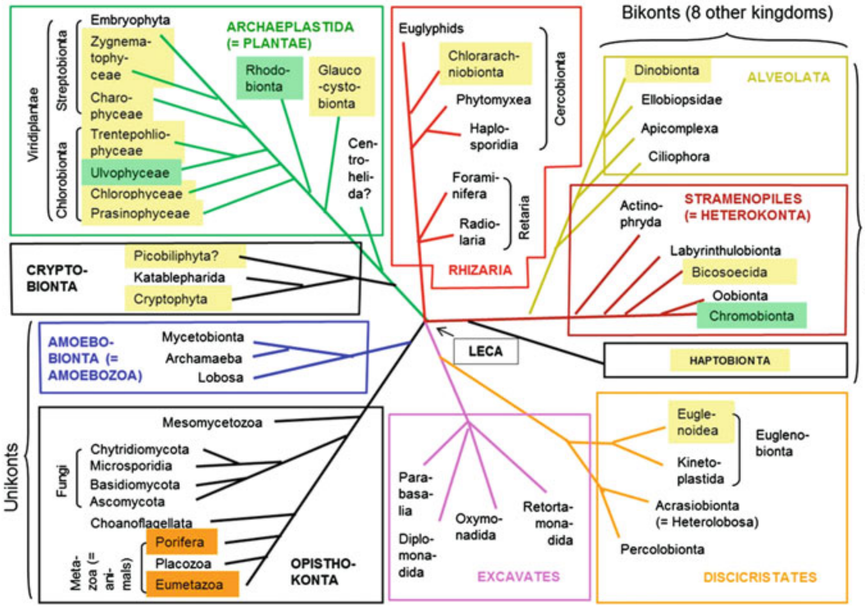

Fig. 1 The simplified phylogenetic tree of eukaryotes: most high-level taxa are not presented, e.g., within Chlorobionta, Dinobionta, Chromobionta, and Metazoa. *Boxes*: kingdoms. To simplify the diagram, certain classes (e.g., within Chromobionta) or most classes (e.g., within Chlorobionta) have not been shown. Highlighted *green* taxa correspond to multicellular "algae" (seaweeds, i.e., macroalgae), prone to constitute seaweed forests. Highlighted *yellow* taxa (in addition to the former) correspond to the customary notion of "algae." Highlighted *orange* taxa correspond to metazoans prone to constitute animal forests. *LECA* last eukaryotic common ancestor (From Boudouresque (2015), modified)

photosynthesis, through the plant. In contrast, higher plants, such as Magnoliophyta, featured the abovementioned characters. Long before the arrival of molecular phylogenies, this simple approach, which dates from the time of Linnaeus, almost three centuries ago, has been questioned and rejected, on the basis of biochemistry, cytology, and anatomy. By the 1980s, molecular phylogenies had confirmed and clarified the breakdown of animal and plant kingdoms into a dozen kingdoms, each one encompassing former plants and animals. Today, "algae" are just a customary notion. They consist in a highly polyphyletic set of taxa, which belongs to seven kingdoms, namely, Archaeplastida, Rhizaria, Alveolata, Stramenopiles, Haptobionta, Discicristates, and Cryptobionta (Fig. 1). As regards "macroalgae," i.e., multicellular photosynthetic organisms (MPOs), they encompass Ulvophyceae and Trebouxiophyceae (Chlorobionta, Viridiplantae, kingdom Archaeplastida; "green algae"), Rhodobionta (kingdom Archaeplastida; "red algae"), and Phaeophyceae (Chromobionta, kingdom Stramenopiles, "brown algae") (Fig. 1; Boudouresque 2015; Boudouresque et al. 2015 and references therein). In the present work, the term "seaweed" is used as a synonym of macroalgae.

Seaweed forests are common worldwide in the infralittoral and circalittoral zones (sensu Pérès and Picard 1964; Pérès 1982) of temperate and cold seas. The autogenic ecosystem engineers generally belong to the Phaeophyceae: Fucales (e.g., genera *Cystophora*, *Cystoseira*, *Durvillaea*, *Phyllospora*, *Sargassum*, *Turbinaria*) and Laminariales (e.g., genera *Agarum*, *Ecklonia*, *Eisenia*, *Laminaria*, *Lessonia*, *Macrocystis*, *Saccharina*) (Boudouresque 1971; Tegner and Dayton 1991; Schiel and Foster 2006; Coleman et al. 2008). Within these forests, sessile and mobile animals (Metazoa) are abundant (species richness, number of individuals) and play a conspicuous role in the functioning of the ecosystems (e.g., herbivores, detritus feeders, suspension feeders, predators). However, in contrast to the canopy-forming seaweeds, they cannot strictly be considered as ecosystem engineers. Canopy-forming species constituting seaweed forests are perennial. Some of them are relatively short-lived, such as *Macrocystis pyrifera* that never exceeds the age of 6 years (Tegner et al. 1997), while others are long-lived, such as *Cystoseira zosteroides* that may exceed 50 years (Ballesteros et al. 2009) and probably much more, perhaps centuries.

Animal forests, i.e., habitats structured by long-lived sessile metazoans, playing the role of autogenic ecosystem engineers (Rossi 2013), are also common worldwide, in the infralittoral and littoral zones, where metazoans can be associated with photosynthetic organisms (mutualistic or not). Animal forests devoid of photosynthetic primary producers are limited to greater depths, beyond the photic zone, e.g., deep-sea corals (Mortensen et al. 2001). The latter habitats are the subject of specific chapters in this book.

Seaweed and animal forests share a number of characters, and can be distinguished by certain other characters, although the differences are far from being clear-cut and there is rather a continuum between them (Table 1).

Here, the juxtaposition, in space or time, of seaweed and animal forests is investigated on the basis of two case studies of emblematic ecosystems: the intertropical coral reefs and the Mediterranean coralligenous. Coral reefs are ecosystems, of which the autogenic ecosystem engineers of the most iconic facies are calcified cnidarians, mainly hexacorallians (Scleractinia) harboring mutualistic photosynthetic dinobionts (Symbiodiniaceae, kingdom Alveolata). The coralligeneous is a Mediterranean ecosystem of which the autogenic ecosystem engineers of the most iconic facies are calcified blade-forming corallines (“red algae”), canopy-forming Fucales (“brown algae”), and/or sea fan gorgonians (Alcyonacea, cnidarians). Both ecosystems, coral reefs and the Mediterranean coralligenous, exhibit a variety of facies (hereafter “communities”), ranging from crustose corallines and sponges, turf macroalgae, low stands of erect macroalgae, high canopy-forming seaweed forests, and high canopy-forming animal forests. These communities depend mainly upon available light, temperature, water movement, nutrients, herbivore pressure, and the overall ecosystem functioning. In space, these communities can constitute a complex mosaic. Over time, these communities can follow each other throughout ecological successions and phase shifts, as a consequence of natural and/or anthropogenic disturbances.

Table 1 Some similarities and differences between seaweed forests and animal forests. These similarities and differences go far beyond those of the ecosystems which are the focus of the present chapter. They concern the proper seaweed and animal forest communities, not the wider ecosystem which these communities are part of (e.g., coral reefs and the Mediterranean coralligenous ecosystem). "Yes" or "No" deals with major and general features, not with marginal processes and/or uncommon exceptions. *POM* particulate organic matter

		Seaweed forests	Animal forests
Structure	Three-dimensional (3D)	Yes	Yes
Habitat	Depth limitation (photic zone)	Yes	No
Life history traits	Long-lived autogenic ecosystem engineers	Yes	Yes
	Climax of a long-lasting succession	Yes	Yes
	Calcium carbonate precipitation	No	Yes
Ecosystem functioning	Importance of diazotrophy	Low	Low
	Importance of chemosynthesis	Low	Low
	Primary production mainly based upon multicellular photosynthetic organisms (MPOs)	Yes	Yes or No
	Primary production mainly based upon unicellular mutualistic organisms	No	Yes or No
	Biomass (primary and secondary producers)	Moderate	High
	Necromass	No	Yes
	Carbon sequestration	No	Yes
	Nutrient sequestration	No	Yes or No
	Conspicuous input of organic carbon	No	Yes
	Major role of filter and suspension feeders	No	Yes
	Herbivory	Low	High
	Food-web length (i.e., the number of trophic levels)	Short or long	Long
	Conspicuous output of organic carbon (POM, detritus)	No	Yes or No

2 The Mediterranean Coralligenous Ecosystem

2.1 Community Structure and Ecosystem Functioning

There is no consensus among scientists studying benthic communities regarding what the Mediterranean coralligenous ecosystem is (Ballesteros 2006 and references therein). According to Ballesteros (2006), a coralligenous reef is a hard substratum of biogenic origin that is mainly produced by the accumulation of calcareous blade-forming and crustose corallines (red algae, Rhodobionta) growing under dim light conditions. It usually develops on almost vertical walls, on gently sloping bottoms near the base of a wall, and on overhangs. The thickness of coralline

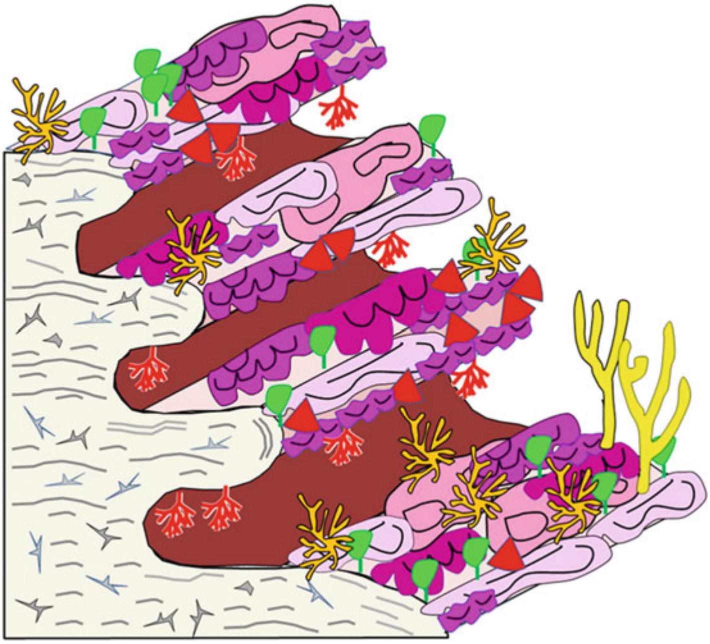

Fig. 2 A 3D sketch of coralligenous biogenic constructions in the form of shelves, near the base of an underwater wall. *Gray* (*left*): dead parts of biogenic constructions, with remains of corallines and metazoans. Dark and light *pink*: blade-forming corallines. *Red* triangles: *Peyssonnelia* spp. (Rhodobionta); *Green*: *Flabellia flabellata* (Chlorobionta). *Light yellow*: *Axinella polypoides* (sponge). *Orange*: bryozoans. *Red* inverted trees: the precious red coral *Corallium rubrum* (cnidarians). *Dark brown*: shady cavities beneath overhanging biogenic constructions (Original drawing (Charles F. Boudouresque))

bioconstructions may reach several dozen centimeters, sometimes several meters (Laubier 1966; Laborel 1987; Sartoretto et al. 1996). Near the base of underwater walls, coralline algae may constitute shelf-like structures, 50–100 cm wide and 20–40 cm thick, with characteristic spatial variations on the vertical and down-facing surfaces (Fig. 2; Virgilio et al. 2006). In addition to these biogenic red algal constructions, where blade-forming corallines are the autogenic ecosystem engineers (Fig. 4), three associated communities are considered here: **(i)** Seaweed forests composed of *Cystoseira zosteroides* and other Fucales (Fig. 3; Ballesteros et al. 2009); **(ii)** Animal forests consisting of gorgonians, e.g., *Eunicella* spp. and *Paramuricea clavata*, large erect sponges such as *Axinella polypoides* (Fig. 4), and bryozoans such as *Turbicellepora* spp. and *Pentapora fascialis*; **(iii)** Stands of crustose but not bio-constructing corallines, with turf and bushy macroalgae and small-sized sessile metazoans belonging mainly to bryozoans, ascidians and sponges (Boudouresque 1973). This last community is often known as “precoralligene” (Fig. 5; Pérès and Picard 1964). Despite the Latin prefix “pre-” (meaning “before”),

Fig. 3 A coralligenous ecosystem at Cap Caveaux (Provence, France), 40 m depth. A seaweed forest (*Cystoseira zosteroides*) occupies most of the scene. On the *right*, an individual of the gorgonian *Eunicella singularis* (Photo © Frédéric Zuberer (courtesy of F. Zuberer))

Fig. 4 A coralligenous ecosystem at La Gabinière Island (Port-Cros National Park, Provence, France), 40 m depth. In the foreground, bioconstruction by blade-forming corallines, covered with soft macroalgae. The brown blades are *Phyllariopsis brevipes*. The fish school is constituted of *Anthias anthias*. In the background, an animal forest of gorgonians, *Paramuricea clavata* (Photo © Sandrine Ruitton)

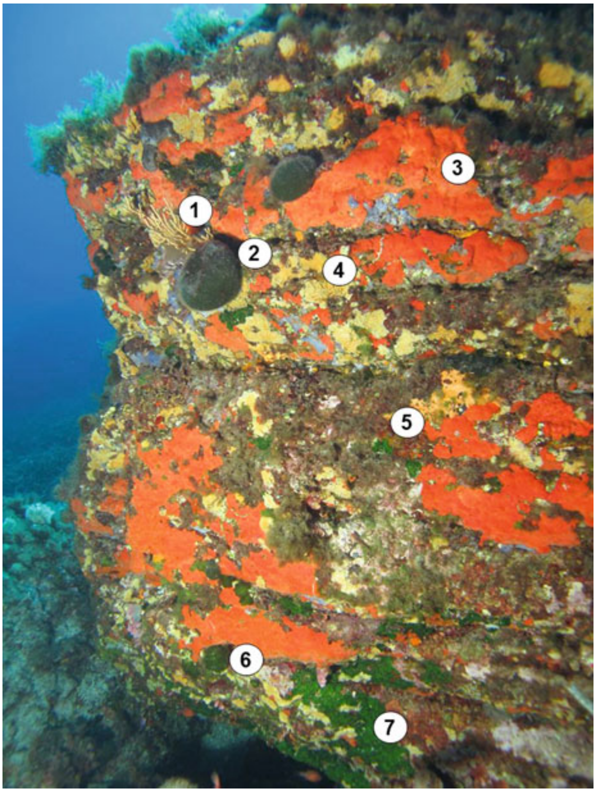

Fig. 5 A coralligenous ecosystem at La Gabinière Island (Port-Cros National Park, Provence, France), 15–18 m depth. The precoralligene community. Numbers indicate the different species and are placed on the right of the shown species. *1 Eunicella cavolini* (Cnidaria). *2 Codium bursa* (Ulvophyceae, Chlorobionta). *3 Crambe crambe* (Porifera). *4* Bryozoa. *5 Peyssonnelia* sp. (Rhodobionta). *6 Codium coralloides* (Ulvophyceae, Chlorobionta). *7 Palmophyllum crassum* (Pyramimonadophyceae, Chlorobionta). (Photo © Sandrine Ruitton)

there is no evidence that the precoralligene community would always represent a stage towards another coralligeneous community.

The reason why these four communities are here considered together is that they are closely intertwined into a mosaic of patches and successional stages, so that on the basis of an ecosystem-based approach, they constitute one ecosystem (Fig. 6; Ruitton et al. 2014). This complexity led Laubier (1966) to consider the coralligenous ecosystem as an ecological crossroad. The mobile fauna (fish, crustaceans, etc.) move from one habitat to the next, while the four communities share most of the features that characterize an ecosystem, namely, the coralligenous ecosystem, such as the importation of organic matter from the water column and adjacent ecosystems, the importance of calcified and long-lived organisms, etc. (see below).

Light, seawater temperature, and sediment deposition are the most important environmental forcing factors with respect to the distribution of the four communities of the coralligenous ecosystem (Morganti et al. 2001; Balata et al. 2005; Ballesteros 2006). Light is very important for the development and growth of coralligenous macroalgae, which need enough light to grow but which cannot withstand high levels of irradiance. They are able to develop at irradiances ranging

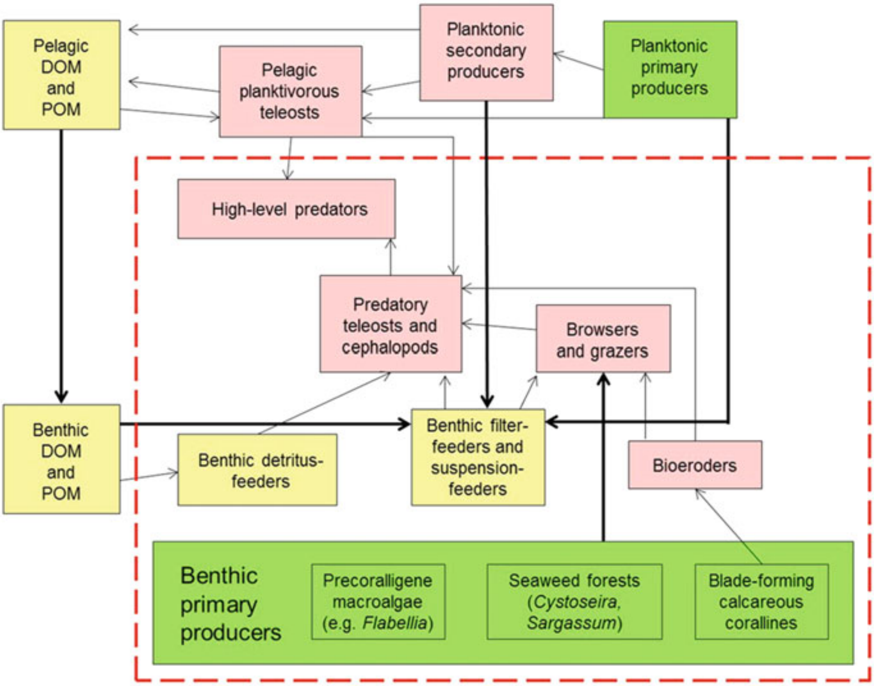

Fig. 6 Conceptual model of the functioning of a coralligenous ecosystem (*red* hatched rectangle). Primary producers are in *green*. Particulate organic matter (POM), dissolved organic matter (DOM), detritus feeders, filter feeders, and suspension feeders are in *yellow*. Bioeroders, browsers, grazers, and predators are in *pink*. *Arrows*, energy flows; *bold arrows*, main energy flows (Modified and redrawn from Ruitton et al. (2014))

from 0.05 to 3% of the sea surface irradiance (Ballesteros 1992). The quality of light should also be taken into account: the light that reaches this habitat belongs only to the blue and green wavelengths (Pérès and Picard 1964; Laubier 1966; Ballesteros 1992, 2006). Most coralligenous organisms withstand a temperature range of 10, 12–20, and 23 °C (minimum, usual range, and maximum) (Laubier 1966; Ballesteros 2006). However, some of them display a relatively high stenothermy, especially those participating in the animal forest community; events of mass mortality affecting gorgonians (e.g., the sea fans *Eunicella cavolini*, *E. singularis*, and *Paramuricea clavata*, and the precious red coral *Corallium rubrum*), other cnidarians (e.g., *Caryophyllia smithii*), and sponges (e.g., *Aplysina cavernicola*, *Cacospongia scalaris*, *Spongia officinalis*) have been attributed to unusually long-lasting periods of high temperature during summer (Cerrano et al. 2000; Perez et al. 2000; Coma et al. 2006; Bensoussan et al. 2010).

Coralligenous communities are widespread in the Mediterranean Sea, with the possible exception of the coasts of Lebanon and Israel (Laborel 1987). The animal forest community, characterized by large erect gorgonians, such as *Paramuricea* *clavata*, is usually restricted to the cooler areas of the Mediterranean. However, this is an artifact, since the knowledge of animal forests can be limited by the depth limit of SCUBA diving, while they thrive, in Greek and Turkish waters, at 60–80 m depth (Gili et al. 2014). The minimum depth (i.e., the upper limit) for coralline bioconstructions and animal forests of the coralligenous ecosystem depends upon the water transparency: 12 m in the Gulf of Fos, near the mouth of the Rhône River (Provence), 20 m around Marseille (Provence), and 50 m at Cabrera (Balearic Islands). They can occur down to 120 m in the southern and eastern Mediterranean (Laborel 1987; Ballesteros 2006). *Cystoseira zosteroides* forests are known down to 100 m in the clearest waters (Aurélie Blanfuné and Thierry Thibaut, unpublished data). The precoralligene community displays an even wider depth range.

The coralligenous ecosystem displays a number of features, the combination of which is unique and therefore characteristic (Fig. 6; Boudouresque et al. 2014; Ruitton et al. 2014). Some of these features are not shared by all the communities delineated here. **(i)** The species richness varies according to the scale, from moderate (point diversity) to high (alpha diversity) for macroalgae and from moderate (point diversity) to very high (alpha diversity) for metazoans. Overall, the coralligenous ecosystem constitutes an important species diversity hotspot, harboring around 20% of the Mediterranean species (Garrabou et al. 2002; Ballesteros 2006; Piazzi et al. 2010; Cánovas Molina et al. 2016). **(ii)** The photosynthetic primary production (PP) is low, because of the oligotrophy of the Mediterranean Sea and the depth, despite the presence of photosynthetic pigments that enhance energy harvesting in the light wavelengths still present at depth; the ecosystem belongs to the low nutrient–low chlorophyll (LNLC) category. The chemosynthetic PP is absent. **(iii)** The biomass of photosynthetic primary producers is low (not taking into consideration the mass of calcium carbonate), especially in animal forests. **(iv)** The ratio between PP and biomass is moderate. **(v)** Part of the PP is palatable and follows the herbivore pathway, while another part is poorly consumed because of mechanical defenses (calcification). However, this non-consumed PP does not enter the litter and the detritus pathway; rather, it constitutes a carbon sink. **(vi)** The importation of organic matter from adjacent ecosystems, as dissolved organic matter (DOM) and particulate organic matter (POM), is pivotal in the ecosystem functioning. Adjacent ecosystems are the pelagic ecosystem (the water column), infralittoral ecosystems such as rocky reefs and the *Posidonia oceanica* seagrass meadows, which exports large amounts of dead leaves and other detritus (Boudouresque et al. 2012; Personnic et al. 2014), as well as circalittoral ecosystems, such as the coastal detritic bottoms (maerl and free-living rhodoliths). The imported DOM and POM play a prominent role as food source for most metazoans of the coralligenous communities, which are either filter feeders or suspension feeders, especially those which play a role in the animal forest. Overall, the ecosystem is a heterotrophic one, with low primary production which cannot support the entire secondary production and which depends therefore upon imported organic matter. **(vii)** In contrast with its high dependence upon organic matter importations, the coralligenous ecosystem is a weak exporter. **(viii)** The growth of blade-forming coralline macroalgae results in a rise of the bottom (in the community of bioconstructions by blade-forming

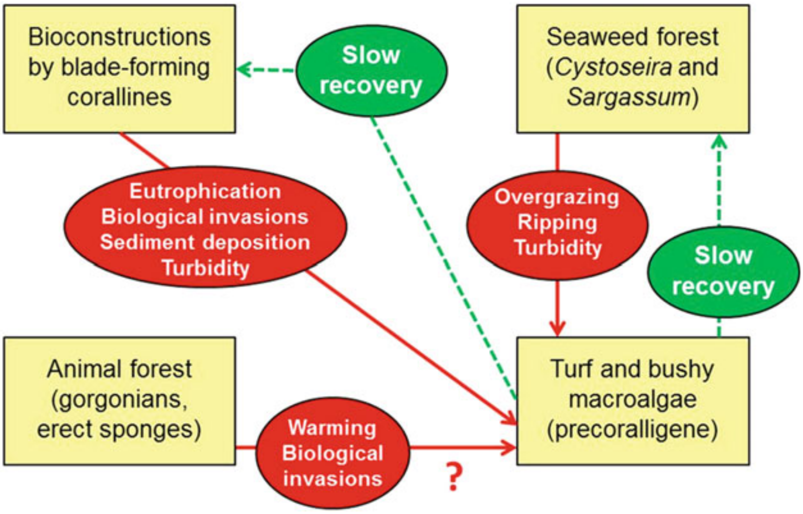

Fig. 7 Temporal dynamics of the four communities that constitute the coralligenous ecosystem, in a context of disturbances (*red* ovals) and recovery (*green* ovals) (Original drawing (Charles F. Boudouresque))

corallines; see Figs. 4 and 7). This trend, however, is offset by organisms that erode or dissolve the bioconstructions. The latter organisms belong to Cyanobacteria (e.g., *Hyella caespitosa*, *Mastigocoleus testarum*, and *Leptolyngbya terebrans*), perforating sponges (e.g., *Cliona celata* and *C. viridis*), boring mollusks (e.g., *Hiatella arctica*, *Lithophaga lithophaga*), sipunculids (e.g., *Aspidosiphon muelleri*), and grazing sea urchins (e.g., *Sphaerechinus granularis*) (Sartoretto and Francour 1997; Sartoretto 1998; Ballesteros 2006). The rise of the bioconstructions depends on a positive balance between building and bioeroding processes (e.g., Garrabou and Ballesteros 2000). **(ix)** The relatively high level of calcium carbonate precipitation is a key character of the ecosystem, more precisely of the community of bioconstructions by blade-forming corallines.

2.2 Macroalgae

At least 315 species of macroalgae have been reported within the four communities of the coralligenous ecosystem, which includes the blade-forming coralline bioconstructions, seaweed forests, animal forests, and the precoralligene community (Boudouresque 1973; Ballesteros 2006).

Blade-forming coralline macroalgae that build the coralligenous bioconstructions belong to a variety of species and genera of Corallinales and Hapalidiales (Rhodobionta). The most important species are *Mesophyllum expansum* (previously misidentified as *M. lichenoides*) and *Titanoderma* sp. (Sartoretto et al. 1996). Other important building species are *Lithophyllum frondosum* (usually reported as

Pseudolithophyllum expansum), *L. stictaeforme*, *L. cabiochae*, *Mesophyllum macroblastum* (previously misidentified as *M. alternans*), *M. macedonis*, *M. sphaericum*, and *Neogoniolithon mamillosum* (Ballesteros 2006). Several species of the genus *Peyssonnelia*, which belongs to the Peyssonneliales (Rhodobionta), mostly *P. polymorpha* and *P. rosa-marina*, also participate in the bioconstruction. These last species precipitate aragonite during calcification (James et al. 1988), in contrast to Corallinales and Hapalidiales, which precipitate calcite (Ballesteros 1992). The presence and the relative abundance of Corallinales, Hapalidiales, and Peyssonneliales vary according to the considered region and depth. A number of calcified non-photosynthetic organisms also contribute to the bioconstruction, e.g., the foraminiferan *Miniacina miniacea* (kingdom Rhizaria), cnidarians, and bryozoans (Metazoa, kingdom Opisthokonta).

Canopy-forming macroalgae that are part of the seaweed forests belong to Fucales (Phaeophyceae, kingdom Stramenopiles). In addition to the most common species, *Cystoseira zosteroides* (Fig. 3), *C. foeniculacea* f. latiramosa, *C. funkii*, *C. jabukae*, *C. spinosa* var. compressa, *C. usneoides*, *Sargassum acinarium*, *S. hornschuchii*, and *S. vulgare* can also be found. A rare species of *Laminaria* (Laminariales, Phaeophyceae), endemic to the Mediterranean Sea, *L. rodriguezii*, can occur, generally at a greater depth (Fredj 1972; Aguilar et al. 2010; Boisset et al. 2016; Žuljević et al. 2016).

The many other species of macroalgae belong to the Rhodobionta (red algae), Ulvophyceae (green algae), and Phaeophyceae (brown algae) and to several functional form groups (sheet, filamentous, coarsely branched, thick leathery, jointed calcareous, crustose). They are long- or short-lived, and most of them are small- or medium-sized, with the exception of e.g., *Phyllariopsis brevipes* (Fig. 4), a non-perennial Tilopteridales (Phaeophyceae). In fact, their only common characteristic is that they are neither builders of calcareous bioconstructions nor canopy-forming fleshy species.

2.3 Seaweed Forests Versus Animal Forests

Within the coralligenous ecosystem, seaweed forests and animal forests coexist, sometimes in close proximity. However, they rarely constitute mixed settlements, i.e., gorgonian forests with some *Cystoseira* and/or *Sargassum* individuals, or *Cystoseira* forests harboring gorgonians (but see Fig. 3). Usually, one of these communities dominates and there is little evidence of competition between them. They occupy slightly differing habitats, in terms of, e.g., depth, slope, light, exposure to currents, and therefore POM/DOM input. Seaweed forests, where *Cystoseira zosteroides* are loosely attached to the substrate, mainly thrive at depth (circalittoral zone), on gently sloping substrates, under dim light, calm conditions, and unidirectional bottom current. On steeper substrates, and with increasing depth and/or decreasing light, the precoralligene community, the bioconstructions with blade-forming corallines, and the animal forests occur successively.

Over time, disturbances can affect seaweed and animal forests. Deep seaweed forests are severely declining throughout the Mediterranean. In many areas, such as the French Riviera and French Catalonia, most *Cystoseira* and *Sargassum* species are locally or functionally extinct (Thibaut et al. 2005, 2015; but see Thibaut et al. 2016). In French Catalonia, *C. zosteroides*, once frequent, is now rare, *C. spinosa* var. compressa, formerly abundant, is currently extinct, together with *C. foeniculacea* f. latiramosa, *C. funkii*, *Sargassum acinarium*, *S. hornschuchii*, and *S. vulgare* (Thibaut et al. 2005). Several factors may be responsible for these regressions: overgrazing by sea urchins, due to the overfishing of their teleost predators (Labridae, Sparidae), ripping by fishing nets, increase in turbidity and biological invasions (Thibaut et al. 2005, 2015, 2016). Extreme storms, such as the 50-year storm (i.e., the most violent storm for 50 years) that occurred on December 26, 2008, in Spanish Catalonia, can also be responsible for massive pulling up of *C. zosteroides* (Navarro et al. 2012; Teixidó et al. 2013). The seaweed forest is then replaced by stands of encrusting, but not bio-constructing corallines, with turf and bushy macroalgae (precoralligene community) (Fig. 7). In the case of *Cystoseira* spp., when the disturbance ceases, the dissemination of the eggs at very short distance (probably a few meters) from the surviving individuals and very low recruitment make any recolonization very difficult and slow.

Blade-forming coralline bioconstructions are threatened by eutrophication (Piazzi et al. 2011, 2012). Nutrient enrichment can cause an increase in turf-forming native macroalgae (Piazzi et al. 2012) and an increased growth of turf-forming invasive macroalgae (Gennaro and Piazzi 2011) that hinder the photosynthesis of blade-forming corallines. Eutrophication also enhances the activity of bioeroder organisms, making negative the balance between bioconstruction and bioerosion (Hong 1980). As a result, blade-forming coralline bioconstructions can be replaced by turf and bushy macroalgae ("precoralligene" community) (Fig. 7). In a context of global change, coralline macroalgae may also be impacted, in the future, by the acidification of marine water (Martin and Gattuso 2009; Martin et al. 2013). Blade-forming coralline bioconstructions are also threatened by turbidity, sediment deposition, and biological invasions, such as *Caulerpa taxifolia*, *C. cylindracea* (Ulvophyceae, Chlorobionta), and *Womersleyella setacea* (Rhodobionta), especially if they occur in concert with other stress factors (Piazzi et al. 2012; Gatti et al. 2015; Cánovas Molina et al. 2016). In the same way as eutrophication, these disturbances putatively hinder the photosynthesis of blade-forming corallines.

Finally, animal forests of gorgonians and erect sponges are threatened by warm episodes (extreme high temperature events), which cause mass mortality episodes, as observed since the late 1990s in the northwestern Mediterranean (Cerrano et al. 2000; Perez et al. 2000; Coma et al. 2006; Lejeusne et al. 2010). The precious red coral *Corallium rubrum* can also be affected (Garrabou et al. 2001). In the context of the global warming, the reduction of the time-interval between extreme warm events (Diffenbaugh et al. 2007), or the persistence of a near-lethal high temperature, might hinder the recovery of the canopy-forming metazoans. Invasive macroalgae, such as *Caulerpa cylindracea* and *Womersleyella setacea*, might also hinder the recovery of gorgonians, by affecting the growth and survivorship of recruits (Cebrian et al. 2012). The animal forest could then be replaced by turf and bushy macroalgae, i.e., the "precoralligene" community (Ponti et al. 2014; Fig. 7).

Professional and recreational fishing activities, with the harvesting of fish and crustacean compartments, of major importance in the ecosystem functioning, and the damage by fishing lines and nets, which uproot gorgonians and large seaweeds, must be taken into account with regards to all the coralligenous communities (e.g., Cánovas Molina et al. 2016).

Overall, the three most emblematic communities of the coralligenous ecosystem (bioconstructions by blade-forming corallines, animal forests of gorgonians and erect sponges, and seaweed forests of *Cystoseira* and *Sargassum* species) can be changed, under the pressure of various disturbances, into the precoralligene community, far less structurally complex, with only turf and bushy macroalgae (in addition to low sessile metazoans) (Fig. 7).

3 The Coral Reef Ecosystem Complex

3.1 Community Structure and Ecosystem Functioning

Coral reefs are intertropical formations. The autogenic ecosystem engineers are calcified cnidarians, mainly hexacorallians (Scleractinia, Metazoa), harboring mutualistic photosynthetic dinobionts (kingdom Alveolata; see Fig. 1). They are found within the north and south isotherms 20–22 °C (minimum temperature) throughout the world's oceans. The calcareous skeletal material of the hexacorallians is made of aragonite and supplies much of the structural bulk of the coral reef, while the cement consisting of calcite is produced by coralline crustose macroalgae (CCMA; Rhodobionta) (Littler and Littler 1988 and references therein). The latter organisms account for ~25–50% of the total precipitation of calcium carbonate (e.g., Eakin 1996; Hart and Kench 2007). As regards the dinobionts, they were for a long time considered as belonging to *Symbiodinium microadriaticum*. In fact, *S. microadriaticum* encompasses a complex of highly diverging clades; each clade probably encompassing a number of described and undescribed species (e.g., Savage et al. 2002; LaJeunesse and Thornhill 2011; Lee et al. 2015). These dinobionts are often called, incorrectly, "zooxanthellae," a misused term coined at a time when their actual nature was unknown (Boudouresque 2015). The symbiosis between calcified hexacorallians (hereafter hexacorallians) and dinobionts is called mutualism, because both partners are thought to derive benefit from the relationship (Fig. 8; Cowen 1988; Grottoli et al. 2006).

In the coral reef ecosystem, nutrients (including N and P) are tenaciously recycled within the system (Fig. 8), so that there is an immense accumulation of biomass (i.e., energy) in a highly oligotrophic environment. The symbiosis between dinobionts and hexacorallians is advantageous to both partners (i.e., a mutualistic symbiosis) only in an oligotrophic high-light environment (see below) (Cowen 1988).

The hexacorallians, i.e., the ecosystem engineers of the "animal forest," derive most of their nutritional resources from the primary production of their mutualistic

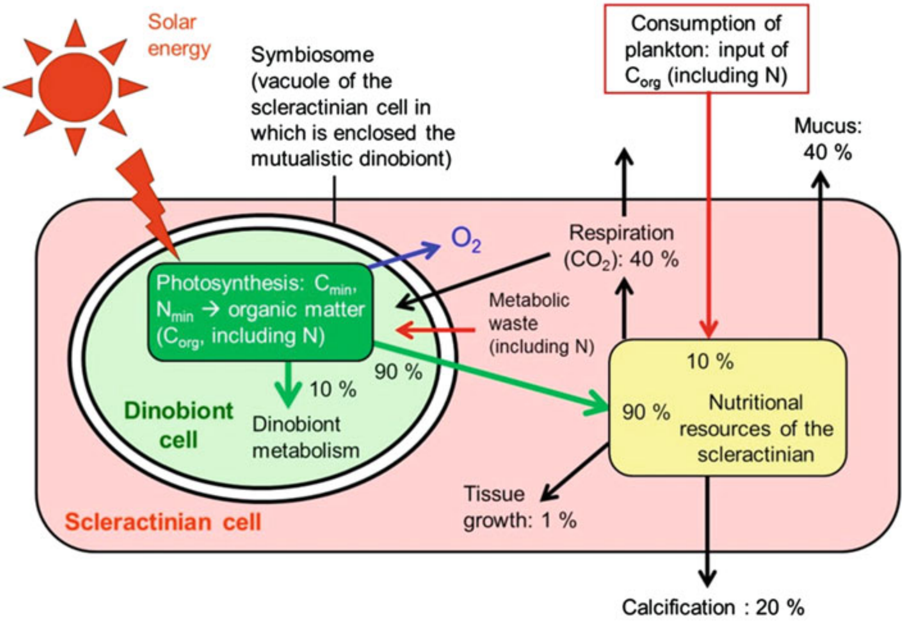

Fig. 8 Model of energy budget of a hexacorallian (scleractinian) and its mutualistic dinobiont. Most of the primary production of the dinobiont is exported toward the hexacorallian, which draws most of its nutritional resources from the mutualistic dinobiont. C_{org}, organic carbon. Data from Cowen (1988) (Redrawn and modified from Paola Furla (Charles F. Boudouresque))

dinobionts (Fig. 8). The proportion of energy transferred from dinobionts to the host, and that used for the host's metabolism and calcification, varies between coral species (Muscatine et al. 1981; Leletkin 2000) and *Symbiodinium* clades and species (e.g., Pettay et al. 2015). As a result, scleractinians could also be regarded as primary producers, and hexacorallian animal forests that characterize coral reefs may be functionally close to seaweed forests.

The coral reef ecosystem is made up of a mosaic of communities (e.g., Pérès and Picard 1969; Bellwood et al. 2004). In addition to the abovementioned hexacorallian forest, the emblematic flagship of coral reefs (Fig. 9), at least four more communities, constitute the coral reef ecosystem. **(i)** Seaweed forests, made up of canopy-forming Fucales (Phaeophyceae, Stramenopiles) such as *Turbinaria* spp. and *Sargassum* spp. (Fig. 10). **(ii)** Non-articulated coralline macroalgae (rhodobionts) of the so-called intertidal algal ridge (Fig. 11). **(iii)** Soft bottom habitats with calcified (in the aragonite form of calcium carbonate) and fleshy chlorobionts belonging to the Bryopsidales and Dasycladales (Ulvophyceae). **(iv)** Turf or mat of filamentous macroalgae and cyanobacteria (Fig. 12). Macroalgae may outcompete corals, through allelopathic compounds (Vieira et al. 2016). A number of other communities, such as animal forests related to gorgonians and sponges and sea urchin barren-grounds, are also important in reef ecosystems (e.g., Bellwood et al. 2004).

Fig. 9 A coral reef ecosystem at Ko Phi Phi Island, Thailand, Adaman Sea, at 8 m depth. An animal forest of hexacorallians. *Left*, branched *Acropora. Right*, tabular *Acropora*. Fish in the foreground: *Chaetodon trifascialis*, a consumer of coral polyps (Photo © Sandrine Ruitton)

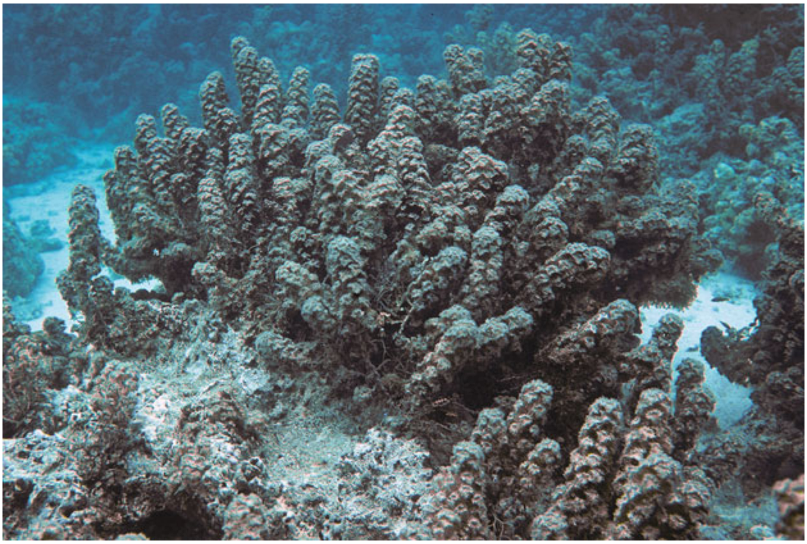

Fig. 10 A coral reef ecosystem at Tiahura, Moorea (French Polynesia). A seaweed forest (*Turbinaria* sp., Phaeophyceae, Chromobionta, Stramenopiles) (Photo © Mireille Harmelin-Vivien)

Fig. 11 A coral reef ecosystem at Tikehau, Tuamotu Islands (French Polynesia). The algal ridge community (Photo © Mireille Harmelin-Vivien)

Fig. 12 A coral reef ecosystem at Bora Bora (French Polynesia). A "garden" of macroalgal turf (center and foreground) on dead hexacorallians, and the farmer damselfish teleost *Stegastes nigricans* (Photo © Sébastien Personnic)

The coral reef ecosystem displays a number of features, the combination of which is unique and therefore characteristic (e.g., Pérès and Picard 1969; Littler et al. 1987; Littler and Littler 1988; Moberg and Folke 1999; Tribollet et al. 2002, 2006; Boudouresque et al. 2014: Glynn and Manzello 2015; Leprieur et al. 2016). Some of these features are not shared by all of the communities delineated here. **(i)** The species richness of macroalgae is between moderate (point diversity) and high (alpha diversity), and that of metazoans is very high (point diversity and alpha diversity). **(ii)** The photosynthetic PP is very high, 50–100 times higher than the PP of the adjacent open ocean. It is enhanced by the efficient retention of nutrients by recycling (Fig. 8) and by nitrogen-fixing (diazotrophic) bacteria (including Cyanobacteria). Endolithic primary producers also significantly contribute to the PP, in dead carbonate substrates. The ecosystem belongs to the low nutrient–high chlorophyll (LNHC) category. The chemosynthetic PP is absent. **(iii)** The biomass of photosynthetic primary producers, not taking into consideration the mass of calcium carbonate, is often regarded as low. In fact, adding the hidden mutualistic dinobiont biomass and the macroalgal biomass, the total biomass of primary producers can be equal to that of the metazoans. **(iv)** The ratio between PP and biomass is low. **(v)** Besides the PP of mutualistic dinobionts (~90% can be transferred to the host; see Fig. 8), part of the macroalgal PP is palatable and follows the herbivore pathway, while calcareous macroalgae, because of mechanical defenses, and fleshy macroalgae, because of chemical defenses, are poorly consumed. Overall, the herbivore pressure is very high and represents a key parameter in the functioning of the ecosystem. **(vi)** The importation of organic matter from adjacent ecosystems, as DOM and POM, plays a role in the ecosystem functioning. Adjacent ecosystems are the pelagic ecosystem (the water column of the lagoon and/or of the open ocean) and infralittoral ecosystems such as seagrass meadows (e.g., *Thalassia hemprichii* in the Indo-Pacific Ocean and *T. testudinum* in the eastern tropical Atlantic Ocean) and mangroves. **(vii)** The coral reef ecosystem is a relatively weak exporter, if compared with seagrass ecosystems (Boudouresque et al. 2014; Personnic et al. 2014). However, a significant part of the secondary production is exported to the open-ocean and deep-sea ecosystems via top predators. **(viii)** The hexacorallian growth results in a rise of the bottom. This trend, however, is offset by organisms that erode or dissolve the bioconstructions. The latter organisms belong to endobiontic Cyanobacteria and chlorobionts, sponges, boring mollusks, and grazing sea urchins and fishes. The rise of the bioconstructions results from a positive balance between calcification as constructive process and bioerosion as destructive process. **(ix)** The very high level of calcium carbonate precipitation constitutes a key character of the ecosystem, and provides ecosystem services of paramount importance (see below) (Jones et al. 2015). **(x)** Coral reefs are typical of an overall top-down control of the food web, especially within the animal forest community; although mats of turf algae could result from the release from this top-down control. Some pristine coral reefs, never impacted by human activities, reveal the possible primeval state of the coral reefs, with a “nasty” top-down control; the brutality of which has perhaps no equivalent in other of the earth’s ecosystems (e.g., Pala 2007; Sandin et al. 2008).

3.2 Macroalgae

The hexacorallian animal forest can seem, at a diver's first glance, to be devoid of macroalgae. In fact, some macroalgae, e.g., corallines, are located beneath or within the hexacorallian canopy. In addition, turf fast-growing macroalgae may seem inconspicuous, because of their steady grazing by herbivores and therefore their very low biomass; although they are responsible for most (70–80%) of the PP of the community (Littler and Littler 1988). Endobiontic boring chlorobionts, cyanobacteria, and fungi, within the hexacorallian skeletal structure, also play a conspicuous role within the animal forest and crustose coralline communities (Tribollet and Payri 2001; Glynn and Manzello 2015).

The canopy-forming seaweed forest (Fig. 10) is restricted to areas where there is more turbulence and little topographic relief, which hinders herbivore activity (sea urchins and fish). Seaweeds belong mainly to the genera *Turbinaria*, *Sargassum* (Phaeophyceae, Chromobionta, Stramenopiles), and *Acanthophora* (Rhodobionta, Archaeplastida).

The intertidal algal ridge community (also called algal crest), which dwells in turbulent areas, is generally dominated by crustose coralline macroalgae (CCMA; Fig. 11) belonging to the genera *Hydrolithon*, *Lithophyllum*, and *Porolithon* (Rhodobionta): *Hydrolithon craspedium*, *H. gardineri*, *Lithophyllum congestum*, *L. kotschyanum*, *L. pygmaeum*, and *Porolithon onkodes*. These species can withstand considerable desiccation and exposure to high sunlight irradiance (Littler and Littler 1988).

Calcified and soft Ulvophyceae (Chlorobionta) predominate mainly in protected shallow areas on soft bottoms, habitats that are unsuitable for most other macroalgae (community: chlorobiont stands on soft bottoms). The former belongs to the genera *Halimeda*, *Penicillus*, *Rhizocephalus*, and *Udotea*, defended from consumption by herbivores and omnivores by calcification, and which strongly contribute to peripheral reef and lagoon sediments. The latter belongs to the genera *Avrainvillea* and *Caulerpa*, protected against herbivores and omnivores by deterrent chemical compounds (terpenes). The animal forest community exports great amounts of coral debris and coral sand toward the chlorobiont stands on the soft bottom community (Fig. 13).

Finally, hard substrates, either rocks or dead coral bioconstructions, can be densely covered by filamentous macroalgae and cyanobacteria, the thickness of the turf or mat being negatively correlated with the herbivore pressure. It is worth emphasizing that the productivity of these mats, either within the present habitat or beneath the hexacorallian forest (see above), is considerably higher than that of the coarser species of the canopy-forming seaweed forest. In addition to the filamentous macroalgae, the mat harbors diazotrophic (i.e., N_2-fixing) Cyanobacteria, such as *Scytonematopsis crustacea*, an important feature that enhances reef productivity (Littler and Littler 1988). The presence of territorial teleost grazers, such as the damselfish *Stegastes nigricans*, which behave as true farmers, reduces herbivory pressure on turf macroalgae and thus might prevent recolonization by hexacorallians or by canopy-forming seaweeds (Fig. 12) (Hata and Kato 2002; Arnold et al. 2010).

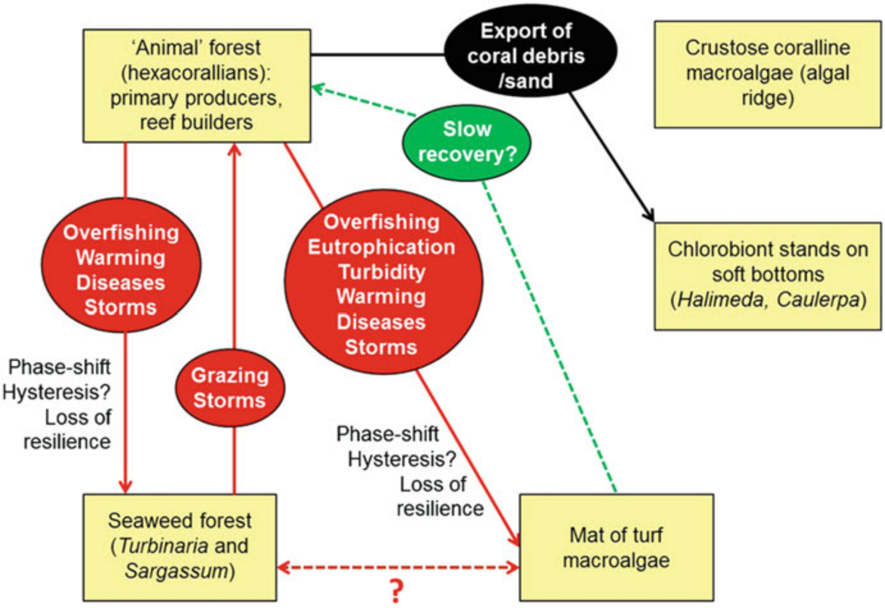

Fig. 13 Temporal dynamics of the five main communities that constitute the coral reef ecosystem, in a context of natural and human-induced disturbances (*red* ovals) and recovery (*green* ovals). Black oval: other processes (Original drawing (Charles F. Boudouresque))

3.3 Seaweed Forests Versus Animal Forests

Within the coral reef ecosystem complex, hexacorallian forests, canopy-forming seaweed forests, and other macroalgal stands compete for space, nutrients, and light. Light is a key factor for all of these communities, as hexacorallians constitute de facto primary producers through their mutualistic dinobionts. Any one of these communities can predominate under specific environmental conditions (Littler and Littler 1988).

Hexacorallian forests are threatened by a variety of natural and/or human impacts, e.g., storm damage, outbreaks of crown-of-thorns starfish (*Acanthaster planci*), diseases, warming resulting in bleaching events, eutrophication, coastal development, overfishing, anchoring, and mining (Smith et al. 2016 and references therein). A phase shift, with possible hysteresis, toward macroalgal turfs or canopy-forming seaweed forests (e.g., *Sargassum* and *Turbinaria*), has been widely reported (Fig. 13) (e.g., Hughes 1994; Bellwood et al. 2004; McManus and Polsenberg 2004; Bruno et al. 2009; Vermeij et al. 2010). Some disturbances (e.g., eutrophication and overfishing) result in a loss of resilience and increased vulnerability to phase shifts (Bellwood et al. 2004). Smith et al. (2016) actually observed that the cover of macroalgal turfs was higher in Pacific inhabited islands than in uninhabited ones, while it was exactly the opposite for the cover of hexacorallian forests (bioconstructions). However, the relationship between macroalgal cover and human impact is unclear, and the apparent link could be due to latitude and then the frequency and intensity of warm events. According to the dataset of Smith et al. (2016), there is no evidence of coral to macroalgal phase shifts, and whether a given community represents a transient state following a disturbance event or is actually an alternate stable state remains unclear (Fig. 13). Besides phase shifts from calcified hexacorallian forests to macroalgal turf or canopy-forming seaweed forests, there are also other phase shifts reported and/or suggested, e.g., from calcified hexacorallians to soft hexacorallians (corallimorpharians)-dominated or to sponge-dominated communities (Norström et al. 2009), which are beyond the scope of the present chapter.

Macroalgal turfs (generally less than 2 cm tall) consist of a mat of filamentous species, in association with Cyanobacteria, that quickly colonize dead hexacorallian skeletons. In contrast to CCMAs, which enhance hexacorallian recruitment, they negatively affect the survival capacity of hexacorallian recruits (Smith et al. 2016). Some macroalgae are even capable of bleaching some hexacorallians, via allelopathic compounds (Vieira et al. 2016). The turf macroalgae, both those that characterize a community and those that constitute an understory beneath the hexacorallian forest, play a prominent role within the coral reef ecosystem. They are ubiquitous in coral reefs, and their cover is probably more significant than usually claimed; however, this group of algae is inconspicuous and less iconic than the hexacorallians, so that it is often ignored or lumped together within categories of "dead coral" or "rubble." Similarly, CCMA (with the exception of the algal ridge) are often lumped together with "bare space" or ignored entirely (Smith et al. 2016). For these reasons, some studies, showing the "worrying" presence, the progression, or the supposed progression, of macroalgal turfs should be treated with caution, in the absence of a relevant baseline.

Finally, the CCMA of the algal ridge and the stands of chlorobionts on soft bottoms are confined to very specific habitats. As a result, these two communities weakly interact with the three former communities (Fig. 13).

4 Discussion, Conclusions, and Future Directions

In the terrestrial realm, forests are made up of perennial, more or less tall and long-lived "plants" (in the popular sense of the term) called "trees." These trees are primary producers and autogenic ecosystem engineers: they directly or indirectly modulate the availability of resources (other than themselves) to other species. The environment change is performed via their own physical structures, i.e., their living and dead tissues (Jones et al. 1994). They therefore structure the space, both above- and below ground. Terrestrial metazoans ("animals" sensu stricto; kingdom Opisthokonta; see Fig. 1) can be allogenic (not autogenic) ecosystem engineers: they change the environment by transforming living or nonliving materials from one physical state to another, via mechanical or other means (Jones et al. 1994). The paradigmatic example of a terrestrial allogenic ecosystem engineer is the beaver, which changes the environment via its activity, e.g., constructing a dam holding a reservoir. In the absence of large terrestrial sessile metazoans, animal forests, built by autogenic ecosystem engineers, cannot occur in the terrestrial realm. Terrestrial termite mounds, which locally are dense enough to constitute a kind of forest, could seem an exception; however, termites are allogenic, not autogenic, ecosystem engineers.

Just the opposite occurs in the marine realm. Large sessile metazoans can play the role of trees as autogenic ecosystem engineers. These "animal trees" can coexist, and/or compete, with more classical primary producer "trees," namely, seaweeds. The theme "animal forests versus seaweed forests" constitutes the central subject of the present chapter.

It focuses on two ecosystems in which animal and seaweed forests are juxtaposed, the intertropical coral reefs and the temperate Mediterranean coralligenous ecosystem, with the aim of disentangling the complexity of their relationships, in space and time.

Most ecosystems consist in a mosaic of patches (here "communities") that functionally are closely interconnected. The delineation of these communities, which actually constitute a continuum, is somewhat arbitrary. Here, four communities were delineated within the coralligenous ecosystem and five within the coral reef ecosystem. Some of these communities are restricted to a particular habitat and therefore are relatively stable over time, e.g., the crustose coralline macroalgae (CCMA) of the algal ridge, within the coral reefs. Other communities can be stages of ecological successions, possible alternate stable states, with transition from one state to another depending upon time and/or disturbances.

Within the two studied ecosystems (coralligenous and coral reefs), animal forests are intertwined with seaweed forests, more broadly with communities that are dominated by canopy-forming macroalgae (seaweed forests sensu stricto), by blade-forming corallines, by CCMA, by chlorobionts on soft bottoms, and/or by turf macroalgae. Surprisingly, few studies have examined the entire ecosystem, i.e., the different communities, which dictate how a given coralligenous or coral reef ecosystem functions, responds to, and recovers from disturbance events. In fact, most studies have focused on the most iconic communities, namely, bioconstructions by blade-forming corallines and animal forests of gorgonians and erect sponges (Fig. 7; coralligenous ecosystem) and animal forests of hexacorallians (Fig. 13; coral reefs), while neglecting more or less completely the other communities dominated by macroalgae. What is worse, when mentioned, these macroalgal communities are only considered as second-rate communities or degraded stages of the iconic ones. Yet all these communities are involved in the functioning and the natural dynamics of the ecosystems; although the baseline of the whole ecosystem (including macroalgal communities), and their overall functioning, are often poorly known, as stressed by some authors (e.g., Pala 2007; Sandin et al. 2008; Smith et al. 2016).

However, it is worth noting that all the communities that constitute the coralligenous and the coral reef ecosystems are not equally vulnerable to natural and human-induced disturbances, and that the ecological goods and ecosystem services they provide do not have the same weight (Moberg and Folke 1999; Salomidi et al. 2012). Bioconstructions of blade-forming corallines (coralligenous) constitute a 3D habitat that strongly structures the space; they contain a labyrinth of cavities and crevices that hosts extraordinary metazoan species diversity, making the coralligenous a hot spot for species diversity in the Mediterranean Sea (Laubier 1966; Ballesteros 2006). The 3D animal forest of hexacorallians (coral reefs) also harbors extraordinary species diversity, accounting for a large part of the world's ocean species diversity. The loss of the 3D coralligenous and coral reef bioconstructions results in a shift to less structured habitats and in a decline in the hosted species diversity. The capacity of animal forests of hexacorallians to precipitate huge amounts of calcium carbonate, and then to build bioconstructions, is one of the most significant services that coral reefs are known for. In addition, the loss of these bioconstructions would lower the flow of coral debris that "feeds" the coral islands located in the background of the reefs, which would threaten the long-term persistence of these coral islands. The animal forests of hexacorallians (coral reefs) and of gorgonians (coralligenous) provide stunning scenery, among the most highly appreciated in the world by divers, and is thus of paramount importance for diving tourism. The recovery of some communities, after their natural or human-induced shift to another community, can be very slow, if it occurs at all (see phase shifts): e.g., bioconstructions of blade-forming corallines, seaweed forests of *Cystoseira* and *Sargassum* (coralligenous), and animal forests of hexacorallians (coral reefs) (Fig. 7 and 13).

A further, and amusing, illustration of the intertwining of animal and plant forests is presented by the two genera *Turbinaria*. Because of the independence of the botanical and zoological codes of nomenclature, *Turbinaria* J.V. Lamouroux is the accepted name for a genus of Phaeophyceae (Chromobionta, Stramenopiles), therefore of macroalgae (Fig. 10), while *Turbinaria* Oken, 1815, is the accepted name for a genus of Hexacorallia (Cnidaria, Metazoa, Opisthokonta), therefore an animal (Boudouresque 2015). Both genera can coexist in the same geographic areas and even within the same ecosystem, the coral reefs, the first constituting part of the seaweed forests, and the second of the animal forests.

The complex relationship between macroalgae-dominated communities (e.g., seaweed forests, precoralligene, algal turfs) and cnidarian-dominated communities (animal forests) autogenic ecosystem engineers, within intertropical coral reefs and Mediterranean coralligenous ecosystems, makes the structure and functioning of these ecosystems highly original, without counterpart in the terrestrial realm.

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Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests

14

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Abstract

Hydroids, one of the dominant components of the zoobenthic communities, share comparable growth patterns with higher plants because of their modular body organization, high potential of asexual reproduction, and phenotypic plasticity. These features, together with the ability to enter dormancy to overcome unfavorable conditions, make hydroids successful organisms adaptable to a wide range of environmental scenarios. Depending on their wide range of shapes and sizes, hydroids form three-dimensional forests at different dimensional scales, establishing both trophic and non-trophic relationships with several other organisms, from virus to vertebrates.

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Despite numerous researches conducted to study the hydroid ecology, the putative importance of hydroids in structuring zoobenthic communities is underestimated. Here, information available about hydroid ecology is summarized, in order to emphasize the role of hydroids as forest formers, as well as their function in the bentho-pelagic coupling.

Keywords
Ecological role • Emerging threats • Hydroid forests • Protection • Seasonal and perennial habitat formers

Contents

1 Introduction

Clonal animals, according to Jackson and Coates (1986), have either uniserial or multiserial growth patterns. Uniserial colonies are also called “runners” and do not form large assemblages, whereas multiserial colonies perform lateral and distal growth and tend to persist, with the possibility of forming large assemblages. Multiserial colonies, hence, are able to form “forests” and behave as trees, whereas uniserial colonies are more similar to weeds. The two strategies are also used to distinguish guerrilla from phalanx species (Humphrey and Pyke 1998). Philopatric colonies (Knowlton and Jackson 1993) can produce a high number of genetically identical colonies (each termed a ramet) that, together, form a genet: an assemblage of genetically identical ramets. This tendency is conducive to the formation of animal forests.

The colonies of the Hydrozoa show highly diverse growth forms that cover both categories (Bouillon et al. 2006). Small polyp colonies (usually less than 1 cm high) are reptant and tend either to grow on other organisms or to form “meadows,” growing directly on primary substrates where they can play a certain ecological role in becoming habitats for other species. Small hydroids are mostly overlooked, being considered as mere epizoites. Consequently, very little information is available on the ecological traits of small hydroids and the role they play in both benthic and pelagic communities. *Clytia hummelincki* (Leloup, 1935) represents a case of meadow-forming hydroid (Gravili et al. 2008).

Large colonies (ranging from 10 cm to 1 m) grow on primary substrates and become substrate for other organisms, forming forests comparable in sizes and abundances to those of either algae or gorgonians, and likely play roles of habitat formers as those documented for anthozoan forests (Cerrano et al. 2010; Ponti et al. 2016; Valisano et al. 2016).

Hydroids are one of the main components of zoobenthic communities. At their relative dimensional scale, hydroids change the features of the geological habitat, becoming habitat formers by affecting water movement and light penetration and providing settling space, shelter, or food to several associated species, so enhancing local biodiversity. Moreover, hydroid forests release a consistent amount of planulae, medusoids, or medusae in the surrounding environment, contributing to bentho-pelagic coupling and affecting biogeochemical cycles (Gili et al. 1998; Rossi et al. 2012).

The modular organization of hydroids gives them a high plasticity and a potentially unlimited growth (Marfenin 1997; Kosevich 2006); hence they can adapt their shape, growth strategies, trophic behavior, and reproductive strategies to a vast array of environmental conditions (Boero 1984; Gili and Hughes 1995; Bouillon et al. 2006).

Even if hydroid ecology is rather well known (Fig. 1), their putative importance in structuring zoobenthic communities is underestimated by benthic ecologists. In spite of several documented cases of hydroids as formers of benthic assemblages comparable to algal forests, in fact, the formal definition of habitats rarely gave them much importance. For the Mediterranean Sea, for example, in the list of habitats assembled by RAC-SPA (2006), there is just a single item comprising all hydroid forests (i.e., facies with large hydrozoa), whereas each type of algal forests is carefully identified with the name of the main species; the same treatment is given to the Bryozoa. Fraschetti et al. (2008) proposed a rationale of benthic habitat classification that allows accommodating hydroid forests into the seasonal or even permanent habitat formers.

One of the reasons why hydroids are neglected is that hydroid specialists contributed less than marine botanists to the formal definition of habitats, and this led to underappreciation of the role of these animals, in respect to algae. Furthermore, at least in the Mediterranean Sea, field activities are mostly carried out in the favorable season when algae dominate benthic assemblages and most hydroids are dormant, leading to underappreciation of their importance in structuring benthic communities.

Analyzing papers focusing on hydroid ecology could help in understanding why hydroid ecological role is overlooked. From 1950 to today (Fig. 1), most of the papers were published during the decade 1980–1989 (over 45 per year); the most explored topic is the study of interactions between hydroids and other organisms (up to about 20 papers per year).

During the last years (2010–2016), there was an increasing interest in studying hydroids belonging to fouling communities, alien species, and effects of climate change on hydroid assemblages.

Among the researches published in the last two decades, very few papers put in relation hydroid distribution and population dynamics with abiotic and/or biotic factors (Azzini et al. 2003; Ronowicz et al. 2008; Orejas et al. 2013; Di Camillo et al. 2012a; Rossi et al. 2012).

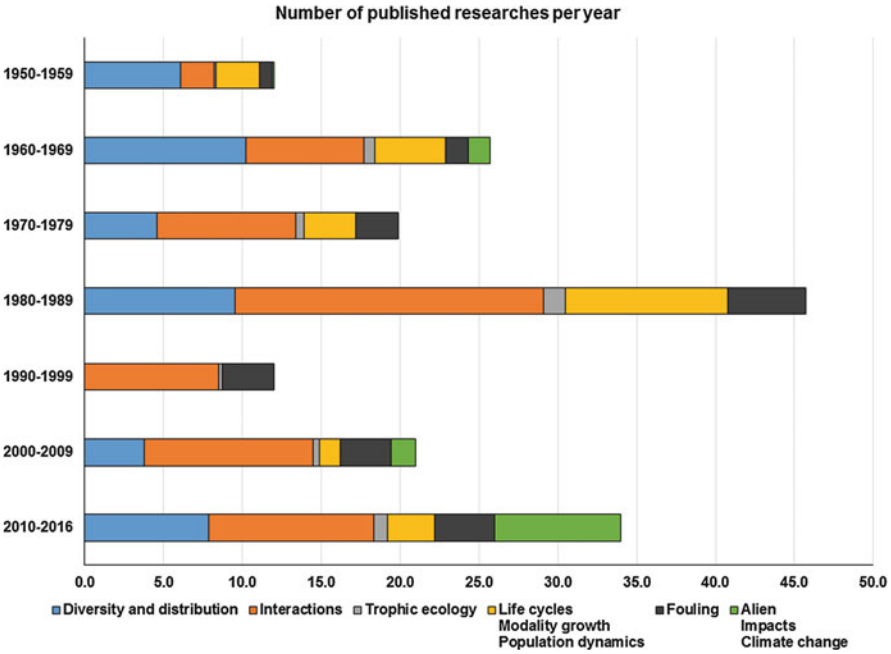

Fig. 1 Trend of published papers per year from 1950 to 2016. Over 1,500 papers focusing on hydroid ecology were considered (Data extracted from BiblioHydro, Gravili et al. 2000)

Similarly to what highlighted by Becerro (2008) regarding sponges, most of researches on hydroid ecology generally are descriptive and focus on one or few species, interesting a narrow readership. Lack of published quantitative data expressed in terms of biomass prevents estimation of the potential of hydrozoan forests in terms of trophic impact, food source, and reproductive output and does not allow the comparison with other animal forests or within the animal forests.

2 Deciduous Hydroid Forests

Deciduous hydroids, typical of shallow waters at cold and temperate latitudes, range from less than 1 mm (many Campanulariids, Campanuliniids) to about 20 cm in height (i.e., several Eudendriids, Pennariids, Tubulariids, Aglaopheniids, etc.). In these seasonal species, hydranth resorption or shedding occurs in response to periodic adverse environmental conditions, followed by dormancy of remaining fragments of tissue (coenosarc) enclosed in stems or hydrorhizae acting as resting stages (Bouillon et al. 2006). When environmental conditions become favorable again, the regeneration of the colonies takes place from the dormant tissue.

Seasonality drives the succession of species with different ecological characteristics; consequently, winter and summer species may occupy the same space, but in distinct temporal windows (Boero and Fresi 1986; Coma et al. 2000; Bavestrello et al. 2006; Puce et al. 2009). The duration of dormancy/active phases can change along bathymetric or geographical ranges characteristic of each species. Deciduous forests undergo strong seasonal variations in their biomass in relation to fluctuation of an intricate mixture of abiotic/biotic factors (i.e., temperature, irradiance, salinity, sedimentation, oxygen concentration, food availability, space competition, predation). Further studies are needed to understand physiological processes triggering quiescence or renovation and to test the duration of dormancy in relation to different ranges of environmental constraints since research focused on a limited number of species (Boero 1994 for a review).

Many studies on hydroid seasonality were conducted in the Mediterranean Sea. Boero and Fresi (1986) were the first to generalize a seasonal pattern of community structure in the Mediterranean benthos while giving paramount importance to hydroids, highlighting the importance of seasonal fluctuations in the composition of the sessile benthos, with a dominance of the algal component in the spring and summer and a prevalence of hydroids in the fall and winter. This was studied in detail for the dominant winter species *Eudendrium glomeratum* Picard, 1951 (Boero et al. 1986) and later better formalized in general studies (e.g., Boero 1994; Coma et al. 2000). Bavestrello et al. (2006) showed that, in the Mediterranean Sea, 50% of the species thrive in the winter, 30% in the summer, and only 20% tend to be always present.

Because of their plasticity and fast growth, deciduous hydroid forests have a prominent role in shaping zoobenthos dynamics. A good example is supplied by the comparison of the different life strategies of *Eudendrium racemosum* (Cavolini, 1785) from different localities. At the Medes Islands (MI), *E. racemosum* is also constantly present (Rossi et al. 2012), whereas it is sharply seasonal in the Adriatic Sea (AS), where temperatures are significantly lower in the winter (Di Camillo et al. 2012a) (Fig. 2). The longer duration of the fertility period and the highest polyp production in the population from the AS are likely related to the conspicuous food availability of this area. The considerable food amounts ingested by the polyps from the AS (Di Camillo et al. 2012a) suggest that (i) the hydroid plays a role in energy cycling and in removing particles from the water column and that (ii) local trophic levels are a key factor regulating variations in biomass of this suspension feeder. Indeed, in the MI, the summer regression of the population of *E. racemosum*, as well as the low polyp production, is probably related to the summer food paucity (Coma et al. 2000; Rossi et al. 2012). Moreover, in the MI, the hydroid growth could be limited in summer due to competition with algae, as occurring at other localities of the Western Mediterranean (Boero 1984; Boero and Fresi 1986; Boero et al. 1986; Rossi et al. 2012).

Under different local conditions, the life cycle patterns of *Eudendrium racemosum* can further differ from those described above: for example, in the Ligurian Sea, *E. racemosum* living on artificial substrates and in eutrophic conditions was observed all year round, while the population living on a natural rocky cliff was present in summer only (Azzini et al. 2003).

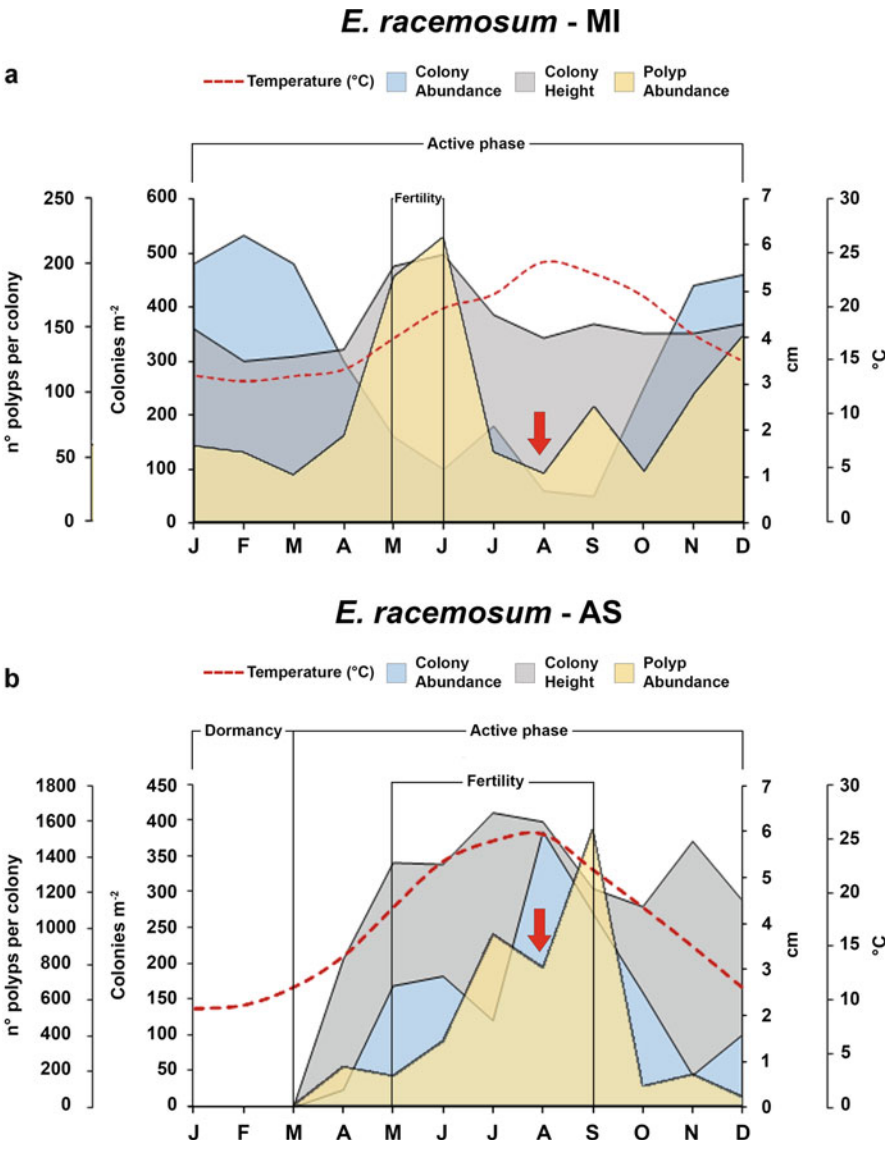

Fig. 2 Comparison of different population dynamics of *Eudendrium racemosum* (Cavolini, 1785) from Medes Islands (MI) (**a**) and Adriatic Sea (AS) (**b**) Red arrows indicate when the nudibranch predation is most intense

These considerations highlight that studies on fast-growing suspension feeders are indispensable to understand how population dynamics mirror environmental pressures and that the natural variability of these phenomena is great.

In tropical areas, seasonality is due to rainfalls, and biomass fluctuations are probably related to variations in food abundance during the wet and dry season

(Boero 1994). In Indonesian waters, the maximal density of hydroids coincides with the period of heavy rainfall and river inputs (Di Camillo et al. 2008). However, most of the projects carried out in tropical waters focused on the census of marine organisms, while long-term monitoring programs are scant. Similar knowledge gaps are present at the poles, where a dark and ice-dominated season alternates with a long period of total darkness (Orejas et al. 2013).

Seasonal forests can regress as a result, for instance, of the impact of global warming on species of cold-water affinity, such as *Eudendrium glomeratum* in the Ligurian Sea (Boero et al. 1986). The regression of seasonal species is usually given less importance than that of perennial species, such as those of gorgonians in the Ligurian Sea (Cerrano et al. 2000). Seasonal species are preadapted to undergo long periods of adverse conditions with dormant phases but, nevertheless, if negative situations become permanent (e.g., with constantly higher temperatures than previous ones), species might become locally extinct.

3 Perennial Hydroid Forests

Perennial hydroids are always present in their erect forms (e.g., the calcareous Milleporidae and Stylasteridae) and are more common than seasonal species where variations in environmental conditions are small. Habitat stability allows enduring species to develop large and sturdy colonies and to reach considerable sizes ranging from 20 cm up to 2 m: for example, *Plumularia elongata* Billard, 1913, *Solanderia* spp., or *Millepora* spp. at tropics; *Lytocarpia myriophyllum* (Linnaeus, 1758) on soft bottoms; *Errina* spp., and *Amphisbetia operculata* (Linnaeus, 1758) on hard substrates from temperate regions (Table 1, Figs. 3 and 4). Perennial hydroids can give rise to animal forests comparable to those formed by gorgonians. Those with calcified skeletons are probably slow growing, but their growth rates are poorly estimated (Lewis 2006). During their theoretically unlimited life span, perennial hydroids host several taxa of sessile and vagile organisms, represent a food source for several animals, and, in their turn, likely collect great amounts of feeding particles from the water column. These forests undoubtedly have a significant – but little explored – role in energy transfer from plankton to benthos (Gili et al. 1998; Gili and Coma 1998). Enduring hydroid forests can be indicators of habitat health conditions: for example, the presence of intact *Errina* gardens on hard substrates (Häussermann and Försterra 2007; Salvati et al. 2010), *Plumularia elongata* on tropical reefs (Di Camillo et al. 2010), and *Lytocarpia miriophyllum* on sandbanks (Di Camillo et al. 2013; Cerrano et al. 2015) is linked to the existence of pristine or scarcely disturbed habitats.

Loss of their habitats would lead to decline or disappearance of the enduring hydroid forests and their ecosystem services, as observed for *L. myriophyllum* in Northern Ireland because of intense bottom trawling (Goodwin et al. 2011). In Ireland and Great Britain, the hydroid is considered a priority species (Goodwin et al. 2011), while, in the Mediterranean, surveys of *L. myriophyllum* should be

Table 1 Summary of the ecological characteristics of some large forest former hydrozoans (*A*, Anthomedusae; *L* Leptomedusae)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
A	*Millepora* spp.	Circumtropical	From reef crest	Hard	Larger colonies branched; calcified skeleton	Eumedusoids	Zooxanthellae, *Wanella elongatum* (Hiro, 1931) (barnacle), *Hermodice carunculata* (Pallas, 1766) (polychaete, predator), several species of crustaceans, echinoderms, mollusks, nemerteans, polychaetes, and sipunculids	Global warming, bomb fishing, pollution
A	*Solanderia* spp.	Tropical and subtropical	Fore reef	Hard	Fan-shaped to bushy; perisarc stiff	Cryptomedusoids or eumedusoids	*Medioantenna* spp., serpulids (polychaetes), *Licnophora* spp. (protozoans), *Jason mirabilis* M.C. Miller, 1974 and *Pleurolidia juliae* Burn, 1966 (nudibranches, predators), bivalves, gastropods,	

							tunicates, ophiuroids, copepods, barnacles, amphipods, bryozoans	
A	*Pseudosolanderia* spp.	Circumtropical	Fore reef	Hard	Fan-shaped to bushy; chitinous or from partly to quite totally calcified	Eumedusoids	*Lagisca zibrowii* Hartmann-Schröder, 1992 (polynoid polychaete), *Pachyprocerastea hydrozoicola* (Hartmann-Schröder, 1992) and *Procerastea simpliseta* Hartmann-Schröder, 1990 (syllid polychaetes)	
A	Stylasterids	Temperate	Deep waters	Hard	Branched colonies; calcified skeleton	Fixed gonophores in ampullae	Algae, other hydrozoans, scleractinians, *Epizoanthus* sp. (zoanthid), sponges, bryozoans, commensal polychaetes, *Pachylasma giganteum*	Destructive fishing techniques

(*continued*)

Table 1 (continued)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
							(Philippi, 1836) (barnacle), *Pedicularia* spp. (gastropods)	
L	*Amphisbetia operculata* (Linnaeus, 1758)	Temperate and subtropical	From shallow waters in cold regions	Hard substrates on soft bottoms	Bushy with pinnate cormoids; perisarc flexible	Cryptomedusoids	Diatoms, macroalgae, ciliates, other hydrozoans, entoprocta, *Doto eireana* Lemche, 1976 (nudibranch, predator), other mollusks, bryozoans, tunicates	
L	*Sertularella diaphana* (Allman, 1885)	Tropical and subtropical	Fore reef	Hard	Fan-shaped to bushy; perisarc stiff	Cryptomedusoids	Bivalves, amphipods	
L	*Sertularia argentea* Linnaeus, 1758	Temperate	From shallow waters in cold regions	Hard	Spiralate colonies; pinnate branches; flexible perisarc	Heteromedusoids		Ornamental harvesting
L	*Hydrallmania falcata* (Linnaeus, 1758)	Temperate	From shallow to mesophotic zone	Hard substrates on soft bottoms	Pinnate cormoids spirally arranged;	Fixed gonophores	Other hydroids	Ornamental harvesting

					perisarc flexible			
L	*Aglaophenia cupressina* Lamouroux, 1816	Indo-Pacific	Between reef crest and fore reef	Hard	Bushy with pinnate cormoids; perisarc very flexible	Fixed gonophores protected by corbulae	Zooxanthellae, *Cuthona diversicolor* Baba, 1975 (nudibranch, predator), cyclopoid copepods, *Hyastenus bispinosus* Buitendijk, 1939 (crab), fish	Global warming
L	*Lytocarpia myriophyllum* (Linnaeus, 1758).	From boreal to subtropical regions	Mesophotic and deep waters	Soft	Bushy with pinnate cormoids; perisarc very flexible	Fixed gonophores	Forams, other hydroids, *Amphianthus dohrnii* (Koch, 1878) (actinian), *Dondice banyulensis* Portmann & Sandmeier, 1960 (nudibranch, predator, egg deposition), bivalves, stalked barnacles, solenogaster, gastropods, caprellids and gammarids, bryozoans	Destructive fishing techniques

(*continued*)

Table 1 (continued)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
L	*Macrorhynchia* spp.	Tropical and subtropical	Fore reef	Hard	Fan-shaped, pinnate cormoids; moderately flexible	Fixed gonophores or medusoids, protected by phylactocarps	Other hydroids (Hebellidae), decapod palaemonids	
L	*Streptocaulus dollfusi* (Billard, 1924)	Eastern Atlantic, Strait of Gibraltar	Mesophotic and deep waters	Hard	Erect and polysiphonic colonies, pinnate cormoids	Fixed gonophores protected by phylactocarps		
L	*Plumularia elongata* (Billard, 1913)	Indo-Pacific	Fore reef	Hard	Fan-shaped to bushy; with pinnate cormoids; strongly polysiphonic and stiff	Fixed or swimming gonophores	*Hydrozoanthus gracilis* (Lwowsky, 1913) and *Hydrozoanthus* sp.1 (zoanthids), pycnogonids	
L	*Pseudoplumaria* spp.	Temperate and subtropical	From shallow to deep waters	Soft	With pinnate cormoids	Fixed gonophores		
L	*Nemertesia* spp.	Cosmopolitan	Mesophotic and deep waters	Hard substrates on soft bottoms	Bushy due to very close unbranched cormoids	Fixed gonophores	Sponges, other hydroids, *Alcyonium digitatum* Linnaeus, 1758 (anthozoan), nemerteans, bivalves,	Destructive fishing techniques

							gastropods (prosobranchs and opistobranchs), *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789) (ophiuroid), *Antedon bifida* (Pennant, 1777) (comatulid), polychaetes, gammarid and caprellid amphipods, copepods, cirripeds, cumaceans, isopods, decapods, pycnogonids, entoprocts, bryozoans, tunicates	
L	*Polyplumaria flabellata* G.O. Sars, 1874	Temperate and subtropical	Deep waters	Hard	Fan-shaped; with pinnate cormoids; stiff perisarc	Fixed gonophores		
L	*Halecium* spp.	Boreal and temperate	Mesophotic and deep waters	Hard	Fan-shaped to bushy, pinnate cormoids	Fixed gonophores		
L	*Hartlaubella gelatinosa* (Pallas, 1766)	Temperate	Deep waters	Mixed substrates	Bushy	Fixed gonophores	Amphipods and caprellids	

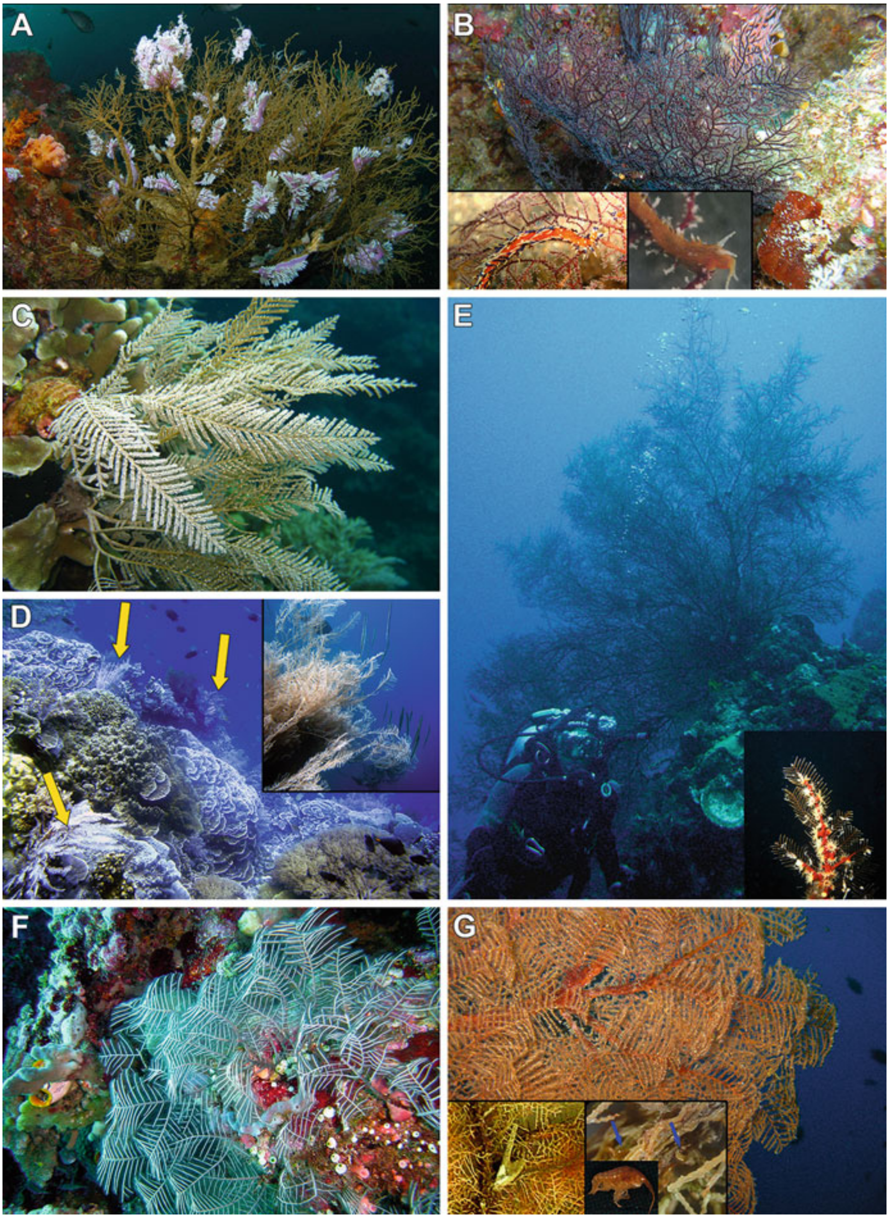

Fig. 3 Some large warm-affinity hydrozoans. (**a**, **b**) The subtropical *Solanderia ericopsis* (Carter, 1873) (**a**) from New Zealand predated by the nudibranch *Jason mirabilis* M. C. Miller, 1974 (photo curtesy of Ian Skip, http://www.ianskipworth.com and *Solanderia secunda* (**b**) from the North Sulawesi. The insets show the polynoid *Medioantenna variopinta* and the nudibranch *Pleurolidia juliae*. (**c**–**d**) *Aglaophenia cupressina* from the North Sulawesi; the inset shows a colony explored by razor fish. (**e**) *Plumularia elongata* from Bali: a large colony completely covered with the zoanthid *Hydrozoanthus* sp. 1 (inset). (**f**–**g**) *Macrorhynchia spectabilis* (**f**) and *Sertularella diaphana* (**g**) from the North Sulawesi. The insets in Fig. (**g**) show a pteriod bivalve and numerous amphipods respectively on the main axis and on hydrorhiza of *S. diaphana*

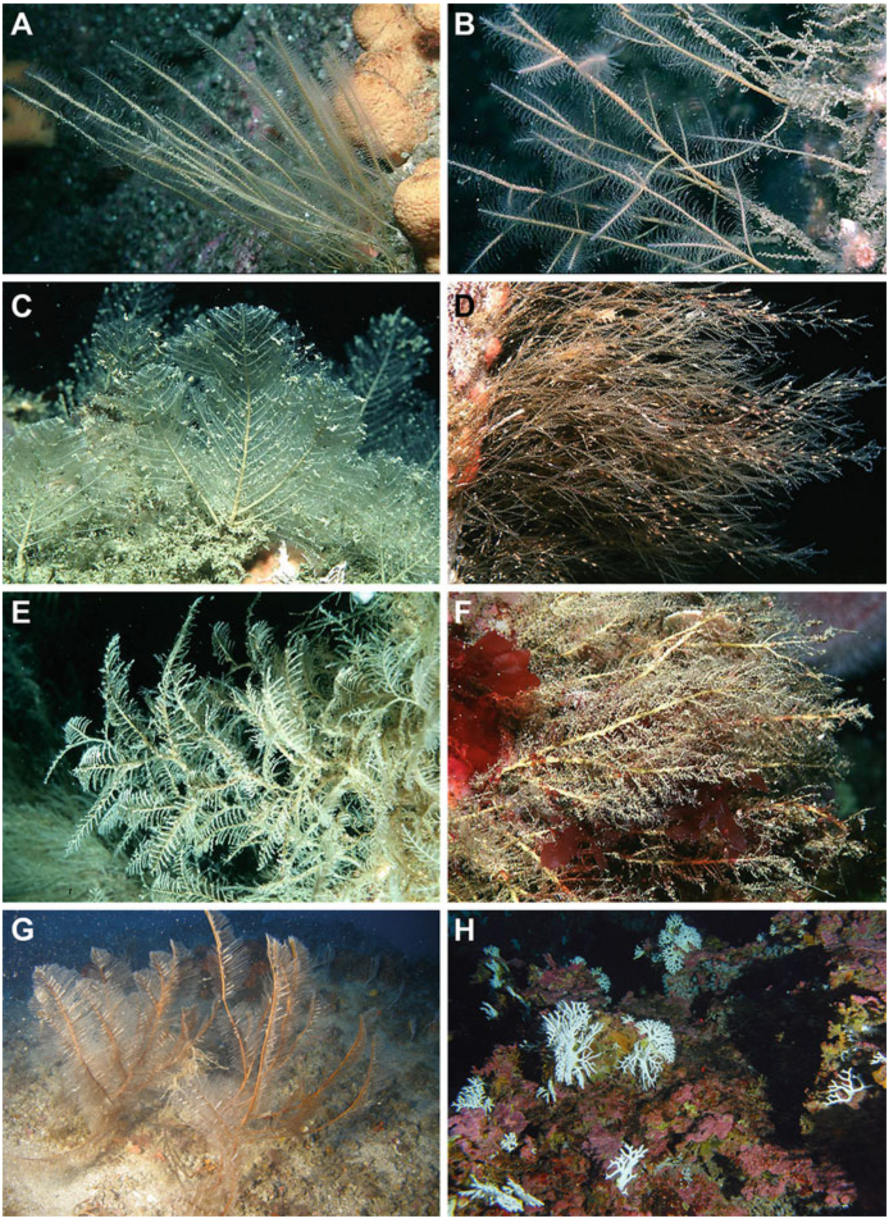

Fig. 4 Some large cold-affinity hydrozoans. (**a**–**f**). Hydrozoans from British Isles, photo curtesy of Dr. Bernard Pictet http://www.habitas.org.uk/marinelife/. (**a**) *Nemertesia antennina.* (**b**) *Nemertesia ramosa*. (**c**) *Polyplumaria flabellata*. (**d**) *Amphibestia operculata*. (**e**) *Hydrallmania falcata.* (**f**) *Halecium muricatum.* (**g**) *Lytocarpia myriophyllum* from the Western Mediterranean. (**h**) The deep stylasterid *Errina aspera* from the Strait of Messina

performed to collect much information about its distribution and abundance and to develop a proper conservation strategy of this species (Di Camillo et al. 2013).

Indeed, the extension of either perennial or seasonal hydroid forests has never been mapped as carefully as other benthic features, such as coralligenous formations or seagrass meadows.

Phenology and distribution of enduring species should be known to evaluate their importance for ecosystem functioning and to plan conservation programs.

4 Interactions with Other Organisms

Hydroids can establish different kinds of symbiotic relationships with several organisms from viruses to vertebrates, and, due to their wide size range, they can be both hosts and epibionts.

Hydroids increase habitat complexity and enhance biodiversity as demonstrated through the study of temporal variations in composition and biomass of the organisms associated to *Tubularia indivisa* Linnaeus, 1758 from the North Sea (Zintzen et al. 2008). The biomass of most of the symbionts was positively correlated to that of the host, and the maximal epibiont density reached very high values (about 450,000 ind. m^{-2}).

Even if several papers describe the entire assemblage of fauna and flora associated to hydroids (e.g., Hughes 1975; Lagardère and Tardy 1980; Bavestrello et al. 1996; Genzano 2001; Zintzen et al. 2008; Meretta and Genzano 2015), the majority of the available literature studies associations involving few taxa, such as endosymbiotic algae (29% of published papers, Fig. 5) and mollusks (19%). There are over 600 papers focusing on interactions between hydroids and other taxa, highlighting that hydroid forests represent a mosaic of microhabitats, exploitable by numerous and diversified organisms. The perisarc composition and the production of secondary metabolites probably affect the attractiveness of hydroid basibionts; moreover, the organic matter trapped by hydroid colonies may support detritus-feeder communities (Bavestrello et al. 2008), whereas other organisms such as amphipods can use the inorganic fraction imprisoned under the hydrorhiza to build their burrows (Genzano 2001). Even the smallest hydroids can host a dense microbiome, composed both of prokaryotic and eukaryotic symbionts (Fig. 6). Stabili et al. (2006) found prokaryotic communities on the perisarcal exoskeleton of *Aglaophenia octodonta* Heller, 1868, while Östman (2000) and Di Camillo et al. (2012b) reported bacteria on the bare epidermis of *Pennaria disticha* Goldfuss, 1820, and *Ectopleura crocea* (L. Agassiz, 1862). Schuett and Doepke (2009) recorded microbes inside the tissues of *Tubularia indivisa* Linnaeus, 1758. Among eukaryotes, the microbiome includes diatoms, sessile ciliata such as *Vorticella* and suctorians (Tazioli and Di Camillo 2013), foraminifera, and macroalgae (Bavestrello et al. 2008).

Millepora spp. and *Aglaophenia cupressina* Lamouroux, 1816, are the only large forest-forming hydroids with conspicuous presences in scleractinian-dominated shallow reefs. The fact that both species host zooxanthellae (*Symbiodinium* spp.)

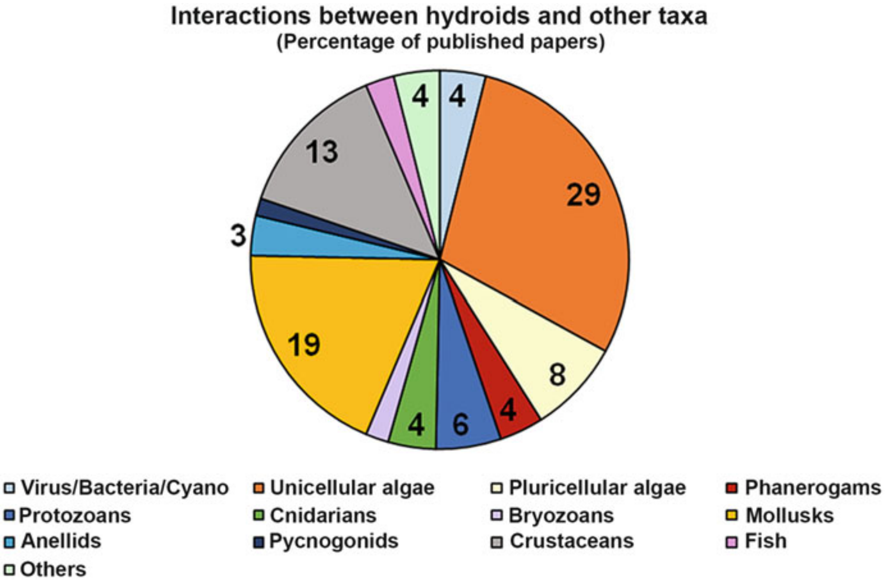

Fig. 5 Percentages of published papers concerning interactions between hydroids and other organisms

suggests that the success of these hydroids on the upper part of the reef could be linked to their ability to obtain part of their nutrition from autotrophic sources (Lewis 2006). On the other hand, many zooxanthellate hydroids (e.g., *Hydra* spp., *Myrionema amboinense* Pictet, 1893, *Eudendrium moulouyensis* Marques, Peña Cantero, Vervoort, 2000, *Halecium nanum* Alder, 1859) do have zooxanthellae but do not form forests.

Large hydroids are basibionts for a conspicuous number of taxa due to (i) the large surface offered by their colonies; (ii) the high variety of microhabitats represented by the hydrorhiza, the proximal polysiphonic portions, and the thinner distal branches; (iii) the elevation from the substrate, allowing the settlement of acrophilous species; and (iv) in some case the stability over time of at least the elder and larger basal portions, where organisms are particularly abundant (Garcia et al. 2009; Hughes 1975, 1977).

Some large hydroids such as *Nemertesia antennina* and *Lytocarpia myriophyllum* form a complex rootlike apparatus, which may be composed by several generations of hydrorhizae (Hughes 1977; Di Camillo et al. 2013). In proximity of the substrate, the anchoring system accumulates sediments due to the reduced current speed (Hughes 1978). This three-dimensional holdfast represents a perennial habitat for several organisms, such as those of meiofauna (Cerrano et al. 2015), sponges, pycnogonids, bryozoans (Hughes 1978), or amphipods. The biomass of associated organisms may reduce in distal portions due to the possible presence of defensive/cleaning zooids (Gili and Hughes 1995; Hughes 1978) or because of a higher turnover of the apical branches.

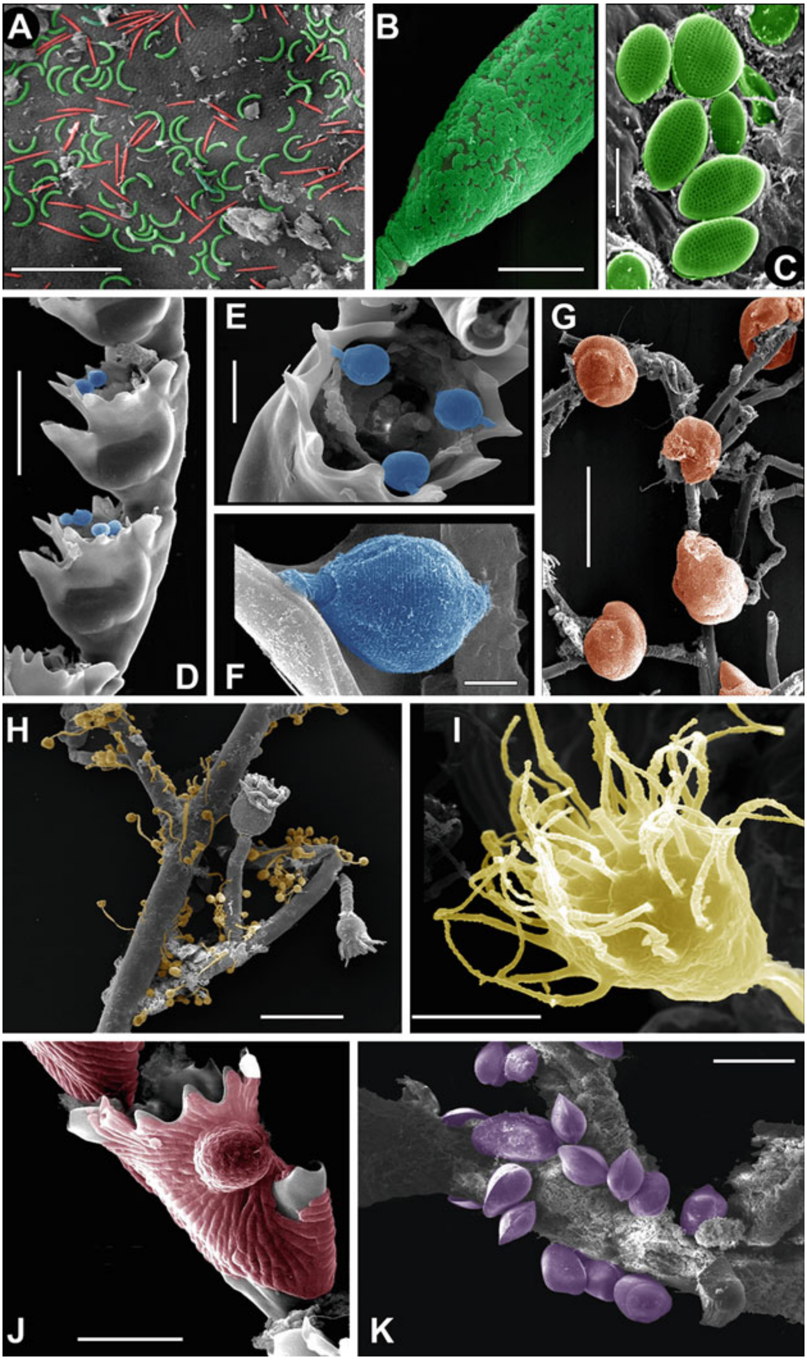

Fig. 6 (continued)

Hydroid's colonies can be the primary substrate for the recruitment of other invertebrates, such as mussel's larvae (Standing 1976; Di Camillo et al. 2012a; Genzano et al. 2003). Big colonies of *Amphisbetia operculata* (Linnaeus, 1758) and *Plumularia setacea* (Linnaeus, 1758) represent the unique filamentous structure in sublittoral outcrops from temperate southwestern Atlantic (Buenos Aires coast), and blue mussel spats use these colonies as primary substrata (Genzano et al. 2003); colonies of *Symplectoscyphus subdichotomus* (Kirchenpauer, 1884) are the main primary settlement substrate of scallop spats in fishing grounds in Argentine sea (Bremec et al. 2008).

Some examples of relationships between large hydroids and associated organisms are summarized in Table 1. *Millepora* spp. form functional biogenic reefs positively influencing fish abundance and species richness, especially in scleractinian-poor Southwestern Atlantic (Coni et al. 2013; Lewis 2006; Pereira et al. 2012; Rogers et al. 2014). Besides fish, *Millepora* forests were found in association with a rich epi- and endofauna represented by crustaceans, echinoderms, mollusks, nemerteans, polychaetes, tunicates, and sipunculids (Cook et al. 1991; Garcia et al. 2009, 2010; Pérez and Gomes 2012).

In temperate waters from southwestern Atlantic Ocean, intertidal colonies of the Anthomedusan *Ectopleura crocea* (Agassiz, 1862) can form dense clumps that support many epizoical microcrustaceans. Colonies also trap sediments under their hydrorhizae where other sediment-associated fauna lives (Genzano 2001). In sublittoral outcrops, two large Leptomedusan hydroid, *P. setacea* and *A. operculata*, represent the most abundant available substrata for numerous vagile and sessile organisms (Meretta and Genzano 2015).

Stylasterid corals enhance habitat complexity offering refuge, food, and a hard substrate to several vagile and sessile invertebrates (Braga-Henriques et al. 2011; Salvati et al. 2010; Pica et al. 2015).

5 Trophic Ecology, Feeding Behavior, and Reproductive Strategies

Hydroid habitat formers do not give rise to large colonies and forests everywhere, suggesting that formation of forests occurs only where food availability can support their development.

Fig. 6 Microforests living on hydrozoans at scanning electron microscope; recolored pictures. (**a**) Two microbial morphotypes, one horseshoe shaped (*green*) and another one fusiform (*red*), living on the bared epidermis of *Ectopleura crocea*. (**b**–**c**) Portion of the hydrotheca of *Clytia linearis* (**b**) almost completely covered by the diatom *Cocconeis pseudonotata* (**c**). (**d**–**f**) Sessile ciliated of the genus *Vorticella* settled on the thecal margin of *Aglaophenia kirkenpaueri*. (**g**) Foraminifers living on cauli of *Eudendrium armatum*. (**h**–**i**) A dense assemblage of suctorians settled on a colony of *Eudendrium racemosum*. (**j**) Hydrotheca of *Aglaophenia tubiformis* covered by the coralline alga *Hydrolithon* cf. *farinosum*. (**k**) Juvenile of *Mytilus galloprovincialis* on *Eudendrium racemosum*. Scale bars: (**a**, **c**, **f**) 10 μm; (**b**, **d**) 200 μm; (**e**) 50 μm; (**g**–**h**) 1 mm; (**i**) 20 μm; (**j**) 100 μm; (**k**) 500 μm

The experimental studies performed to define the trophic role of hydroids in marine communities (Table 2) show that hydroids can exploit large quantities of seston, contributing to control the secondary production in coastal waters (Gili and Coma 1998; Gili et al. 1998). Zooplanktonic preys, eggs, merobenthic larvae, phytoplankton, bacteria, and detritus represent the preferential food items of hydroids. The prey composition and predation rates vary in relation to hydroid species, sizes of preys and hydranths (feeding polyps), characteristics of the study areas, temporal fluctuations of environmental parameters (such as temperature, salinity, current intensity), and biotic factors (i.e., predation and competition). Captures are related to the food availability, which can vary daily or seasonally (Table 2). Predation rate is inversely correlated to digestion time (Coma et al. 1994) which, in its turn, is related to hydroid characteristics but also to environmental conditions (i.e., temperature and salinity, Kinne and Paffenhöfer 1965; Gili and Hughes 1995). Besides the size, other features of the ingested preys can condition digestion times, such as the presence of stiff exoskeletons (Orejas et al. 2013). Times required for digestion of some hydrozoans are compared in Table 3.

Different preys have diverse carbon contents; however, the total carbon intake (mg C m^{-2} day^{-1}) of the considered hydroid species is comparable to that of other suspension feeders (Gili and Coma 1998, Table 1), suggesting that hydroids play a key role in energy transfer from the pelagic to the benthic realms (Coma et al. 1995, 1998). In particular, hydroids forming large, multibranched colonies could have a great impact on seston since they have a number of feeding polyps much higher than small hydroid species. Large colonies of *Lytocarpia myriophyllum* from the Ligurian Sea have about 1,300,000 feeding polyps m^{-2} (Cerrano et al. 2015), that, applying the lowest feeding rate reported for a cnidarian (0.01 mg C $polyp^{-1}$ day^{-1}, Gili and Coma 1998), could remove up to 13,000 mg C m^{-2} day^{-1}.

Standing (1976) and Sutherland and Karlson (1977) showed that hydroids resist overgrowth when present in dense aggregations (forests) being able to prevent the settlement of competitors by feeding on their approaching larvae. This behavior contributed to the proposal of the inhibition model as one of the modes of community development (Connell and Slatyer 1977) and can explain the processes that lead to the establishment of hydroid forests: once established, the forests inhibit the settlement of other species by eating the larvae of potential competitors.

The trophic role of hydroids with medusae is double since they predate both in the benthos and in the plankton. To our knowledge, the complete trophic role of a species with both polyps and medusae has never been studied in detail, accounting for both domains.

Concerning trophic behavior, Miglietta et al. (2000) reviewed a vast array of strategies in the various hydroid species, ranging from passive filter feeding, with the outstretched tentacles used as a filter, to active feeding achieved by movement of the whole polyp in a “searching” pattern, to rhythmic tentacle contraction causing microcurrents that convey small prey toward the mouth. As it might have been expected, specific studies (Gili et al. 1996; Miglietta et al. 2000) showed that small polyps mostly eat small food items, usually protists, whereas large polyps catch larger prey, ranging from crustaceans to other planktonic and

Table 2 Predation rates of some hydroids from different localities

Species	Locality	Dominant preys	Predation rate	Carbon intake (mg C m^{-2} day^{-1})	References
Campanularia everta Clark, 1876	Western Mediterranean	POM (88), copepod eggs (7%)	From 4,000 (summer) to 800,000 (winter) preys m^{-2} day^{-1}	6.4	Coma et al. 1995; Gili et al. 1998
Ectopleura crocea (Agassiz, 1862)	Mar del Plata	Diatoms (100% in winter), crustaceans (summer)	115·(summer), 93 (autumn), 77 (winter), 200 (spring) preys $ind.^{-1}$ day^{-1}	–	Genzano 2005
Ectopleura larynx (Ellis & Solander, 1786)	Cumbrae (SW Scotland)	Crustacean eggs, nauplii, copepodites	From 36 (day) to 360 (night) preys $ind.^{-1}$ day^{-1}	89.9	Gili et al. 1996, 1998
Eudendrium racemosum (Cavolini, 1785)	Medes Islands (Mediterranean)	–	372,000 preys m^{-2} day^{-1} in June	30.7	Rossi et al. 2012
Eudendrium racemosum (Cavolini, 1785)	North Adriatic Sea (Mediterranean)	Bivalve larvae (43%), tintinnids (32%), invertebrate eggs (7%), invertebrate larvae (6%), amphipods (4%)	Over 6,000 preys m^{-2} day^{-1} in summer (without considering POM)	13	Di Camillo et al. 2012
Eudendrium racemosum (Cavolini, 1785)	Western Mediterranean	Copepod eggs (28%), Copepods (22%), invertebrate larvae (10%)	120,000 preys m^{-2} day^{-1}	12	Gili et al. 1998
Eudendrium racemosum (Cavolini, 1785)	Western Mediterranean	Above all zooplanktonic preys (crustacean fragments, copepods, larvae)	100,000 preys m^{-2} day^{-1}	–	Barangé and Gili 1998
Lytocarpia myriophyllum (Linnaeus, 1758)	Ligurian Sea	–	–	13,000[a]	Cerrano et al. 2015
Millepora complanata Lamarck, 1816	Barbados	Copepods (63%)	480,000 preys m^{-2} of the corallum's surface day^{-1}	360,000 mg C m^{-2} of the corallum's surface day^{-1}	Lewis 1992

(*continued*)

Table 2 (continued)

Species	Locality	Dominant preys	Predation rate	Carbon intake (mg C m^{-2} day^{-1})	References
Nemalecium lighti (Hargitt, 1924)	San Blas Islands (Panamá)	Diatoms (28%), POM (23%); invertebrate larvae (19%); bivalve larvae (11%)	400,000 preys m^{-2} day^{-1}	6	Gili et al. 1998; Coma et al. 1999
Obelia dichotoma (Linnaeus, 1758)	Kongsfjorden (Spitsbergen, Arctic)	Fecal pellets (up to 57% of the total ingested food), phytoplankton (up to 50%), and organic matter (up to 35%)	261,182 preys m^{-2} day^{-1}	5.5–8.9	Orejas et al. 2013
Obelia geniculata (Linnaeus, 1758)	Chile	Fecal pellets (48%), Copepod eggs (29%), diatoms (17%)	3,200,000 preys m^{-2} day^{-1}	48	Gili et al. 1998
Silicularia rosea Meyen, 1834	King George Island (Antarctica)	Benthic diatoms (95%), eggs (2%)	4,000,000 preys m^{-2} day^{-1}	66	Gili et al. 1996, 1998

[a] Estimated applying the lowest capture rate calculated for cnidarians (0.01 mg C $ind.^{-1}$ day^{-1}, from Gili and Coma 1998)

Table 3 Digestion time of some hydroids estimated in experimental conditions

Species	Sampling site	Rearing conditions	Preys	Digestion time (h)	References
Ectopleura larynx (Ellis & Solander, 1786)	Cumbrae (SW Scotland)	15 °C	Small	2–3	Gili et al. 1996
			Large	5	
Ectopleura crocea (Agassiz, 1862)	Mar del Plata			4–5	
Obelia dichotoma (Linnaeus, 1758)	Arctic waters	6 °C	A single diatom	20	Orejas et al. 2013
Hydractinia echinata (Fleming, 1828)	Knähaken Reef (Øresund, NE Atlantic)	4 °C		40	Chistensen 1967
		16 °C		5	
Silicularia rosea Meyen, 1834	King George Island (Antarctica)	0–2 °C	Diatoms	12	Gili et al. 1996
Campanularia everta (Clark, 1876)	Medes Islands (NW Mediterranean)	18 °C		2	Coma et al. 1995
Clava multicornis (Forsskål, 1775)	Helgoland (North Sea)	12 °C (32‰ S)	Artemia larvae	8	Kinne and Paffenhöfer 1965
		17 °C (32‰ S)	Artemia larvae	6	
		22 °C (32‰ S)	Artemia larvae	4	
Garveia franciscana (Torrey, 1902)	Russia	23–26 °C		3–4	Simkina 1980
Eudendrium racemosum (Cavolini, 1785)	Medes Islands (NW Mediterranean)	18 °C		5	Barangé and Gili 1988

benthic prey. Miglietta et al. (2000) distinguish active filter feeders that produce microcurrents that draw food particles toward the mouth (e.g., *Aglaophenia*) and passive filter feeders that extend their tentacles and wait for prey (e.g., *Tubularia*). The subantarctic hydroid *Silicularia rosea* Meyen, 1834, from the intertidal communities of King George Island ingests above all benthic diatoms resuspended by tidal current. The hydroid rhythmically expands and contracts its tentacles in order to increase the flow of particles toward the mouth (Gili et al. 1996). Some species with small hydranths such as *Lytocarpia myriophyllum* and *Aglaophenia cupressina* produce conspicuous amount of mucus probably acting as a trap of organic matter (Puce et al. 2002).

Hydroids hosting zooxanthellae (i.e., *Myrionema* spp., *Eudendrium molouyensis*, *Millepora* spp., *Aglaophenia cupressina*) probably adopt a mixotrophic strategy and exploit products of the photosynthesis in oligotrophic waters.

Trophic strategies are finalized to optimize the hydroid reproductive effort: since the reproductive period overlaps, at least partially, with the higher food intake and the maximal colony size, it is hypothesizable that hydroids store the energy necessary to produce gametes or medusae (Rossi et al. 2012 and references therein). Thanks to their plasticity, hydroids can adapt the shape of their colonies to increase the feeding surface and to give rise to an efficient three-dimensional predation system (Gili and Hughes 1995; Rossi et al. 2012).

The reproductive patterns do have a major role in the persistence of perennial hydroid forests. Large polyp colonies with fixed gonophores such as the *Eudendrium* studied by Wasserthal and Wasserthal (1973) produce planulae that settle directly in the vicinity of the mother colony, so contributing to the persistence of the forest. Hughes (1977) observed similar patterns for *Nemertesia*. Furthermore, these large colonies do spend the adverse season as resting hydrorhizae and continue to occupy the substrate. Boero et al. (1986) showed that the forest-forming *Eudendrium glomeratum* has a mixed strategy, with new colonies deriving from planulae and old colonies that regenerate from the resting stolons. The life histories of most species, however, are unstudied, and further research is needed to substantiate these patterns. The presence of medusae, due to the high vagility of this life form, should have more opportunistic polyps, even though the medusa stage is present in most of the very specialized forms that live in strict symbiosis with other animals (Puce et al. 2008), whereas those associated with plants do not follow this rule.

6 Emerging Threats for Hydroid Forests

As other "animal forests," hydroid assemblages represent fragile and diverse systems that could suffer severe threats from direct and indirect impacts and for the lack of a clear responsibility for some human activities in coastal and offshore benthic systems (Rossi 2013).

As shown in Fig. 1, researches on hydroids and environmental/anthropogenic stresses have been increasing. These papers highlight that the three-dimensional habitats formed by hydroids could be threatened from direct (bottom trawling, pollution, urban expansion, tourism, harvesting of precious corals, aquaculture, mining, introduction of alien species) and indirect (ocean acidification and global warming) anthropic impacts (Rossi 2013).

Bottom trawling, among fishing activities, is the most devastating practice for animal forests (Rossi 2013), due to the destruction of the fragile species and the sediment compactness, leading to the simplification of the benthic ecosystems (Althaus et al. 2009; Clark et al. 2010; Rossi 2013). Hydroids living on dredgeable soft substrates, such as *Lytocarpia myriophyllum* and *Nemertesia* spp., are vulnerable to the effects of mechanical disturbances. Up to now, the role of soft-bottom habitat formers received little attention despite they create secondary hard substrata

(Hughes 1975, 1977, 1978; Ammons and Daly 2008; Cerrano et al. 2015; Di Camillo et al. 2013).

Global warming is leading to changing in the benthic domain (Boero and Bonsdorff 2007; Lejeusne et al. 2010) favoring the establishment of tropical non-indigenous species (Coll et al. 2010; Lejeusne et al. 2010) and leading to the regression or disappearance of autochthonous, cold-affinity species (Boero et al. 2008; Rivetti et al. 2014; McCauley et al. 2015). Analysis of records over time can provide "early warning signals of species" that may encounter higher probabilities of local extinction involving several mechanisms at different spatial and temporal scales (Gravili et al. 2013, 2015). According to Puce et al. (2009) and Gravili and Boero (2014), in the Mediterranean Sea, larger *Halecium* species (e.g., *Halecium beanii*, *H. halecinum*, *H. labrosum*) are regressing compared to smaller ones (e.g., *Halecium petrosum*, *H. pusillum*, and *H. tenellum*). Large-size *Halecium* species, in fact, can be considered as habitat modifiers that create wide marine forests maintaining and modifying habitats (Fraschetti et al. 2008; Piraino and Fanelli 1999; Piraino et al. 2002). Ocean acidification could affect hydroid producing calcified skeletons, such as stylasterids and milleporids, or the partly calcified such as the Alaskan hydractiniid *Schuchertinia antonii* (Miglietta 2006).

Moreover, intensive aquaculture is responsible for composition changes of the animal forest by water eutrophication, pollution, introduction of invasive species with evident changes in the trophic chain, simplification of the ecosystems, and accumulation of sediments (Borja et al. 2009; Rossi 2013).

Some hydroid species are harvested for ornamental purposes, such as *Sertularia argentea* and *Hydrallmania* (Hancock et al. 1956); *S. cupressina* Linnaeus, 1758 (Wagler et al. 2009); or stylasterids (Cairns 2011), with presumably negative consequences on their conservation status. Moreover, this state is worsened by the deficiency of clear legal rules in the management of marine communities (Rossi 2013).

Other hydroids take advantage from anthropic impacts, such as those able to proliferate on artificial or modified substrates (e.g., among the genera *Clytia*, *Obelia*, *Ectopleura*, and *Pennaria*) (Morri and Boero 1986).

Deciduous and enduring hydroid forests probably respond in different ways to the effects of the abovementioned threats. Seasonal hydroids, due to their fast growth, plasticity, and above all their ability to enter dormancy, could overcome temporal unfavorable environmental conditions (Di Camillo and Cerrano 2015). Enduring forests formed by large, slow-growing hydroids could be more vulnerable to environmental changes (Di Camillo et al. 2013), especially considering species producing calcified or strongly polysiphonic skeletons or those associated with zooxanthellae (Banaszak 2003).

7 Conclusions

The scientific literature on hydroids here reported clearly highlights a gap in supplying quantitative data, limiting the possibility to compare information on hydroids with those available for other suspension feeders, to evaluate the impact of hydroids on seston, to calculate energy budgets, and therefore to define their actual role in benthic-pelagic coupling.

Moreover, most of studies focused above all on species easy to rear (i.e., *Hydra* spp.) or on shallow-water hydroids easy to study in situ. Since several species live in environments difficult and/or expensive to be explored, there are very few data available on cryptic, tropical, polar, and deep hydroids, suggesting that we have only a partial knowledge on hydroid ecology.

Data on enduring species – forming the largest hydroid forests – are still insufficient to understand their function in benthic communities and to assess their vulnerability to climate changes.

Knowledge on ephemeral hydroids allows using them as indicators of several environmental conditions (Mergner 1987). Long-term studies on hydroid diversity and life histories may allow to detect early signs of the effects of water warming and other environmental stresses or to pinpoint nonindigenous species, identifying variations in composition, abundance, and reproductive periods (Puce et al. 2009; Gravili 2016).

The importance given to algal canopies in the description of habitats and in the determination of conservation policies must be extended also to animals that, in the past, where named “zoophytes,” since they have a similar structural role to that of algae as habitat formers, extending also at depths where algal growth is not optimal. Hydroids do have a higher trophic level than algae and represent an important link between the benthic and the planktonic realms, due to the production of medusae and to predation on both benthic and planktonic organisms.

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Evolution of the Marine Animal Forest: EvoDevo of Corals, Sea Anemones, and Jellyfishes

15

Emma Rangel-Huerta, Griselda Avila-Soria, and Ernesto Maldonado

Abstract

Cnidarians are the sister group of Bilaterians, so they are in a unique position to provide essential clues about the evolution of developmental pathways in animals. It is surprising that with only 10,000 described species, they come in so many different forms, shapes, sizes, and colors. Reef corals, that certainly look as a rich marine forest, are the clearest example of this phenotypic plasticity. Cnidarians are an ancient phylum that together with Porifera, Placozoa, and Ctenophora stand at the base of the animal kingdom tree. Cnidarians share with Bilaterians the main molecular *toolkit* genes used for patterning cells and tissues and build the basic animal body plan. Plasticity in the *Wnt*, *Fgf*, *Bmp*, and *Hox* molecular pathways is a key factor to understand such morphological evolution, as these are the main players in the patterning of the anteroposterior and the dorsoventral axes and therefore fundamental to ultimately shape the reef *seascape*. We intend to provide a link between the diversification of the *toolkit* versatile genetic pathways to the myriad of shapes of corals, sea anemones, and jellyfishes. The objective is the understanding of how all that morphological richness is produced transforming the molecular repertory. Coral reef species variability makes you appreciate the diversity of forms of marine organisms and makes you understand why conservation efforts must be a priority if we want to preserve this special case of biodiversity.

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Contents

1 Introduction

Many of the diverse colors and shapes forming the seascape in marine reefs belong to corals, sea anemones, and jellyfishes. These animals are so unique and beautiful that very often are seen in illustrated books or websites, as drawings or watercolors, usually made by naturalists themselves. For example, the artist and naturalist Ernest Haeckel (unfortunately remembered for its tendentious animal embryos drawings) (Hopwood 2015) makes stunning artwork of several marine invertebrates during his trips to the *Canary Islands* off the southern coast of Morocco or to *Ischia* and *Capri islands* at the Gulf of Naples, continuing this work in the Sicilian city of *Messina* in *Italy*. He also traveled to the Red Sea in order to draw and study marine organisms like coral reefs. A selection of his drawings was printed in 1899–1904 *Kunstformen der Natur* (Artforms in nature) (Haeckel 1998) and became part of 100 lithography's and halftone prints in this zoological treaty. This book includes many Cnidarians, like the campanularian hydroids (*class Hydrozoa*, *order Leptomedusae*), tubularian hydroids (*class Hydrozoa*, *order Anthomedusae*), stalked medusa (*class Staurozoa*), disk jellies (*class Scyphozoa*), sea wasps or box jellyfishes (*class Cubozoa*), and some Hexacorallians (*class Anthozoa*) as well. A recurrent theme in Haeckel's sketches and drawings, from these marine organisms, is symmetry, polarity, and organization. In fact, Haeckel believed that organisms' geometry may well be a discipline by itself and even proposed a name for it "promorphology" (Haeckel 1866).

Cnidarians are the main inhabitants and builders of coral reefs, including stony corals, soft corals, sea pens, sea fans (gorgonians), sea anemones, tube-dwelling anemones, jellyfishes, stalked jellyfishes, and box jellyfishes, among others. They could be as small as 2 mm (e.g., myxozoan parasitic *Buddenbrockia plumatellae*) or as large as the *Nomura's jellyfish* (*Nemopilema nomurai*) that have a 2 m bell and weighs about 200 kg (McClain et al. 2015). Some *Elkhorn corals* (*Acropora palmata*) form massive branches that may reach 3.5 m in diameter. The more striking thing about the phylum Cnidaria is that with only 10,000 known species, they have a remarkable diversity size, forms, and colors. For comparison, there are 350,000 known species of beetles and 25,000 known species of nematodes. So, the interesting question is: Why Cnidarians are so incredibly phenotypically diverse?

Developmental biology and evolution are both research fields where scientists study the reasons of change in species. Animal form is, in part, governed by two processes: (i) genetically and epigenetically driven cellular divisions, differentiation, communication, and movements, taking place during development, and (ii) evolutionary change that produces organism phenotypes as adaptations to specific circumstances. The field that studies such phenomena is known as EvoDevo (Moczek 2012). Interestingly, development and evolution are both directly influenced by the environment (Laland et al. 2008). Therefore, some researchers in the field are focusing in EcoEvoDevo (Gilbert et al. 2015). In the present chapter, we want to synthesize the updates on the high diversity of forms in Cnidarians, describing some clues of what is known about the molecular basis of how Cnidarians develop. Symmetry and polarity are recurrent themes along this text, because one elemental approach is to understand how corporal patterns are made during early stages of development, and compare these between ancient and modern animals.

2 An Ancient Origin for the Basic Body Plan of Cnidarians

Cnidarians have a simple body with basic shapes, like polyps of cylindrical form with a mouth surrounded by tentacles and stinging nematocysts like sea anemones. Some Cnidarians also have a free-floating stage called medusa (as in jellyfish). Most corals are colonial polyps joined one another, by a calcareous skeleton. The basic body plan in most animals is the result of symmetry forming and breaking events occurring during development and growth (Manuel 2009) (see as an example the development of the *Acropora palmata* coral in Fig. 1). Such sequence of events happens as a succession of highly regulated and invariant cell divisions, which, in combination with cell polarizing movements, produce the major body axis. Cnidarians have a radial symmetry; therefore, they were called “Radiata” by Georges Cuvier (Cuvier 1817). These animals possess one primary axis (*oral-aboral*) that is crossed by multiple planes. Bilaterians, in contrast, were defined as animals with a twofold symmetry, in which one primary axis (*anteroposterior*) is crossed by a secondary axis (*dorsoventral*) (Hollo 2015). Based on body symmetry, Radiata and Bilateria were considered different groups of animals (Hatschek 1888). Classifying animals, however, by its radial or bilateral symmetry is an oversimplification: Metazoans could have up to five different forms of symmetry (asymmetry, spherical symmetry, cylindrical symmetry, radial symmetry, and bilateral symmetry) and even sometimes could have different symmetries in different developmental or life stages. As an example, some Echinoderms (as starfishes) have bilateral symmetry as larvae and radial symmetry as adults (Manuel 2009).

As mentioned before, Radiata is a very small group of organisms, when compared with Bilaterians. Radiata only has three phyla, Ctenophora (comb jellies), Cnidaria, and Trilobozoa (extinct), that have between 15,000 to 10,000 species that are

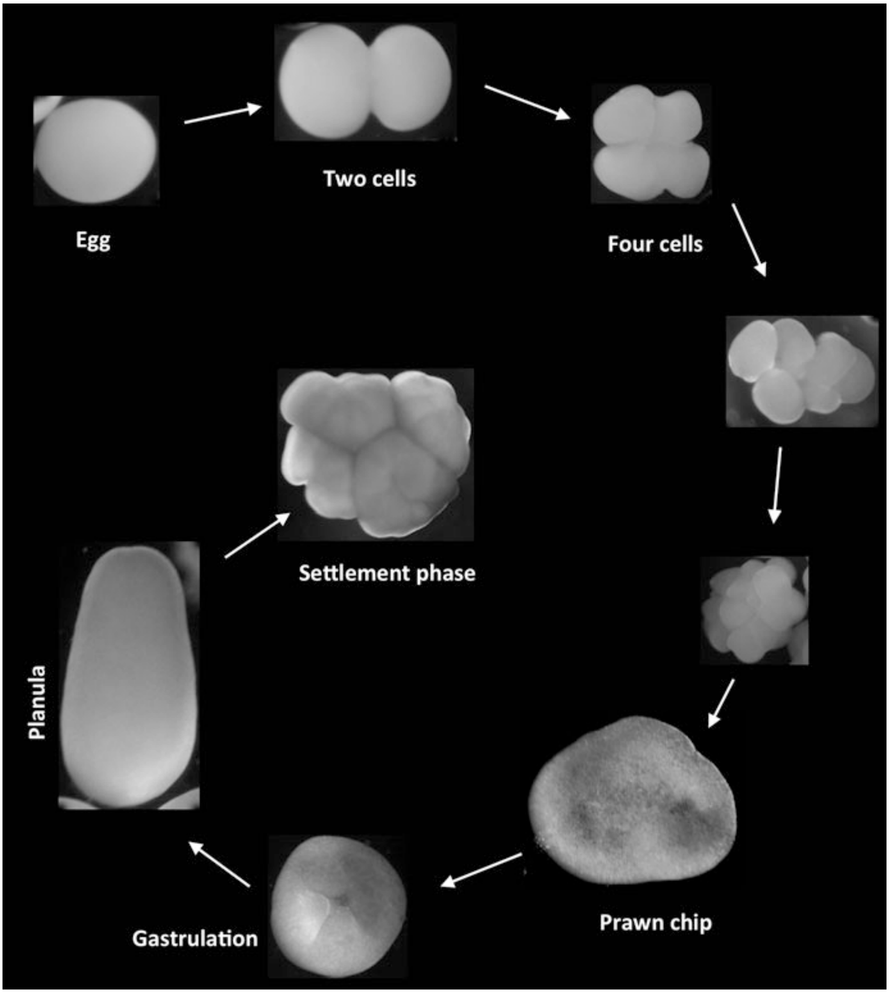

Fig. 1 Development of the elkhorn reef coral *Acropora palmata*. After several rounds of cell divisions and about 10 h postfertilization, the embryo takes a flattened shape called a "prawn chip." Later on, about 24 h, postfertilization gastrulation begins. Cnidarians are diploblastic and only ectoderm and endoderm are formed. The embryo then changes to one elongated form and is called a "planula," which swims actively and finally gets settled on the substrate, and only then, the formation of the polyp initiates

gathered under this taxonomic umbrella. In contrast, there are at least 36 phyla in the Bilaterian group, with one phylum (Arthropoda) containing more than 1,170,000 described species. Therefore, the significant differences in body plan between Radiata and Bilaterians may be in part explained since Radiata is an early divergent group in the metazoan taxa. Cnidarians along with phyla Placozoa, Porifera, and Ctenophora had an ancient origin within metazoa that precedes the Bilaterians. The phylogenetic origin for most non-Bilaterians taxa is not completely understood, and there is a plethora of conflicting phylogenetic hypothesis. Although it seems clear that organisms with radial symmetry are in basal positions with respect to animals with bilateral symmetry, it remains unknown what is the precise phylogenetic position of the Ctenophora, Porifera, and Placozoa groups (Collins et al. 2005; Dunn et al. 2008; Nosenko et al. 2013; Pick et al. 2010).

Recently, with the advent of next-generation DNA sequencing, a massive amount of genomic sequencing data became available and made feasible to build phylogenomic trees, which may be important to solve the phylogenetic relationships between these groups. For example, selecting genes that evolve slowly across all metazoan lineages, the authors decreased systematic errors and improved the recovery of phylogenetic signals, which, they claim, is the first step toward understanding why, in basal groups, different genes tell different phylogenetic stories (Nosenko et al. 2013). At the moment, we are certain of two things: Metazoans are most likely derived from Choanoflagellata (free-living unicellular colonial flagellate eukaryotes) and early animal diversification occurred 700–550 million years ago, by ancient rapid radiations or close diversification events (Nosenko et al. 2013).

3 Genetic Pathways in the Cnidarian *Toolkit*

There is a general consensus that during animal evolution body symmetry evolved from asymmetrical to radial and then to bilateral symmetry. At the center of this idea is a climb in a ladder of complexity where bilateral symmetry is the final innovation that allowed sessile or slow-moving animals to become active burrowers and swimmers (Finnerty 2003; Jenner 2000). This concept is now disputed for several reasons. The first one is that bilateral symmetry seems equally complex than radial symmetry. By sequencing several genomes from basal organisms like the Demosponge *Amphimedon queenslandica* (Srivastava et al. 2010), the Placozoan *Trichoplax adhaerens* (Srivastava et al. 2008), the sea anemone *Nematostella vectensis* (Putnam et al. 2007), and the Ctenophore *Pleurobrachia bachei* (Moroz et al. 2014), the researchers realized that many genes required, for the development of complex traits in higher animals, were already present in basal metazoans (Ball et al. 2004; DuBuc et al. 2012; Kusserow et al. 2005). Therefore, evolution to complex traits, we currently see in Bilaterians, was not constrained by a lack of molecular diversity. In other words, emergent properties of bilateral symmetry not necessarily involved genetic innovations, as these could be directed by physical constraints (Newman et al. 2006) and by natural selection (Lanna 2015; Manuel 2009).

When molecular biologist became immersed in the field of developmental biology, they showed a surprising and unexpected finding. Different types of animals, as different as a jellyfish, a butterfly, a gorilla, and a squid, are basically built using the same set of genes. This concept motivated the extensive work of many researchers that yield the conclusion that all animals share a common *toolkit* of master genes that drive the patterning of the body development (Carroll 2008; Shubin et al. 2009). The

Table 1 Comparison of "Toolbox genes" function between Bilaterians and Cnidarians

Name	Functions in Bilaterians	Conserved homologs in basal metazoans	Functions in Cnidarians
Wnt[a]	Gastrulation, AP[b] and DV[c] patterning	Po[d], Pl[e],Ct[f], and Cn[g]	Gastrulation, OA[h] patterning
Bmp[i]	Gastrulation, DV patterning, neural, heart, blood vessels, and skeleton development	Po, Pl, and Cn	Gastrulation, DA[j] patterning, mesenteries development, and regulate staggered Hox[k] expression
Shh[l]	AP patterning, neural, somites, tooth, and limb development	Po (Shh like) and Cn	Planar and transepithelial signaling in gut and germline development
Fgf[m]	Gastrulation, AP patterning, mesoderm induction, neural and limb development	Po and Cn	Gastrulation and neural cells development
Notch	Embryo polarity, somitogenesis, angiogenesis, neural, gut, and heart development	Po, Pl, Ct, and Cn	Head regeneration and tentacle patterning in *Hydra*. Nematocytes differentiation
Pax[n]	Neural tissue and eye development	Po, Pl, and Cn	Neuroectoderm development. Eye development in Cubozoans
Hox	Body plan and give identity to segments. Forming antennae or wings in some Arthropoda or ribs and vertebrae in vertebrates	Cn (Ghost Hox cluster in Pl)	These genes are expressed in a staggered-like fashion along the OA axis and neural, pharynx, and tentacles development
Para-Hox	Brain, mouth, gut, and posterior structures of the body	Pl and Cn (Ghost Para-Hox cluster in Po and Pl)	Neurogenic functions. Proliferation of apical neuronal progenitors and nematoblast in *Hydra*

[a] Wingless
[b] Anteroposterior
[c] Dorsoventral
[d] Porifera
[e] Placozoa
[f] Ctenophora
[g] Cnidaria
[h] Oral-aboral
[i] Bone morphogenetic protein
[j] Directive axis
[k] Homeotic box genes
[l] Sonic hedgehog
[m] Fibroblast growth factor
[n] Paired box

main toolkit genes that are essential for animal development are *Wnt*, *Shh*, *Bmp*, *Fgf*, *Notch*, *Pax*, *Ho*x, and *Para-Hox* (Table 1, each of the used acronyms is explained).

Each of these *toolkit* genes is part of signaling cascades that are essential during development, by inducing cellular identity, by regulating cell division rates, by establishing new intercellular communication, or by guiding cellular migrations.

These genetic pathways have been mainly studied in Bilaterians model organisms (like *Drosophila melanogaster*, *Caenorhabditis elegans*, *zebrafish*, or *mouse*), where it was found how these pathways are involved in establishing the body axes or the formation of different tissues or organs during development; for example, the *Wnt*, *Shh*, and *Fgf* take part in anteroposterior (AP) specification, while *Bmp's* genes participate mainly in dorsoventral (DV) patterning. *Fgf* was also found to be involved in mesoderm induction and limb development; however, the hedgehog (*Shh*) signaling pathway also has a role in limb formation. Both *Shh* and *Notch* genes modulate somitogenesis, while *Bmp* and *Notch* pathways regulate heart development and blood vessel formation. In the differentiation of the neural system, *Shh*, *Fgf*, *Notch*, *Pax*, and the *Hox* genes have also an essential role. Furthermore, *Pax* genes are also required for eye development, while the *Hox* and *Para-hox* set of genes control the basic body plan and segmentation along the AP axis.

In the basal branches of the animal evolutionary tree, sponges possess *Wnt*, *Bmp*, *Fgf*, *Pax*, and *Notch* genes, while *Hox* and *Para-hox* genes are absent (Table 1) (Srivastava et al. 2010). Using analyses of gene neighborhoods and genomic synteny (*comparative analysis*, *among different organisms*, *of gene location in conserved loci*), a *Hox* "ghost" locus was found in the genome of the sponge *Amphimedon queenslandica*; in other words, the loci are conserved, but the *Hox* gene is absent. This suggests Hox genes were lost in Porifera (Mendivil Ramos et al. 2012). Placozoa (*Trichoplax adhaerens*) have *Wnt*, *Bmp*, *Notch*, and *Para-hox* signaling genes but lack components from the *Hox*, *Shh*, and *Fgf* signaling pathways (Srivastava et al. 2008). Ctenophora do not have *Bmp*, *Shh*, *Fgf*, *Hox*, and *Para-hox* pathway genes but have *Wnt* and *Notch* genes (Moroz et al. 2014; Ryan et al. 2013). Cnidarians, which are the focus of this review, possess all of the genetic *toolkit* genes: *Wnt*, *Bmp*, *Shh*, *Fgf*, *Notch*, *Pax6*, *Hox*, and *Para-hox*. Similarities in morphological patterns very often are the result of common ancestry. Expression patterns and function of the genes inherited by this ancestor, to modern animals, in combination with analyses of gene family diversification, gene co-option, and gene loss, provide essential clues about the evolutionary process in Cnidarians and Bilaterians.

4 Cnidarian Gastrulation and the Organizer

During early developmental stages, most animals carry out a series of morphogenetic movements known as "gastrulation," where cells in the marginal zone involute through a blastopore resulting in formation of meso-endoderm and ectoderm germinal layers, which marks the initiation of the AP and DV regionalization (Kaneda and Motoki 2012). Gastrulation is mediated by at least three of the *toolkit* signaling pathways *Wnt*, *Bmp*, and *Fgf*. It is remarkable that just a few cells located in the dorsal margin, known as *the organizer*, induce and control the gastrulation. The inductive capacity of the organizer was studied first in Bilaterians during 1924, at the Freiburg University in Germany, where *Hilde Mangold* and *Hans* Spemann transplanted the dorsal blastopore lip from a salamander embryo to a host salamander embryo's ventral side, inducing the formation of a secondary axis. They noticed that most of the new secondary axis was formed by the host tissue (Spemann 1924). For this finding, Spemann was awarded the 1935 Nobel Prize in physiology or medicine. The genes in play at the organizer function were later identified by *Richard M. Harland*, *Edward De Robertis*, and many others (De Robertis 2006; Smith and Harland 1992).

Emulating the *Mangold/Speeman* experiment, *Ulrich Technau* research group at the *University of Vienna* found that by transplanting the ectodermal part of the *Nematostella* blastopore lip, they could induce as well an ectopic secondary axis in the host (Kraus et al. 2007), confirming the existence of an organizer in Cnidarians. This suggests a pre-Bilaterian origin of the organizer and the molecules that take part on it, predating the 500 Ma divergence of Cnidaria and Bilateria. The genes that take part in the organizer function have been detected around the blastopore lip from *Nematostella vectensis*, the region with organizer activity during gastrulation. These genes are *Bra* (*brachyury/T-Box*) (Scholz and Technau 2003), *FoxA* (*forkhead*) (Martindale et al. 2004), *Gsc* (*goosecoid*) (Matus et al. 2006) *Bmp2/4*, and *Chd* (*chordin*) (Saina et al. 2009). Equivalent expression patterns for the same set of genes were observed in embryos from the coral *Acropora millepora* (Hayward et al. 2015); however, while *forkhead* demarcate the ectoderm/endoderm boundary in *Nematostella*, it is the gen *brachyury* that define the ectoderm/endoderm borders in *Acropora*. As in Bilaterians, these proteins cross talk with the *Wnt*, *Bmp*, and *Fgf* genetic pathways in Cnidarians, which are highly conserved, being essential for the body axis patterning.

5 Cnidarians Axis Patterning

In basal metazoans, including Cnidarians, it has been a challenge to compare the body axes with those of Bilaterians (Hayward et al. 2015; Matus et al. 2006). The equivalent axis of the Bilaterian anteroposterior (AP) axis is known as the oral-aboral (OA) axis in Cnidarians and basal animals. The AP axis in Bilaterians is known to be regulated by the *Wnt* signaling pathway that controls the expression of *Hox* genes. In two sponges from the phylum Parazoa (*Sycon ciliatum* and *Amphimedon queenslandica*), with a clear radial symmetry at the larval stage, the expression of *Wnt* genes was found to be involved in OA specification (Adamska et al. 2007; Leininger et al. 2014). In Cnidarians and Bilaterians, the *Wnt* gene family is equally complex. For example, *Nematostella* possess 11 out of the 12 known *Wnt* Bilaterian genes. In sea anemones *Wnt* genes are expressed during development, in segmented stripes along the OA axis; interestingly this is similar to the AP staggered expression of *Hox* genes in Bilaterians (Kusserow et al. 2005). *Hydra vulgaris*, *Nematostella vectensis*, and other Cnidarians possess the *Gsk3*, disheveled, *β-catenin*, and *Tcf/Lefty* genes that are the downstream components of the *Wnt* pathway (Hobmayer et al. 2000; Kusserow et al. 2005; Wikramanayake et al. 2003). These observations suggest that AP or OA patterning is a widely shared characteristic of animal design that is not restricted to Bilaterian symmetry.

There is growing evidence that Cnidarians have a secondary body axis, known as the "directive axis" that could possibly be related to the DV axis from Bilaterians (Ball et al. 2004; Finnerty et al. 2004; Genikhovich et al. 2015; Kusserow et al. 2005; Saina et al. 2009). The expression patterns in *Acropora* and *Nematostella* of *Bmp* genes, and their antagonists, provide one of the most convincing lines of evidence that Cnidarians (Anthozoans in particular) do have a secondary axis that crosses the AP axis. As mentioned before (Table 1), *Bmp* genes are essential for the formation of the DV axis in Bilaterians. *Bmp* signaling is regulated by extracellular antagonists, like the secreted proteins Chordin and Gremlin, that block the interaction of Bmp and the Bmp-receptor. This diffusible system of extracellular Bmp and Chordin proteins promotes signaling in a gradient, since its strength depends on how far the signal diffuse. Bmp's belong to the TGF-β family of proteins; the binding of Bmp and the Bmp receptor leads to the phosphorylation of Smad proteins that form heterodimers entering the nucleus and transcriptionally activating several target genes. For a detailed review about the *Bmp* genetic pathway, see Bier and De Robertis (2015).

In Bilaterians, *Bmp* and *Chordin* homologs are expressed at opposite sides of the DV axis in the developing embryo. In contrast *Nematostella Bmp* and *Chordin* are co-expressed in the same side of the embryo (Genikhovich et al. 2015; Saina et al. 2009). This same pattern has been observed in sea urchins (Lapraz et al. 2009). It was proposed that while *Bmp* expression domain must vary, it is *Chordin* expression that must remain constant (Genikhovich et al. 2015). Several studies have shown shared functions in genes from the *Bmp* genetic pathway among Bilaterians and Cnidarians (Finnerty et al. 2004). For example, *Bmp2/4* from the coral *Acropora millepora*, when expressed in *Drosophila*, showed dorsalizing properties (Finnerty et al. 2004; Hayward et al. 2002). The DV patterning properties of *Bmp* pathway were also recently compared between the sea anemone *Nematostella* and the amphibian *Xenopus laevis*. While some expected similarities were detected, some differences were also found: The *Bmp* agonist *Gdf5* and *Bmp* antagonist *Gremlin* both have a role in the initial *directive axis* specification in *Nematostella* but not in *Xenopus*. Additionally, instead of specifying the central nervous system, as in *Xenopus*, *Nematostella Bmp* signaling is used to pattern the mesenteries and regulate expression of *Hox* and *Gbx* genes in the endoderm (Genikhovich et al. 2015). It is puzzling that in Cnidarians *Hox* genes are regulated by *Bmp* signals since, in Bilaterians, these are regulated by the *Wnt* pathway. For some authors this suggests that *Wnt* genes may have an ancient function in gastrulation and axial differentiation (Kusserow et al. 2005), and at some point along the road of animal evolution, these functions were relayed to the *Bmp* and *Hox* genetic pathways.

6 Cnidarian *Hox* Genes

Hox genes coordinate the development of body structures along the AP axis, so there are considered major regulators in organizing the basic body plan in metazoans. These transcription factors determine segment identity, but do not form the segments themselves. *Hox* genes special features for animal development were discovered by *Christiane Nüsslein-Volhard*, *Edward Lewis*, and *Eric F. Wieschaus*, through the analysis of mutations modifying the identity of different body segments in the fruit fly *Drosophila*. For this work, these scientists received the 1995 Nobel Prize in physiology and medicine. The *Hox* genes are also known as *homeotic genes*, a name based on the term *homeosis* coined by *William Bateson* in 1894, and given to a class of biological variations in which *one element of a segmentally repeated array of organismal structures is transformed toward the identity of another* (Bateson 1894). For example, the *Bithorax* mutation in *Drosophila* produces flies with four wings, instead of the normal number, which is two, and this happens because the third thoracic segment is transformed toward the second one. In *Drosophila Hox* genes are arranged in tandem and these clustering constraint embryonic expressions in a specific order (colinearity) along the AP body axis (Carroll et al. 2005). Cnidarian *Hox* genes have been described for Hydrozoans like *Hydractinia symbiolongicarpus* and *Hydra viridissima* (Murtha et al. 1991; Schummer et al. 1992), sea anemones like *Nematostella* and *Metridium senile* (Finnerty and Martindale 1997), or the jellyfish *Cassiopea xamachana* (Kuhn et al. 1999) and corals *Acropora digitifera* (DuBuc et al. 2012). The staggered expression of *Hox* genes in *Drosophila* or vertebrate embryos has a clear and direct consequence: the segmented bodies of adult fruit flies (body segments with antennae, legs, or wings) or vertebrates (vertebrae with or without ribs). *Nematostella* sea anemone, however, do not have segmented bodies as adults, and their embryos have a semi-staggered expression of *Hox* genes along the OA axis (Fig. 2) (Finnerty et al. 2004; Matus et al. 2006).

There is a clear picture for the expression of *Hox* genes in *Nematostella* along the OA axis during development. In Anthozoans, *Hox* genes are known as "*Anthox*" genes. The genes *Anthox6*, *Anthox8*b, *Anthox8*a, and *Anthox7* are expressed at the oral and central (anterior/central) regions along the OA axis, while *Anthox1* and *Anthox1a* are preferentially expressed in aboral (posterior) zones. Specifically, the *Anthox7* and *Anthox8* mRNAs are first expressed at the endoderm, close to the blastopore, but later its expression becomes extended along the outer endoderm wall. Eventually, they join the pharynx at the oral (anterior) regions; *Anthox6* is expressed in the pharynx endoderm. At the opposite side, Anthox*1* is expressed early in a broader area of the aboral blastoderm, and after gastrulation its expression becomes restricted to a round patch of ectoderm at the aboral pole (Fig. 2) (Finnerty et al. 2004).

It is worth to mention a set of genes that represent the evolutionary paralog group to the *Hox* genes known as the *Parahox* family; these genes are also involved in developmental morphogenesis. In the phylum Placozoa (*Trichoplax adhaerens*), no *Hox* genes have been detected; however, a *Parahox* gene, with the name *Trox2*, was found. In sponges (phylum Porifera), despite many efforts to find them, no *Hox* or *Parahox* genes have been found (Table 1), being a matter of debate if this represents a secondary loss (Manuel 2009; Mendivil Ramos et al. 2012). The three basic *Parahox* genes *Gsx*, *Pdx*, and *Cdx* have been cloned and studied in Cnidarians

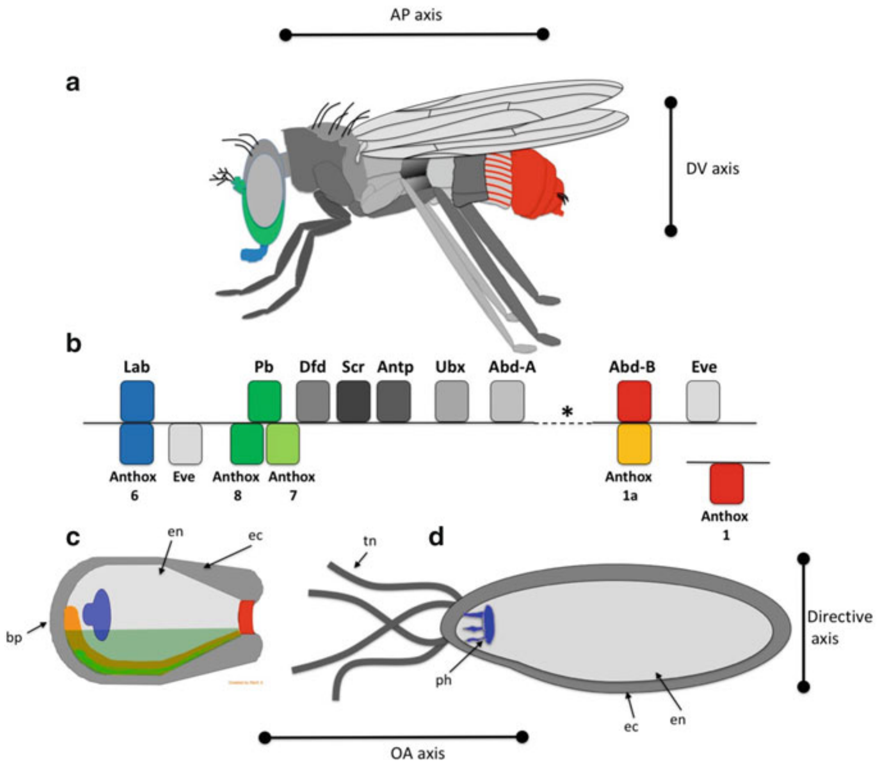

Fig. 2 Conserved *Hox* gene expression between Bilaterians and Cnidarians. (**a**) Drawing of an adult fruit fly (*Drosophila melanogaster*). Only the segments, specified by Hox genes present in Cnidarian genomes, are shown in different colors. While the genes *Lab* (*labial*) (*blue*) and *Pb* (*proboscipedia*) (*green*) regulate the formation of structures in anterior regions, the genes *Abd-B* (abdominal B) (*red*) specify posterior zones. (**b**) The *Lab* gene is homolog to the *Anthox 6* gene (both in *blue*) in *Nematostella* and other Cnidarians, while the gen *Pb* has two homologs, *Anthox 8* and *Anthox 7* (in different tones of *green*) in Cnidarians. The *Abd-B* gene is homolog to the *Anthox 1a* and *Anthox1* gene (in *orange* and *red*, respectively). The asterisk is to show that while the gene *Anthox 1a* is not contiguous to other *Anthox* genes in *Nematostella*, the same gene from *Acropora digitifera*, is located next to the other *Anthox* genes. *Anthox 1* is in a different location. There are not homologs in Cnidarians for the *Drosophila* genes *Dfd* (*deformed*), *Scr* (*sex combs reduced*), *Antp* (*antennapedia*), *Ubx* (*ultrabithorax*), and *Abd-A* (*abdominal-A*). All the *Drosophila* Hox genes are aligned in the same cluster. The *Eve* gene (*even-skipped*) is not a *Hox* gene, but is required for proper segmentation in *Drosophila* and is at the *Hox* cluster in both Cnidarians and Bilaterians. (**c**) Planula larvae stage of *Nematostella*, *Anthox 6* is expressed at the endoderm near the blastoporal pore; *Anthox 1a* is also located at the endoderm close to the blastopore and in a thin strip along the body wall. *Anthox 1a*, *Anthox 8*, and *Anthox 7* overlap its expression at the endoderm, along the OA axis. *Anthox 1* expression is restricted to a small round patch at the ectoderm in the aboral pole. (**d**) In the young polyp, *Anthox 6* is expressed in the outer endodermal layer of the pharynx. The *Drosophila* diagram is based on Maeda and Karch (2006). The expression patterns from *Nematostella* larvae and young polyp are based on experiments by Finnerty (2004). AP anteroposterior, OA oral-aboral, DV dorsoventral, bp blastopore, ec ectoderm, en endoderm, tn tentacles, ph pharynx

(Gauchat et al. 2000; Quiquand et al. 2009). The most conserved sequence in *Hox* genes is named the homeobox, which encodes a 60 residues motif known as the homeodomain. Some other genes with homeobox domains, originally found in *Drosophila*, are *Ems* (*empty-spiracles*) and *Otd* (*orthodenticle*), which have conserved roles in AP patterning along Bilaterians. In *Acropora millepora* coral embryos, the *Ems-Am* gene (as is known in corals) was found expressed in neurons at the oral body region and more broadly throughout the ectoderm that is similar to the known expression pattern of *Ems* in *Drosophila* (de Jong et al. 2006). However, coral *Ems-Am* could not substitute the function of the *Ems Drosophila* gene (Hartmann et al. 2010). The *Acropora* homolog *Otx-Am* is expressed at early developmental stages around the blastopore and later at the base of the ectoderm. *Acropora* also has a second *Otx* gene expressed at the presumptive endoderm during gastrulation and planula developmental stages (de Jong et al. 2006).

Marine animals dominate the marine forest seascape: there are around 195,000 species of marine animals, being the 85.5% of the 228,000 known marine eukaryotes already described (Leray and Knowlton 2016). It is estimated that up to half a million more species of marine animals have yet to be described (Appeltans et al. 2012). As mentioned before, there are about 10,000 Cnidarians species that have been already described, and it is likely that many more will be found in the future. For example, *Plumularia setacea*, one Hydrozoan, was recently found by genetic methods to have – according to the author – "…a multitude of genealogical lineages that deserve species status…" (Schuchert 2014). Like this, in many other Cnidarians, cryptic species have been described and new ones will appear in a near future. We believe that new Cnidarian morphological forms, shapes, and colors may also be found in the future, since this group of animals possesses a great phenotypic plasticity (as individuals and as colonies). As an example, in the evolutionary history of the class Hydrozoa, the medusa stage has been lost around 70 times (Miglietta and Cunningham 2012). Much of the genetic repertoire, responsible for Cnidarian phenotypes, has been described by many research groups that have found that the same set of genes have evolved to produce many different phenotypes in Bilaterians.

7 Future Directions

The future for studying Cnidarian evolution and biodiversity looks more exciting and promising than ever. Classic animal models, as mice, *Drosophila*, and zebrafish, no longer have exclusive rights for mutagenic screenings or genomic and transcriptomic studies. Furthermore, CRISPR/Cas9 genome editing, that is currently the state of the art genetic method to study gene function, has been successfully performed the sea anemone *Nematostella* (Ikmi et al. 2014). These experiments open the door for performing, more precise, lack of function genetic and phenotypic studies in other Cnidarians as corals, Hydrozoans, and jellyfishes. The genomes of the reef coral *Acropora digitifera*, the sea anemone *Nematostella vectensis*, and the hydra called *Hydra magnipapillata* (Chapman et al. 2010; Putnam et al. 2007;

Shinzato et al. 2011) have been completely sequenced (Putnam et al. 2007; Shinzato et al. 2011), among other Cnidarian genomes already deciphered.

Performing transcriptomic studies in Cnidarians could be highly informative. For example, specific genes related to the RNA interference-mediated gene silencing pathways were found to be highly expressed in disease-resistant *Acropora* corals (Libro and Vollmer 2016). Furthermore, reference transcriptomes were recently assembled for three Scleractinian corals *Fungia scutaria*, *Montastraea cavernosa*, *Seriatopora hystrix*, and one clonal sea anemone *Anthopleura elegantissima* (Kitchen et al. 2015). Current advances in microfluidics and RNA-seq libraries construction (Macosko et al. 2015) have open the possibilities to not only carry out transcriptomic projects in whole organisms or tissues but in individual cells as well. It will be interesting to scrutinize deeply the transcriptomic behavior even for different cell types of Cnidarian organisms during development as a way to understand how basal organisms evolved to new shapes and new body designs.

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Metabarcoding Techniques for Assessing Biodiversity of Marine Animal Forests

16

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Abstract

The “marine animal forests” are among the most diverse ecosystems in the Biosphere. However, exhaustive biodiversity assessment of these communities has been so far elusive. The real extent of biodiversity and its temporal and spatial variability patterns remain unknown for most animal forests, mainly due to the inability of traditional taxonomy methods to cope with such degree of diversity and structural complexity.

The development of metabarcoding techniques has revolutionized biomonitoring. Using this approach, thousands of species present in any environmental sample can be detected by high-throughput DNA sequencing and identified using public databases. Though initially limited to homogeneous substrates such as plankton or sediments, the applications of metabarcoding have been recently extended to communities on heterogeneous complex hard bottom substrates.

Here we present novel metabarcoding protocols, based on the use of short fragments of 18S rRNA or cytochrome *c* oxidase I genes as genetic markers. We aim to develop methods for robust, reproducible eukaryotic biodiversity assessment of structurally complex communities such as marine animal forests, allowing characterization of communities living on hard-bottom substrates or other marine benthic ecosystems.

We propose some guidelines focusing on sampling techniques, sample preprocessing, DNA extraction, selection of genetic markers, and bioinformatic

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pipelines, including steps such as sequence filtering (removal of low quality reads), clustering algorithms for delimiting molecular operational taxonomic units, and automated taxonomic assignment using reference databases. We expect these recommendations will help marine ecologists to become familiar with the paradigm shift that metabarcoding represents in the way marine ecosystems will be monitored and managed in the next future.

Keywords

Marine biodiversity assessment • Eukaryotic community assessment • Hard-bottom substrates • Marine benthos • Metabarcoding pipelines

Contents

1 Introduction

Marine benthic communities living in three-dimensional structures built mostly by sessile suspension feeders, the so-called animal forests (Rossi et al. 2012), are among the most diverse ecosystems in the Biosphere, playing a crucial role in providing planetary ecosystem services (Duarte 2000). However, due to a number of factors such as their staggering structural complexity, the massive, colonial or modular morphology of many of their species, and the abundance of small epibionts, these communities have been largely inaccessible to exhaustive qualitative or quantitative biodiversity assessments. Given the unfeasibility of complete enumeration of all the biodiversity present, ecologists have traditionally relied on partial analyses, focused on just a few groups of identifiable macrospecies, to characterize these communities. But the real extent of biodiversity and their temporal and spatial patterns of variability remain unknown in most instances of animal forests.

In the last few years, the development of metabarcoding techniques (Hajibabaei et al. 2011; Taberlet et al. 2012) has revolutionized our concept of biomonitoring. Using a metabarcoding approach, thousands of species present in an environmental sample can be detected by high-throughput DNA sequencing and automatically identified using molecular taxonomy databases. These techniques are sensitive to detect not only DNA from living organisms ("community DNA"), but also an array of different types of "extra-organismal DNA" originated from dead bodies, gut contents, tissue fragments, exudates, reproductive or fecal material, or simply extra-cellular DNA (Barnes and Turner 2016). Together, community DNA and extra-organismal DNA form what is now known as environmental DNA by molecular ecologists (Creer et al. 2016).

The application of this technology to complex, hard bottom eukaryotic communities has been hindered due to several factors, such as the lack of standardized techniques for quantitative sampling, the lack of universal primers capable of amplifying the wide array of taxonomic groups that compose these communities, and the underdevelopment of bioinformatic algorithms capable of coping with the complex datasets generated from these extremely diverse communities.

The time is now ripe for all these past impediments to be overcome. Some recent advances towards complete analysis pipelines are presented here, including repeatable sample treatment and DNA extraction, novel sets of degenerated primers capable of amplifying suitable fragments of highly variable genetic markers such as the mitochondrial cytochrome *c* oxidase I (COI) or the small ribosomal subunit RNA (18S) in most Eukaryotic groups, bioinformatic algorithms for delimitation of the molecular operational taxonomic units (MOTUs), and efficient methods for taxonomic assignment which take advantage of the massive information deposited in public databases. Our proposed pipelines have been successfully used to characterize the eukaryotic diversity present in diverse hard-bottom marine benthic communities (Wangensteen et al. 2015) and could be implemented, with few modifications, as a robust, affordable, and relatively fast technique for biodiversity assessment of a wide array of different marine, freshwater, or even terrestrial eukaryotic communities.

After briefly reviewing the crucial elements which led to the development of metabarcoding procedures and introducing some of the current issues regarding the metabarcoding of eukaryotic community-DNA, we will summarize proposed pipelines for two different molecular markers (18S and COI). Most methods presented here are not exclusive for marine samples and could be applied to other types of communities with little modifications. Sections 3, 4, and 5 focus on the peculiarities of working with marine benthic complex samples, whereas Sects. 6, 7, 8, 9, and 10 are more widely applicable to metabarcoding of eukaryotic samples, not exclusively marine.

Since we do not expect most marine ecology researchers to be familiar with the specific vocabulary related to molecular genomics and metagenomics techniques, we have included a small glossary of some common terms used in the metabarcoding literature, as a reference for the readers (Table 1).

2 DNA-Barcoding and Metabarcoding

The simple idea that just a short fragment of a DNA sequence could suffice for unequivocally identifying an unknown organism and assigning it to a given species is known as DNA-barcoding. This concept, introduced by Hebert et al. (2003), initially faced a number of detractors among both traditional taxonomists and geneticists, but eventually gained adepts among biodiversity researchers, as it proved to be incredibly fruitful for cataloguing and analyzing the vast biodiversity remaining to be discovered in many taxonomical groups and in poorly explored habitats or geographical regions. The success of DNA-barcoding relies on the coexistence of two factors, one natural and other technological: (1) a genetic marker universally present in every species, which could be easily sequenced using standardized protocols. This marker should have enough sequence variability to allow distinction among related species but must be surrounded by regions conserved enough so that universal primers could be designed. And (2) a massive public database containing the known sequences of this marker for the maximum possible number of different species, which must be searchable by automated algorithms, so that unknown sequences could be matched to a known species. The identification by DNA-barcoding is evidently as good and reliable as complete and accurate this reference database is.

With the introduction of high-throughput sequencing technologies over the past 10 years, the sequencing of heterogeneous DNA templates without cloning became possible, and the era of one-sequence-at-a-time was superseded. The simultaneous identification of many specimens by DNA-barcoding opened new avenues for biodiversity research. This intersection between taxonomic identification by means of short DNA sequences and massive simultaneous sequencing of millions of DNA fragments came to be known as metabarcoding (Riaz et al. 2011; Taberlet et al. 2012). This application uses DNA-barcodes not for taxonomically identifying a single sequence from an unknown specimen, but for characterizing the full community of species present in a set of complex environmental samples, by taxonomically identifying the sequences of hundreds of thousands to millions of small DNA fragments amplified from the DNA contained in these samples.

3 Specific Challenges of Marine Hard-Bottom Communities

The metabarcoding technology has now been successfully used for characterizing the microscopic biodiversity present in relatively homogeneous substrates, such as plankton (Pearman and Irigoien 2015; de Vargas et al. 2015), soil (Epp et al. 2012; Schmidt et al. 2013) or marine sediments (Chariton et al. 2010; Fonseca et al. 2014;

Table 1 Glossary of terms for molecular biodiversity assessment

Assignment	The bioinformatic step for adding taxonomic information to the sequences or MOTUs detected in a barcoding or metabarcoding procedure. The reliability and level of detail of the taxonomic assignment will depend on how complete and dense the reference database is
Chimera	A sequencing artifact consisting in a DNA molecule which two or more fragments from two or more different mother sequences, usually originated by incomplete extension of a mother sequence during a polymerase chain reaction cycle, which is continued using another template at random in a following cycle
Clustering	The bioinformatic step for delineating all the MOTUs present in a dataset of raw sequences. Most clustering algorithms are based in a constant arbitrary similarity threshold, though other algorithms (such as Bayesian clustering or step-by-step aggregation methods) result in a set of MOTUs with variable similarity thresholds
Community DNA	The fraction of environmental DNA extracted directly from the living or recently dead organisms (macroscopic or microscopic) isolated from their habitat, which forms the community (or biocoenosis) from which the sample was taken, as opposed to extra-organismal DNA
Demultiplexing	The bioinformatic step for detecting and reading the library-tags and sample-tags from a dataset of many reads obtained from a high-throughput sequencer and assigning each read to the corresponding original sample where it belongs
eDNA	(also envDNA). Environmental DNA includes all the DNA molecules present in an environmental sample, either in the organisms or in their habitat. It may have different original sources (living cells, egestion, excretion, secretion, exfoliation, decomposition, reproductive, trophic, parasitic...) and be in different physical forms (intraorganismal, intramembranous, extramembranous, particulate, adsorbed, free). It can be considered to be composed of two main fractions: community DNA and extra-organismal DNA
Extra-organismal DNA	The environmental DNA which is extracted from the nonliving fraction of the environmental sample. It is physically present in the form of tiny particles, able to be filtered away by washing and sieving
MOTU	Molecular Operational Taxonomic Unit. It is the working proxy for "species" in molecular ecology. Eukaryotic metabarcoding borrowed this term from microbial taxonomy where it is widely used. The different MOTUs are delineated from a set of raw sequences by means of a clustering algorithm. Typically a MOTU is a set of related sequences which present a similarity degree higher than a given arbitrary similarity threshold. However, MOTUs can also be defined by clustering methods which use variable similarity thresholds
Multiplexing	A way to decrease the cost per sample of a high-throughput sequencing run. Multiple samples can be processed together, as long as they are individually tagged using oligo-tags. Multiplexed samples are usually pooled together and processed jointly to build a sequencing library. The more samples in a multiplexed library, the less sequencing depth per sample will be accomplished
Oligo-tag	A short sequence of DNA (usually 4–8 nucleotides) designed for being attached to the DNA molecules of a sample in order to identify this sample,

(*continued*)

Table 1 (continued)

	so that many tagged samples can be sequenced together in a multiplexed high-throughput sequencing run
Paired-end sequencing	A high-throughput sequencing technology which allows the sequencing of both ends of a short DNA fragment, so that longer sequences than in single-end procedures can be obtained. Paired-end sequences are usually aligned during the first steps of the bioinformatic pipeline and the aligned pairs are analyzed as single reads
Pipeline	The sequence of multiple steps of bioinformatic procedures used to analyze the raw data obtained from a high-throughput sequencer is usually called "a pipeline." The term comes from the fact that the output of a process is used as the input for the following one, an operation that in Unix systems is carried out by the pipe operator "|"
Reference database	A database of as many known sequences of the chosen metabarcoding marker as possible, taxonomically identified (preferably at the species level), in order to be used for taxonomic assignment of a metabarcoded sequence dataset
Sequencing depth	The number of total reads per sample. It depends on the sequencing technology, on the number of multiplexed samples which are processed together, and on random variation during the library preparation and sequencing processes
Sequencing library	A DNA sample (or, more usually, a set of multiplexed samples) ready to be processed in a high-throughput sequencing apparatus. The fragments of DNA to be sequenced must be surrounded by a set of adapters attached at one or both ends. These adapters are usually a row of: (1) a sequence for attaching to the sequencer matrix, (2) a specific sequencing primer, (3) a library-tag, and (4) a sample-tag. In paired-end sequencing methods, both ends must have a different set of specific adapters

Guardiola et al. 2015; Lejzerowicz et al. 2015). However, its application for characterizing more heterogeneous substrates such as marine hard-bottom communities and for identifying relatively big colonial or modular organisms such as those present in a typical marine animal forest is still little explored. The work by Leray and Knowlton (2015) on marine communities colonizing artificial substrates in Southeastern USA and the study by Pearman et al. (2016) using the same collectors in the Red Sea are some of the few published works dealing with marine communities of such complexity. However, animal forest ecosystems are even more heterogeneous and of higher structural complexity than the artificial fouling communities studied in those works. No published research work has as yet dealt with natural community-DNA metabarcoding of fully developed marine animal forests.

One crucial problem related with structural complexity is the representativeness of the sampling. How big should a sample be in order to adequately represent the community it belongs to? How many replicates must be sampled in order to get a good characterization of the biodiversity present in the community? The minimum sampling size is related to the destructiveness of the sampling process, which may be a factor to consider in vulnerable marine ecosystems (VMEs), which are in many cases endangered, such as coral reefs. The sampling effort needed for a good characterization of the communities depends on the spatial heterogeneity of the habitat. In the case of extremely complex communities such as marine animal forests, a high number of samples may be necessary to achieve saturation of species richness curves. For example, in the analysis of fouling communities on artificial substrates (Leray and Knowlton 2015), nine replicates per condition were not yet enough for reaching diversity saturation. Thus, an even higher number of replicates would be recommended if an exhaustive characterization of biodiversity is to be carried out. However, a lower number of replicates could still be useful for tracking temporal or spatial changes in communities, for detecting the presence of introduced species or, in the case of deep benthic ecosystems, even a few samples may provide invaluable information. Preliminary studies are always advisable, in order to determine the right sampling effort needed depending on the community type and the question investigated.

Another challenge is the wide range of body sizes of the organisms to analyze. While traditional metabarcoding approaches deal with organisms having roughly similar sizes (e.g., meiofaunal communities, Guardiola et al. 2015; Lallias et al. 2015 or planktonic communities, de Vargas et al. 2015), in a developed animal forest community, the samples will be composed of organisms whose sizes span several orders of magnitude, from protists to macroscopic colonies of stony corals or large sponges. One possible approach is to sort the samples into different size fractions using a nested column of sieves. The smallest fraction is expected to be the most species rich, not only because of the higher diversity expected for small-sized organisms, but also because small portions of DNA-containing tissue from bigger organisms will be filtered through the sieves and detected in the smallest fractions. Thus, the smallest size fractions are expected to qualitatively represent most of the species richness present in the whole sample. However, if the quantitative biomass proportion of each species in the full sample is to be assessed, then the DNA abundances obtained from the biggest fractions will probably better represent the composition of the whole sample.

One last issue is the hardness and composition heterogeneity of both the substrates and the organisms which form the animal forest, which will introduce additional difficulties to sampling and DNA extraction procedures. Before the DNA extraction, a good homogenization step is crucial. This step needs to be done using a powerful blender unit, capable of crunching hard materials. The smaller the size of the fragments in the final homogenate, the better the yield of the DNA extraction procedure. Advanced DNA extraction kits and procedures should be used, formulated for extracting good quality DNA from samples containing high proportions of a variety of potentially interfering, difficult components, such as calcium carbonates, silicates, proteins, algal polysaccharides, or humic acids. Fortunately, a number of kits for DNA extraction from soils are commercially available, which can be used for marine benthic samples, rendering excellent yields (Mahmoudi et al. 2011; Eichmiller et al. 2016).

4 Sampling and Preservation

Samples from shallow complex communities may be easily collected using scuba diving equipment. In these communities, 25-cm quadrats have been successfully used as sampling units (Fig. 1a). Using chisel and hammer, the substrate is thoroughly scraped and all the organisms present inside the quadrat are carefully collected in a polyethylene bag which is sealed underwater. Smaller particles of substrate and sediments may be collected using a scrub brush or a portable underwater suction sampler. For loose substrates such as maërl or dead coral remnants, a cylindrical PVC corer can be used to delimit the sampling unit (Fig. 1b).

We recommend all samples to be stored in ethanol (a good preservative for DNA samples) as soon as possible. The seawater in the sample bags can be eliminated by filtering through a 63-μm sieve and replaced by 95% ethanol. The material retained in the sieve may be recovered using a wash bottle with ethanol. A thorough wash of the filtering sieve is necessary between samples to avoid cross-contamination. The use of diluted bleach and rinsing with distilled water is recommended between uses of the sieves. When the use of ethanol is not an option, a good alternative is using DESS (DMSO-EDTA-Saturated NaCl solution) as a preservative (Dawson et al. 1998). Preservation methods using formaldehyde are known to degrade the DNA and should be always avoided when working with samples aimed at molecular studies.

Sampling of deeper benthic communities represents a bigger technological challenge. The selective sampling of these communities would require the use of costly new technological devices such as mechanical-arm equipped ROVs. However, a satisfactory, though less selective sampling of deep benthic communities may be generally achieved using less expensive traditional methods such as grabs or corers (Jamieson et al. 2013). In the specific case of hard substrates in deep areas, ROVs and manned submersibles are currently the best alternative,

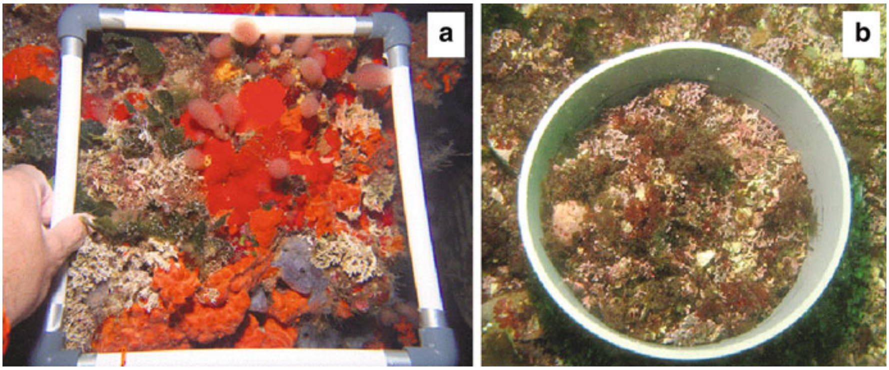

Fig. 1 Examples of sample units for scraping with chisel and hammer on hard bottoms such as coralligenous outcrops (**a**) or collect manually on loose bottoms such as maërl (**b**)

even if not optimal, since designing a proper sampling protocol is not always easy. The use of destructive methods such as trawls or sledges should be avoided in these VMEs.

5 Sample Preprocessing and DNA Extraction

In any sampling preprocessing for metabarcoding, the objective is to get well-homogenized samples, suitable for DNA extraction and representative of the studied community. Special care must be taken in the design of good separation procedures, which should allow transforming a complex sample into one or several homogenates from which DNA samples, representative of the community, will be extracted. We have successfully used an approach including size fractionation of complex samples through three stainless steel sieves (with successive mesh sizes of 10 mm, 1 mm, and 63 μm) by thoroughly washing them under high-pressure water, in order to obtain three size fractions per sample (Fig. 2). After separation, each fraction is independently homogenized using a 600 W kitchen blender and stored in ethanol at −20 °C until DNA extraction. The extraction should be ideally performed as soon as possible, although storage times of up to 6 months in these conditions are not expected to significantly affect DNA integrity.

It should be noted that, after this sieving procedure, with a final mesh size of 63 μm, the smallest particles are expected to be effectively washed away by the high-pressure washing. Thus, most of the extra-organismal DNA fractions will be removed, as well as most free-living bacteria. Thus, this separation procedure allows the metabarcoding study of eukaryotic community-DNA samples (excluding extra-organismal DNA), rather than whole environmental DNA. This is best suited for characterizing the living eukaryotic community of organisms inhabiting the sampled ecosystem, while removing most prokaryotic cells and the majority of the small free DNA, which might have been transported *postmortem* from external localities (Deiner et al. 2014).

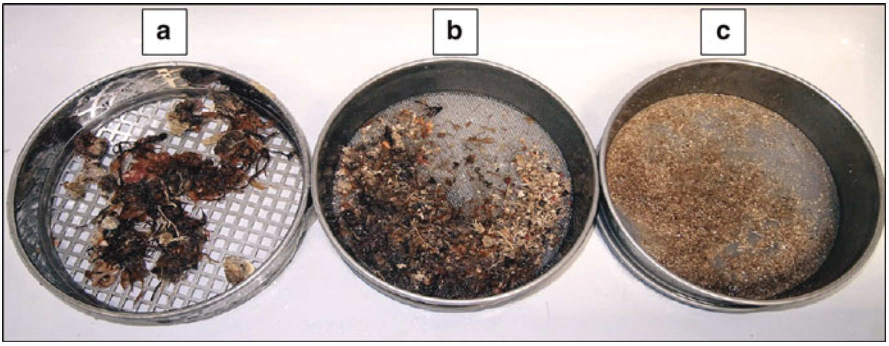

Fig. 2 Complex samples may be separated into size fractions before extracting the DNA. In the image, fractions of: (**a**) >10 mm, (**b**) 1–10 mm and (**c**) 63 μm–1 mm were obtained

A number of commercial kits for DNA extraction from soils are available and are recommended to be used for marine samples. A good solution for using a good representative quantity of community sample is PowerMax soil DNA extraction kit (MO-BIO Laboratories, http://mobio.com/), which allows to extract a relatively big amount of sample (up to 10 g of homogenate), with excellent yields. We recommend extracting 10 g of each fraction homogenate, using this standardized amount for obtaining comparable results. The PowerMax soil DNA extraction procedure includes an initial step of cellular lysis during which the DNA is released from the living tissues, followed by several purification steps which remove major contaminants that could interfere with the downstream PCR amplification steps. For a thorough lysis of all cellular material present in the samples, we recommend to perform this incubation step in an oven at 65 °C with shaking, using an extended time span (3 h).

6 Primer Design, Sample Multiplexing and PCR Protocols

In order to choose a suitable genetic marker for metabarcoding, a genomic region with enough sequence variability must be targeted to allow distinguishing among closely related species, whereas this variable region must be flanked by conserved regions, which will act as primer docking sites. Moreover, a region with many copies per cell is preferable, since the amplification will then be facilitated by the natural abundance of the DNA sequences. Thus, organelle genomes, such as mitochondrial or chloroplast DNA, or ribosomal RNA clusters (present in hundreds of copies along nuclear genomes), are usually preferred targets for metabarcoding. Two attributes are crucial and must be kept in mind for the design: fragment length and universality or specificity of the primers to be designed.

For metabarcoding purposes, the target fragment length must be kept short. This is mainly due to technical issues: the recommended method for environmental high-throughput sequencing (the Illumina MiSeq technologies; http://www.illumina.com) has currently a maximum effective read length of around 600 bp (2 × 300 bp paired-ends). This must include not only the fragment of interest, but also the flanking primers, sample tags, and other shorter adapter sequences used (but it does not include the Illumina adapters nor the library tag). In order to keep sequencing error rates low, smaller fragments are preferred. Furthermore, these smaller fragments will benefit from a longer overlap during the paired-end alignment step. There is another good reason for recommending smaller lengths: environmental DNA will be degraded to small fragments over time when removed from living tissues. So, the chances for amplifying the full length of the marker from extra-cellular DNA are inversely proportional to the length of the chosen marker. Thus, if we are interested in amplifying not only living tissue, but also the dead remnants and extra-cellular DNA present in the environment (e.g., when working with palaeoecological samples), the ideal length for a suitable metabarcoding marker should not exceed 350 bp.

The universality or specificity of the primer set depends on which is the main purpose of our research. For example, if we are only interested in arthropod diversity, we could design a primer set specific for this group (Zeale et al. 2011). If the research is taxonomically narrower, smaller groups can be targeted with suitable primers (Valentini et al. 2016). Conversely, if we target the whole community of eukaryotic organisms, then we will be interested in designing a primer set as universal as possible. That is, able to recognize the sequences flanking the marker in most taxonomic groups, so that all these groups could be adequately amplified by PCR. Until recently, very few truly "universal" primers were able to amplify the full taxonomic range of a community for highly variable markers such as COI. Thus, truly universal primers were usually restricted to markers with more conserved regions (e.g., 18S, Guardiola et al. 2015). However, the recent introduction of primers including deoxyinosine (a nucleotide which complements any of the four natural bases present in the DNA) in the fully degenerated sites of the sequence has improved the universality of primer sets. Using this strategy, Geller et al. (2013) introduced universal primers for COI barcoding of metazoa. Their primers amplify a 658-bp region based in the classic Folmer fragment (Folmer et al. 1994), but this region is still too long to be useful for metabarcoding purposes in Illumina series. Leray et al. (2013) introduced an internal primer to this region, able to amplify a shorter 313-bp fragment (hereafter called Leray fragment), which has proven to be most useful for characterizing marine benthic communities (Leray and Knowlton 2015; Aylagas et al. 2016). Some useful universal primer sets for different metabarcoding markers are summarized in Table 2.

Even though the suitability of COI for metabarcoding purposes has been criticized (Deagle et al. 2014) due to the high variability in the primer binding sites, the use of COI as a metabarcoding marker is the only way to benefit from the massive and ever growing information deposited in the Barcode of Life Database (http://www.boldsystems.org/). Thus, the development of satisfactory pipelines for COI-metabarcoding can be considered a necessary step towards comprehensive molecular biodiversity assessment tools. This is especially true for the case of Metazoa, but also for other groups such as Rhodophyta or Stramenopiles, to which great amounts of barcoding effort have been dedicated.

Once a suitable metabarcoding marker is chosen, we need to multiplex our samples. This implies attaching a short sequence oligo-tag (usually 6–8 bp) for identifying each sample, in order to prepare a multiplexed mix which will be sequenced together in a single run. In this way, a high number of samples (usually up to 100) could be simultaneously processed at a reasonable cost. When designing these tags, care must be taken to make them different enough (e.g., differing in at least 3 out of 8 positions) so to be able the unambiguous assignment of each read to its original sample, even in the presence of some sequencing errors. Software such as oligotag (Coissac 2012) has been developed to automatize the design of these tags. We suggest using the same tags at both primers for each sample. This will easily reveal any intersample chimeric read generated in the sequencing process if the tags at both ends of the sequence did not match. As a single marker is usually sequenced, there will be a low variability in the nucleotides that are being sequenced at every sequencing cycle (many positions will have the same nucleotide across all samples). This is undesirable for the efficiency of many sequencers and might increase the

Table 2 Universal primer sets for Eukaryotic metabarcoding markers

Marker	Primers	Sequence	Size (bp)	Refs.
COI Leray fragment	mlCOIintF jgHCO2198	5′-GGWACWGGWTGAACWGTWTAYCCYCC-3′ 5′-TAIACYTCIGGRTGICCRAARAAYCA-3′	313	(Leray et al. 2013) (Geller et al. 2013)
18S v4 region	TAReuk454FWD1 TAReukREV3	5′-CCAGCASCYGCGGTAATTCC-3′ 5′-ACTTTCGTTCTTGATYRA-3′	200–300	(Stoeck et al. 2010)
18S v7 region	18S_allshortsF 18S_allshortsR	5′-TTTGTCTGSTTAATTSCG-3′ 5′-TCACAGACCTGTTATTGC-3′	100–110	(Guardiola et al. 2015)
18S v9 region	Euk_1391f EukBr	5′-GTACACACCGCCCGTC-3′ 5′-TGATCCTTCTGCAGGTTCACCTAC-3′	120–134	(Hino et al. 2016)

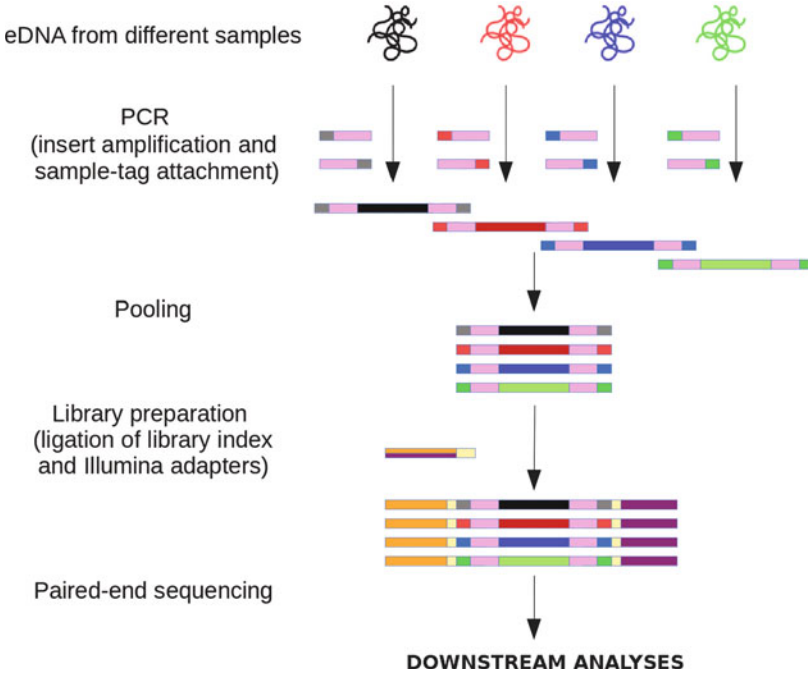

Fig. 3 Scheme of the 1-PCR protocol for amplifying a metabarcoding marker from multiple samples. The only PCR step uses metabarcoding primers tagged at 5′ with individual short tags of known sequences (barcodes) so that the reads belonging to the different samples could be identified after sequencing the multiplexed pool

sequencing error rates. To increase sequence variability, it is advisable to add a variable number (2, 3, or 4) of fully degenerate positions (Ns) at the beginning of each primer. In this way, the first position of the amplified gene will be lagged in some samples with respect to the others, and this will effectively increase the nucleotide diversity at each cycle. If our primer design does not include these degenerate positions, another way to increase sequencing diversity is adding a given proportion (20–25%) of a highly variable genomic library (e.g., PhiX phage genomic library) to our sample, though this will effectively reduce the number of available reads for our analyses. Alternatively, designs implying the simultaneous sequencing of two or more libraries prepared from different markers might be used.

For the amplification step, a typical PCR program at constant annealing temperature, whose conditions will depend on the primer sequences, is usually enough to amplify the samples (Fig. 3). Some tips to consider when designing the PCR program are setting a low annealing temperature (so to allow the primers to bind to targets with some mismatches) and setting a long extension time in every cycle and a low total number of cycles, in order to minimize the formation of chimeras (artificial amplicons stemming from two or more parent sequences, formed by incomplete template extension) (Edgar et al. 2011).

The quantitative value of procedures involving a single PCR amplification step which use sampling oligo-tags attached to the metabarcoding primers has been recently questioned (O'Donnell et al. 2016) due to the bias introduced by the mismatches of the short sequences used as oligo-tags. Instead, these authors recommended a two-step procedure, with a first PCR amplification step using just the metabarcoding primers (without oligo-tags), followed by a second PCR in which the sample oligo-tags are attached, for a better quantitative reproducibility. This procedure, however, could increase errors linked to PCR amplification, such as chimera formation, and the untagged fragments remaining in the final library might decrease the rate of reads successfully assigned to multiplexed samples.

7 High-Throughput Sequencing

There are a number of different technologies available for high-throughput sequencing, which differ in the total number of reads and in the length of these reads. When a good quantitative characterization of the samples is desirable, the best solution is the one which provides the highest number of reads. For metabarcoding purposes, the read length is not so critical, since short sequences can be successfully used for taxon assignment. Pyrosequencing technologies such as Roche 454, which yield long sequences (up to 1000 bp), but in lower numbers (up to one million), were the most used in the first years of metabarcoding studies, but due to the above considerations, they are being abandoned in favor of higher-throughput methods.

The most adequate technology presently available for metabarcoding is the Illumina series. This technology is currently able to sequence a high number of single-end or paired-end short reads, from 100 to 300 bp each. The Illumina MiSeq series is currently able to provide up to 25 million of 2 × 300 bp reads per run in a single cell, being probably the best solution for medium-sized metabarcoding laboratories, whereas the HiSeq series would be indicated for higher workloads, being able to yield up to 4×10^9 sequences (2 × 250 bp), separated into 8 lanes/cell. The sequence length and output are continuously increasing.

Other promising emerging technologies, such as nanopore sequencing, might improve the standards of high-throughput sequencers in the near future, though its suitability for reliable metabarcoding studies is yet to be demonstrated.

The choice of the sequencing technology determines the design of the sequencing library. Most technologies have specific adapter sequences which must be attached to the DNA fragments to be sequenced. There are many different commercial kits available for library preparation for each sequencing system, using either PCR-based or PCR-free methods for adapter attachment, which provide DNA libraries of variable quality. We favor PCR-free methods such as TruSeq DNA PCR-free library preparation kit (http://www.illumina.com/) or NEXTflex PCR-free DNA sequencing kit (http://www.biooscientific.com/), since every amplification cycle may introduce errors and biases. The library preparation is always a crucial step to obtain good quality sequencing results, which should be ideally performed by experienced staff. Fortunately, some companies provide sequencing services including library preparation, which can be a good solution for ecology laboratories with little molecular experience.

Finally, we advocate for the use of paired-end sequencing libraries for metabarcoding, even though this would not seem necessary for the shortest markers. Sequencing in both directions provides not only longer reads, but also a general improvement in the quality of the reads. If the overlap is wide, the final bases of one strand (which have the least quality) can be checked against the initial bases of the other strand and the correct sequence assembled.

8 Bioinformatic Analyses

Though many bioinformatic pipelines have been proposed for analyzing metabarcoding data, all of them are basically composed of three sequential steps: (1) quality control and demultiplexing, (2) clustering of the sequences that passed the quality control into MOTUs (a molecular proxy for "species"), and (3) taxonomic assignment of the obtained MOTUs. We will explain below the most commonly used alternatives among the many existing for each of these steps.

8.1 Quality Control and Demultiplexing

High-throughput sequencers are provided with an automated initial quality control step, which removes those reads having a low signal-to-noise ratio. The CASAVA software (through the CHASTITY filter) serves this function in the Illumina series, though this software is in process of discontinuation in favor of other online applications available in BaseSpace (http://basespace.illumina.com), a free web portal for genomic cloud-computing. The output of the sequencer is a file in FASTQ format, a text file which includes the sequences and the quality information for each base, so that further quality control procedures can be performed. Free software such as FASTQC (http://www.bioinformatics.babraham.ac.uk/projects/fastqc/) allows for a quick graphic evaluation of the quality of FASTQ sequences. The last positions of long sequenced fragments are usually of lower quality, and this problem worsens for the second thread of the paired end. Thus, a good practice is trimming all the fragments of both threads to a maximum length (depending on the mean quality scores achieved in the sequencing run) before proceeding to align the paired ends. This trimming can be done by using free software such as FASTX-toolkit (http://hannonlab.cshl.edu/fastx_toolkit/).

For most of the next steps of the analysis pipeline, we recommend the use of the OBITOOLS package (Boyer et al. 2016), a powerful suite of tools for metabarcoding analysis that has proven very useful for eukaryotic metabarcoding using different markers. Most steps of the pipelines we propose here (with some exceptions) are based on this software. Although the user can select other software, the explanations given are nevertheless illustrative, as similar steps must be performed. After the initial quality control, the next step is the alignment of the paired ends. This can be achieved by the OBITOOLS illuminapairedend command, which also provides a quality value for the alignment. Reads with alignments not passing a given quality threshold must be removed from the dataset.

With the remaining reads, the next step is demultiplexing the data in order to assign each read to its corresponding sample. This can be done by the OBITOOLS ngsfilter command, which will look for known sample oligo-tag sequences and will also remove the metabarcoding primers from every read, leaving just the amplified fragments. Sequences with tag mismatches and those with different tags at both ends (inter-sample chimeras) will be discarded.

In this step, only the original amplified sequences remain in every read (having removed all the adapters, tags and primer sequences). Then, a dereplication step can be done by using the OBITOOLS obiuniq command, which will group all the identical sequences, keeping track of their abundances in each of the multiplexed samples.

Further quality control procedures are usually applied to the dereplicated sequences, including a length filter, which will keep only sequences within the expected length range for the metabarcoding marker. The removal of singleton sequences at this step (sequences which appear only once in the dataset and are probably related to random sequencing errors) is also often applied. However, we recommend the removal of singletons at this step only in the case of short markers (18S), since longer markers (COI) are more prone to random point sequencing errors, and their early removal could result in an excessively pruned dataset. For markers over 300 bp, the removal of singletons is better done after the clustering process for delimiting the MOTUs.

After this step, the authors of OBITOOLS recommend the pruning of reads carrying putative sequencing errors by using a filtering procedure called obiclean. However, we have noticed that this procedure may be too stringent for long markers showing high natural variability levels, such as COI. Thus, we recommend performing instead a chimera removal step, using programs such as uchime (Edgar et al. 2011). The removal of chimeras may be performed in uchime using two different algorithms, depending on the availability of an extensive and well-curated database of reliable sequences. Since this is not usually the case for eukaryotic metabarcoding, we will need to run the uchime_de_novo algorithm, which is based on the comparison of all the reads present in the dataset between themselves, in order to detect if any of them is derived from the 5′ end of one parent sequence and the 3′ end of another. Those sequences that are questioned as putative chimeras will be removed, and only the ones passing the filter will be kept for further analyses. The VSEARCH software (http://github.com/torognes/vsearch) provides a free implementation of uchime that can be run in multiple processors, shortening computation times considerably.

8.2 Clustering Methods for Delimiting MOTUs

The dataset of reads that passed all the quality control filters usually includes a still overwhelming number of different sequences. This high diversity of sequences is a result of three different sources of variability: (1) true diversity of species present in the samples, (2) true intraspecific diversity (e.g., the presence of different alleles or mitochondrial lineages), and (3) errors produced during the PCR amplification or during the sequencing procedure, not pruned in previous steps. For reducing this dataset, we need a clustering algorithm able to group the related sequences into clusters, so that the resulting clusters (MOTUs) reflect the real species diversity present in the samples as accurately as possible. Note that, at this step, sequences containing a few sequencing errors will nevertheless cluster with the right sequence (which will be usually more abundant), so no informative sequences will be lost. That is why we do not recommend too stringent initial filtering procedures for long sequences. There are three different main approaches for clustering, discussed below.

The simplest clustering algorithms are based in grouping the related sequences with a similarity degree above a constant arbitrary similarity threshold (whose value depends on the chosen marker). Since there is not an objective way of evaluating the accuracy of the results, these algorithms belong to the category of unsupervised machine learning methods and are implemented in popular software for microbial metabarcoding such as CD-HIT (Fu et al. 2012), USEARCH or UCLUST (Edgar 2010). Besides the arbitrariness in the selection of a suitable similarity threshold, these methods have the drawback of being sensitive to the initial order of the sequences in the dataset (an initial sorting of sequences by decreasing order of abundances is thus recommended before performing the clustering). Despite some flaws, the speed and simplicity of these methods make them commonly used for delimiting MOTUs in the case of microbial communities or when studying a group of taxonomically related organisms. However, the constant similarity threshold is not suitable (neither theoretically nor in practice) when clustering a dataset which includes sequences of distantly related groups. A constant similarity threshold would always underestimate the real diversity in those groups that have suffered recent evolutionary radiations, whereas it would overestimate the number of species in groups with high mutation rates. It is no wonder that finding the adequate threshold for clustering is always a contentious matter (Chen et al. 2013), and none is likely to suit studies with wide taxonomic breadth.

A more complex possibility is the use of Bayesian clustering algorithms, such as the one implemented in the CROP software (Hao et al. 2011). The resulting clusters from this algorithm show different similarity thresholds for the diverging branches of the phylogenetic tree, which is probably more accurate for reflecting real species diversity. However, it has the big disadvantage of requiring time-consuming calculations, even when using powerful multiprocessor computing clusters. Moreover, given the heuristic nature of Bayesian algorithms, the reproducibility of CROP is somehow low, so that different runs on the same input dataset might result in variable numbers of resulting MOTUs. The choice for the correct values of the parameters for optimized calculations is not straightforward, and the performance of the algorithm will depend on the complexity of the input data, which is difficult to be estimated a priori. Notwithstanding these disadvantages, CROP has been successfully used for characterizing complex marine communities using different metabarcoding markers, with strikingly robust results (Leray and Knowlton 2015; Wangensteen et al. 2015). In the case of datasets with high sequence heterogeneity, the distribution by abundance of the output clusters may not be fully satisfactory, in the sense that a low number of superclusters might be formed which would include a high amount of sequences, not so closely related, artificially clustered together, whereas the most divergent sequences will not be clustered at all, yielding many low-abundance clusters with one or a few included sequences. When this happens, a reclustering method can be used, by selecting only the sequences included in the superclusters and submitting them to a second iteration of CROP. The removal of the divergent sequences during the first step usually results in a much better performance of the CROP algorithm during the second step, producing a suitable output table of MOTUs, more accurately representing the real species diversity of the samples.

The last family of clustering algorithms are those based in step-by-step aggregation procedures, such as SWARM (Mahé et al. 2015). This method has the advantage of being deterministic, so it yields robust and repeatable results. Every resulting cluster is a network of sequences, somehow comparable to the haplotype networks used in population genetics. However, it also bears the arbitrariness of having to choose a value of the distance threshold for including a sequence into a growing cluster. SWARM is an iterative process which also requires large amounts of computing time for completion.

Whichever clustering method is chosen, it must be followed by a recounting step, where the abundances of the different reads belonging to every resulting cluster must be aggregated and recalculated for each sample. Given the different file formats used by the software implementing these clustering algorithms, this step would generally require a custom user script to perform this calculation.

8.3 Methods for Taxonomic Assignment

The results from the clustering step will be a shortened list of sequences, representatives of every cluster (MOTUs). The most abundant or the topologically central sequence of each cluster is usually selected as the representative of each MOTU. The next step of every metabarcoding pipeline is the automated taxonomic assignment of these representative sequences by comparison with the identified sequences present in a reference database.

A common choice for performing this assignment is the use of BLAST (Altschul et al. 1990) against the Genbank nucleotide database. However, this approach has a number of drawbacks. First, the search algorithm may be too slow when thousands of sequences must be assigned. Second, for many sequences, a blast hit with enough similarity for identification at the species level will not be found, and then a phylogeny-based approach (which cannot be performed automatically by BLAST) would be needed to find the lowest taxonomic level which could be assigned to these sequences. On the other hand, for low-variability markers (such as 18S), the opposite problem could also occur. Namely, that a query sequence matches exactly two or more sequences in the database corresponding to different species (or even different genera or families). Then, a phylogenetic approach would be also useful to find the lowest taxon including all these sequences. Moreover, the sequences in the Genbank are not necessarily well curated by expert taxonomists. Consequently, misidentifications and errors do occur among the deposited sequences, which sometimes may lead to problems in an automated assignment procedure.

For all these reasons, a curated database with a reliable taxonomy and an algorithm which is able to integrate phylogenetic information in the assignment process are always preferable. An integrated approach reconciling classical taxonomic knowledge and molecular barcoding methods is needed for curating useful databases. Errors resulting from sequences of organisms that have been clearly wrongly identified by nonexpert researchers or sequences showing too much divergence from their relatives (which might result, for example, from the amplification of DNA from some symbiont or prey organism, wrongly assigned as the host or predator sequence) should be removed from the reference databases. In this sense, morphological taxonomic expertise is crucial and still much needed for the development of reliable metabarcoding reference databases. Depending on the metabarcoding marker chosen, there are different instances of curated databases. In the case of the small subunit of the ribosomal DNA (16S for bacteria/18S for Eukaryotic organisms), the SILVA database (Quast et al. 2013) would be a good choice. In the case of COI, the Barcode of Life Data System, BOLD (Ratnasingham and Hebert 2007) is the natural choice. Both public databases hold massive amounts of sequencing data with curated taxonomic identification, so that the number of misidentified sequences is almost negligible and the assignment problems much less frequent.

The problem with the speed of the assignment procedure can hardly be resolved when using on-line resources. For huge sequence datasets, it is preferable to query a local personal reference database, which may be based on the information extracted from the on-line databases, personally customized by the user. The use of a local implementation and the possibility of executing the software in a multiprocessor computing cluster highly accelerate the assignment procedure.

A good choice for an assignment algorithm for eukaryotic sequences which uses a local, customizable, reference database, is the ecotag software (Pegard et al. 2009). This software is based in two steps: first, it uses a Needleman-Wunsch algorithm (Needleman and Wunsch 1970) for finding the most similar hit to the query sequence in the reference database; then the phylogenetic information from the NCBI taxonomy tree is incorporated, so that the resulting taxon assignment will be the last common ancestor of the most similar sequence and all the sequences in the database that are equally or more similar to it than the query sequence is. Thus, the query sequences may be assigned to different taxonomic ranks, depending on the marker variability and the completeness of the reference database. This procedure has the advantage that the reference database may be obtained either from Genbank or from other databases using the ecoPCR software for *in silico* PCR (Ficetola et al. 2010) with the same primers used for the amplification of the samples. The resulting reference database may be customized by adding new sequences and new species to the local taxonomy tree, using the OBITOOLS obitaxonomy command, whenever new sequences are available. In the current version of ecotag, if a MOTU is assigned to the rank of order or lower (family, genus, or species), then the higher taxa will not be added (this is intended for avoiding the volatility of disputed higher classifications, with the proliferation of intermediate ranks in some groups). Thus, a custom script should be used for assigning the higher taxonomic ranks above the order level, according to the user's preferences in taxonomic matters.

The phylogenetic assignment is not exempt of problems. The most obvious being that commonly accepted taxonomic trees (especially those branches relying upon doubtful morphological traits) are often in conflict with molecular phylogenies. Moreover, some molecular phylogenies based on different molecular markers can often be in conflict as well. Even in the presence of phylogenetically coherent taxonomic information in the reference database, the problem remains that the phylogenetic tree obtained from using just a short fragment of marker (unavoidable in metabarcoding) is not expected to match perfectly the real phylogeny. Thus, incongruences and ambiguities are common in any phylogenetic procedure intended to assign metabarcoding data using reference sequences with low similarities, resulting in many query sequences being assigned to higher taxonomic levels or even to wrong taxa. The only way to improve these assignments would be adding as many sequences as possible to the reference databases in order to grow them denser. When any sequence in the reference database matches the query closely (with an identity of 95% or higher in COI), the assignment procedure is reliable, fast, and useful. Sadly, the reliability drops quickly as the similarity with the matching references decreases, so that even assignments at the phylum level with identity percentages less than 85% in COI should be considered questionable and treated with caution.

8.4 Refining of the Final Matrix

In multiplexed metabarcoding analyses, particularly in those using PCR-based methods for library preparation, a small degree of cross-sampling is always to be expected. That is, a small (but usually not negligible) number of reads will be assigned to the wrong sample. The cross-sampling rates will depend on the total abundance of the MOTU. Thus, a small number of reads of the most abundant MOTUs of the dataset will appear randomly spread through most of the sample columns in the raw final matrix resulting from the MOTU clustering procedure. Quantitatively, this would be unimportant, but it represents a big difference for methods based on presence/absence. Thus, the refining of the read abundance distributions for all the MOTUs present in the final matrix is highly recommended before proceeding to the final analyses. Different methods for applying these corrections have been proposed. A simple method consists in equating to zero the number of reads of a MOTU in all samples representing less than a given percentage (usually 3%) of the total abundance of that MOTU. A less stringent approach (which we recommend) is based in sorting the samples by the cumulative abundance of the MOTU to be normalized and equating to zero the values of all samples until that whose cumulative frequency accounts for 3%. We call this procedure “abundance renormalization.” This procedure leads to the loss of a small proportion of the reads of every MOTU, but it will remove almost all false-positive presences.

Including some blank samples or negative controls from the beginning of the process is always a mandatory practice. At least two kinds of negative controls are possible. A negative control for the procedures of sample pretreatment and DNA extraction may be obtained by extracting the DNA from 10 g of muffled sand (sand that has been heated in an oven at 400 °C for 24 h to remove all traces of DNA) using the same separation through sieves and extraction protocol used for the samples. On the other hand, a PCR blank or negative control for the amplification procedure may be obtained (as usual) by amplifying a volume of water (or, even better, of elution buffer from the DNA extraction kit), using the same master mix than the DNA samples, but with no DNA template added. During the final refining of the data matrix, a blank correction should be performed, where all the MOTUs appearing in significant numbers in the negative controls or in the blanks (e.g., MOTUs for which the abundance in the blanks to total abundance ratio is higher than 10%) should be removed.

If one of the objectives of our study is the detection (presence/absence) of some particular MOTUs in our samples, we would also want to apply a filter of minimal abundance, by fixing an arbitrary minimal number of reads as a detection limit (which should be established considering the total number of reads in the final matrix). All the MOTUs with a number of reads under this detection limit will be removed. Given that the total abundance of reads for each MOTU in the samples will usually follow a negative binomial distribution, a big number of MOTUs with low abundance will be removed during this filtering procedure, which could significantly affect qualitative diversity measurements. So, the detection limit should be always chosen with caution, and there is no clear rule of thumb for it. Rather, for each project, the compromise between getting rid of noise while not throwing the baby out with the bath water should be carefully thought of.

Even after the removal of the MOTUS present in the negative controls and the minimal abundance filtering, some MOTUs would still remain in the final matrix that are clearly contaminations of terrestrial origin. For example, in marine samples from shallow seawater, shallow benthic ecosystems, and even deep sediments, we have regularly detected the presence of some sequences of human, bovine, or porcine origins. For an accurate assessment of natural biodiversity, these MOTUs should be removed from the dataset by manual filtering.

9 Summary of Pipelines for Eukaryotic Metabarcoding

A summary of the proposed complete pipeline for metabarcoding of two different markers (18S and COI), designed to take into account most of the guidelines discussed here, is presented in Table 3. The summary intends to comprehend all the critical steps, from sampling and molecular biology laboratory to bioinformatic data treatment. The recommended software for each step of the bioinformatic pipeline is represented in Courier font. Of course, alternative software may be used for most of the steps. Eukaryotic metabarcoding is still a developing new technology, which is in continuous evolution. The pipelines proposed are to be

Table 3 Summarized pipeline for the complete metabarcoding procedure including two markers: COI and 18S. In case of choosing just one marker, only one of the columns should be followed. Software names beginning in "owi_" are custom R scripts (Available at http://github.com/metabarpark)

Sampling (preservation in ethanol)		
Pre-processing: (separation in size fractions and homogenization)		
DNA extraction: (PowerMax Soil DNA extraction kit)		
	Pipeline for COI	**Pipeline for 18S**
PCR-1	Leray primers	All_short primers
PCR-2	Tagged Leray primers	Tagged Allshort primers
Library preparation	TrueSeq DNA kit or similar	TrueSeq DNA kit or similar
HT Sequencing	Illumina MiSeq 2 × 250 bp	Illumina MiSeq 2 × 150 bp
Raw sequences QC	fastqc fastx_trimmer	fastqc Trimming not usually needed
PE alignment	illuminapairedend	illuminapairedend
Demultiplexing	obiannotate/obisplit ngsfilter	obiannotate/obisplit ngsfilter
Length filter	obigrep 300–320 bp	obigrep 75–180 bp
Dereplication	obiuniq	obiuniq
Rename identifiers	obiannotate	obiannotate
Chimera removal	vsearch uchime_denovo	vsearch uchime_denovo
Clustering	CROP l = 3 u = 4 obitab owi_recount_crop	CROP l = 0.3 u = 0.5 obitab owi_recount_crop
Re-crop superclusters	owi_extract_crop_cluster CROP l = 3 u = 4 owi_recount_crop	Not needed
Taxonomic assignment	ecotag using db_COI_BOLD	ecotag using db_18S
Add higher taxa	owi_add_taxonomy	owi_add_taxonomy
Final refinement	Blanks correction Abundance renormalization Minimal abundance filtering Removal of contamination MOTUs	Blanks correction Abundance renormalization Minimal abundance filtering Removal of contamination MOTUs
Community analyses and integration of the results		

regarded as first approximations. Building on them, the particulars of each project will determine the final implementation of the procedures.

10 Reporting the Results

The resulting output from the metabarcoding pipeline is a table of MOTU abundances with as many rows as MOTUs have been detected in the sample set and as many columns as samples have been included in the analysis. Usually, the taxonomic information and the representative sequences for each MOTU are included as additional columns, along with the degree of similarity with the closest sequence in the reference database, which gives valuable information on the reliability of the assignment. Reporting the MOTU table along with the publication of results (often as supplementary material, or deposited in public repositories) is mandatory. Making available the original set of sequences is also advisable should anyone be interested in reanalyzing the data or trying different pipelines.

The MOTU table is amenable to many traditional statistical methods for biodiversity assessment, always taking in consideration that the quantitative abundances reflected in the table are the absolute numbers of reads for each MOTU obtained from the samples. Whether this abundance of reads reflects or not the real biomass of the MOTUs in the original samples is a disputed matter (Elbrecht and Leese 2015; Thomas et al. 2016; Wares and Pappalardo 2016). For some authors, only the qualitative (presence/absence) information is reliable and should be used. In general, however, it is accepted that numbers of reads grossly correlate with abundance ranks (Egge et al. 2013; Pearman and Irigoien 2015; Evans et al. 2016), so at least a semi-quantitative value can be assigned to read abundances (Valentini et al. 2016). In any case, within a given project, quantitative changes are likely to be informative, as in principle biases must remain similar in all samples (Pawlowski et al. 2016).

The number of different MOTUs detected and the percentages of them which could be taxonomically assigned to a given taxonomic rank are usually reported in metabarcoding works. Apart from this, many methods of traditional community ecology for describing α- and β-diversity in the analyzed samples may be applied.

When comparing diversity patterns, the differences in the total number of reads obtained from each sample in the sequencing run must be considered. The "ecological sampling effort" may have been kept constant for all samples by the researchers during the sampling design and sampling procedures. However, the "molecular sampling effort" will not be so constant. The total number of reads obtained from each sample in a multiplexed library will be subject to stochastic processes during the library preparation and the sequencing procedures. Thus, the absolute abundances of the reads must be normalized for every sample as proportions of the total number of reads from that sample. It is therefore advisable to use relative, rather than absolute, number of reads for quantitative inference (Pawlowski et al. 2014; Leray and Knowlton 2015). Furthermore, if the number of multiplexed samples in the library is high, some samples might randomly yield too small a number of reads to be representative. These samples must then be removed from the final analyses.

For analyzing α-diversity patterns, rarefaction methods (Sanders 1968), using the number of reads as a proxy for sample size, must be applied. Values for MOTU richness of every sample would be rarefied to a number of reads equal to that of the sample having the least total reads. In order to analyze β-diversity patterns, methods based in presence/absence of MOTUs (such as Jaccard dissimilarities) or methods based on relative abundances (such as Bray-Curtis distances) may be applied. The R package vegan (Oksanen et al. 2016) is useful for carrying out this kind of community ecology analyses, while PERMANOVA methods (Anderson 2001) are well suited for statistical inference about the factors determining the community structure. Furthermore, if sequence divergence information is to be included in β-diversity calculations, a weighted UniFrac distance calculation procedure (Lozupone et al. 2007), implemented in the R package phyloseq (McMurdie et al. 2013) may be used.

11 Future Perspectives

With the ever-increasing number of published metabarcoding ecological studies, reconciliation between morphological taxonomists and molecular ecologists has finally been possible, as molecular identification increasingly proves its utility for biodiversity assessment. Comparisons of morphological and molecular diversity estimates of marine benthos (Aylagas et al. 2016; Pearman et al. 2016) have proven that molecular approaches usually yield a higher number of taxa than those based exclusively in morphology. This often strikingly higher number of molecularly detected taxa are not exclusively due to the occurrence of species distinguishable only by molecular tools (cryptic speciation) but is mainly attributable to the increased detectability of otherwise neglected groups of taxa such as eukaryotic microbial species, endosymbionts, or meiofaunal metazoans. These usually neglected taxa are likely to play vital roles in biogeochemical and ecological processes within marine benthic ecosystems, roles which can be objectively studied only using a community-DNA metabarcoding approach. In the near future, a number of correlation studies linking ecological variables to the presence of certain molecular taxa are expected to appear, which will allow the emergence of new bioindicator sequences (Pawlowski et al. 2016). Interestingly, these new bioindicators do not need to be assigned to any described and valid morphological species. Sequences might still be useful as ecological indicators, even if we do not currently know the names of the organisms to which they belong.

Besides its ability to detect neglected taxa, the metabarcoding approach to marine benthic ecology has several additional advantages. An obvious benefit is the objectivity in the automated taxonomic assignment of the detected sequences, in contrast with the subjectivity related to the morphological identification bias (probably related to the unavailability of taxonomic expertise). Another big advantage, related to the latter, is the traceability of the results. Whereas the original specimens used for morphologically identified inventories are very rarely (if ever) deposited in public collections, the lists of detected sequences are routinely stored in public data repositories, a custom which is strongly encouraged by scientific journals and research institutions. The presence/absence or abundance data associated to the stored sequences may be revisited again and again by future researchers for comparative ecological studies. Moreover, those sequences which are not currently assignable to a given taxon due to gaps in reference databases (and are thus currently labeled as "unassigned") may be possibly revisited and accurately assigned in the future, using improved reference databases. The massive amount of objective, traceable, and quantitative data from future metabarcoding studies to be carried out in different geographical areas will surely revolutionize the way in which research in biodiversity distribution is approached, including distribution changes related to Global Change (Cristescu 2014).

Eukaryotic metabarcoding is an emerging field in continuous evolution. Many significant technical developments are expected to occur during the next years. A significant part of these developments will be undoubtedly directed to deal with the problem of primer-bias (the bias introduced by the mismatches in the primer docking sequences), which would allegedly prevent the PCR amplification procedures from quantitatively reflect the real abundance of the sequences in the samples.

Many efforts are thus being dedicated to the so-called PCR-free methods, where total extracted environmental DNA is sequenced directly without any amplification step. However, the overwhelming complexity of the mixed sequence datasets resulting from these methods (which includes short fragments of genomic DNA from all the diversity of organisms present in the sample) currently precludes any successful effort for characterizing natural eukaryotic communities based on this information. Some progress is being achieved with the so-called mitochondrial metagenomics techniques (Crampton-Platt et al. 2016), where mitochondrial sequences can be isolated from the total sequenced pool and analyzed for taxonomic assignment. However, this technique currently can take advantage of less than 1% of the total sequenced reads, since most of the sequenced dataset belongs to nuclear genomes or to unknown mitochondrial genomes, which cannot be ultimately assigned. Thus, the big challenge of these techniques is to achieve the sequencing depth needed for a reliable assembly of mitochondrial genomes. Some mitochondrial enrichment protocols are being tested, which could partially solve this problem (Liu et al. 2016), though the bias introduced by this enrichment step is yet to be determined. Anyway, the success of mitochondrial metagenomics depends on the development of a massive database of complete mitochondrial genomes that does not yet exist, and a substantial investment should be done before these methods could be useful for routine analyses.

Yet, during the next few years, the improvement of the current PCR-based metabarcoding methods is still the most promising development. There is still much room for improvement in the design of universal primers (by incorporating deoxyinosine nucleotides in crucial positions) as well as in the design of specific primers for selected groups of organisms of special interest, which would allow the selective amplification of just the target group of organisms, with the resulting increase in the sequencing depth of target sequences. No doubt new metabarcoding markers will be discovered, which will lead to enhanced quantitative and qualitative biodiversity assessment.

Another crucial point where improvement is expected in the near future is the increasing breadth and coverage of existing reference databases. Although for particular studies it is possible to generate the database of interest (e.g., by sequencing all species of a given group known to occur in very local studies), for most studies concerned with assessment of general biodiversity, the correct assignment of MOTUs is directly dependent on dense and correctly curated databases. Marine barcoding databases are currently much less populated than their terrestrial counterparts, and significant portions of the tree of life are still under-represented or missing altogether. We urge marine biodiversity researchers to contribute to the growth of denser and more useful reference databases by sequencing at least the most prominent taxa found in marine metabarcoding studies, thus obtaining a validation of the assignments and contributing to improve the databases. Of course, ecological inferences are possible even in the absence of a precise taxonomic assignment, but the lower the number of "unassigned" MOTUs (or assigned just at high taxonomic levels), the better the knowledge we will obtain of the structural properties and the functioning of the ecosystems.

Finally, as the cumulative knowledge and the number of metabarcoded samples from different geographic origins grow, some spectacular developments may be expected from the emerging fields of population metagenomics and metaphylogeography, where haplotype frequencies and genetic population structure of hundreds of species could be obtained simultaneously by using a single multiplexed metabarcoding assay, facilitating and significantly decreasing the costs of population genetics approaches for benthic organisms, and rendering possible so far intractable studies of population genetics of small organisms, such as protists or meiofaunal metazoans.

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Deep-Sea Suprabenthic Communities: The Forgotten Biodiversity

17

Inmaculada Frutos, Angelika Brandt, and Jean Claude Sorbe

Abstract

Suprabenthos includes all swimming bottom-dependent animals (mainly small peracarid crustaceans) living in the water layer just above the sea floor. Although being widespread in all oceans from estuaries and shallow waters to the deep sea, this fauna has been poorly examined and remains virtually unknown for most marine areas. Suprabenthic communities are more often neglected in ecological studies, although they highly contribute to global benthic biodiversity (with many species new to science, frequently discovered in this near-bottom environment). In deep-sea areas, suprabenthic communities may constitute hotspots of biodiversity. Furthermore, some suprabenthic taxa are known to play a major trophic role in benthic ecosystems. As many of these taxa have good swimming capacities, efficient devices are necessary to catch this faunal component that is not sampled with conventional box-corers or dredges.

This chapter provides an account of the most recent quantitative studies on diversity and abundance of deep suprabenthic communities from different areas ranging from temperate to polar seas, including data on ecology, biogeography, and biology of species and trying to understand their role in the marine animal forest.

Keywords

Peracarida • Eucarida • Suprabenthos • Sledges • Biodiversity • Community structure • Marine animal forest

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Contents

1 Introduction

The so-called marine animal forest is characterized by sessile animals, e.g., corals and sponges, which provide an appropriate habitat to a permanent or occasional associated fauna living in, on, or above them. Formerly referred as "forest" or "thicket-like" habitats for the large gorgonians in the Northeast Channel off Nova Scotia (Buhl-Mortensen and Mortensen 2004, 2005), these living structures are known to constitute refuges and places for feeding and/or breeding, especially for fishes, cephalopods, crustaceans, and other invertebrates in coastal as well as in deeper waters (Husebo et al. 2002; D'Onghia et al. 2010). However, little is known about the motile invertebrate communities associated to these forests.

According to the definition given by Brunel et al. (1978), the suprabenthos includes all swimming bottom-dependent animals (mainly peracarid crustaceans) which perform, with varying amplitude, intensity, and regularity, seasonal or daily vertical migrations above the seafloor. This component of the benthic biota is mainly represented by amphipods, isopods, cumaceans, lophogastrids, mysids, and tanaids (superorder Peracarida), as well as by decapods and euphausiids (superorder Eucarida). In general terms, the abundance and diversity of these groups are related to depth: mysids and euphausiids are dominant on shelf bottoms (30–250 m), amphipods and cumaceans at bathyal depths (300–2000 m), and isopods and tanaids on the abyssal plain (4800–5800 m).

Due to the actual swimming capacities of its main components, the suprabenthic fauna occurs both within the animal forest and in its vicinity, being an important food source for many benthic/demersal fishes (Sorbe 1981, 1984; Cartes 1998; Preciado et al. 2009) and decapod crustaceans (Cartes 1994; Fanelli and Cartes 2004). Suprabenthic species also constitute highly productive populations in the benthic environment: they can annually produce between 5 and 10 times their mean annual biomass as demonstrated by their estimated P/B ratio (Sorbe 1984; Cartes et al. 2000, 2002; San Vicente and Sorbe 2013). Furthermore, peracarid populations are very sensitive to contamination events such as oil spills. They are quickly and severely

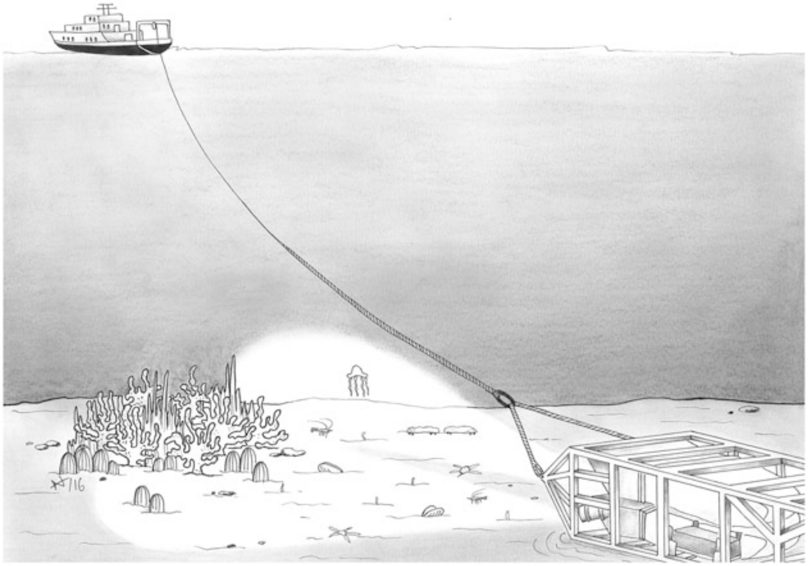

Fig. 1 Artistic representation of a sampling operation carried out with a camera-epibenthic sledge (see also Brandt et al. 2013) towed in the deep-sea "meadows" (Drawn by Nele Heitland)

impacted and need many years for full recovery (Dauvin and Zouhiri 1996; Poggiale and Dauvin 2001). In spite of its role in benthic ecosystems, the suprabenthic fauna has been generally neglected in many ecological studies because it is inefficiently sampled by conventional benthic samplers (i.e., grabs and box corers).

The suprabenthic fauna can be quantitatively sampled in the near-bottom waters by means of specific devices such as sledges towed over the sea floor (Eleftheriou and Moore 2005). Originally conceived for flat soft-bottoms (sandy to muddy substrata), such sledges can also be used on "trawlable" areas located at the immediate proximity of animal forests (Fig. 1). However, within animal forest habitats (3-D habitats), the use of these towed samplers is excluded due to possible damage for the animal forest and also due to the high risk of device loss. Therefore, other non-invasive sampling methods have been tested such as pushed nets, bottom closing nets, water pumps, and different trap systems (Emery 1968; Schroeder 1974; Potts 1976; Sale et al. 1976; Hobson and Chess 1978; Hamner and Carleton 1979; Rützler et al. 1980; Kawagushi et al. 1986; Lasenby and Sherman 1991; Setran 1992; Metaxas and Scheibling 1994; Buhl-Mortensen and Mortensen 2004; Madurell et al. 2012a). Furthermore, Carleton and Hamner (1987) conceived and used a diver-operated device to catch the motile fauna of these peculiar 3-D habitats.

Suprabenthic communities can be easily sampled in littoral/shallow waters with hand-pushed or diver-operated small devices but need heavier logistics on deeper bottoms (research vessels equipped with adequate winches, sufficient wire length for towed devices, acoustic systems to control in real time the sampler position above the sea floor). Moreover, such suprabenthic samplings are extremely difficult to operate (if not impossible) on deep 3-D structured habitats and hard bottoms, many of them considered as Vulnerable Marine Ecosystems (VMEs) where the use of invasive methods should be avoided. Thanks to improvements in the development of new samplers, non-invasive samplings of suprabenthos start to be possible in these vulnerable habitats.

The present chapter attempts to describe the patterns of occurrence of suprabenthic taxa in some deep animal forest habitats and soft-bottoms surrounding areas.

2 Sampling the Deep-Sea Suprabenthos

Initially referred as "hyperbenthos," suprabenthos studies started with Beyer' work (1958), but this research theme was mostly developed during the 1980s and 1990s with the use of adequate samplers. Mees and Jones (1997), followed by Dauvin and Vallet (2006), summarized all the terminology used to designate this near-bottom motile fauna and listed the plethora of sampling devices used for its study in distinct areas of the world ocean, from tropical to high latitudes and from coastal to the deepest abyssal bottoms. Even if many studies have been carried out in neritic and bathyal areas during the last decade, modern investigations on deeper abyssal environments are still scarce due to methodological difficulty in deep samplings and cost of remote oceanic expeditions.

The new non-invasive methods to sample the suprabenthos in hard bottoms were recently attempted in cold-water coral (CWC) ecosystems at bathyal depths. In Cap de Creus Canyon (NW Mediterranean), Madurell et al. (2012a) used a suction sampler piloted from a manned submersible whereas in Northeast Channel off Nova Scotia (NW Atlantic) the suction sampler was mounted on a Remote Operated Vehicle (ROV; Buhl-Mortensen and Mortensen 2004, 2005). In Avilés Canyon (S Bay of Biscay), Sánchez et al. (2013) used a plankton net mounted on a photogrammetric gear towed over the coral reefs. In soft-bottom areas surrounding these animal forests, many kinds of bottom sledges were successfully used to catch the near-bottom swimming fauna (Eleftheriou and Moore 2005). Basically, these sledges show a metallic chassis mounted on runners, equipped with one or more nets (to describe the near-bottom vertical distribution of the taxa) associated with an opening and closing system acting by contact with the sea floor (to prevent contamination by pelagic organisms from the water column). These sledge nets are equipped with flowmeters to estimate the haul length on the bottom.

The diverse studies presented below were carried out with different kinds of sledges (see Fig. 2), most of them with superimposed nets (500 μm mesh-size). They are referred in the literature as suprabenthic (Sorbe 1983; Cartes et al. 1994; Dauvin et al. 1995; Frutos 2006), hyperbenthic (Koulouri et al. 2003), or epibenthic sledges (Brattegard and Fossa 1991; Brandt and Barthel 1995; Brenke 2005, Brandt et al. 2013). Some of these denominations are apparently in contradiction with the definitions given by Brunel et al. (1978) and Huberdeau and Brunel (1982) for the

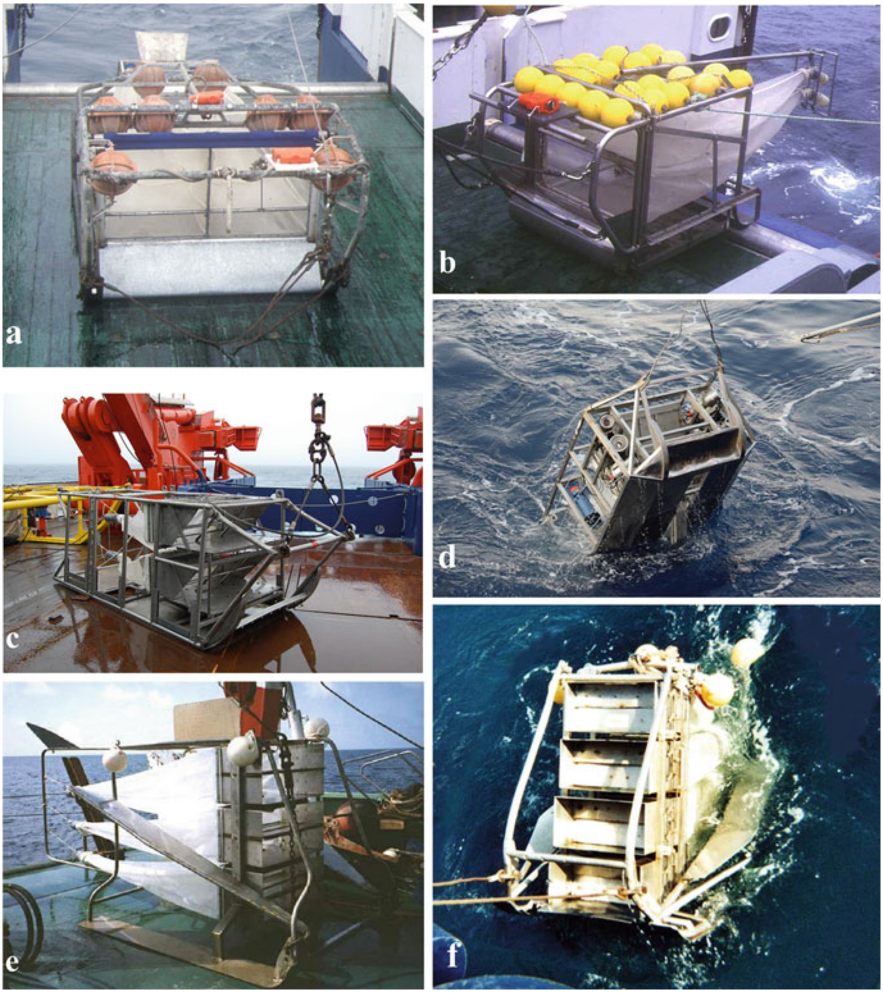

Fig. 2 Different deep-sea sledge models used in some of the studies referenced in this chapter (see also Table 1). The sledges are named after their published original description. (**a**) Sorbe 1983, (**b**) Frutos 2006, (**c**) Brenke 2005, (**d**) Brandt et al. 2013, (**e**) Cartes et al. 1994, (**f**) Dauvin et al. 1995 (Authors: Inmaculada Frutos (**a**) and (**b**), Nils Brenke (**c**), Thomas Walter (**d**), Joan E. Cartes (**e**), and Jean Claude Sorbe (**f**))

different components of the benthic biota according to their respective position with respect to the sediment-water interface (endobenthos, epibenthos, suprabenthos) (see also Dauvin and Vallet 2006). However, in the subsequent sections, the original denomination of sledges will be maintained, as initially mentioned by the authors in their respective publications. For all of them, their efficiency in sampling suprabenthos has been largely demonstrated.

3 Suprabenthos in Deep-Sea Areas of the World

A summary of 26 studies is presented below, carried out on deep suprabenthic communities from the Atlantic Ocean (from off East Greenland, Iceland, Bay of Biscay, Vema Fracture Zone, Angola Basin to the Beagle Channel), the Southern Ocean (at South Shetland Islands, Bellingshausen Sea, Weddell Sea, and Ross Sea), the Mediterranean Sea (Western and Eastern part), and the Pacific Ocean (in the Sea of Japan, Kuril-Kamchatka area, and New Zealand waters) with different sledge models. They took place either on soft-bottoms surrounding marine animal forest (most of them) or within such forest (few examples), allowing in this last case comparisons between both areas. Some of these relationships between the suprabenthos and the animal forest are shown in a further section.

4 Atlantic Ocean

In the North Atlantic the composition, abundance, and diversity of bathyal peracarid crustaceans have been examined off East Greenland in the North East Water Polynya (174–1809 m) as well as north of Iceland at the Kolbeinsey Ridge (830–1100 m) by means of two sledges models (see Table 1).

Off East Greenland, a highly diverse fauna of peracarids occurred, where amphipods were the most speciose taxon followed by isopods and cumaceans (Fig. 3). Overall, in the northernmost areas (~79°N), cumaceans were the most abundant taxon. Brandt (1995) showed the highest abundance of peracarids around 300 m depth and in the deeper stations (492–517 m), isopods were the most abundant and speciose taxon. A later study carried out in a deeper range (Brandt and Berge 2007) reported the highest abundance at the deepest station (1809 m) dominated by cumaceans. The middle stations (411–1151 m) cluster together where isopods are the most abundant taxon, while the shallow ones (188–310 m) are dominated by amphipods. Within this studied area, differences in peracarid composition, abundance, and diversity reflect hydrography, ice cover, and mainly food availability (phytoplankton and ice algae), depending on temporal and spatial opening of the polynya (Brandt 1995; Brandt et al. 1996; Brandt and Berge 2007).

Further south off Greenland (~75°N, 197–2681 m), the diversity of taxa showed the same trend than in northern areas, but here isopods became the most abundant taxon (Fig. 3). Isopods were dominant in most stations and contributed with higher abundances down 1500 m at the stations where the total abundances were the highest as well (Brandt 1997). These high abundances at the deepest stations could be explained by an episodic input of organic matter, probably related to a deep water formation process in an area of high ice dynamics (Brandt 1997).

In the Kolbeinsey Ridge (~68°N), the peracarid species composition followed the trend found off East Greenland, but the abundances were similar to the results from 75°N also dominated by isopods (Fig. 3). The gradient in faunal composition observed between the western and eastern sides of the ridge is probably related to differences in sediment composition, to the heterogeneity of the environment, as

Table 1 Faunal composition of suprabenthic communities in deep-sea temperate to polar marine areas, sampled by means of different sledges

Study area	Depth range (m)	Sledge	Species richness		Abundance	References
			Total	Dominant taxon	Dominant taxon[a]	
Atlantic Ocean						
Off East Greenland	45–517	Brattegard and Fosså (1991)	229	Amphipods (130 sp.)	Cumaceans (33.1%)	Brandt et al. 1996
	197–2681	Brandt and Barthe1(1995)	200	Amphipods (97 sp.)	Isopods (51.5%)	Brandt 1997
	188–1809	Brandt and Barthel (1995)	180	Amphipods (94 sp.)	Cumaceans (37%)	Brandt and Berge 2007
N Iceland	830–1100	Brattegard and Fosså (1991)	92	Amphipods (>36 sp.)	Isopods (59.7%)	Brandt 1993
Cap Ferret Canyon margin	ca.400	Sorbe (1983)	109	Amphipods (56 sp.)	Isopods (42.9%)	Sorbe and Elizalde 2014
Capbreton Canyon	162–987	Dauvin et al. (1995)	184	Amphipods (106 sp.)	Amphipods (48.2%)	Corbari and Sorbe 2001
Kostarrenkala	175–1000	Sorbe (1983)	205	Amphipods (76 sp.)	Amphipods (30.7%)	Frutos and Sorbe 2014
Avilés Canyon	207–1024	Frutos (2006)	199	Amphipods (89 sp.)	Amphipods (48.7%)	Frutos et al. 2012
Le Danois Bank	486–1062	Sorbe (1983)	303	Amphipods (121 sp.)	Amphipods (37.9%)	Frutos and Sorbe 2008
Vema Fracture	4986–5735	Brandt et al. (2013)	>200	Isopods (>100 sp.)	Isopods (74.4%)	Frutos et al. 2015
Angola Basin	5125–5415	Brenke (2005)	241	Isopods (100 sp.)	Isopods (60.7%)	Brandt et al. 2005
Beagle Channel	25–663	Brandt and Barthel (1995)	>94	Amphipods: (-)	Amphipods (60.1%)	Brandt et al. 1997

(*continued*)

Table 1 (continued)

Study area	Depth range (m)	Sledge	Species richness		Abundance	References
			Total	Dominant taxon	Dominant taxon[a]	
Mediterranean Sea						
NW Mediterranean	389–1859	Cartes et al. (1994)	157	Amphipods (82 sp.)	Amphipods (55.3%)	Cartes and Sorbe 1995,1997,1999; Cartes et al. 1994
S Balearic Islands	249–1623	Cartes et al. (1994)	104	Amphipods (45 sp.)	Mysids (36.7%)	Cartes et al. 2003
N-S Mallorca	150–750	Cartes et al. (1994)	187	Amphipods (90 sp.)	Mysids: (–)	Cartes et al. 2011
Ionian Sea	473–603	Cartes and Sorbe (1993)	66	Amphipods (25 sp.)	Mysids (63.2%)	Madurell and Cartes 2003
N Creta	50–300	Koulouri et al. (2003)	96	Amphipods (45 sp.)	Mysids: (–)	Koulouri et al. 2013
Southern Ocean						
South Shetland Islands	45–649	Cartes et al. (1994)	300	Amphipods (140 sp.)	Amphipods (60.2%)	San Vicente et al. 2007; Sorbe and Jimeno, 2012

Bellingshausen Sea	45–3280	Cartes et al. (1994)	66 families	Amphipods (76 sp.)	Amphipods (50.4%)	San Vicente et al. 2009
Weddell Sea	231–2119	Brandt and Barthel (1995)	-	-	Cumaceans (38.8%)	Linse et al. 2002
	201–840	Brandt and Barthel (1995)	115	Amphipods (56 sp.)	Amphipods (59.5%)	Lörz and Brandt 2003
	774–6348	Brenke (2005)	>674	Isopods (674 sp.)	Amphipods (43%)	Brökeland et al. 2007; Brandt et al. 2007a
W Ross Sea	474–3490	Brenke (2005)	-	-	Amphipods (68.8%)	Lörz et al. 2013
S Polar Front	2732–4327	Brenke (2005)	>107	Isopods (107 sp.)	Isopods (49%)	Brandt et al. 2014
Pacific Ocean						
Sea of Japan	455–3666	Brandt et al. (2013)	146	Amphipods (65 sp.)	isopods (37%)	Golovan et al. 2013
Kuril-Kamchatka Trench	4830–5780	Brandt et al. (2013)	343	Isopods (207 sp.)	isopods (58.5%)	Brandt et al. 2015

[a] Percentage of total peracarid collected, (–): data not available

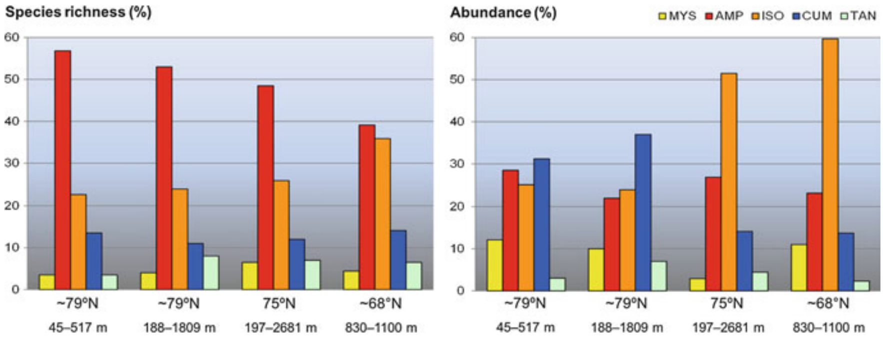

Fig. 3 Relative species richness and abundance of the bathyal peracarid fauna from Greenland and Icelandic waters. Data from Brandt et al. (1996), Brandt and Berge (2007), Brandt (1997), and Brandt (1993), from *left to right*. AMP Amphipoda, CUM Cumacea, ISO Isopoda, MYS Mysida, TAN Tanaidacea

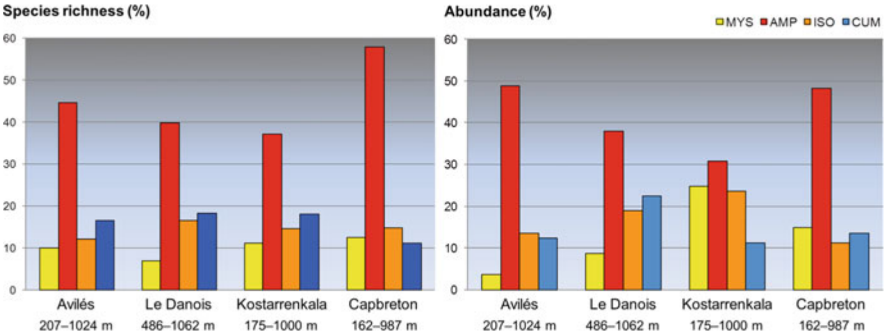

Fig. 4 Relative species richness and abundance of the bathyal peracarid fauna from the S Bay of Biscay. Data from Frutos et al. (2012), Frutos and Sorbe (2008 and unpublished data), Frutos and Sorbe (2014), and Corbari and Sorbe (2001), from *left to right*. Tanaids not represented (contribution <1%). AMP Amphipoda, CUM Cumacea, ISO Isopoda, MYS Mysida

well as to the quality and quantity of organic carbon reaching the seafloor (Brandt 1993; Brandt and Piepenburg 1994).

In the southern Bay of Biscay, the suprabenthos from bathyal depths was studied on open slopes, within canyons and on seamounts structures (Fig. 4). On the southern margin of the Cap Ferret Canyon (ca. 400 m depth, muddy sand bottom), the suprabenthic assemblages were monthly investigated in 1991–1992 (Sorbe and Elizalde 2014) with a multi-net sledge (Fig. 2a; see Sorbe 1983). In this temporal study, amphipods were the most speciose taxon and isopods the most abundant one (see Table 1). Species richness picked in August and dipped in November, mainly due to fluctuations in the number of amphipod species. Total abundances were maximal in July and minimal in November, due to both mysid and isopod abundance fluctuations. During the annual cycle, three successive phases were noted: phase

February–April with the dominance of the isopod *Munnopsurus atlanticus* (Bonnier, 1896) (Fig. 5k) and the mysid *Parapseudomma calloplura* (Holt and Tattersall, 1905) (64.1% of total abundance), phase May–August with the dominance of the same species but with higher abundances (61.0%), and phase September–January with the dominance of the mysids *Erythrops neapolitanus* Colosi, 1929 (Fig. 5a) and *Mysideis parva* Zimmer, 1915 (42.7%). All these species are permanent components of the community (they occurred in all samples). Although located in a deep environment known to be more stable than the adjacent neritic areas in terms of near-bottom temperature, salinity, dissolved oxygen, and sediment disturbance, this bathyal suprabenthic assemblage shows wide fluctuations of structural indices during the year, mainly related to population dynamics of a few key species such as the foraminifer-eating isopod *M. atlanticus* and the detritivorous/omnivorous mysid *E. neapolitanus* (Elizalde et al. 1999; Cartes et al. 2000).

Located in the southeastern part of the Bay of Biscay as well, the Capbreton Canyon was visited between 1997 and 2001 (Marquiegui and Sorbe 1999; Corbari and Sorbe 2001) and suprabenthic samplings were carried out with a 4-superimposed net sledge (Fig. 2f; see Dauvin et al. 1995) in several sites between 162 and 987 m depth (see Table 1, Fig. 4). At each site, both specific richness and density of the fauna sampled by the four nets of the sledge showed decreasing values from the lower to the upper net, as yet observed in many previous studies. The canyon and adjacent slope sites showed a species richness higher than at the shelf site, whereas density values showed some decrease with depth. Nevertheless, a maximal value was observed at the northern flank site of the canyon, probably related to higher bottom deposition of organic matter after turbidity events known to occur in that area (Frutos and Sorbe 2015). Amphipods were numerically dominant at all sites. Due to the Mediterranean outflow water detected below 500 m depth in the S Bay of Biscay, some of these species (e.g., the amphipods *Arrhis mediterraneus* Ledoyer, 1983; *Carangoliopsis spinulosa* Ledoyer, 1970; *Mediterexis mimonectes* (Ruffo, 1975); *Pardalisca mediterranea* Bellan-Santini, 1984; *Parvipalpus major* Carausu, 1941; and the mysid *Erythrops neopolitanus*) cannot be anymore classified as Mediterranean "endemics". Furthermore, following Rowe (1972), some suprabenthic species such as the amphipods *Cleonardopsis carinata* KH Barnard, 1916*, Tmetonyx similis* (Sars, 1891), the isopod *Arcturopsis giardi* (Bonnier, 1896), and the decapod *Calastacus laevis* de Saint Laurent, 1972 can be classified as "canyon indicator species" (Marquiegui and Sorbe 1999).

Within the Capbreton area, "Kostarrenkala" is a well-known fishing ground located on the southern flank of the canyon. The new mapping of that area (Bourillet 2007) revealed the presence of many circular pockmarks (diameter ≤600 m; depth ≤100 m) aligned along faults perpendicular to the canyon thalweg. However, a study carried out by Sorbe et al. (2010) on the benthic/suprabenthic fauna associated with these depressions demonstrated that they are presently inactive (at least the shallower ones). The suprabenthic communities of the surrounding soft-bottoms were studied in a bathymetric transect between 175 and 1000 m depth (Frutos and Sorbe 2014; Table 1), using a multi-net sledge (Fig. 2a). Amphipods were the most speciose taxon followed by cumaceans and isopods, thus confirming the general trends

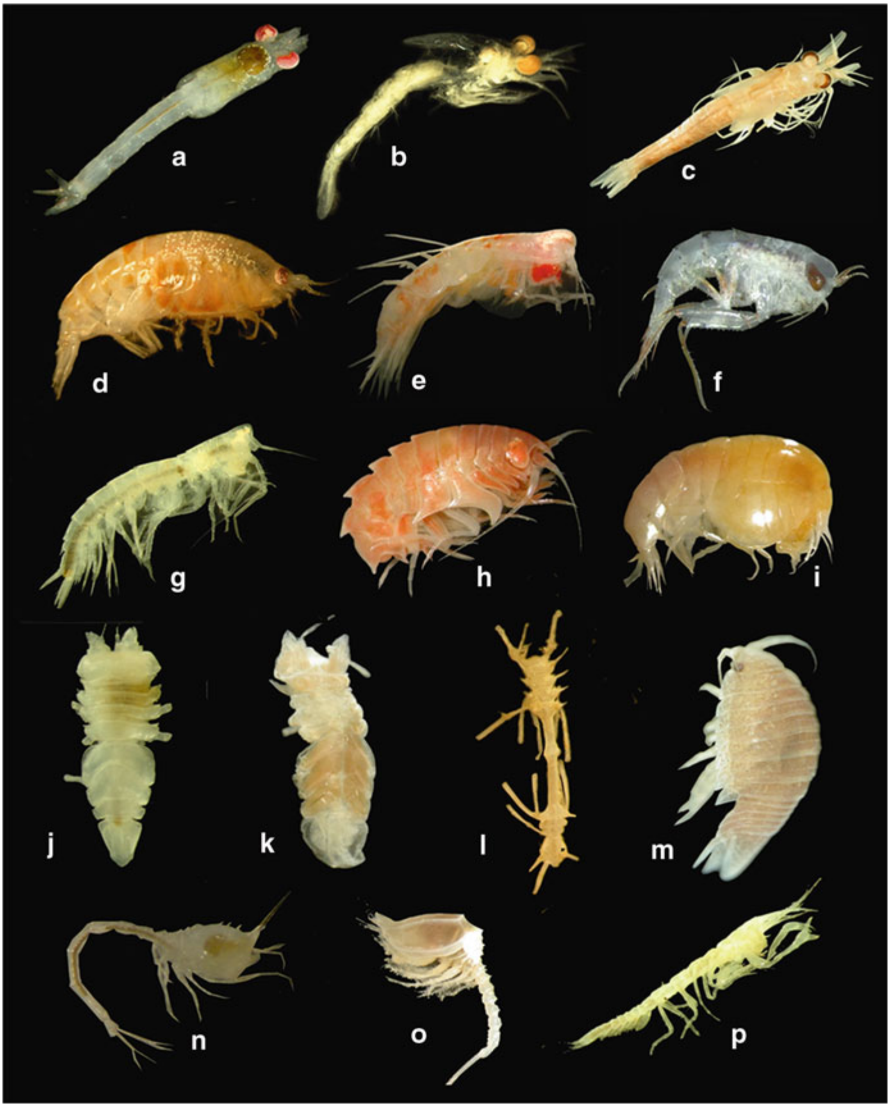

Fig. 5 Pictures of some suprabenthic species from deep-sea areas. Mysids: (**a**) *Erythrops neapolitanus* Colosi, 1929; (**b**) *Mysidopsis cachuchoensis* San Vicente, Frutos and Sorbe, 2012; (**c**) *Boreomysis tridens* GO Sars, 1870. Amphipods: (**d**) *Scopelocheirus hopei* (Costa, 1851); (**e**) *Syrrhoe affinis* Chevreux, 1908; (**f**) *Themisto compressa* Goës, 1865 (**g**) *Pseudotiron bouvieri* Chevreux, 1895; (**h**) *Epimeria parasitica* (M Sars, 1858); (**i**) *Stegocephaloides auratus* (GO Sars, 1882). Isopods: (**j**) *Ilyarachna longicornis* (GO Sars, 1864); (**k**) *Munnopsurus atlanticus* (Bonnier, 1896); (**l**) *Cornuamesus longiramus* (Kavanagh and Sorbe, 2006)*;* (**m**) *Metacirolana hanseni* (Bonnier, 1896). Cumaceans: (**n**) *Styloptocuma gracillimum* (Calman, 1905); (**o**) *Campylaspis vitrea* Calman, 1906. Tanaid: (**p**) *Apseudes spinosum* (M Sars, 1858) (The pictures were taken on board immediately after sampling. Author: Inmaculada Frutos)

observed in the bathyal suprabenthic communities of the S Bay of Biscay (Fig. 4). Total densities decrease with depth, whereas diversity values increased significantly (Shannon index, 3.83–5.72). A multivariate analysis of the abundance data discriminated three assemblages according to depth, each one characterized by a distinct dominant species: the amphipod *Westwoodilla caecula* (Bate, 1857) at the shelf break (175–182 m), the isopod *Munnopsurus atlanticus* on muddy sand bottoms of the upper slope (298–405 m), and the amphipod *Rhachotropis gracilis* (Bonnier, 1896) on mid-slope muddy bottoms (724–1000 m) below the mud line. Such a structure of bathyal communities seems to be common for the whole margin of the Bay of Biscay.

In the central part of the southern Bay of Biscay, the seamount-like Le Danois Bank (declared as the Marine Protected Area “El Cachucho” by the Spanish Authorities since 2011 and belonging to the Natura 2000 Network) was investigated with the purpose to model the functioning of its benthic ecosystem, characterized by a mosaic of soft- and hard bottoms (Sánchez et al. 2008). In that area, distinct benthic communities were characterized: a *Callogorgia-Chimaera* community located in the northern area of the top of the Bank, where the sediment coverage is relatively thin, including the presence of rocky outcrops; a *Gryphus-Galeus* community on the southern area; a *Phormosoma-Trachyrincus* community on the sedimentary terraces characterizing the break of the bank; a *Pheronema-Deania* community (the most extensive one) in the deeper and muddy flat grounds of the inner basin (Sánchez et al. 2008). Image analyses conducted by Sánchez et al. (2009) on the hard bottoms of the Le Danois Bank summit by means of a photogrammetric sledge showed that 3-D structured habitats occurred, characterized by the gorgonian *Callogorgia verticillata* (Pallas, 1766), the large-sized sponges *Asconema setubalense* Kent, 1870 and *Geodia megastrella* Carter, 1876 together with the corals *Caryophyllia smithii* Stokes and Broderip, 1828 and *Acanella arbuscula* (Johnson, 1862).

During this survey, the suprabenthic fauna of the Le Danois Bank was also studied on soft-bottom areas (Frutos and Sorbe 2008), sampled with a multi-net sledge (Fig. 2a). In the whole material collected, amphipods were the best represented taxon in terms of abundance and number of species (Fig. 4, Table 1). A multivariate analysis of abundance data discriminated two assemblages reflecting differences in environmental features (surficial sediment, bottom currents, organic input from surrounding waters): one on top of the bank (486–500 m) dominated by amphipods, mainly represented by *Pseudotiron bouvieri* Chevreux, 1895 (Fig. 5g) and the second one in the inner basin (828–831 m) dominated by cumaceans. Following the species composition trend of the bathyal communities of the S Bay of Biscay, the high values of species richness ($\geq$100 species) and diversity (>5; Shannon index) at all sampled stations demonstrate that the Le Danois Bank is actually a true biodiversity hotspot, probably related to the mosaic-structured benthic habitats of the bank (Frutos and Sorbe 2008; unpublished data). According to this study, some boreal amphipods (*Amphilochus manudens* Bate, 1862, *Metambasia faeroensis* Stephensen, 1923, *Melphidippa borealis* Boeck, 1871, *Dulichiopsis nordlandica* (Boeck, 1870), and some “endemic” Mediterranean ones (*Bathymedon monoculodiformis* Ledoyer, 1983, *Oediceroides pilosus* Ledoyer, 1983, and

Pseudotiron bouvieri) extended the limits of their geographical distribution. Furthermore, several peracarid species were described as new to science: the amphipods *Liropus cachuchoensis* Guerra-García, Sorbe and Frutos, 2007 and *Leucothoe cathalaa* Frutos and Sorbe, 2013; the isopods *Cornuamesus longiramus* (Kavanagh and Sorbe, 2006), (Fig. 5l), *Politolana sanchezi* Frutos and Sorbe, 2010, *Paranthura santiparrai* Frutos, Sorbe and Junoy, 2011, and *Ischnomesus harrietae* Kavanagh, Frutos and Sorbe 2015; and the mysid *Mysidopsis cachuchoensis* San Vicente, Frutos and Sorbe 2013 (Fig. 5b). Many others (16 amphipods, 12 isopods, and 10 cumaceans) are putatively new to science.

Also located on the Cantabrian margin near the Le Danois Bank area, the bathyal suprabenthic communities of the Avilés Canyon were sampled between 207 and 1024 m depth (Frutos et al. 2012) using a suprabenthic sledge (Fig. 2b; see Frutos 2006). Amphipods represented the most speciose group and the most abundant as well (Fig. 4, Table 1). A multivariate analysis of abundance data discriminated three suprabenthic assemblages located: at shelf break (207–211 m), with the dominance of the euphausiid *Nyctiphanes couchii* (Bell, 1853); on the upper slope (365–380 m), with the dominance of the amphipod *Scopelocheirus hopei* (Fig. 5d); on the mid-slope (462–1024 m), with the dominance of the isopod *Munnopsurus atlanticus*.

The 3-D structured habitats of the Avilés Canyon were investigated along transects by video records performed with either a ROV or a photogrammetric sledge (Sánchez et al. 2013). Beside direct observations on the epibenthic megafauna, both devices allowed a qualitative survey of the suprabenthic fauna associated with deep-water corals (mainly *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758). During two ROV transects in the upper bathyal (844–777 and 891–605 m depth, respectively), suction samplings carried out in the near-bottom water layers collected the amphipods *Themisto compressa* Goës, 1865 (the most abundant species, Fig. 5f) and *Ichnopus* sp., the mysid *Parerythrops* sp., and the tanaid *Apseudes* sp. The photogrammetric sledge was equipped with a plankton net (500 μm mesh-size, 0.3 × 0.3 m opening), fixed on top of the frame in order to gently sample the near-bottom motile fauna. A total of 12 taxa were sampled along a transect carried out between 398 and 528 m depth. Mysids were the most abundant group (46.8% of total abundance), represented by *Boreomysis arctica* (Krøyer, 1861) and *Pseudomma affine* Sars, 1870. Amphipods (31.9%) were represented by *Apherusa bispinosa* (Bate, 1857), *Scopelocheirus hopei* (Costa, 1851), unidentified Photidae, *Stegocephaloides auratus* (Fig. 5i) and *Themisto compressa*. Euphausiids (17%, with *Euphausia krohnii* (Brandt, 1851), *Meganyctiphanes norvegica* (M Sars, 1857), and *Nematoscelis megalops* Sars, 1883), lophogastrids (2.1% with *Gnathophausia zoea* Willemoes-Suhm, 1873), and cumaceans (2.1%, with females belonging to one of the unidentifiable lampropid genera *Hemilamprops/Mesolamprops*) were recorded as well. Such observations actually demonstrate that these motile peracarids, well represented in soft-bottom surrounding areas of coral reefs, are also present in the close vicinity of these habitats.

In the tropical Atlantic Ocean, abyssal bottoms between 4986 and 5735 m were studied in the Vema Fracture area to know the species turnover at both sides of the

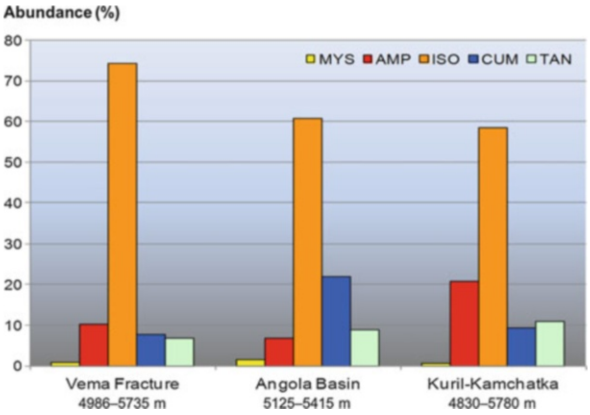

Fig. 6 Relative abundance of the abyssal peracarid fauna from the Atlantic and Pacific oceans. Data from Frutos et al. (2015) and Brandt et al. (2005, 2015), from *left to right*. AMP Amphipoda, CUM Cumacea, ISO Isopoda, MYS Mysida, TAN Tanaidacea

Mid Atlantic Ridge in terms of abundance and diversity (Devey et al. 2015). Sampled with a camera-epibenthic sledge (Fig. 2d; Brandt et al. 2013), isopods were the dominant peracarid group (>70% of the total number of peracarids). Amphipods, cumaceans, and tanaids were also well represented (Fig. 6; Frutos et al. 2015).

In the southern Atlantic, the diversity and abundance of abyssal peracarid crustaceans were investigated in the Angola basin off Namibia between 5125 and 5415 m depth by means of an epibenthic sledge (Fig. 2c; see Brenke 2005). Here, isopods were the most abundant and speciose taxon (Fig. 6, Table 1). Most of these abyssal species were new to science, but the distribution of the few knowns ones indicates that the Walvis Ridge acts as an effective distribution barrier to the deep-sea fauna (Brandt et al. 2005).

In the Beagle Channel (Patagonia), Brandt et al. (1997) studied the abundance of peracarids between 25 and 665 m depth by means of an epibenthic sledge (see Brandt and Barthel 1995). In that channel, amphipods were the most abundant taxon (but not identified to species level), followed by isopods and cumaceans (see Table 1). Abundances generally decreased from east to west with a single peak registered at a station located east of Punta Yámana. Species richness increased with distance from the eastern entrance of the Beagle channel towards Burdwood Bank and was generally lower in the Beagle Channel, assuming the sediment composition might be one of the factors that affect the peracarid fauna (Brandt et al. 1997).

5 Mediterranean Sea

In the Catalan Sea (NW Mediterranean), the bathyal suprabenthos was sampled between 389 and 1859 m depth by means of a multi-net suprabenthic sledge (Fig. 2e; see Cartes et al. 1994). The diversity patterns of the different peracarid groups were extensively studied by Cartes and Sorbe (1993, 1995, 1997, 1999) according to depth across the Catalan Sea slope. Amphipods represented the dominant group in terms of both species richness and abundance (Table 1). Cumaceans were progressively more abundant with increasing depth, being the dominant taxon on the lower slope (Cartes and Sorbe 1993).

In subsequent works, these observations were compared with suprabenthic data from bathyal bottoms in a depth ranging from 249 to 1622 m of the Southern Balearic Islands (Cartes et al. 2003; W Mediterranean). Amphipods were the most speciose group, while mysids were the most abundant (Table 1). Both sites appear quite similar with respect to their species composition, with three slope faunal belts discriminated according to depth: an upper slope belt above 400 m where species diversity and biomass are low, a medium slope belt (400–1200 m) where both diversity and particularly biomass attain maximum values; and a lower slope belt (below 1200 m) where diversity and biomass decrease with depth.

This pattern was also observed in the case of suprabenthic assemblages from N and S Mallorca during 2003–2004 (Cartes et al. 2011; W Mediterranean). Amphipods were the most speciose group (Table 1) followed by cumaceans. Three assemblages were discriminated according to depth: a shelf-break assemblage (150 m) dominated by the mysid *Leptomysis gracilis* (Sars, 1864); an upper slope assemblage (350 m) dominated by the cumacean *Hemilamprops normani* Bonnier, 1896; and a middle slope assemblage (650–750 m) with the isopod *Munnopsurus atlanticus* as dominant species. Diversity was low at the shelf-break and higher values were registered on the slope. Most of the new species described in these deep Mediterranean areas are in fact widely distributed and relatively abundant in both western and eastern basins (see Cartes et al. 2011)

In the Cap de Creus Canyon (NW Mediterranean; ca. 233 m depth), Madurell et al. (2012a) tested a submarine coupled multi-filtration pump (SC-pump) in order to collect the zooplankton associated with CWC from hard bottoms. According to Orejas et al. (2009), followed by Madurell et al. (2012b), the three most abundant coral species in the canyon showed distinct spatial distribution patterns: patches of varying sizes for *M. oculata*, isolated colonies for *L. pertusa,* or alone or in small groups for *Dendrophyllia cornigera* (Lamarck, 1816). The preliminary density data obtained with the SC-pump revealed that the motile macrofauna collected with the near-bottom zooplankton was not diverse but abundant, represented by typical suprabenthic species (such as the amphipod *Melphidippella macra* (Norman, 1869) as well as the mysids *Anchialina agilis* (G.O. Sars, 1877) and *Leptomysis gracilis*). However, more sampling effort needs to be carried out to confirm such preliminary results.

In the Ionian Sea (E Mediterranean), the suprabenthic peracarids collected at bathyal depths (473–603 m) were studied by Madurell and Cartes (2003). Amphipods were the most speciose taxon while mysids were the most abundant (see Table 1). Qualitative comparison with the deep suprabenthic fauna from the western Mediterranean showed a similar composition and diversity in both areas. However, a number of dominant species from the lower slope (1200–1350 m) in the western basin actually showed a shallower distribution in the Ionian Sea.

On the shelf and upper slope of northern Creta (E Mediterranean, 50–300 m depth), Koulouri et al. (2013) sampled suprabenthic communities by means of a hyperbenthic sledge (Koulouri et al. 2003). Amphipods were the most speciose group whereas mysids were the most abundant one (see Table 1).

6 Southern Ocean

San Vicente et al. (1997) published the first work that demonstrated the existence of the suprabenthos in Antarctic waters. Over there, the suprabenthic communities from South Shetland Islands and Bransfield Strait were sampled with a multi-net suprabenthic sledge (Fig. 2e; see Cartes et al. 1994) between 45 and 649 m depth (San Vicente 2011; San Vicente et al. 1997, 2007). Amphipods were the most speciose and abundant taxon (see Table 1). Abundances showed a maximum value at South Livingston Island (163 m) whereas the minimal value was recorded at Brandsfield Strait (361 m). Four assemblages were discriminated in the study area, apparently more structured by the degree of shelter-exposure and development of sessile epifauna than by depth or sediment features. On shallow bottoms, the macro-epibenthos is mainly represented by suspension-feeders that constitute 3-D habitats (Hexactinellida, Demospongia, Bryozoa, and Ascidiacea), whereas at deeper depths it is represented by organisms showing a great variety of trophic strategies: Ophiuroidea and Asteroidea down to 400 m; Polychaeta Sedentaria at greater depths (Arnaud et al. 1998).

San Vicente et al. (2009) studied the suprabenthic communities of the Bellingshausen Sea and off the western Antarctic Peninsula at depths ranging from 45 to 3280 m by means of a suprabenthic sledge (Fig. 2e). Amphipods were the most representative taxon followed by mysids (see Table 1), whereas amphipods and isopods contributed with the highest number of taxa. Five suprabenthic assemblages were discriminated, mainly structured by environmental features related with the depth gradient (sediment mud content). Sorbe and Jimeno (2012) identified at least 76 species of amphipods. *Melphidippa antarctica* Schellenberg, 1926 and *Lepidepecreum urometacarinatum* Andres, 1985 were the numerically dominant species (22.5% and 17.6% of the total individuals, respectively). San Vicente et al. (2009) noticed that, except for the coastal zones <100 m depth, the Bellingshausen Sea and W Antarctic Peninsula are characterized by soft bottoms, high sedimentation rates, and low primary production, influenced by iceberg scouring. The lack of the dense 3-D communities of long-lived filter-feeders reported from the Weddell and Ross seas could also be an important factor affecting suprabenthic assemblages in this area (San Vicente et al. 2009).

Linse et al. (2002) studied the bathyal suprabenthic fauna by means of the sledge described by Brandt and Barthel (1995) in the southern part of the Weddell Sea (231–2119 m depth). Within peracarids, cumaceans, and amphipods were the dominant components of the near-bottom motile fauna (Linse et al. 2002). Then, Lörz and Brandt (2003) reported 115 species in a shorter depth range, where amphipods were the most speciose and abundant taxon (see Table 1). Later on, Brökeland et al. (2007) sampled at bathyal and abyssal depths between 774 and 6348 m by means of the sledge designed by Brenke (Fig. 2b). Within the peracarids collected, amphipods were the most abundant taxon and Brandt et al. (2007a, b) reported 674 species in the whole isopod collection (see Table 1).

Kaiser et al. (2008) studied the macrofauna associated with the shelf and slope in the South Sandwich arc by means of the sledge designed by Brenke (Fig. 2c). Within the peracarid collection, amphipod dominated at the shallow shelf station (~300 m) while tanaids were the dominant group in all the deeper ones (500–1500 m), displaying a decline in abundance with increasing depth.

In the western Ross Sea, Lörz et al. (2013) studied the suprabenthic communities from the shelf break down to the abyssal plain by means of the sledge described by Brenke (Fig. 2c). Amphipods were the most abundant group followed by isopods (see Table 1). Across the transition zone between the shelf break and the base of the slope, isopods increased their proportion with increasing depth matched by a decline in the proportion of amphipods, this last one being dominant at most stations (Lörz et al. 2013). The high peracarid abundance on the Ross Sea shelf break may reflect overall high surface productivity of the Ross Sea region (Arrigo et al. 1998) or could be also caused by the patchy distribution of fauna or by seasonal effects (Rehm et al. 2006).

Further north in the South Polar Front, Brandt et al. (2014) sampled the benthic macrofauna at depths ranging between 2732 and 4327 m with an epibenthic sledge (Fig. 2b). In the whole material collected, crustaceans were dominant, and within peracarids, isopods were the most abundant taxon, followed by amphipods and tanaids (see Table 1). However, the results were comparatively low in comparison with data from Weddell Sea (Brökeland et al. 2007).

7 Pacific Ocean

In the NW Pacific Ocean, the peracarid fauna from the slope and the deep-basin of the Sea of Japan was sampled at depths ranging from 455 to 3666 m depth by means of a camera-epibenthic sledge (Fig. 2d). Golovan et al. (2013) reported 146 species, where 93 were new records for that marine area which 42 were new to science. Isopods were the most abundant taxon while amphipods were the most speciose (see Table 1). The highest number of amphipods and cumaceans on the shallower stations decreased when increasing depth while isopods and tanaids increased their abundance at bathyal depths. The multivariate analysis discriminated three assemblages related to depth: a first assemblage for the slope stations (450–1500 m) characterized by the isopod *Baeonectes brandtae* Malyutina, Golovan and Elsner, 2013; a second assemblage for the lower slope stations (2500–2700 m) characterized by the amphipod *Anonyx derjugini* Gurjanova, 1962; a third assemblage grouping the deepest stations characterized by the isopod *Eurycope spinifrons* Gurjanova, 1933.

The benthic macrofauna of the abyssal plain adjacent to the Kuril-Kamchatka Trench (northwestern Pacific Ocean) was sampled between 4830 and 5780 m depth with a camera-epibenthic sledge (Fig. 2d). Isopods were most important peracarid taxon in terms of number of species and abundance (Fig. 6, see Table 1). As a general rule, the number of individuals decreased with increasing depths. All the stations located close to the trench margin yielded the highest abundances as well as high species richness values in comparison with adjacent abyssal plain stations. In general, the non-isolated Kuril-Kamchatka Trench area is characterized by higher abundances and higher species richness than the geographically isolated and young deep-sea basin of the Sea of Japan (Brandt et al. 2015).

In New Zealand waters (southwestern Pacific), the benthic macrofauna from the upper slope was sampled between 218 and 1213 m in two sites by means of the sledge described by Brenke (Fig. 2c). In peracarids, amphipods were the most abundant (47.9% of total peracarid abundance), followed by isopods and cumaceans. But no clear correlation of abundance or species richness with depth was observed (Lörz 2011).

8 Deep-Sea Suprabenthos Distribution Patterns

The study of suprabenthos carried out with efficient specific samplers demonstrates the regular occurrence of the near-bottom motile fauna in deep-sea benthic ecosystems. The aforementioned studies took place in distinct marine areas from temperate to polar latitudes displaying the suprabenthos as a permanent component of the deep-sea benthos (Table 1). Furthermore, the quantitative sampling of these assemblages provides knowledge of their structure in terms of abundance and diversity and allows describing the distribution patterns of suprabenthic taxa. Generally, suprabenthic abundances decrease with increasing depth, concomitantly with diversity increase. The eight main crustacean groups that compose the suprabenthic fauna (amphipods, cumaceans, isopods, lophogastrids, mysids, tanaids, decapods, and euphausiids) occurred in all the previously mentioned studies, but their relative abundance and diversity was related to depth (and associated co-factors). In this way, mysids, euphausiids, and decapods are the most abundant groups on shelf bottoms (Atlantic Ocean; Cornet et al. 1983, Sorbe 1989, Frutos et al. 2012). Although euphausiids are mainly pelagic species, they can interact with the seabed during daytime and feed at the benthos or sediment-water interface (e.g., *Meganyctiphanes norvegica* (M. Sars, 1857), see Schmidt 2010). The aggregations of euphausiids (swarms) come into contact with the slope due to horizontal impingement from the pelagic to the benthopelagic environments, as evidenced Mauchline and Gordon (1991) for some species. Then, wind-driven and tidal upwelling circulation cells reinforces the up-slope aggregation where also topography play a role in the concentration of this fauna in specific areas such as canyon heads (see Simard and Harvey 2010). In the same way, the suprabenthic behavior of lophogastrids is well documented for the mesopelagic *Lophogaster typicus* M. Sars, 1857 and the bathypelagic *Gnathophausia zoea* Willemoes-Suhm, 1873 (Lagardère and Nouvel 1980), but their occurrence in the near bottom environment is always reported to be very low. Amphipods and cumaceans are dominant on slope areas (Atlantic Ocean, Mediterranean Sea, and Southern Ocean), the last group becoming more prevalent at higher depths while the first group shows some abundance decrease. Isopods are dominant at abyssal depths (Atlantic, Pacific, and Southern oceans) where the presence of tanaids is also noticeable as well.

According to the available information reported in the 26 aforementioned studies (see Table 1), the observed number of species reported in the different geographical areas ranged from 92 peracarid species in N Iceland up to 674 species only for the isopod group in the deep Weddell Sea area (Brandt et al. 2007b). According to these authors, 86% of this huge value represented species new to science.

Most previous studies were dedicated to the spatial distribution of deep-sea suprabenthic communities, both from a geographical and bathymetric viewpoint. Only a few ones (Sorbe and Elizalde 2014; Cartes et al. 2008) described the variability of their faunal composition (species richness and abundance) according to seasons. The observed fluctuations within these communities seemed to be related to the population dynamics of their key species (Elizalde et al. 1999; Cartes et al. 2000; Sorbe and Elizalde 2014).

9 Suprabenthos in the Deep-Sea Animal Forests

In the open ocean, the soft-bottom areas inhabited by suprabenthic communities could be considered equivalent to terrestrial "meadows." In these deep-sea meadows, some "animal trees" could appear as scattered organisms in wide areas or grouped in some peculiar location, generating an animal forest with different degrees of development. As the suprabenthic organisms exhibit good swimming capacities, they probably occur both in meadows and in animal forest habitats. If the occurrence of suprabenthic communities is well reported and quantified in deep-sea meadows (see Table 1), their presence within deep-sea animal forests is so far poorly documented (Buhl-Mortensen and Mortensen 2004, 2005; Madurell et al. 2012a; Sánchez et al. 2013) due to methodological constraints (problematic sampling of small motile organisms in 3-D habitats). As species richness is known to increase with habitat heterogeneity, such a trend is to be also expected within deep sea animal forests. Sampling the animal forest could provide the capture of the motile fauna previously recorded in the surrounding areas (Madurell et al. 2012a; Sánchez et al. 2013), demonstrating its relationship with these three-dimension habitats.

On shallow hard-bottoms, it is well documented that "animal trees" such as sponges and madreporarian or alcyonarian corals provide a settle where amphipods, mysids, and isopods could be associated (Wägele 1987, 1991; Thomas and Klebba 2006, 2007; White 2011; White and Reimer 2012a, b, c; Wittman et al. 2014; Thomas 2015; Krapp-Schickel et al. 2015) and even being their source of food (e.g., mysids preyed by sponges; Vacelet and Boury-Esnault 1995, 1996). Furthermore, the symbiotic relationships between mysids and epibenthic organisms such as madreporarian corals, sea anemones, sabellid polychaetes, crustacean pagurids, sea urchins, and ophiurids have been widely documented (see Wittman et al. 2014).

However, in the deep sea, more studies must be carried out to know the mutual link between both motile and sessile fauna within these 3-D habitats that constitute the animal forest. Despite our weak general knowledge on motile fauna within animal forests, some punctual observations can be mentioned on this topic.

Buhl-Mortensen and Mortensen (2004) reported crustaceans associated to the two deep-water gorgonian corals *Paragorgia arborea* (Linneus, 1758) and *Primnoa resedaeformis* (Gunnerus, 1763) sampled on the slope off Nova Scotia by means of a suction sampler. Crustacean composition was different for each coral species, probably related to the differences in size and morphology of the coral, but amphipods were the most abundant and speciose taxon in both coral species. The two most common amphipod species (*Metopa bruzelii* (Goës, 1866) and *Stenopleustes malmgreni* (Boeck, 1871) occurred mainly on hydroids attached to the coral, which make corals with hydroids a suitable substratum for these peracarids (Buhl-Mortensen and Mortensen 2004). *Munna boecki* Krøyer, 1839 was the unique isopod species recorded in this habitat.

The motile fauna collected in coral habitats is highly dependent on the sampling method, even being underestimated in case of an inappropriate sampler. In this way, Buhl-Mortensen and Mortensen (2005) showed that the fauna associated to the same coral species collected by ROV or video-grab were more abundant and varied than collected by bottom trawl; especially for amphipods caught by suction sampler. Off northern Norway, the associated fauna observed on *P. arborea* was dominated also by crustaceans, mainly amphipods, where stegocephalids were reported as the most common family (De Clippele et al. 2015). However, despite stegocephalids are well known as micro-predators of cnidarians, this video study was not conclusive with respect to the use of corals as a settle habitat or as a food source for these amphipods (De Clippele et al. 2015).

Some peracarid species (16 amphipods, 7 isopods, and 1 tanaid) were reported as fauna associated with sponges in the upper slope of the NE Atlantic, all of them using sponges as substratum (Klitgaard 1995). As these peracarids are known to belong to the local geographical communities, their association with sponges seems to be facultative in temperate to cold waters, in contrast to the great number of obligate associates reported on Porifera from warm tropical waters (Klitgaard 1995).

Within amphipods, leucothoids are most often reported as commensal inhabitants of sessile invertebrates such as sponges, ascidians, and bivalves, where they find a stable microhabitat that provides access to food resources and possible protection from predators (Crowe 2006; Thomas and Klebba 2006, 2007; Thomas and Krapp-Schickel 2011). *Leucothoe cathalaa* is a new leucothoid recently sampled on bathyal sandy bottoms of the Le Danois Bank. All the specimens collected showed a free-living behavior at the moment of their capture (no sign of commensalism) (Frutos and Sorbe 2013). However, additional trawlings and photogrammetric observations on epibenthic communities from the same area (Sánchez et al. 2008, 2009) showed the presence of several sponge species, including the whitish cup-shaped *Asconema setubalense* (up to 1 m in height above bottom). This sponge is thought to be the best host candidate for *L. cathalaa*, offering to this whitish amphipod a cryptic lifestyle inside its erected cup.

As aforementioned, animal forests represent complex habitats characterized by high values of diversity and abundance of their associated motile fauna, also observed in the case of suprabenthic communities living in their close vicinity. For instance, at the top of the Le Danois Bank, the scattered presence of rocky outcrops on fine sandy bottoms actually increases habitat heterogeneity of that area, explaining the high diversity of the surrounding suprabenthic communities (suprabenthic "hotspots") when compared to bathyal assemblages without rocky outcrops from soft bottoms of the Bay of Biscay (Frutos and Sorbe 2008, 2014; unpublished data).

In the Antarctic region, the relatively high proportion of hard bottoms is related to the local presence of drop stones (Thomson 2006). Such hard bottoms represent animal forests with different complexity degrees, harvesting peculiar benthic communities characterized by a high abundance of amphipods. In most studies dedicated to the Antarctic shelf, amphipods represent the most abundant peracarid taxon (Brandt 2001; Rehm et al. 2006, 2007). A very similar pattern was also reported in the deep areas of the Southern Ocean (Linse et al. 2002; Lörz and Brandt 2003; Brökeland et al. 2007; San Vicente et al. 2007, 2009; Lörz et al. 2013) with amphipods being most abundant down to 4000 m. This tremendous evolutionary and ecological success of amphipods on the Antarctic shelf (Arntz et al. 1994; De Broyer and Jazdzewski 1996; De Broyer et al. 2003) is related to the lack of a thermocline in the water column and to the unusual extension of the shelf down to 600 m depth, favoring species submergence and emergence. The general rule that macrobenthic abundances decrease with depth due to decreasing food availability (Hessler 1974; Gage and Tyler 1991) is not fully confirmed in this area (Brökeland et al. 2007). Overall peracarid abundances below 3000 m tend to be lower than at shallower depths, but there is no regular decline in abundance with depth. Furthermore, the high proportion of hard bottoms or the influence of down-welling water mass could possibly explain higher values of species richness and abundance in some isolated stations (Brandt et al. 2007b, c).

10 Conclusions

Despite the wide geographical range of studies presented herein, the deep-sea suprabenthic communities of many areas in the world still remains unknown. Furthermore, our knowledge of this near-bottom motile fauna is much better at bathyal depths than in abyssal plains. If the sampling methodology carried out on soft-bottom areas needs to be more standardized (e.g., height of sampling above the bottom, haul length, duration of haul, use of electronic devices), recent new technologies should be developed and improved in the case of the marine forest. When these objectives will be achieved, better faunal comparisons could be realized between marine forests associated fauna and surrounding soft-bottom communities. New perspectives could be also considered with respect to the problematic quantitative study of suprabenthic fauna on hard-bottoms (e.g., cold seeps, hydrothermal vents).

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11 Cross-References

- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests of the World: an overview
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests

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Part II

Structure and Function of the Animal Forests

Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects

18

Katell Guizien and Marco Ghisalberti

Abstract

Long-lived hard and soft coral species that are able to develop dense patches with a complex, three-dimensional structure form an animal forest canopy, similar to trees in terrestrial systems. Aside from the shelter provided by this canopy to other organisms, the animal forest can significantly modify the local physical and biogeochemical environment.

In the first part of this chapter, the modification of benthic boundary layer hydrodynamics in and above canopies is described, with a focus on the impacts of canopy density and flexibility. In the second part of this chapter, the structure of diffusive and advective mass transfer in canopies will be presented and discussed in relation to the biogeochemical transformations observed in animal forest canopies. Ongoing challenges in the conceptualization of physical and biogeochemical processes in animal forest canopies are also exposed. In the third part of this chapter, we review the factors that form the basis of a mechanistic explanation of the development of micro-niches, which explain the large diversity hosted in animal forest canopies.

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Keywords

Benthic boundary layer • Flow instability • Drag • Micro-niche • Spatial heterogeneity • Gradients • Turbulence • Biotic-abiotic interactions • Ecosystem engineers

Contents

1 Introduction

The concept of the "marine animal forest" was initially introduced based on aesthetic similarities between trees and large erect colonial animal communities (e.g., corals, Bruno and Bertness 2001) that cover some marine substrates (see Fig. 1, as well as Gutt et al. (2015) in this book). Similarly to terrestrial forests, marine animal forests form a sheltered habitat by reducing the foraging efficiency of consumers (Bartholomew 2000; Beukers and Jones 1994) and providing refuge for motile species like fishes or vagile invertebrates (Ross and Quattrini 2007). The similarities between marine and terrestrial forests extend beyond the provision of shelter, however, and include the manner in which these systems modify the local physical and biogeochemical environment. Despite differences in spatial scale and the properties (density, viscosity, heat capacity) of the fluid to which they are exposed, steady flows over atmospheric (O(10–100 m)) and aquatic canopies (O(0.1–1 m)) display a common characteristic flow structure, as detailed in Sect. 2. Because of such similarities, we use the terms "forest" and "canopy" interchangeably here.

Organisms forming canopies are typically considered "ecosystem engineers," a term which refers to organisms that, through causing changes in the local physical or biogeochemical conditions, directly or indirectly control the availability of resources

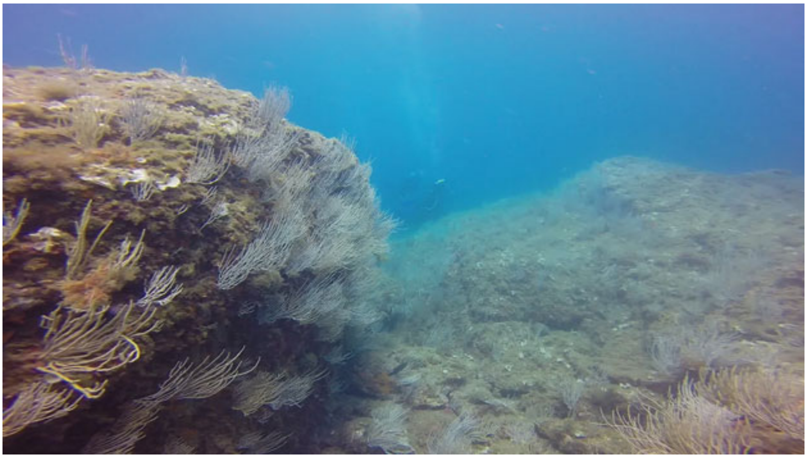


Fig. 1 The white gorgonian, *Eunicella singularis*, covering a boulder at 15 meters depth in Cap L'Abeille (Réserve Naturelle Marine de Cerbère-Banyuls, NW Mediterranean sea, Photograph by Katell Guizien)

(other than themselves) to other organisms and, thus, modify, maintain, or create habitats (Lawton 1994). Autogenic engineers modify their environment through physical changes, while allogenic engineers do so through chemical transformations (Jones et al. 1994). Six factors have been identified by Jones et al. (1994) as defining the scale of impact of an ecosystem engineer: (1) the lifetime activity of individual organisms; (2) the population density and size; (3) the spatial distribution of the population, both at the local and regional level; (4) the length of time a population has been present at a site; (5) the durability of constructs, artifacts, and impacts in the absence of the original engineer; and (6) the number and types of resource flows that are modulated by the constructs and artifacts and the number of other species dependent upon these flows. On the basis of these factors, trees have always been considered the paradigmatic example of ecosystem engineers in terrestrial habitats (Holling 1992).

Marine animal forests have been shown to act as autogenic ecosystem engineers in marine systems through the provision of habitat, colonization opportunities, and increasing habitat complexity. For corals, these effects are well established in shallow tropical environments, but also recognized in temperate (Scinto et al. 2009; Cerrano et al. 2010) and deepwater environments (Cordes et al. 2008; Freiwald and Roberts 2005). Animal forests also act as autogenic ecosystem engineers through modification of the mean and turbulent flow structure. The lower levels of turbulence inside the canopy increase sedimentation (Luckenbach 1986), causing the retention of propagules and enhancing larval settlement (Eckman 1985; Smith and Witman 1999; Bruno 2000). At the top of the canopy, the enhanced turbulence generated by the large canopy roughness augments the delivery of food and critical metabolites by reducing the thickness of the diffusive boundary layer on organism surfaces

(Dennison and Barnes 1988; Thisle and Eckman 1990; Shashar et al. 1996). Flow modification by marine forests encompasses a variety of processes on a range of spatial scales (reviewed for coral reefs by Monismith 2007), and it is now clear that the hydrodynamics of marine forests demonstrate strong similarities, regardless of whether the forest is comprised of plants (e.g., kelp forests or seagrass meadows, Eckman et al. 1989; Duarte 2000) or animals. This flow modification likely leads to the creation of highly dynamic microenvironments, which ultimately select those organisms able to feed, grow, and reproduce within the marine forest.

Animal marine forests can also act as allogenic ecosystem engineers, although in the opposite manner to vegetation canopies. Indeed, marine forests of autotrophic primary producers are expected to be carbon sinks (like their terrestrial counterparts) through atmospheric carbon fixation by photosynthesis (Goreau 1992). In contrast, marine forests of heterotrophic consumers (except corals living in symbiosis with autotrophic algae) release inorganic carbon during organic matter assimilation in respiration. Nevertheless, the allogenic impact of the “wall of mouths” of marine animal forests is expected to significantly alter the local biogeochemical conditions near the sea floor (Fabricius and Metzner 2004).

The objective of this chapter is to review the state-of-the-art understanding of the hydrodynamics and biogeochemistry of marine animal forests and their impact on living conditions inside the animal forest.

2 The Hydrodynamics Inside and Above the Marine Animal Forest

Marine animal forests can be found in both shallow and deep environments, exposing them to a range of hydrodynamic conditions in terms of the magnitude and steadiness of the flow. At the marine forest scale, steady flows include those generated by wind, buoyancy, or tides, with surface waves (seas and swell) generating an unsteady flow. Flow in the oceanic bottom boundary layer is therefore often decomposed into a quasi-steady unidirectional component (the current) and a series of periodic components (waves). This decomposition is of utmost importance when considering the hydrodynamics inside and above the marine animal forest, as the bottom boundary layers associated with steady and unsteady flows differ greatly in their size and structure.

2.1 Structure of the Turbulent Boundary Layer Over Flat Beds in Steady Flows

The bottom boundary layer is the region where the flow velocity is impacted by the bed (reaching a zero velocity at the bottom) and where flow energy is dissipated as heat. In steady aquatic flows, the thickness (δ) of the bottom boundary layer is typically O (1–10 m). The flow in a steady turbulent boundary layer exhibits a well-known vertical structure, with three distinct regions (Wilcox 2000): (1) the viscous

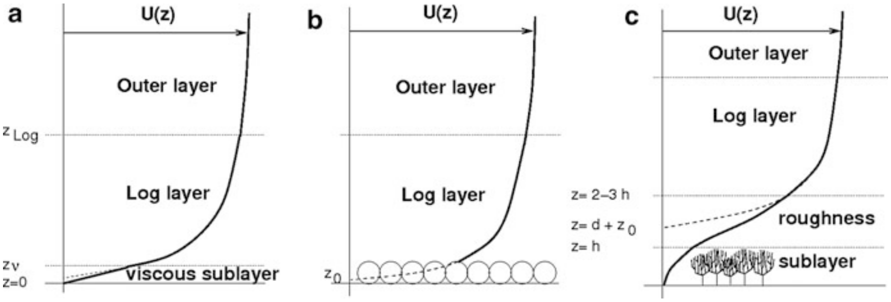


Fig. 2 Schematic diagram of the vertical structure of the mean velocity in (**a**) a smooth-bottom boundary layer, (**b**) a rough-bottom boundary layer, and (**c**) a canopy boundary layer formed by obstacles of height *h*

sublayer nearest the bed, where the velocity is low and viscous forces dominate inertial forces; (2) the logarithmic (or inertial) layer, where viscous forces are progressively overwhelmed by inertial forces; and (3) the outer layer, where the flow velocities are greatest and exceed the bottom friction velocity by an order of magnitude (Fig. 2a). The viscous sublayer and logarithmic layer form the inner part of the boundary layer, which extends over a distance of roughly 0.1δ. In these layers, the flow velocity scales on the bottom friction velocity u* (defined as the square root of the bed shear stress divided by the fluid density). In the viscous sublayer, velocity increases linearly with distance from the bed up to $z_\nu \approx 10\ \nu/u_*$. In the logarithmic layer (of O (10 cm) in height for the typical flow considered above), the velocity increases logarithmically with distance from the bed according to the "law of the wall" (Fig. 2a) expressed as

$$U(z) = \frac{u_*}{\kappa} \ln \left[z/z_0 \right] \quad \text{for } z_\nu < z < \mathrm{z}_{\mathrm{Log}} \tag{1}$$

where $\kappa = 0.41$ is the von Karman constant, z is the distance from the bottom and z_0 is the bottom roughness length.

Over a rough bed, the viscous sublayer can vanish between roughness elements (Fig. 2b). This is seen when $u_* k_s/\nu > 70$ (Sleath 1984), where k_s is the average height of the roughness elements ($k_s \approx 30\ z_0$, Nikuradse 1933).

2.2 Structure of the Turbulent Boundary Layer Over Large Obstacles in Steady Flows: The Canopy Effect

When ocean beds are covered by large obstacles (i.e., a canopy) which extend into the theoretical logarithmic layer of the unobstructed flow, the classical boundary layer structure can be significantly modified. This is typically the case in animal forests formed by erect organisms larger than a few centimeters. The wakes produced by these obstacles create strong spatial variations in the flow, over a region (embedded within the boundary layer) known as the roughness sublayer (RSL, Fig. 2c). In a homogeneous canopy (of elements of height *h*), the RSL is estimated to extend to approximately 2–3 *h* above the bed (MacDonald 2000). Above the RSL, where the flow is horizontally homogeneous, there is again a logarithmic dependence of velocity on height but the profile in (1) is shifted upward by a displacement height, *d* (Raupach et al. 1980). Within the canopy (i.e., in the lower part of the roughness sublayer, below $z = h$), the vertical profile of horizontally averaged flow velocity has been approximated by an exponential decay from its value at the top of the canopy (U_h) down to the bed (MacDonald 2000; Cheng and Castro 2002). The mean flow velocity, $U(z)$, inside and above animal forests is thus typically modeled as

$$U(z) = \frac{u_*}{\kappa} \ln\left(\frac{z-d}{z_0}\right) \qquad \text{for } z > 2-3\ h \tag{2}$$

$$U(z) = U_h \exp\left[\alpha\left(\frac{z}{h}-1\right)\right] \qquad \text{for } 0 < z < h \tag{3}$$

where u_* is the friction velocity (which can be related to the flow velocity far above the canopy through a bed friction coefficient), α is the attenuation coefficient of velocity within the canopy (which increases with canopy density, MacDonald 2000), and z_0 is the canopy roughness length. Many attempts have been made to relate the displacement height and roughness length of vegetation canopies to the packing density of the obstacles as well as their arrangement and shape (e.g., Wooding et al. 1973). Similar studies are far less numerous for animal canopies, but similarly point out the difficulty in parameterizing drag and roughness in these systems (Rosman and Hench 2011). The mean velocity between the top of the canopy and the bottom of the logarithmic layer has not been fully described, but has been shown to contain characteristic features that engender strong similarities across the range of canopy flows (as discussed below).

The proposed exponential decay of horizontally averaged velocity within the canopy (Eq. (3)) is in fact a crude approximation to the highly spatially variable flow that develops in dense canopies. Figure 3 displays the horizontally averaged flow between two-dimensional rippled topography and shows that a steady return flow appears near the bed as the spacing between ripples decreases. This renders an exponential fit inappropriate deep within the roughness. Moreover, simulations show that the flow inside the canopy depends not only on the roughness density but also on obstacle shape.

2.3 Inherent Similarities of Canopy Steady Flows

A key feature of the mean velocity profile in canopy flows is the characteristic inflection point (i.e., a point of maximum velocity gradient) that is generated at the top of the canopy, the interface between the low-speed in-canopy flow and

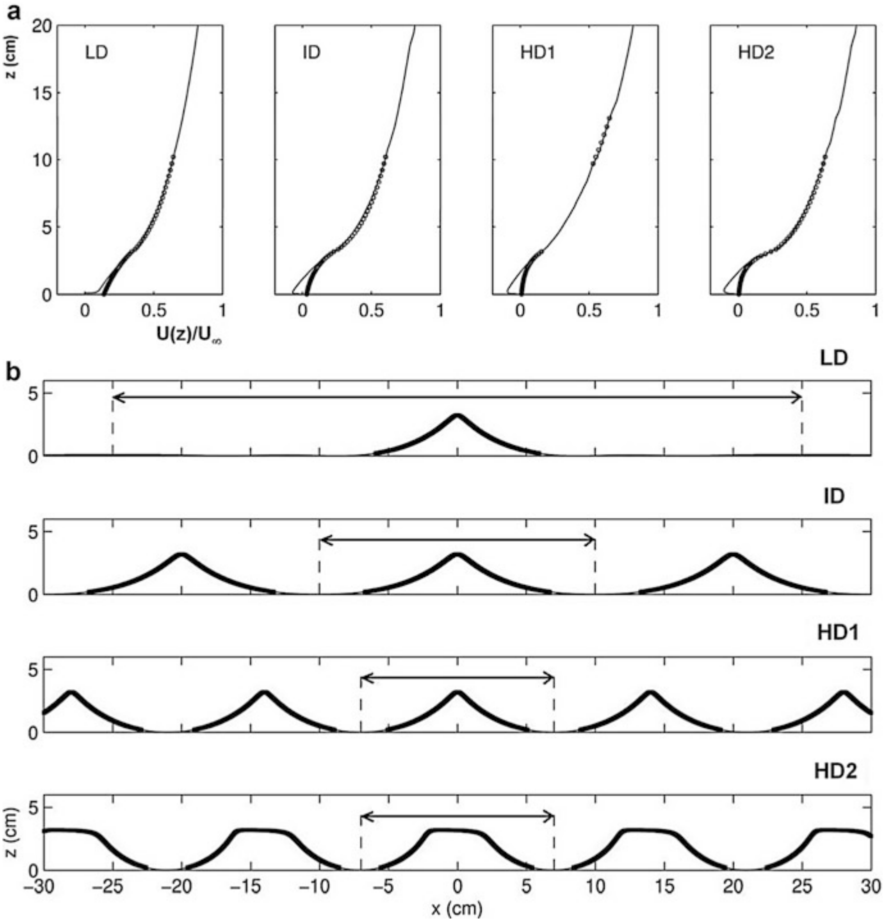


Fig. 3 (**a**) Vertical profiles (solid lines) of the nondimensional temporally and horizontally averaged longitudinal velocity ($U(z)/U_\infty$) for a steady flow of strength U_∞ above rippled beds with different densities. Fits for the logarithmic layer and for the exponential decay of velocity within the roughness are indicated by the circles; clearly, the exponential fit breaks down deep within the roughness. (**b**) The varying densities and geometries of the rippled beds (*LD* low density, *ID* intermediate density, *HD* high density, from Moulin et al. (2007), with kind permission of EDP Sciences)

high-speed above-canopy flow. This inflection point yields the flow inherently unstable to Kelvin-Helmholtz-type vortices (Fig. 4) that dominate the transport of mass and momentum across the top of the canopy (see, e.g., Ghisalberti and Nepf 2005, 2009).

Based on the dominance of these characteristic vortices, Ghisalberti (2009) demonstrated strong similarities across a range of canopy-type flows (termed “obstructed shear flows”), including atmospheric flows over forest canopies and

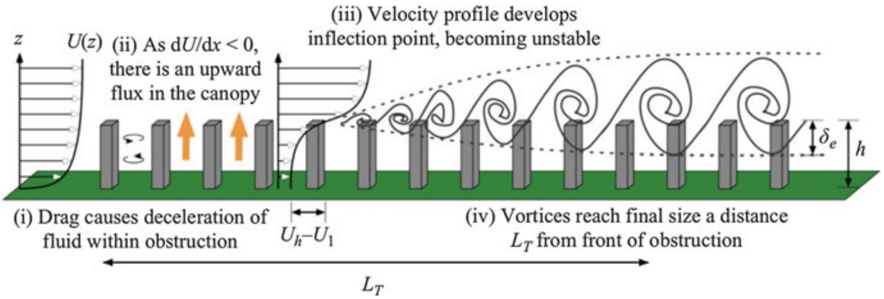


Fig. 4 The streamwise evolution of steady canopy flow. The coherent vortices are a characteristic hydrodynamic feature of canopy flows (From Ghisalberti 2009, with kind permissions of Cambridge University Press)

aquatic flows over coral reefs and seagrass meadows. These similarities exist across a range of canopy scales (from O(mm) – O(10 m)) and provide predictive capability for the structure of the mean and turbulent flow in animal forests. For example, the thickness (δ_e) of the region within the canopy where the vortices drive rapid transport (Fig. 4) is shown to scale inversely with canopy density (given here as the canopy frontal area per unit volume, a), according to

$$\delta_e = \frac{1}{3}(C_D a)^{-1} \tag{4}$$

where C_D is the drag coefficient of the obstacles in the canopy. $(C_D a)^{-1}$ is termed the canopy drag length scale. Similarly, the intensity of vertical turbulent fluctuations (w_{rms}) at the top of the canopy is directly related to the friction velocity:

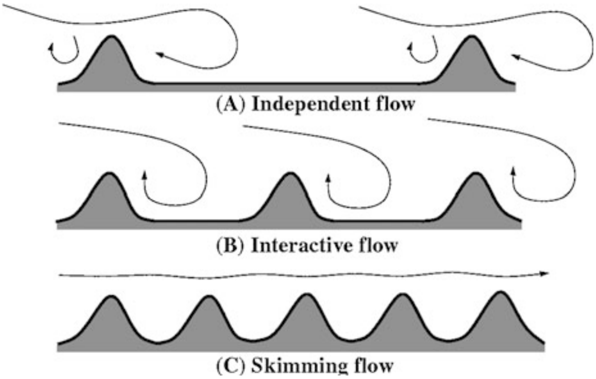
$$w_{rms} = 1.1\ u_* \tag{5}$$

Canopy drag coefficients (as employed in Eq. 4) are not typically known with a high degree of accuracy. Drag coefficients for certain (isolated) geometric shapes are well known, and simplifications have been made using morphological approximations. Vogel (1994) reports drag coefficients of 0.74 for a rectangular solid, 0.76 for an erect cylinder, and 0.32 for a hemisphere. Such approximations may prove useful for some organisms in animal forests (e.g., hemisphere-like stony corals, Hench and Rosman 2013) but, in general, canopies present the additional complications of (a) significant morphological complexity, including variation over height and (b) organisms potentially existing in the wake of upstream elements, which can greatly affect the drag coefficient. Drag estimation becomes complicated further when animal forests are comprised of organisms with a range of ages and hence a range of sizes and shapes, as is frequently observed in highly diversified tropical environments. Moreover, quantification of canopy drag coefficients has remained elusive. Values of canopy drag coefficients are typically in the range 0.4–1.5 (MacDonald et al. 2006), and are at least an order of magnitude greater than bed friction coefficients estimated either from flow measurements over coral reefs (Reidenbach et al. 2006), or used in reef flow modeling (Rosman and Hench 2011).

2.4 Variation of a Steady Flow with Canopy Density

Qualitatively, three regimes of flow within and immediately above animal forests have been identified. These regimes are distinguished by the packing density of the forest and are schematized in two dimensions in Fig. 5 (adapted from Vogel (1994)). At low density, each individual in the forest is not in the wake of the closest upstream individual, and the forest impacts the mean velocity profile only in the vicinity of the individual canopy elements. Both the displacement height (d), and roughness length (z_0), remain small in this regime. As packing density increases, organism wakes begin to interact, such that individual wakes can no longer be identified. The in-canopy flow becomes strongly three dimensional, and local velocities depend strongly on the precise arrangement of organisms. The apparent roughness increases in this regime, but the displacement height remains small. As packing density increases further, forest drag produces a sufficiently strong blockage that a "skimming" flow (where the strength of the in-canopy flow is minimized) occurs above the canopy. This corresponds to a decrease in the roughness length together with a rapid increase in the displacement height. Density thresholds delineating these three flow regimes in real canopies depend on the size of the wake that develops behind each organism, thus varying with organism size and shape as well as flow speed. In the case of atmospheric flows over vegetation canopies, the onset of skimming flows occurs for frontal area density (i.e., the canopy frontal area per unit bed area) larger than 0.2 (MacDonald 2000).

Fig. 5 Three typologies of flow modification in the vicinity of obstacles with increasing packing density (Adapted from Vogel 1994)



2.5 Variation of a Steady Flow with Canopy Flexibility

A significant complication in predicting the flow structure in animal forest canopies arises when dealing with flexible organisms like soft corals (Ghisalberti and Nepf 2006). It has been seen that, even in steady flows, flexible canopies exhibit a coherent, large-amplitude waving (Ghisalberti and Nepf 2002; Ghisalberti and Nepf 2004), termed the *monami* in vegetation canopies (Ackerman and Okubo 1993). The generation mechanism of the *monami*, although still under debate (Singh et al. 2016), has been explained by the passage of the vortices at the top of the canopy, which create strong sweeping motions as they pass (Ghisalberti and Nepf 2006). This coherent waving of flexible canopies significantly modifies the structure of the mean and turbulent flow above and inside the canopy, increasing (relative to rigid canopies) mean velocities inside the canopy and reducing the friction velocity (Ghisalberti and Nepf 2009).

2.6 Structure of the Canopy Boundary Layer in Oscillatory Flows

Marine animal forests are not exposed only to steady unidirectional flows (i.e., currents) but also to oscillatory flows driven by wind waves (shorter periods) and swell waves (longer periods). A description of wave-driven flow requires two parameters: the amplitude of the orbital velocity, U_w, and the wave period, T.

As in steady flow, a boundary layer forms near the bed, within which the wave orbital velocity decreases as the bed is approached. In the absence of a canopy, boundary layers in oscillatory flow are considerably thinner than their unidirectional counterparts. While tidal boundary layers frequently extend over several meters, the boundary layer under a 10-sec wave may extend over only a few centimeters. The thickness of a turbulent oscillatory boundary layer can be approximated by $\sqrt{\nu_t T}$ where ν_t is the eddy viscosity (Nielsen 1992). With flow energy dissipated in such a thin layer, maximum bottom friction velocities can be up to an order of magnitude larger in wave flows than in the corresponding unidirectional flow (Jonsson 1966). As with other turbulent quantities, bottom friction velocities in a wave boundary layer exhibit oscillatory variations at half the wave period (Sleath 1987). However, when velocities are phase averaged, i.e., keeping track of the flow phase along the periodic flow outside the boundary layer, the law of the wall (i.e. logarithmic velocity profile and a linearly increasing mixing length) is observed along a large part of the wave cycle (Jenssen et al. 1989), validating quasi-steady modeling of wave boundary layers (e.g., Grant and Madsen 1979). However, describing with accuracy turbulent quantities within a turbulent oscillatory boundary layer, and particularly the phase lagging of turbulent quantities across it, motivated many more complex numerical modeling (reviewed by Fredsoe and Deigaard (1992), Guizien et al. (2003)).

In the presence of a canopy, a wave boundary layer is considerably less affected than a steady flow boundary layer. The porous nature of the canopy, even at high

Table 1 Summary of the key aspects of flow modification by animal forests

	Low population density	High population density
Current-dominated flow	Flow speed reduced within canopy, fairly uniform rates of mixing through the canopy	Flow speed strongly reduced within canopy, strong turbulent mixing in upper region of canopy, with reduced mixing near the bed
Wave-dominated flow	No significant attenuation of flow within canopy, enhanced mixing in canopy due to unsteady wakes	Moderate flow attenuation within canopy, greatly enhanced mixing at top of canopy

densities, offers comparatively little resistance to pressure transmission within the canopy, and velocity reduction inside the canopy will be smaller than in unidirectional flow (Lowe et al. 2005). No simple description exists for the vertical profile of orbital velocity inside a canopy under wave-driven flow, although Lowe et al. (2008) have developed a unique model for prediction of the overall velocity attenuation of canopies in oscillatory flows. The model is based on the idea that the local velocity deviates from that in the absence of the canopy as a result of both shear stress and canopy flow resistance. Ultimately, however, its use relies on estimation of friction and drag coefficients.

Similarly to steady flows, vortex generation at the top of the canopy is also observed under oscillatory flows. This occurs when two key dimensionless parameters, namely, the Reynolds number (the ratio of fluid internal forces to viscous forces) and Keulegan-Carpenter number (the ratio of the timescale of flow oscillation to that of shear layer formation), exceed threshold values such that an unstable shear layer forms on each wave half cycle (Ghisalberti and Schlosser 2013). This means that vortices are preferentially seen in long and energetic waves over dense canopies.

In summary, developing predictive capability for the structure of the mean and turbulent flow in real marine canopies remains challenging. Nevertheless, a qualitative classification of the effect of the canopy on flow velocity and mixing can be proposed for animal forests (Table 1).

3 The Biogeochemistry Inside and Above the Canopy of the Animal Forest

From a biogeochemical perspective, the analogy between terrestrial forests and marine animal forests is not straightforward given their opposite trophic pathways: trees as autotrophs synthesize organic matter from inorganic nutrients, absorbing CO_2, while animals degrade organic matter into inorganic compounds, releasing CO_2 (N.B. the analogy works somewhat better with tropical corals whose symbiotic association with autotrophic algae puts them in the category of semi-autotrophs). Despite their reversed trophic pathways, an analogy between trees and marine animal forests can be based on their life span; long-lived biota, either autotrophs or heterotrophs, act as carbon sinks through carbon sequestration (albeit temporarily) as long as they grow and thus influence the global carbon cycle in a similar manner.

Furthermore, a change in density of aquatic canopies can shift their role in global biogeochemical cycles from carbon sink to carbon source. While the reduced flow and low turbulence deep in dense aquatic canopies can promote burial of undegraded particulate organic matter due to hypoxic conditions (carbon sink), higher levels of near bed turbulence within canopies of intermediate density can maintain an oxygen supply sufficient to enhance the degradation of sedimenting organic matter (carbon source). The role of marine animal forests in global biogeochemical cycles is also linked to their stability and to the diversity they host. Biogeochemical conditions are essential drivers of the growth of large organisms and cell division in microorganisms. Therefore, it is critical that we understand how the regulation of mass transfer inside and above canopies controls the uptake of biogeochemical compounds necessary for the development of organisms living in or forming canopies, in order to predict their resilience to disturbances (Holling 1973).

3.1 Bulk Mass Transfer Rates Across Canopy Boundaries

At the canopy scale, turbulent mixing regulates the exchange of dissolved and particulate species across the top of the canopy boundaries. Indeed, mass transfer across the top of the canopy is typically related by analogy to turbulent momentum transfer, which is governed by the interfacial hydrodynamics. Turbulent momentum transfer (indicated by u_*) between the in-canopy and above-canopy flows has been described through a momentum exchange velocity, U_E (Bentham and Britter 2003):

$$u_*{}^2 = U_E\left(\mathrm{U}_{ref} - U_c\right) \tag{6}$$

where U_{ref} is the flow velocity at $z = 2.5\ h$ (i.e., near the bottom of the logarithmic layer) and U_c is the depth-averaged velocity inside the canopy.

By analogy, the rate of vertical mass transfer (ϕ) of a dissolved compound across the top of the canopy is thought to be controlled by the same exchange velocity as momentum and expressed by

$$\phi = U_E\left(C_c - C_{ref}\right)/Sc \tag{7}$$

(Moulin et al. 2007) where C_{ref} is the compound concentration at $z = 2.5\ h$ and C_c is the depth-averaged concentration inside the canopy. The compound is characterized by its Schmidt number (Sc), equal to the ratio of the kinematic viscosity of sea water (ν) to the diffusion coefficient of the compound in sea water (D). This characterization of mass transfer can also be described in terms of the Stanton number (St), which represents the ratio of the mass transfer coefficient $\phi/(C_c - C_{ref})$ to fluid advection (U_{ref}):

$$St = \phi/\left[U_{ref}\left(C_c - C_{ref}\right)\right] = U_E/\left(U_{ref}Sc\right), \tag{8}$$

and depends only on the mean flow structure (and a Schmidt number correction). Given its practical utility, formulations of the Stanton number as a function of canopy drag coefficient (as used by Bilger and Atkinson 1992) have been developed to avoid the necessity of explicitly measuring the in-canopy flow and mass transfer rate.

3.2 Uptake Inside the Canopy

For all the progress in understanding rates of mass transfer across canopy boundaries, downscaling bulk fluxes at the canopy scale to the microscale heterogeneity of concentration within the canopy remains a challenge. Within the canopy, transfer to organismal surfaces is expected to be regulated by molecular diffusion in the organism's diffusive boundary layer, which extends over a portion (approximately 10%) of the viscous sublayer. In canopies, the developed surface area where a diffusive boundary layer (DBL) can be present is considerably enhanced compared to uncovered beds in one study of a coral reef, it was found to be 15 times the planar reef area (Dahl 1973).

With the thickness of the DBL proportional to the viscous sublayer thickness, it decreases with the local Reynolds number around the organism and will vary between canopy elements based on the local flow speed and turbulence intensity. Active motile cilia on the epidermis of an organism disrupt the viscous and diffusive boundary layers (Fig. 6), increasing mass transport locally; up to a fivefold enhancement of mass transfer rates to organism surfaces has been observed due to vortical ciliary flows (Shapiro et al. 2014). Among cnidarians which often form animal forests, motile epidermal cilia are present in scleratinian corals (Yonge 1930), but absent in octocorals (Lewis 1982). It is worth noting that not all erected species rely on the physical disruption of the diffusive boundary layer to increase mass transfer; many are active filter feeders that create biomixing (Riisgard and Larsen 2015, this book).

In addition to the spatial heterogeneity of mass transfer inside the canopy, the canopy organisms contribute to strong concentration gradients through their consumption or production. Coral polyps (indicated by red dots in Fig. 7a), where biogeochemical transformations take place through respiration, calcification, uptake, and release of organic and inorganic forms of phosphorous and nitrogen, form a complex three-dimensional distribution of concentration (Fig. 7b).

Mapping the microscale physical and chemical environment that organisms experience requires high-resolution, 3D measurements of both flow and concentration. The current capacity is limited to simultaneous 2D visualization of flow and concentration through a combination of particle image velocimetry (PIV) and particle laser-induced fluorescence (PLIF, e.g., Koehl and Reidenbach 2007, Fig. 7b). Significant advances should be sought to improve the 3D mapping of flow and concentration, which may come from medical (positron emission tomography) or material science (Raman spectrometry, Du et al. 2015) technologies.

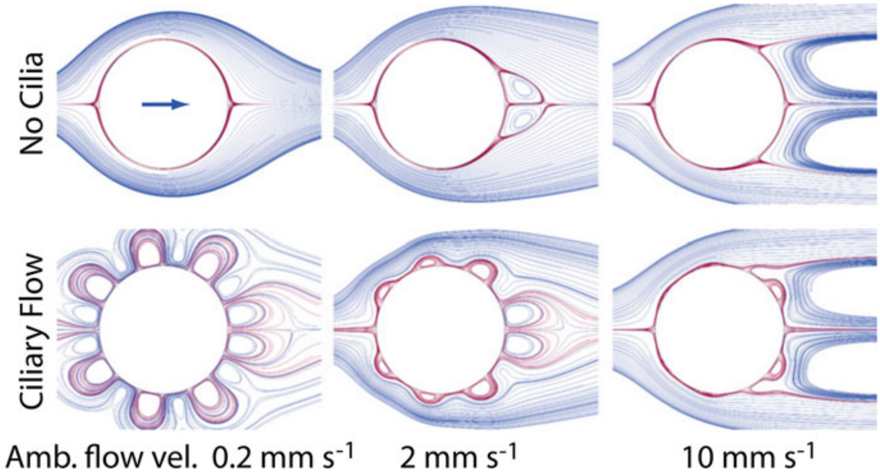


Fig. 6 Streamlines (*shown in blue*) from numerical simulations of flow around a coral branch (diameter = 5 mm). Streamline spacing can be taken as proxy for DBL thickness: the greater the spacing, the thicker the DBL. Ciliary vortical flows (*lower panel*) significantly impact the flow topology and decrease the DBL thickness at low-to-moderate ambient flow velocities, relative to the no-cilia case (*upper panel*). The *arrow* marks the direction of the ambient flow. Streamlines shown in red are those passing within 50 μm of the branch (From Shapiro et al. 2014, with kind permission of PNAS Editions)

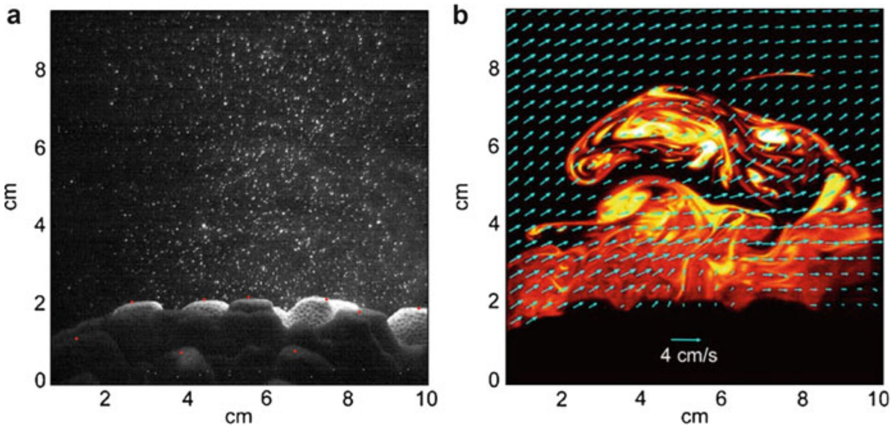


Fig. 7 Example of simultaneous PIV and PLIF measurements over *Porites compressa* coral in a wave-dominated flow (with a weak current present) in a flume. (**a**) A PIV frame, on which opening polyps are indicated by *red dots*. (**b**) A PLIF image of dye concentration released from the coral coating, recorded 0.02 s after the image shown in (**a**). The velocity vectors during this interval are shown in *blue* (From Koehl and Reidenbach 2007, with kind permissions of Springer)

3.3 Relating Bulk Mass Transfer Across the Canopy to Local Mass Transfer Limitations

An important application of the Stanton number characterization of bulk mass transfer across canopies was in the demonstration that local nutrient uptake by coral reef organisms is frequently mass transfer limited and not biologically controlled. It has been shown that Stanton numbers for phosphate in experimental coral reefs (assuming infinitely rapid uptake, i.e., taking $C_c = 0$) agree well with those estimated from engineering formulations that only consider the hydrodynamic influence of the reef roughness (Bilger and Atkinson 1992). Other methods for quantifying the influence of fluid-canopy interactions on nutrient supply can be based on comparisons of timescales of nutrient consumption (if known) and canopy flushing (e.g., Kregting et al. 2011). Mass transfer limitation on reef flats has been shown for ammonia and nitrate, including under waves (Falter et al. 2004), demonstrating the high demand for these compounds in coral reefs. Similarly, mass transfer limitation has been shown for ammonia in seagrass and macroalgae canopies (Cornelisen and Thomas 2009; Stephens and Hepburn 2014). For heterotrophic forest-forming species, such as temperate gorgonians, the validity of assuming mass transfer limitation for basic resources (oxygen and organic compounds) must be investigated.

Eddy correlation techniques allow direct measurement of turbulent diffusive fluxes of a compound, provided a high-frequency, small-scale technique exists to measure the compound concentration and its turbulent fluctuations. In marine systems, such measurements can currently only be provided by microelectrode sensors, which effectively limits the technique to quantification of fluxes of dissolved oxygen (Berg et al. 2003). Importantly, eddy correlation techniques allow quantification of local fluxes under both wave- and current-dominated flows. The eddy correlation approach has been used to monitor spatial and temporal variability of respiration and photosynthesis rates over the slope and crest of a coral reef (Long et al. 2013). In this study, respiration rates increased with current velocity, suggestive of mass transfer limitation. Rates of respiration and gross primary production were higher on the reef crest (dominated by gorgonians and soft corals) than on the reef slope (dominated by sand and pavement).

4 Living in the Canopy of the Animal Forest

Habitat complexity has long been recognized as increasing biodiversity and biomass, explained through the provision of a diversity of niches (MacArthur and MacArthur 1961). Aquatic canopies built by flora or fauna display structural complexity and have been shown to host higher diversity and biomass than bare beds (Benedetti-Cecchi et al. 2001; Emslie et al. 2014). Yet, the relationship between canopy complexity (measured through precise canopy descriptors) and the hosted diversity and biomass still needs to be defined. In a recent study, the overall fish population biomass (driven by large fishes) was positively correlated with the density of kelp stipes forming a canopy over temperate rocky reefs (Trebilco et al. 2015). The fish population structure, however, was more closely correlated to the roughness of the undercanopy rocky substratum. While this study is clearly a step toward a more quantitative description of understory species habitat, it highlights the lack of a mechanistic conceptualization of habitat complexity, one that integrates the effects of the underlying substratum roughness and the canopy to predict the overall flow structure. Moreover, although canopy density likely influences the living conditions of fishes inside the canopy, the increase of fish biomass with canopy density is not straightforward given the nonlinear effect of density on the canopy flow structure. Indeed, near bed turbulence intensity first increases with density (as indicated by an increase in roughness length) but then decreases with the onset of skimming flow in dense canopies (increase in displacement height, Vogel 1994).

Elucidating the functional role of canopies requires consideration of the combination of all physical and chemical factors that are (1) locally or globally modified within a canopy and (2) that define the fundamental niche of a hosted species. A fundamental niche (sensu Hutchinson 1957) is defined as the set of abiotic conditions in which a species can live. Fundamental niche explorations should rely on different experimental or observational strategies according to the motility of hosted species. For sessile species, fundamental niches should be sought with an Eulerian approach, that is, monitoring in fixed locations, determining regions where temporal variations in physical and chemical conditions are within acceptable ranges. For mobile species, fundamental niches should be sought with a Lagrangian approach, that is, monitoring conditions along potential organism paths.

4.1 Living in a Sparse Animal Forest

In marine animal forests with low population density, the flow intensity will display some localized variation, creating a dependence on organism arrangement of rates of mass transfer to organism surfaces. Hosted and more precisely associated fauna and flora are expected to display a spatial structure reflecting the wakes developing behind each individual. In such open forests, mass transfer into the canopy will not be significantly affected, and the biogeochemical conditions are expected to be similar to those in the absence of the animal forest (except in individual wakes), such that the physical conditions will be dominant in structuring the biota, particularly in determining colonization processes (settlement and post-settlement survival). Individual wakes should increase local larval retention and could potentially facilitate densification of the forest by self-recruitment of the canopy-forming species as long as intraspecific competition remains small. However, such densification may be slow compared to algal growth in photic areas, suggesting that shallow animal forests would be less resilient to perturbation than deeper ones.

4.2 Living in a Moderately Populated Animal Forest

In marine animal forests of intermediate population density, canopy patchiness leads to spatial heterogeneity of mass transfer into the canopy and flow intensity (together with some light penetration) which should promote diversification of trophic niches, enabling the development of slow-growing sessile autotrophs competing for space with sessile heterotrophs. In this context, despite high local retention of larvae by the animal forest, recruitment success will probably be low due to strong intra- and interspecific competition. The settlement of sessile heterotroph larvae in these environments should be favored in regions of rapid mass transfer into the canopy. The larvae of some species are able to respond sufficiently quickly to turbulent fluctuations so as to change and adapt their locomotory behavior to more precisely follow chemical cues to appropriate sites (Koehl et al. 2007). The ability of larvae with low motility to maintain themselves in the appropriate Lagrangian niche seems to depend on the larval sinking speed: only those larvae with a sufficiently high density or rapid behavioral changes (e.g., velum retraction, cessation of swimming) will settle rapidly enough. Patchy flow conditions and partial visual occlusion should limit the size of highly mobile species (like fishes) seeking low-flow refuge in animal forests. In summary, marine animal forests of intermediate population density are expected to be characterized by (1) a high diversity of sessile species, autotrophic and heterotrophic, whose distribution could reflect the colonization ability of larvae advected from distant sites, and (2) strong intra- and interspecific competition. Hosted mobile species are expected to be diversified, due to the variety of trophic resources associated with the diversity of sessile species and the spatial variability of the flow (Finelli et al. 2009). Such hosted species are expected to be limited in number and size, depending on the size and shape of the canopy-forming organisms. In marine animal forests of intermediate density, the choice of spatial and temporal scales used to describe in-canopy conditions is incredibly important, as canopy-averaged values may differ greatly from those actually experienced by organisms. Upscaling procedure should take into account not only average but also variance and covariance descriptors. Quantile descriptors should also be considered to express the proportion of time or space over which given conditions are experienced.

4.3 Living in a Dense Animal Forest

In dense canopies (of either autotrophs or heterotrophs), the reduction of rates of mass transfer near the bed associated with the low in-canopy flow is expected to lead to the accumulation of compounds excreted by the canopy-forming species. Similarly, the consumption of compounds useful to the canopy-forming species can lead to their depletion. Local modification of the biogeochemical and mass transfer conditions below dense assemblages of macroalgae growing on sessile corals was found to be deleterious to the development of sessile corals, due to the reduction in oxygen concentration and increase in dissolved organic carbon concentration (Hauri et al. 2010). Combining limited diffusion and high rates of consumption, sessile species hosted in dense canopies are expected to be limited to those having a different trophic regime than the canopy-forming species. However, near the bed in dense heterotrophic marine forests, low light conditions should also prevent the development of algae. In the absence of competition with algae in a low-flow environment, bacteria associated with hypoxic environments will likely be favored, in turn leading to low biomass and a uniform composition of sessile species. One could expect a dense canopy to be monospecific, or at least formed by species sharing similar growth traits. Indeed, a canopy will adjust so as to have a large surface area in the high-velocity, turbulent region of the canopy flow, where the DBL around the organism surface is thin. Such a mechanism was proposed recently to explain the existence of the oldest known marine animal forest in the deep ocean of the Precambrian era (Ghisalberti et al. 2014). In the low-flow and nutrient-rich conditions of the Precambrian ocean, tall rangeomorphs could have grown up to 2 m relying on osmotic uptake only, due to an increased mass transfer to the organism surface resulting from a thinned DBL. As a consequence of limited diffusion and flow velocity in the lower part of the canopy, one can expect dense canopies to be cleared of smaller sessile species, freeing space for mobile species like fishes looking for shelter from predators and low-flow conditions to rest. The amount of open space in the lower canopy might even increase as the canopy grows, as some canopy-forming species with a treelike shape experience population density decay though a self-thinning mechanism (Cau et al. 2016). In this case, the hosted biomass is expected to increase with the growth of the canopy-forming species. In summary, one could expect dense marine animal or vegetal forests to (1) be composed of sessile species of similar height, (2) host a diverse and large biomass of highly mobile species like fishes that are using the canopy as refugia, and (3) a diverse microbiota subsisting on by-products of macrobiota function.

5 Conclusions and Future Directions

Local modification of the physical and biogeochemical environment by erect animals living on the sea floor has long been recognized as a key factor generating high biodiversity and biomass in the understory. While there is a fairly comprehensive understanding in the environmental fluid mechanics community of the modification of the flow structure generated by these animal forests, these modifications are not well known among the biological community studying these diverse assemblages. In this sense, marine animal forests are archetypal of ecosystems whose study requires more interdisciplinarity and reciprocal pedagogy to advance knowledge. Indeed, going beyond the term “habitat complexity” to explain species associations in a unified framework to yield a typology of forest requires an understanding of physically relevant parameters such as canopy planar and frontal density, roughness and drag coefficients, and nondimensional parameters such as the Reynolds, Keulegan-Carpenter, and Stanton numbers.

Research into the physical and biogeochemical environments around scleratinians has demonstrated the relevance of such an interdisciplinary approach in explaining species function. Drawing scientific attention to scleratinians in the last 40 years was possible given the climatic and overfishing threats that they face. However, other marine animals, such as gorgonians, soft corals, and sponges (Maldonado et al. 2015, in this book), form animal forests that may colonize areas freed up by scleratinians and provide an alternative complex habitat for understory species. The flexibility of soft coral species contrasts with the stiffness of scleratinian species, making their hydrodynamic influence similar to that of vegetation canopies.

The ultimate goal of such interdisciplinary research should be to develop models of marine animal forest functioning and to compare predictions and observations of niche extent in a meta-community approach. Such models will then be useful in the prediction of biodiversity evolution under climatic and anthropogenic stresses, thereby assisting conservation efforts.

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Demography of Animal Forests: The Example of Mediterranean Gorgonians

19

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Abstract

Gorgonian corals may form dense canopies, resembling miniature forests. Similarly to terrestrial forests, gorgonian canopies can increase local complexity and biodiversity. The demographic study of gorgonian populations can supply valuable tools to our understanding of their complex, long-lasting life cycles. In this chapter we report on the demographic history of two Mediterranean gorgonian corals provided of opposite reproductive strategies: *Paramuricea clavata* and *Corallium rubrum*. The two study cases show how a demographic approach can

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be applied to study the effects of disturbances (mass mortality in *P. clavata* and harvesting in *C. rubrum*) on long-lived species. The population of *P. clavata*, object of our study, dwells at the edge of the summer thermocline in the NW Mediterranean Sea. It has been strongly affected by two high mortality events in 1999 and 2003, associated with an anomalous high temperature of the water column. Long-term data (12 years) allowed the analysis of the population structure before and after the mortality events which killed 78% of the colonies. Nowadays the population is recovering, exhibiting a fivefold increase in recruitment density despite the reproductive output reduced to 7.25%. Our observations support the hypothesis of an over abundant reproductive output of the species and a strict density-dependence control of recruitment operated by larger colonies in crowded, stable *P. clavata* populations.

C. rubrum is a long-lived, slow-growing, and low reproductive gorgonian, whose populations living in the shallower part of the species bathymetric distribution range (between 20 and 50 m depth) are mainly composed by crowded colonies having a small size/early age at first reproduction and high recruitment rates. Deep populations (deeper than 50 m), mainly composed by large colonies, are the main target of commercial fishing nowadays. The minimum harvestable colony size is 7 mm of colony basal diameter, according to General Fisheries Commission for the Mediterranean (GFCM) Scientific Advisory Committee (SAC). Report of the transversal workshop on red coral Ajaccio (Corsica) (5–7 Oct 2011) stated that sexual maturity is reached at an age of about 30–35 years. The assessment of population structure in size/age classes of reproductive and survival rates allowed to project population structure over time.

Keywords

Octocorals • Mesophotic corals • *Paramuricea clavata* • *Corallium rubrum* • Demography • Population dynamics • Mediterranean Sea

Contents

1 Gorgonians: The Mediterranean Miniature Animal Forests

Corals are the main ecosystem engineer species forming the so-called animal forests. With their three-dimensional structure, they modify the environment facilitating the settlement of other species (Chapter 38, Paoli et al. Ecosystem Functions and Services of the Marine Animal Forests). The disappearance of these engineer species may have indirect effects on the whole community, changing habitat conditions (flow regime, food availability, and shelter; Soulé et al. 2003). Similarly to the trees in the terrestrial habitat (i.e. Kwit et al. 2004), corals are characterized by long life cycle that in some cases can exceed centuries (Roark et al. 2006, 2009; Benedetti et al. 2016; ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species”, Lartaud et al.,). Demographic studies on long-lived, slow-growing circalittoral species require dedicated long-term research, which provides basic knowledge on the complex dynamics of their populations. Such knowledge is essential for planning rational measures for conservation and management (Caswell 2001).

Gorgonian corals are long-lived, slow-growing species, forming patches of dense canopies which resemble miniature terrestrial forests (Rossi 2013; chapter 14, Guizien and Ghisalberti. Living in the Canopy of the Animal forest: Physical and Chemical Aspects). They are main components of the Mediterranean *coralligenous species assemblages*, characterized by one of the world’s highest biodiversity (Ballesteros 2006 and references therein), and play a pivotal role in the transfer of energy from the less stable, high-turnover planktonic system to the more stable benthic one due to their suspension feeding strategy which implies the capture of seston via their three-dimensional fans (Gili and Coma 1998; Chapter 17, Sebens et al. Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders; Chapter 23, Rossi et al. Benthic-pelagic Coupling: New Perspectives in the Animal Forests).

Long-term data showed high variability in life history traits between gorgonian populations of different species. Reproductive output, in particular, can vary over broad ranges (Santangelo and Bramanti 2010; Torrents and Garrabou 2011). Some variability in life history traits have been observed also between populations of the same species (Tsounis et al. 2007; Linares et al. 2010; Priori et al. 2013; Bramanti et al. 2014; Montero-Serra et al. 2015; Cau et al. 2016). Different life histories may produce different population dynamics, and hence gorgonians may exhibit species- and population-specific responses to high mortality events.

In this chapter we review the demographic features of two Mediterranean gorgonian corals: *Paramuricea clavata* (Risso 1826) and *Corallium rubrum* (L 1758).

P. clavata form dense canopies on vertical and subvertical cliffs with low irradiance and intense water flow (within the *coralligenous* species assemblages; Ballesteros 2006). The species has been found on rocky shoals down to 120 m depth (Bo et al. 2012), but the highest population abundance is reported between 15 and 35 m (Linares et al. 2008), and the size of the colonies can reach 1.5 m height (Linares et al. 2008). *P. clavata* populations are widespread in the Western Mediterranean Sea (Carpine and Grasshof 1975) and in the Adriatic Sea (Kipson et al. 2014) but are less common in the Aegean Sea (Öztürk et al. 2004).

The Mediterranean red coral (*C. rubrum)* is a long-lived, slow-growing species, distributed throughout the Mediterranean Sea and adjacent Atlantic rocky shores. Its bathymetric distribution is comprised between 10 and 800 m, but it is more common between 30 and 200 m (Costantini et al. 2010; Cau et al. 2016). This species has gained considerable attention from the scientific community because of its cultural and economic relevance, which is linked to the use of its red calcium carbonate ($CaCO_3$) skeleton in the jewelry industry (Santangelo and Abbiati 2001; Tsounis et al. 2010 and references therein).

Due to the differences in their reproductive parameters (Linares et al. 2007; Santangelo and Bramanti 2010; Viladrich et al. 2016), the comparative study of these two Mediterranean gorgonian species may provide valuable insights on the responses of gorgonian coral populations to drastic mortality events.

2 Recovery After Drastic Mortality Event: The Study Case of a *Paramuricea clavata* Population in the Gulf of La Spezia (Ligurian Sea)

Paramuricea clavata (Risso 1826) is a long-living (50 years; Coma et al. 1995) species, with high reproductive output with respect to other Mediterranean gorgonians (Cupido et al. 2012; Viladrich et al. 2016). Synchronous spawning occurs twice a year from June to August, with spawning episodes lasting 2–3 days and separated by several days (Linares et al. 2007; Cupido et al. 2012). After spawning, oocytes remain on the surface of the parental colony for some days (surface brooding). Large colonies may produce hundreds of thousands oocytes, and due to the density of the patches, hundreds of thousands or even millions oocytes per m^2 can be released (Cupido et al. 2012; ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species”, Lartaud et al.,). *P. clavata* populations are generally considered to have low recruitment rate and slow dynamics, due to the high mortality rates of early settled larvae (Linares et el. 2008). Our long-term data showed that these features can drastically change under increased mortality rates.

During late summer 1999 and 2003, a population of *P. clavata* dwelling in La Spezia Gulf (Ligurian Sea, Italy) suffered two mass mortality events linked to an anomalous temperature increase (Cerrano et al. 2000). Thanks to the availability of demographic data collected in 1998 (before the mass mortality) and in the following years, a comparison between the pre- and post-mortality populations and simulations of population trends has been carried out. The demographic structure and the dynamics of the affected population have been examined, and in particular, three features have been object of detailed study:

1. Population structure in terms of size/age classes based on the mean annual colony growth rate and mortality/survival
2. Size at first reproduction, fertility, and fecundity of polyps and colonies of the different classes

3. Reproductive output and recruitment density of the impacted population

Pre- and post-mortality data were compared, and a detailed transition matrix averaged over 3 years following the mortality event was set up and used to project population trends over time (Table 1 and simulations in Fig.4).

The following paragraphs provide a brief summary of the methods adopted; a detailed description can be found in Cupido et al. (2008; 2009; 2012) and Santangelo et al. (2015).

2.1 Study Site, Sampling, and Model Parameterization

Long-term data have been collected in the period 1998–2012 on a population living at the western edge of the Gulf of La Spezia (Ligurian Sea, Italy, 44°.01’ N, 09°.50’E), off the western edge of Tinetto Island, on a vertical cliff just below the upper bathymetric limit of the summer thermocline (between 17 and 25 meters depth). High turbidity characterizes the sampling area. Because the studied population was small, likely geographically isolated, and heavily impacted, the research has been based as much as possible on nondestructive samplings and measurements (photographs and direct colony measurements taken in the field on fixed and random plots). Annual recruitment included all new colonies found on the fixed plots, just before spawning. Population sex ratio, fertility, fecundity, and reproductive output of female colonies have been examined on freshly collected tips from colonies of different sizes (n = 205), just before spawning (Cupido et al. 2012).

The mean annual growth rate (in height) was measured on a sample of labeled colonies (n = 243) over 3 years and used to divide the population in size/age classes assigning to each colony the most probable age for its size (henceforth they will be called size/age classes; Santangelo et al. 2007; Bramanti et al. 2014). This division allows a temporal resolution of the model, supplying a time step for iterating the population size structure in simulations (Bramanti et al. 2014; ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species”, Lartaud et al.,). The demographic model set out to simulate population trends was based on a modified *Leslie* transition matrix (Caswell 2001) which takes into account the individual fate of colonies recorded on fixed plots over the period 2007–2010. The possible fates of the colonies have been schematized as follow:

1. Colony survives and grows passing to the next, larger class.
2. Colony survives but does not grow, remaining in the same class.
3. Colony survives and grows faster skipping to a class larger than the next one.
4. Colony survives but shrinks, passing to a smaller class.
5. Colony dies.

Values in the diagonal of the matrix represent the proportion of colonies remaining in the same class in a single time step (1 year; Table 1).

Table 1 Transition matrix for the *Paramuricea clavata* La Spezia population. The matrix presents percentage colonies that grow by one size class each year (in bold), percentage colonies that grow by a number of classes each year (they grow more), percentage of colonies remaining in the same size class, and the few colonies that regress to a smaller class due to the loss of apices

Size class	1	2	3	4	5	6	7	8	9	10	>10	survival
1	0.18	**0.38**	0.10									**0.66**
2		0.21	**0.38**	0.19								**0.78**
3			0.27	**0.40**	0.16							**0.83**
4				0.24	**0.40**	0.24						**0.88**
5				0.11	0.37	**0.31**	0.09					**0.88**
6					0.12	0.38	**0.32**	0.11				**0.93**
7						0.09	0.41	**0.28**	0.14			**0.93**
8								0.49	**0.43**			**0.92**
9								0.22	0.49	**0.25**		**0.96**
10										0.67	**0.25**	**0.92**
>10											0.72	**0.72**

2.2 Mortality and Recovery Dynamics

2.2.1 Density

Population density before the mortality event (1998) was high (35.7 colonies m^{-2}). In 1999 and 2003, 78.3% of the colonies were affected by partial or total mortality bringing density to low values (7.9 colonies m^{-2}; Santangelo et al. 2015). Density remained low between 2004 and 2006 (Fig. 1), and population structure shifted to smaller sizes. Between 2007 and 2010, the population experienced a positive growth ($\lambda > 1$), and colony density increased up to about half of the pre-mortality values (Fig. 1).

2.2.2 Recruitment

A decrease in recruitment was recorded immediately after the mortality events. Recruit density decreased from 2.6 ± 0.5 in 1998 to around 0.8 ± 0.3 recruits m^{-2} between 2004 and 2006 (Santangelo et al. 2015). Recruitment levels increased in the period 2007–2010 during which recruitment rates were fivefold higher (Fig. 1). A twofold increase in recruit density following a mass mortality event was found by Cerrano and colleagues (Cerrano et al. 2005).

2.2.3 Size Structure

Based on the mean annual colony growth rate (3 ± 0.7 cm y^{-1}), the population was divided into size/age classes. All the size/age structures found in the different years showed *monotonic*, regularly decreasing patterns, in which recruitment (the first age class) was the dominant class (Fig. 2). The proportion of large colonies increased in 2009 and 2010.

The population was completely gonochoric, and sex ratio was balanced (not diverging significantly form a 1:1 ratio). According to nearest neighbor, chi-square analyzes the spatial distribution of nearest-neighbor colonies of the same sex diverged significantly from randomness, suggesting some sexual segregation in the population (Cupido et al. 2012). The size at first maturity of female colonies was 8.5 cm (approximately 3 years old), but only 20% of colonies were sexually mature at this size. The percentage of mature colonies reached 100% in bigger/older colonies (over 31.5 cm and 11 years), and the number of polyps increased exponentially with size. Also polyp fecundity increased with colony size (up to 20 mature oocytes per polyp), resulting in an overall increase of fecundity with colony size which can easily reach 250,000 oocytes per colony (Fig. 3). The majority of the population reproductive output (77%) is produced by classes 6–10 representing only one fifth of the overall population; in contrast, colonies in classes < 6, despite their abundance (77%), accounted for only 3.8% of the population reproductive output due to their smaller size and lower fecundity and fertility. Largest-oldest colonies accounted for about 20% of the reproductive output (Linares et al. 2007; Cupido et al. 2012; Santangelo et al. 2015).

After the two high mortality events, the estimated population reproductive output reduced by 92.5% (from 2,000,000 to 145,000 oocytes m^{-2}) due to reductions in

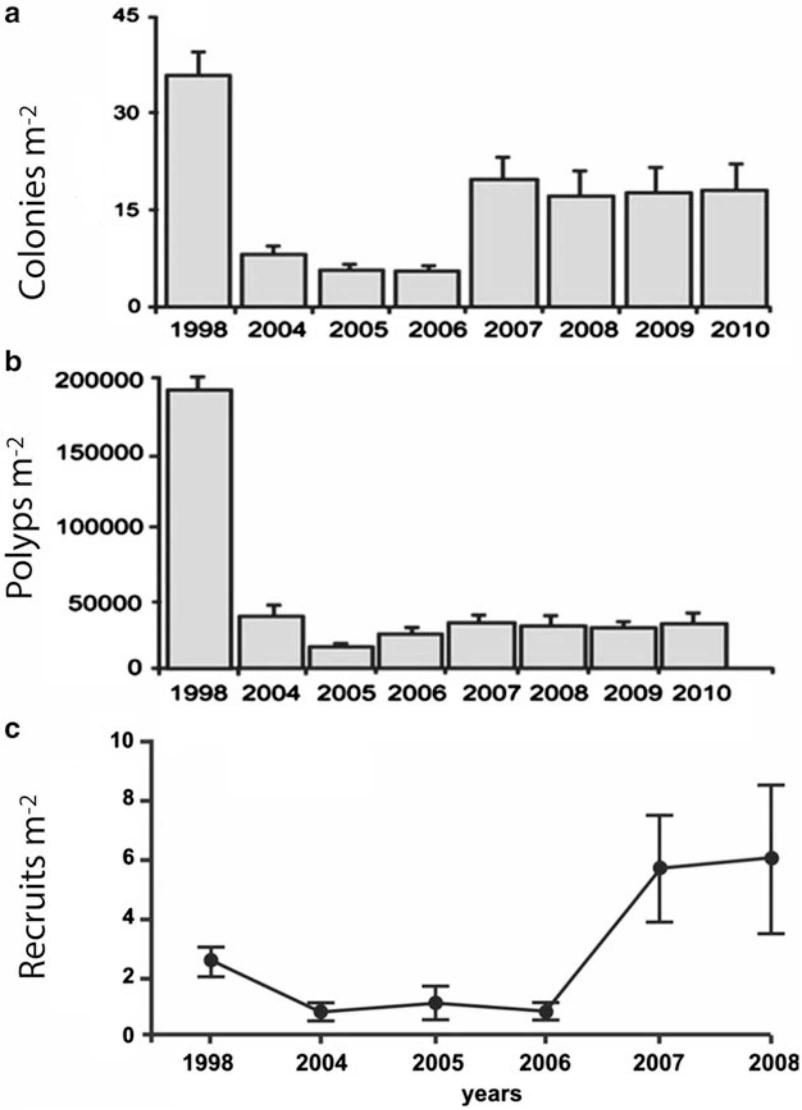

Fig. 1 Trends of colony density (**a**), polyp density (**b**) and recruitment density (**c**) in the *Paramuricea clavata* population of La Spezia (Italy). (Modified after Santangelo et al. 2015)

both colony density and size; at the same time recruitment increased fivefold (Cupido et al. 2012).

All the survival values recorded in the fixed plots over the period 2007–2010 are included in the population matrix averaged over 3 years (see Santangelo et al. 2015); this matrix allowed to project population trends over time (Table 1; Fig. 4). The projections exhibited damped oscillations and then stabilized after several cycles at a

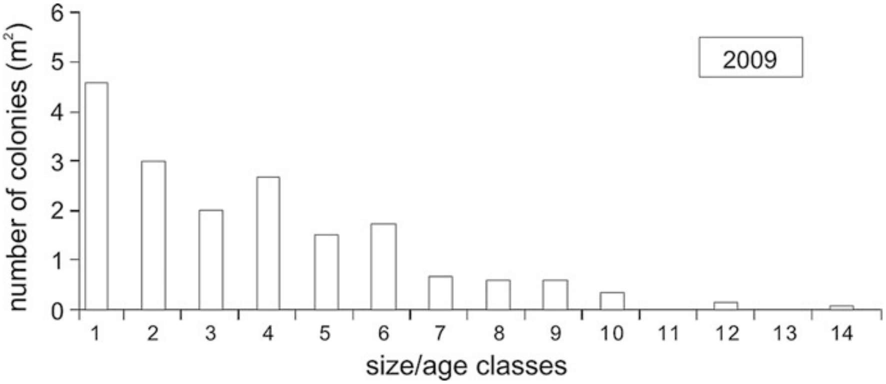

Fig. 2 Size structure of the *Paramuricea clavata* population of La Spezia (Italy) (Modified after Cupido et al. 2008)

Fig. 3 Exponential fit of colony size/age and fecundity in the *Paramuricea clavata* population of La Spezia (Italy) (Modified after Cupido et al. 2008)

polyp density that was about 1/4 of the pre-mortality value, which has not ever been reached.

3 The Mediterranean Red Coral *Corallium rubrum* (L. 1758): An Exemplary Case Study of an Overexploited Gorgonian

The Mediterranean red coral (*Corallium rubrum*) is one of the marine species with the highest commercial values. Due to the use of the red carbonate skeleton in jewelry industry, this octocoral has been harvested and traded for over 2,000 years

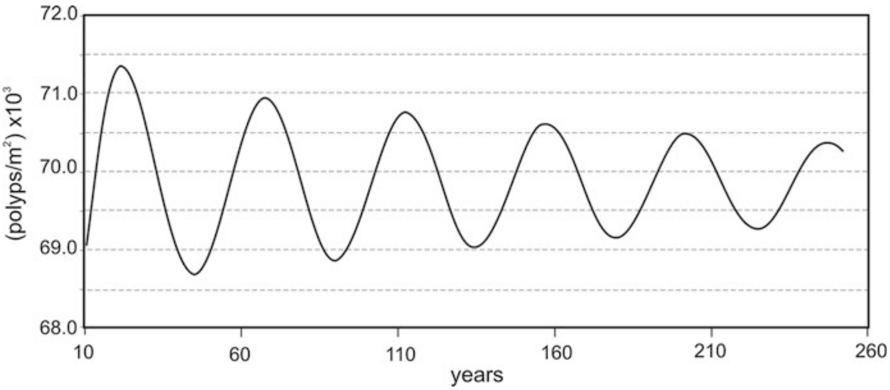

Fig. 4 Simulation of *P. clavata* population trends. After some damped oscillations, the population is near stabilizing at a polyp density about 1/3 of that in the pre-mortality population (Modified after Santangelo et al. 2015)

(Tsounis et al. 2010 and references herein), and several populations have been overexploited (e.g., Cicogna and Cattaneo 1993; Santangelo et al. 1993; Tsounis et al. 2013). *C. rubrum* is a component of the deep circalittoral rocky bottoms *miniature animal forest* (Ballesteros 2006), exhibiting an extensive bathymetric distribution (Carpine and Grasshoff 1975; Costantini et al. 2010; Cau et al. 2016).

3.1 Shallow Populations

In the recent years, the main demographic and reproductive features of the populations dwelling within 50 m depth have been deeply studied, and the resulting picture reveals that *C. rubrum* is a gonochoric species with *discrete* (time-limited) reproduction (in summer), low polyp fecundity (Santangelo et al. 2003; Tsounis et al. 2006; Torrents and Garrabou 2011), and high adult colony and recruit densities (300 colonies and 600 recruits m^{-2}; Bramanti et al. 2005; 2014; Santangelo et al. 2012). Colony growth rate is extremely slow (0.24–0.36 mm y^{-1} in basal diameter; Garrabou and Harmelin 2002; Marschal et al. 2004; Torrents et al. 2005; Gallmetzer et al. 2010; Bramanti et al. 2014; ▶ Chap. 22, "Growth Patterns in Long-Lived Coral Species", Lartaud et al.,), and life-span may overcame one century (Garrabou and Harmelin 2002; Priori et al. 2013). Colony reaches early (and at a small size) the age at first reproduction (Santangelo et al. 2003; Gallmetzer et al. 2010; Bramanti et al. 2014), and genetic differentiation has been found at small spatial scale (Ledoux et al. 2010; Costantini et al. 2011). Due to the intense harvesting, shallow populations (shallower than 50 m depth) are generally characterized by small and crowded colonies (with the exception of populations dwelling in enforced marine protected areas which can reach larger sizes, Bramanti et al. 2014; Cau et al. 2016). Despite the low commercial value of the small colonies, some shallow populations are still subjected to overexploitation; moreover some of them have been affected by mortality events (Garrabou et al. 2001; Bramanti et al. 2005). Recently, the General Fisheries Commission for the Mediterranean (GFCM) has promoted a ban on the fishing of these populations, as well as a minimum legally harvestable size (colony basal diameter of 7 mm, corresponding to an average age of 30–35 years; GFCM 2011).

3.2 Deep Populations

The size shift observed in the shallow populations due to the intense harvesting pushed fishermen to harvest on populations deeper than 50 m depth which have now become the main fishing target (Tsounis et al. 2010). These populations are mainly composed of large, sparse colonies, and the main demographic features (e.g., population density, size and age structure, mortality, fertility, fecundity, larval output, recruitment) are still poorly known (Rossi et al. 2008; Santangelo and Bramanti 2010). Only very recently some researches gathered further demographic and genetic knowledge on these populations (Costantini et al. 2011; Priori et al. 2013; Angiolillo et al. 2015; Cau et al. 2016).

3.3 Demography of *Corallium rubrum*

Life history tables summarize the demographic traits of the individuals inside a population and are useful tools for the compilation of transition matrices. Demographic models based on transition matrices allow to project population structure over time (Caswell 2001; Santangelo et al. 2007). In the case of *Corallium rubrum*, a population model based on a Leslie matrix has been parameterized with data on growth rates, recruitment, fecundity, and mortality collected in some shallow populations (Table 2) (Bramanti et al. 2009, 2014; Santangelo et al. 2015).

3.3.1 Growth Rates

Colony growth rates in *C. rubrum* are determined by staining and counting the growth rings on thin sections (50 μm). To this purpose, the organic matrix staining method (OMS), validated by Marschal et al. (2004), is applied (see details on methods and results in ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species”, Lartaud et al.,).

3.3.2 Recruitment

Recruit density varied between years and on a small spatial scale exhibiting high values in the shallow populations in which it was studied ($0.56–6 \times 10^2\ m^{-2}$, Bramanti et al. 2005; 2007; Santangelo et al. 2012). At higher spatial scale, tenfold differences in recruitment rates have been recorded (Garrabou and Harmelin 2002; Bramanti et al. 2005, 2007, 2014; Santangelo et al. 2012).

Table 2 Life table of a *red coral shallow* population (Calafuria Livorno, Italy) (Modified after Santangelo et al. 2007)

Class	Colonies	Survival	Fertility	N° of Planulae/polyp	Sex ratio	N° of polyps/colony	N° of Planulae/colony	N° of Planulae/class
1	822.00	0.89	0.00	0.87	0.58	0.00	0.00	0.00
2	731.00	0.63	0.00	0.87	0.58	6.20	0.00	0.00
3	463.00	0.70	0.36	0.87	0.58	15.91	0.15	1338.86
4	323.00	0.52	0.64	0.87	0.58	31.06	10.03	3240.58
5	167.00	0.44	0.82	0.87	0.58	52.18	21.59	3605.88
6	73.00	0.29	0.97	0.87	0.58	79.72	39.02	2848.47
7	21.00	0.57	0.98	0.87	0.58	114.06	56.41	1184.57
8	12.00	0.33	0.99	0.87	0.58	155.58	3.26	932.65
9	4.00	0.75	1.00	0.87	0.58	204.24	103.23	412.91
10	3.00	1.00	1.00	0.87	0.58	261.33	131.87	395.61
11	3.00	0.33	1.00	0.87	0.58	326.14	164.57	493.71
12	1.00	1.00	1.00	0.87	0.58	399.23	201.46	201.46
13	1.00	–	1.00	0.87	0.58	480.87	242.65	242.65

Recruitment is the dominant class (Santangelo and Bramanti 2010), and the frequency distribution of size-age classes exhibits a monotonic, regularly decreasing trend (Santangelo et al. 2007;Bramanti et al. 2014) in the studied shallow populations (Fig. 2), suggesting that these populations are in *steady state*. Such colony size distribution may exhibit different patterns if sampling is selective for larger colonies, either in small samples or samples collected in areas marginal to the main populations and therefore irregularly colonized by *C. rubrum* (Priori et al. 2013; Santangelo and Bramanti 2010; Doughty et al. 2014; Angiolillo et al. 2015).

3.3.3 Reproductive Features

C. rubrum is a gonochoric internal brooder (oocytes are internally fertilized and developed larvae are released). The minimum size at first reproduction is 1.8 mm (basal diameter), corresponding to an age of about 3 years, and the sex ratio is balanced (Priori et al. 2013; Bramanti et al. 2014). The average fecundity (larvae polyp^{-1}) is low with respect to other octocorals (Torrents and Garrabou 2011) and is similar in shallow and deep populations (0.93–0.87 oocytes per polyp, respectively; Santangelo et al. 2003; Priori et al. 2013). Larval production depends on the size/age of the colony with old and large colonies producing up to 6,500–7,000 larvae (Priori et al. 2013), almost 300 times higher than a small colony, suggesting that there should be large differences in larval output between populations with different size and age structures. Fertility (percent of fertile colonies) is usually high (between 76% and 94%; Priori et al. 2013; Bramanti et al. 2014).

3.3.4 Population Trends

In Fig. 5 simulations of two different scenarios based on demographic data from Calafuria population are reported (Santangelo et al. 2007; Bramanti et al. 2009): the first scenario simulates a population subjected to a single mortality event (such that recorded locally in 1999), showing that the population, if affected by a single mortality event, should return to initial density in about 20 years (Fig. 5a). In the second scenario (Fig. 5b), the population is driven to local extirpation under the effect of a periodic mortality event occurring at 3-year intervals (Santangelo et al. 2007; Bramanti et al. 2009).

4 Recovery Dynamics of the Studied Populations

4.1 *Paramuricea clavata*

In late summer 1999 and 2003, several populations of *Paramuricea clavata* in the North Western Mediterranean were impacted by high mortality events associated to temperature increase (Cerrano et al. 2005; Garrabou et al. 2009). In the *P. clavata* population of La Spezia, large colonies were mainly affected, causing a dramatic reduction of density and a shift of the size/age structure of the population toward smaller sizes (Cupido et al. 2009). The frequency distribution of size classes based on average annual colony growth in La Spezia population revealed a pattern of

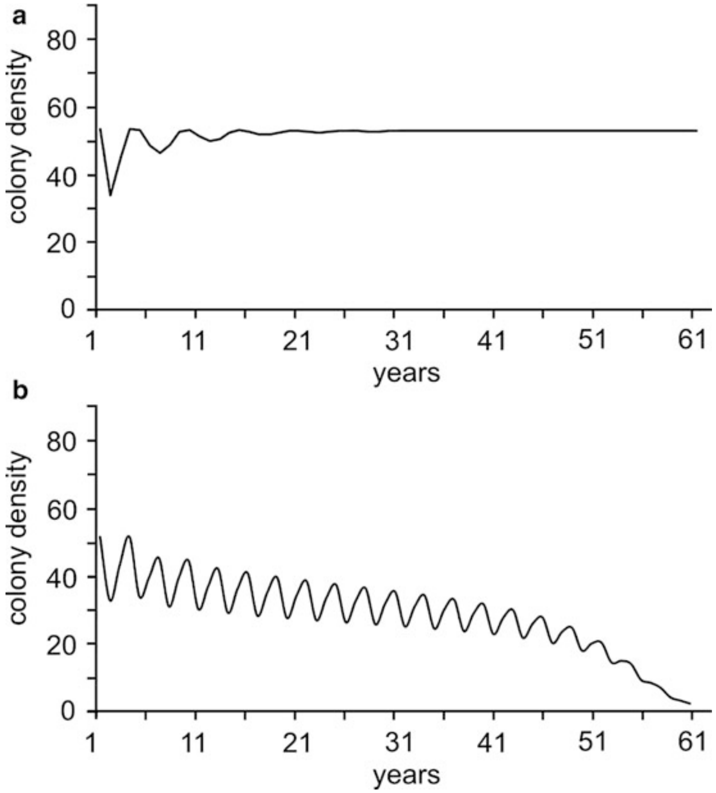

Fig. 5 Simulations of population density trends based on abundance, survival, and reproduction coefficients of a red coral population living in the shallower part of the species bathymetric range (Calafuria population, NW Mediterranean, Italy). (**a**) after a single mortality event the population recovers in about 15 years; (**b**) a population affected by repeated high mortality events occurring every 3 years is driven to local extirpation (Modified after Santangelo et al. 2007)

regularly decreasing abundance with increasing size/age. Throughout the years examined, recruits were the dominant class (Fig. 2). After 3 years of low mortality, density of recruits and adults increased to about 1.5 and 5 times the pre-mortality values, respectively. Population growth coincided with the detachment of dead colonies, suggesting that the density of both living and dead larger colonies has a negative effect on population recovery (Cupido et al. 2009; 2012).

The minimum size at first reproduction corresponds to an age of about 3 years; however, only 20% of colonies were ripe at this size. Colony reproductive output increases exponentially with size (Fig. 3) due to the higher number of polyps and higher fecundity and fertility of older polyps and large colonies (Cupido et al. 2012). Early onset of reproduction and high fecundity are basic features of successful colonizer octocorals (Benayahu and Loya 1985).

In La Spezia population, 7 years after the mass mortality events, the estimated population reproductive output was only 7.3% of the pre-mortality population one

(Cupido et al. 2012) and about 20% of that determined in other undamaged stable populations (Coma et al. 1995). The population showed a recovery trend with increased adult colony and recruit densities although with a sharp fall in the reproductive output; these findings could be likely due to a negative density dependence of recruitment and a still overabundant reproductive output. However, La Spezia population could also be part of a *metapopulation* with larval input from distant populations (Padrón PhD thesis and Padrón and Guizien 2015). Despite previous studies showed that *P. clavata* populations are structured at fine spatial scale (Mokhtar-Jamaï et al. 2011; Arizmendi-Mejía et al. 2015), the presence of distant migrants in the populations has been shown (Mokhtar-Jamaï et al. 2011) suggesting that distant populations can be connected. Moreover a recent PhD thesis (Padrón 2015) showed that the *P. clavata* population of La Spezia can receive larvae from other Ligurian Sea populations. Pilczynska et al. (2016) investigated the genetic structure and connectivity in the highly threatened populations from the Eastern Ligurian Sea and showed that the maximum larval dispersal was between 20 and 60 km. Authors demonstrated that larvae may disperse from La Spezia to the adjacent Punta Mesco population (20 km distance) and vice versa. Short distance migration (hundreds of meters) is likely to be the dominant mode of dispersal in *P. clavata*, but Pilczynska et al. (2016) suggested that migration from close undisturbed sites may be a significant source of recruits for disturbed areas to recover.

Despite gorgonians have generally been considered species exhibiting slow dynamics (Lasker 1991; Linares et al. 2007), the impacted population object of our study exhibited unexpectedly rapid dynamics, mainly driven by high recruitment rates. However, the population is still far from its original size/age structure, having attained only half of its pre-mortality density and is likely stabilized around lower values. This finding is consistent with the results of simulations and the observed survival of colonies in subsequent years, which suggest that the population will remain stable at lower densities after deep, dumping oscillations probably reaching a new equilibrium state (Santangelo et al. 2015). A long-term (more than 30 years) study of the population growth trends should enable determining whether this equilibrium between mortality and recruitment rates will be stable.

4.2 *Corallium rubrum* Recovery Dynamics

The small size and early age at first reproduction of *C. rubrum* colonies could have fostered the survival of the overharvested populations in the shallower part of the species distribution range; such shallow populations are mainly composed small-sized and crowded colonies (Santangelo and Abbiati 2001; Santangelo et al. 2003; Tsounis et al. 2006; Gallmetzer et al. 2010). It is worth to notice that recruitment values regularly found in the population of Calafuria are the highest ever reported for the species (Garrabou and Harmelin 2002; Santangelo et al. 2012; Bramanti et al. 2014) and also the highest with respect to other gorgonians: 20–50 times higher than that measured in *Paramuricea clavata* populations (Linares et al. 2007; Cupido et al. 2012) and even 100–1000 times higher than those reported in other gorgonians (e.g., Grigg

1988; Lasker et al. 1998; Doughty et al. 2014). Unfortunately, it has not been possible (until recently) to measure recruitment rates in the sparse, deep-dwelling populations.

Contrary to recruitment, fecundity of red coral polyps is among the lowest reported in gorgonians (Torrents and Garrabou 2011), with less than one larva produced per polyp, on average (Santangelo et al. 2003; Priori et al. 2013; Bramanti et al. 2014). The reproductive output (oocytes m^{-2}) calculated in a crowded, shallow-water population (Calafuria Livorno Italy, Santangelo et al. 2007) was about 38,000 mature oocytes, 20–50 times less abundant than that measured in *P. clavata* populations (720,000–2,000,000 mature oocytes m^{-2}; Coma et al. 1995; Cupido et al. 2012).

The simulations revealed that the local shallow red coral population studied has a high recovery capability after a single high mortality event. Nonetheless, the increase in the frequency of such events could lead populations to local extirpation in about 60 years.

5 Conclusive Remarks

The two temperate gorgonian populations whose basic life history features are outlined in this chapter are paradigmatic of two different demographic strategies: high recruitment densities and low reproductive output in *C. rubrum* and high reproductive output and low recruitment in *P. clavata*. It is worth to notice that despite the results presented are particularly focused on two populations (Calafuria population for *C. rubrum* and La Spezia population for *P. clavata*), they can be generalized to species/populations with different demographic and reproductive features (as in Bramanti and Edmunds 2016).

Although several demographic studies on gorgonian have been performed (e.g., Grigg 1977; 1988; Babcock 1991; Chadwick-Furman et al. 2000, Goffredo and Chadwick-Furman 2003; Linares and Doak 2010), only few of them have been used as a base for management and conservation measures (Linares et al. 2007; Bramanti et al. 2014; Montero-Serra et al. 2015). Focusing on engineering species such as *P. clavata* and *C. rubrum* gives double advantage as their demography can be linked to the associated community (via canopy effect; ▶ Chap. 18, "Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects", Guizien and Ghisalberti,) allowing to protect the entire animal forest also if conservation efforts are focused on charismatic species.

Determination of colony age, growth rates (Lartaud et al., ▶ Chap. 22, "Growth Patterns in Long-Lived Coral Species"), and recruitment (▶ Chap. 20, "Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages", Adjeroud et al.,), as well as colony and population reproductive output, are basic steps in the study of population dynamics. However, to date only a meager body of literature on marine benthos deals with descriptors able to link the age structure of a population with its reproductive output in a unique demographic model (Santangelo et al. 2007; Bramanti et al. 2009; 2014; Edmunds 2010).

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Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages

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Mehdi Adjeroud, Mohsen Kayal, and Lucie Penin

Abstract

Recruitment is now widely recognized as a fundamental process governing spatial patterns, dynamics, and maintenance of marine invertebrate communities. Moreover, recruitment is a critical factor for successful recovery following disturbances and thus resilience of ecosystems. Over the last decades, tropical coral reefs, which are one of the most diverse ecosystems on Earth and provide goods and services to ~500 million people, have been confronted with various types of natural and anthropogenic disturbances, causing widespread mortality of reef-building coral species. In this context, understanding processes of coral recruitment and their patterns in time and space is a fundamental step to understand, detect, and predict the effects of climate change on reef ecosystems. Despite major advancements in the last three decades, our understanding of some critical phases of coral recruitment processes remains too limited for their integration into management and conservation actions that are urgently needed for this unique ecosystem. Here, we synthesize and analyze existing literature on coral recruitment to determine the state of knowledge, identify knowledge gaps, and suggest future lines of research. We particularly focus on the spatiotemporal variability of recruitment and its controlling factors, the relative importance of

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pre- and post-settlement events and life strategies in the maintenance of adult assemblages, and the critical role of recruitment for the recovery and resilience of disturbed reef communities.

Keywords
Coral reefs • Scleractinian corals • Recruitment • Post-settlement processes • Regulation • Resilience

Contents

1 Introduction

1.1 The "Coral Reef Crisis"

Coral reefs are one of the world's most iconic marine ecosystems, often referred to as "rainforests of the sea." They act as natural breakwaters, protecting coastal areas and provide important economic, social, and esthetic goods and services, which are critical to the survival of ~500 million people (Moberg and Folke 1999). As tropical rainforests, coral reefs are characterized by an exceptional biodiversity and complexity and are among the most productive ecosystems on Earth. Hermatypic scleractinian corals, with their endosymbiotic single-celled algae (zooxanthellae), are the primary framework builders of the reef ecosystem and are a key component of coral reef health and diversity. As trees, corals build a complex tridimensional structure and provide essential or important habitat for hundreds of thousands of reef-dwelling organisms. Due to the sedentary nature of corals and their narrow tolerance range for environmental conditions, reef ecosystems are highly vulnerable to acute stressors and may change rapidly in their structure and functioning (Hughes and Connell 1999; Harrison and Booth 2007). Like many marine ecosystems, coral reefs are becoming increasingly exposed to various chronic and/or episodic threats and are expected to be highly vulnerable to future climate change (Hughes et al. 2003; Edmunds et al. 2014). While some physical and biological disturbances are a routine part of reef community dynamics, there is growing concern that the frequency and severity of various types of natural and anthropogenic disturbances, which have increased over the last three decades, will continue to do so (Hoegh-Guldberg et al. 2007). Among the broad range of large-scale disturbances that affect coral reefs, thermally induced coral bleaching events, cyclones, and outbreaks of keystone species, such as the coral-killing sea star *Acanthaster planci* in the Indo-Pacific, have the potential to significantly alter the biological and ecological processes that maintain coral communities (De'ath et al. 2012; Kayal et al. 2012). Coral reefs are also under increasing pressure from the combined effects of local human-induced stressors including overfishing, water pollution, dredging activities associated with coastal development, tourism, and recreational impacts (Grigg and Dollar 1990). Consequently, coral reefs have been affected by widespread mortalities of keystone organisms and habitat degradation and in many cases have undergone a striking phase shift in community structure. Classically, these phase shifts have involved the replacement of stony corals by algae, which results in the deterioration of the ecosystem goods and services previously supplied by corals (Harrison and Booth 2007). In the context of "confronting the coral reef crisis" (Bellwood et al. 2004), understanding the processes that maintain coral populations is of critical importance to better evaluate the resilience of reef ecosystems (defined here as the ability of an ecosystem to recover its structure and functions after a perturbation; see further developments of this concept in ▶ Chap. 43, "Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998" by Bianchi et al.) and to understand, detect, and predict the effects of climate change. These outcomes are also crucial to identify appropriate actions for coral reef conservation and management (Mumby and Steneck 2008; Anthony et al. 2015).

1.2 The Importance of Recruitment Processes

Coral assemblages often show strong spatiotemporal variations which are governed by a variety of interacting physical and biological processes that vary in frequency, intensity, and spatial scale (Hughes and Connell 1999; Harrison and Booth 2007). Among these processes, recruitment is widely recognized as being fundamentally important in the dynamics of local populations and recovery following disturbances, though both pre- and post-settlement processes may also influence the local abundance and spatial distribution of adult assemblages (Caley et al. 1996; Cowen et al. 2000; Doropoulos et al. 2015). In fact, the supply of coral larvae, their successful settlement and metamorphosis, and their subsequent survival and growth can have a marked influence on local population structure. The relative contribution of these processes vary greatly across geographic scales given dissimilarities in adult coral assemblages, local hydrodynamics, disturbance history, competition, and sources of predation (Hughes et al. 2000). In some cases, spatial heterogeneity of adult distribution can be largely influenced by stochastic variations in early recruitment rates (Caley et al. 1996; Cowen et al. 2000). But post-settlement mortality in scleractinian corals is generally high (up to 90% within the first year), thereby representing a critical process for coral population dynamics, that can greatly distort patterns established at settlement (Vermeij and Sandin 2008; Penin et al. 2010). One of the key questions for ecologists then is to determine the degree to which spatial heterogeneity in the abundance of adult corals is influenced by pre- vs. post-settlement processes and to identify major intrinsic and extrinsic biological and physical factors that drive these patterns.

1.3 Complexities of the Coral Life Cycle

With the high complexity of their life cycles and the inter- and intraspecific diversity of their life strategies, scleractinian corals are a challenge for demographic and population dynamics studies (Hughes and Jackson 1985; Kayal et al. 2015). Like most marine invertebrates, corals have a bipartite life cycle in which larvae develop as plankton before settling and attaching to the substratum (Fig. 1). As seeds for trees, coral larvae are the predominant means for dispersal and colonization of new habitats, enabling recolonization following disturbance and genetic exchange among subpopulations (Caley et al. 1996; Cowen et al. 2000). In addition to the typical recruitment, growth, and mortality processes observed in other benthic organisms, most corals have a clonal life-form and undergo fragmentation, fission, fusion, and partial mortality (i.e., shrinkage or negative growth), which distort age-size relationships (Hughes and Jackson 1985; Harrison and Wallace 1990). Moreover, corals are exceedingly small in size at settlement compared to their adult form and have a long life span. Most corals require several years of benthic life to become sexually mature (i.e., become “adults”). The nonreproductive benthic phase of corals, which can last for up to 5 years, can thus be separated into a recruit and a juvenile stage, that are ecologically very different (Fig. 2; see Penin et al. (2010) for further distinctions between recruits and juveniles). Sizes vary by up to an order of magnitude between these stages, and many processes such as growth and mortality are size dependent in corals (Vermeij and Sandin 2008; Kayal et al. 2015). In addition, organisms interacting through competition or predation with recruits are likely to be different from those interacting with juveniles and/or have differing severity in their effect on recruits vs. juveniles. Consequently, juvenile corals can be seen as immature colonies from several successive cohorts, providing a short-term history of settlement patterns combined with early post-settlement growth and mortality, whereas early recruits reflect variability in larval supply (Penin et al. 2010). Most studies conducted on recruitment and post-settlement mortality of corals have focused either on recruits or juveniles, but rarely on both partly because the techniques used to investigate each

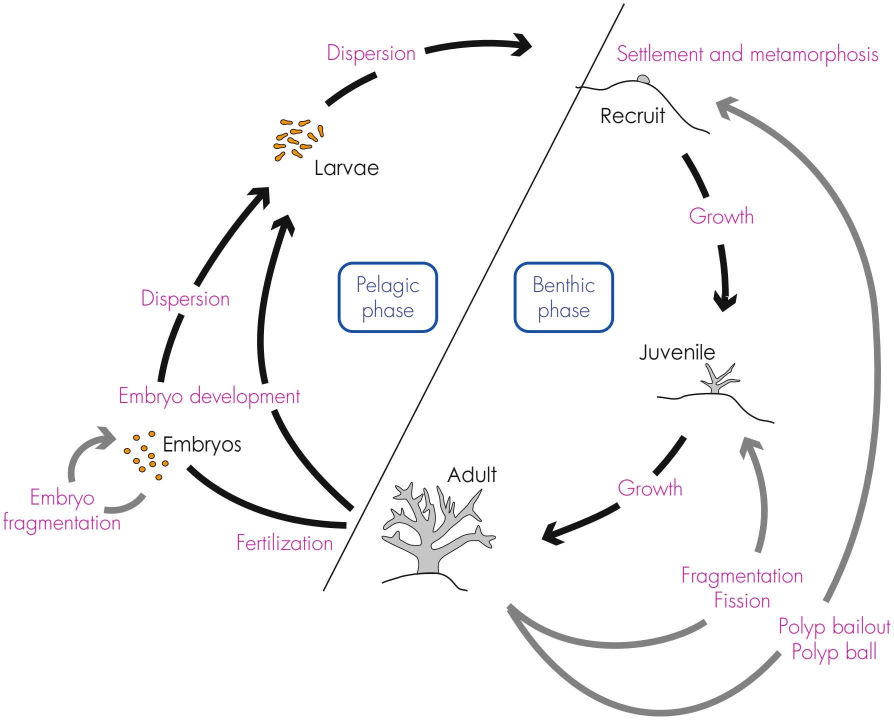
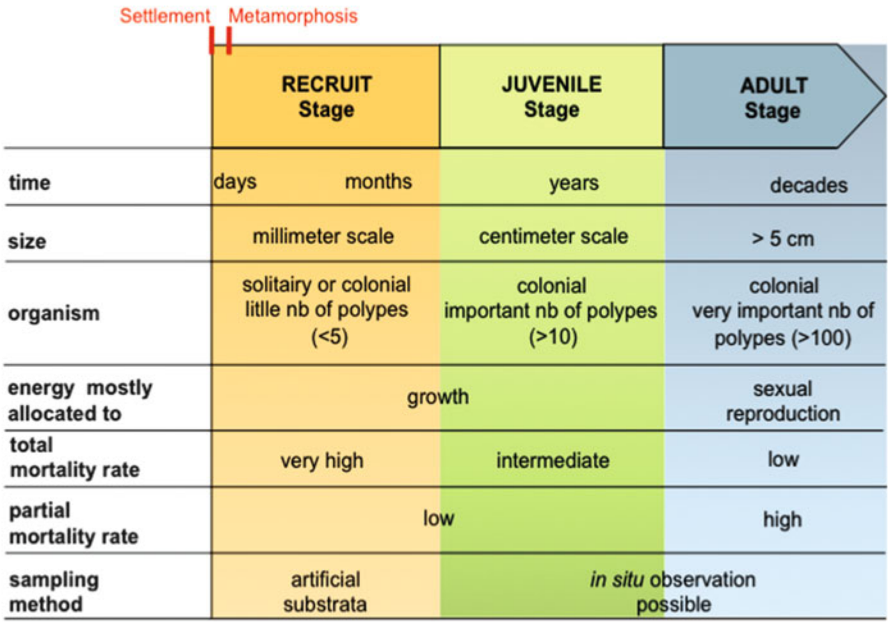


Fig. 1 Coral life cycle showing the critical pelagic and benthic phases. Most of the coral species have adult colonies that are attached to the substratum. Sexual reproduction occurs in two forms: fertilization and brooding of the larvae within the polyp and external fertilization and development. Several modes of asexual reproduction are known, such as fragmentation, fission, polyp bailout, polyp balls, asexual brooded planulae, and embryo fragmentation. Following their pelagic phase, coral planulae must settle, metamorphose, and grow to form the next generation of adults

stage differ (i.e., deployment of artificial substrates and observations under microscope in the laboratory for early recruits vs. in situ survey for juveniles). Consequently, the relative importance of events occurring during each of these stages remains largely unknown.

1.4 Objectives of This Chapter

Since the 1980s, several studies have been conducted on recruitment and post-settlement processes in corals that have led to major advances in our understanding of the ecology of coral populations and communities that form coral reefs. However, some critical phases of these processes have yet to be examined. The recent decline of some coral reefs and their vulnerability to future climatic changes suggest the need to develop new areas of research, not only to improve our fundamental



	RECRUIT Stage	JUVENILE Stage	ADULT Stage
time	days months	years	decades
size	millimeter scale	centimeter scale	> 5 cm
organism	solitairy or colonial litlle nb of polypes (<5)	colonial important nb of polypes (>10)	colonial very important nb of polypes (>100)
energy mostly allocated to	growth		sexual reproduction
total mortality rate	very high	intermediate	low
partial mortality rate	low		high
sampling method	artificial substrata	*in situ* observation possible	

Fig. 2 Main characteristics of the recruit, juvenile, and adult phases in coral reefs. Recruits are invisible to the naked eye on natural substrata, generally aged less than 1 year, whereas juveniles are observable in situ (>1 cm) and typically aged at least 1 year. Growth and mortality are size dependent in corals. Total mortality is very high during the first months of the benthic life and decreases with increasing size of coral colonies. Large adult colonies are mainly affected by partial mortality

knowledge but also to help implement adequate conservation actions. In this chapter, we synthesize and analyze existing literature on major advances in our understanding of recruitment process in corals (variability in recruitment, post-settlement and regulation processes, importance of recruitment in recovery and resilience). Our intention is not to achieve an exhaustive review of the literature, but rather to determine the state of knowledge, identify major gaps, and suggest future lines of research.

2 Spatiotemporal Patterns of Recruitment and Major Controlling Factors

One of the most striking characteristics of coral recruitment is its strong spatial and temporal variability at almost every scale investigated. Patterns of recruitment also vary among coral taxa in relation to their life history traits. This high variability in coral recruitment is partly explained by the numerous biological and physical factors (i.e., “positive” and “negative” cues) that may influence the abundance and distribution of coral recruits.

2.1 Spatial Patterns

Marked spatial variation in recruitment patterns has been recorded at various scales, from geographic (i.e., between Indo-Pacific and Atlantic reefs; see Ritson-Williams et al. 2009) to local scales (i.e., within reefs or between sites of the same region), and even within sites, among adjacent settlement tiles, and between upper and lower surfaces of tiles (Fisk and Harriott 1990; Hughes et al. 2002; Adjeroud et al. 2007). At local scales, recruitment patterns and settlement preferences often vary with hydrodynamic and wave energy exposure and with depth gradients (Ritson-Williams et al. 2009; Edmunds et al. 2010). Some of the physical factors associated with these patterns include sedimentation, water quality, availability and composition of adequate substrate, the preference of larvae for certain wavelengths of light or substrate color, and sound (Vermeij et al. 2010; Mason et al. 2011). Biotic interactions such as predation or allelopathy may also greatly influence spatial patterns of coral recruitment (Ritson-Williams et al. 2009). In particular, competing algae may affect coral recruitment and adult distribution through space pre-emption, overgrowth, and chemical cues (Kuffner et al. 2006; Dixson et al. 2014). Conversely, some encrusting coralline algae enhance recruitment success of coral species through the production of chemical cues that induce larval settlement and metamorphosis (Ritson-Williams et al. 2009). Specifically, preferred encrusting coralline algae tend to exhibit poor antifouling defense strategy, thus providing a substratum that is suitable to early post-settlement survivorship of corals (Harrington et al. 2004). At regional scales, spatial variation in the fecundity of coral species may explain a large part of the variation in recruitment, as it was demonstrated for *Acropora* on the Great Barrier Reef (Hughes et al. 2000). In the Indo-Pacific, the oceanic island of Mo’orea and several subtropical reefs in Taiwan, Hong Kong, Gneering Shoals, or Houtman Abrolhos Islands are characterized by low recruitment rates (~40 recruits m^{-2} $year^{-1}$ at Mo’orea; Adjeroud et al. 2007) which are an order of magnitude lower than those found on tropical Western Pacific reefs (~200 to 700 recruits m^{-2} $year^{-1}$ and up to 4590 recruits m^{-2} $year^{-1}$ in the central Great Barrier Reef; Hughes et al. 1999). Moreover, the relative contribution of the different families of recruits differs highly at this scale. In Mo’orea and most subtropical reefs in the Indo-Pacific, recruits are typically dominated by Pocilloporidae (>60%) with Acroporidae representing less than 15%, whereas on tropical Western Pacific reefs, Acroporidae are more abundant, representing up to 85% of the recruits (Fisk and Harriott 1990; Hughes et al. 2000). Despite the low recruitment rates and the rarity of Acroporidae recruits at Mo’orea and some subtropical reefs, adult densities and living coral cover may reach relatively high values similar to those recorded on some reefs of the GBR (Hughes et al. 2002). These results suggest that low levels of recruitment are compatible with a relatively abundant adult population for some species. One of the hypotheses to explain this outcome is that early post-settlement mortality in coral populations is particularly reduced at these reefs. Alternatively, these results may indicate a higher contribution of fragmentation, one of the several asexual reproductive modes of corals, in the maintenance of local populations of some species, which can also be a major driver in recovery after perturbations (Roth et al. 2013).

For example, recent observations suggest that populations of branching *Acropora* in French Polynesia produce a high number of fragments that possess a 90% chance of survival and reattachment, while other species like massive *Porites* use fission and fusion processes to maintain their local populations (Kayal et al. 2015).

2.2 Temporal Changes

Monitoring surveys have all demonstrated that the density of recruits varies among seasons and years (Fisk and Harriott 1990; Adjeroud et al. 2007). This interannual and seasonal variability of coral recruitment appears to be mainly related to the spawning patterns of coral assemblages. Specifically, changes in climatic and oceanographic conditions affect the fecundity, pre-settlement mortality (which is highly weather dependent), dispersal, and early post-settlement events (Harrison and Wallace 1990). Small sublethal changes in the fecundity of corals could also result in major reductions in recruitment. These changes in coral fecundity may be caused by the effects of large-scale perturbations such as thermally induced bleaching events or chronic stressors such as water pollution, which result in the depletion of the larval pool at regional scales (Mumby 1999; Adjeroud et al. 2007). This interannual variability in fecundity, settlement rates, and post-settlement events may therefore result in “good” and “bad” years for recruitment. In fact, adult population densities seem to be the results of 10-year averages of variation in larval production and early juvenile mortality, and present-day populations probably reflect successful recruitment events that occurred years or decades earlier (Hughes et al. 1999). Some authors even suggest that some coral populations may rely on sporadic episodes of high recruitment for their maintenance and recovery (i.e., the “storage effect”; Warner and Chesson 1985).

2.3 Perspectives

Major advances have been made in characterizing the spatiotemporal patterns in coral recruitment, and the interactions of various and complex biophysical drivers of this variability have been identified for some reefs. However, the evolutionary and ecological factors that may explain the high variation in recruitment rates at geographic scales are still unclear. The link between interannual variation in fecundity, larval supply, and successful recruitment at regional scales remains poorly understood. The recent progress on coral recruitment mainly concerns a few subsets of coral taxa from a few families (mainly Acroporidae, Pocilloporidae, and Poritidae in the Indo-Pacific) indicating a critical lack of information concerning recruitment of other taxa that are also major components of adult assemblages. This is primarily due to the difficulty in identifying early coral recruits because at this stage of development, the micro-architecture of the corallum is not sufficiently developed to allow high-resolution identification (Babcock et al. 2003). It is also plausible that some coral taxa do not recruit on the artificial settlement tiles used in some recruitment surveys. These taxa may also rely on occasional episodes of high recruitment (that have few chances to be detected in classical recruitment surveys that rarely exceed 5 years) or on asexual reproduction for their maintenance. Nonetheless, efforts need to be placed on monitoring these "rarely recruiting taxa" in order to avoid over-simplifications and to allow more holistic examination of mechanisms of population regulation within coral communities. This will require the development of approaches to better discriminate early recruits (Hsu et al. 2014). Another critical information gap concerns the origin of recruits. If population genetic studies have greatly improved our knowledge on connectivity among established subpopulations of corals, the question of self- vs. allorecruitment remains open. This future line of research calls for the development of genetic tools for corals, such as the DNA parentage analysis which has been successfully applied to reef fishes. This challenging task, coupled with the monitoring of the spatiotemporal variability in recruitment rates, will provide an insight into the extent to which larvae recruit into populations on their natal reef, or are dispersed between reefs, leading to the identification of potential reef "sources" and "sinks" at regional scales.

3 Post-settlement Events, Regulation Processes, and Life Strategies

A critical step in understanding the dynamics and regulation of coral populations is to determine the relative contribution of pre- and post-settlement processes (Fig. 3). Pre-settlement processes, such as distribution and abundance of larvae, integrate regional scales (i.e., up to several hundreds of kilometers), whereas post-settlement processes like competition or predation occur at a much smaller scale (i.e., within reef habitats). As a consequence, the relative importance of pre- and post-settlement events may appear to be very different depending on the scale considered, and a high variation in mechanisms of population regulation is expected among regions. Moreover, the relative contribution of pre- and post-settlement processes in the dynamics of adult populations varies greatly among coral species within the same reef, underlying the importance of intrinsic life history strategies in mechanisms that maintain local populations.

3.1 Post-settlement Events and Regulation Processes

For many benthic organisms, rates of mortality are very high during the first days or weeks following settlement, which has significant implications on population structure, dynamics, and recovery capacity after disturbance (Gosselin and Qian 1997). However, in situ studies addressing the effects and mechanisms of positive and negative settlement cues are limited (Penin et al. 2010, 2011). This is mostly due to the very small size of newly settled coral recruits and their preference for cryptic habitats, which make their observation difficult. The major sources of mortality of early recruits are unsuitable environmental conditions, competition, and predation.

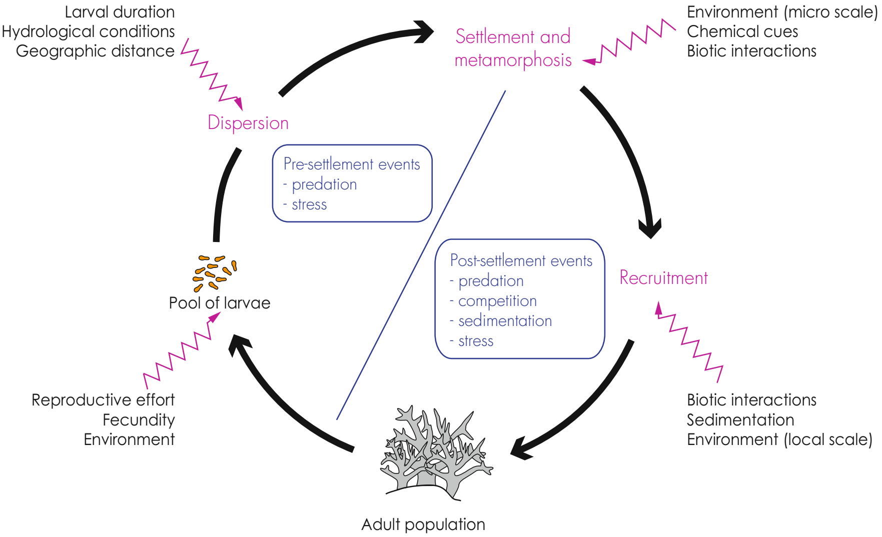


Fig. 3 Major factors influencing larval dispersal, settlement, and recruitment of corals. Dispersion patterns of larvae are largely determined by their physiology (duration of the planktonic phase, competency period, vertical distribution in the water column), the prevailing hydrological conditions (mainly hydrodynamic patterns), and geographical distances. Settlement and recruitment patterns are influenced by factors acting at the local and/or at the small spatial scales. Pre-settlement mortality is mainly due to predation by fishes, whereas predation by fishes and sea urchins is a major component of the post-settlement mortality. Competition is also playing an important role in recruitment patterns, particularly when space occupancy is high

Effects of competition on early benthic stages of corals have received little attention. However, the presence of adult corals and other benthic organisms such as turf algae has been shown to increase early post-settlement coral mortality (Ritson-Williams et al. 2009). Conversely, established coral colonies can also benefit early survivorship through creation of diverse habitats and provision of refuges from multiple stresses (Ritson-Williams et al. 2009). Sedimentation also limits early survivorship through abrasion or burial of colonies (Hunte and Wittenberg 1992), and sediment trapping can be an indirect reason for the detrimental effect of competition with turf algae (Penin et al. 2011). Since they are very small at settlement, coral recruits mostly face incidental predation linked with dislodgement by grazers during their first days or weeks of benthic life. Grazing is an important ecological process in coral reefs, benefiting corals in their competitive interactions with algae (Mumby et al. 2007). However, altering grazer abundance, through caging experiments, for example, demonstrates a potentially strong effect of incidental predation on recruitment success (Penin et al. 2011). Contrasting effects of grazing on early post-settlement survivorship have been revealed in different reefs. When grazer abundance is low, algae grow and compete with early settlers, trapping sediment thus increasing early post-settlement mortality. Conversely, high grazer abundance reduces the development of turf algae, but induces incidental predation on coral recruits. The current consensus is that the presence of macrograzers is beneficial for coral resilience, tipping the scales of coral/algal interactions in favor of corals, enhancing coral recruitment and growth, and improving recovery after disturbances (Bellwood et al. 2004; Mumby et al. 2007). However, there is a critical need to further examine the "collateral damage" made by grazers to the different life cycle stages of corals and to better understand the cost/benefit ratio of grazing processes on coral reef resilience (Rotjan and Lewis 2008).

3.2 Supply-Side Ecology

The relative contribution of early recruitment patterns and post-settlement events may vary among coral reefs. The contribution of larval supply and early recruits to the structure of the adult assemblages is evident in some situations, while post-settlement events and differential rates of post-settlement growth and mortality appear to have a stronger effect on other reef systems. Divergences between recruitment patterns and adult assemblage distribution may also be due to contrasting effects of environmental factors and perturbations on these different life stages. Mortality is size specific, and some disturbances do not have the same impact on all size classes (Kayal et al. 2015). Contrasting patterns of distribution of adults and recruits may also indicate that asexual reproduction plays an important role in population maintenance as suggested for the branching *Acropora* corals. The positive link between spatial distribution of adult and recruit abundances may be viewed as an indication of strong stock-recruitment relationships (where the adults drive the number of recruits), recruitment-limitation relationships (where recruits drive the number of adults), or as the result of preferential settlement of recruits near established adult colonies. On the contrary, strong dissimilarities in spatial patterns between recruits and adult corals have been used to argue that coral populations are not strongly regulated by patterns of recruitment, but rather are highly dynamic. Correlations between adult abundance and local densities of coral recruits are generally expected for species with short competency periods (most brooding species) or in closed systems where larvae are not dispersed far away from the natal reef. However, this relationship is likely to break down in large open systems where advection tends to mix larvae from natal and distant reefs, particularly for broadcast spawning species with long larval durations (Caley et al. 1996; Cowen et al. 2000). One of the implicit assumptions of the hypothesized recruitment-limitation relationship is that juvenile and adult patterns are temporally constant, such that current patterns of adult coral abundances were generated by patterns of recruit and juvenile abundances similar to contemporary levels. However, recruitment rates and early post-settlement mortality can fluctuate greatly among successive years (Hughes et al. 1999; Adjeroud et al. 2007). It is thus necessary to determine whether observed relationships between juvenile and adult abundances are temporally consistent through the implementation of long-term monitoring programs routinely measuring recruitment rates and juvenile abundance. Moreover, the effects of larval input on adult abundance may be difficult to detect because adult abundance reflects the accumulation of recruits over many successive cohorts and infrequent years of very high recruitment might have a disproportionate influence on adult abundance. Scientific opinion regarding the extent to which coral populations are open or closed has varied in recent decades. Since the majority of coral reefs are broadcast spawners with potentially long dispersal capacities, coral populations were largely considered open and driven by recruits from distant locations (Caley et al. 1996; Cowen et al. 2000). But recently, there has been renewed interest in the possibility that populations of a broad range of taxa, including scleractinian corals, can be remarkably closed even though they have dispersive larvae (van Oppen et al. 2008; Cowen and Sponaugle 2009). In fact, the current consensus is that populations of many marine organisms occupy a gradient from fully open to fully closed, with their position on this gradient determined by a complex assortment of biological and physical processes.

3.3 Life Strategies

Several studies underline discrepancies among coral taxa in terms of maintenance processes that are most likely linked to differences in life history traits such as reproduction strategies, stress tolerance, growth capacities, or competitive abilities, each modifying maintenance processes (Penin et al. 2010). For example, Pocilloporidae corals tend to settle in disproportionate abundance compared to other families in places like the Central Pacific and subtropical or equatorial locations, but then most likely show higher rates of early post-settlement mortality (Adjeroud et al. 2007). This may be linked to the fact that this family is represented by opportunistic genera, capable of high recruitment, but presenting high turnover and mortality. In these reefs, Pocilloporidae clearly represent the opportunistic species, with higher recruitment rates, high potential for larval dispersal and colonization, fast growing, and low resistance to perturbations. For these taxa, post-settlement events seem to be preponderant. On the opposite, taxa like massive Poritidae usually show a resistant life strategy with the production of fewer offspring endowed with a higher capacity for survival (Penin et al. 2010; Kayal et al. 2015). Their populations are characterized by slow growth, slow turnover among individuals, large-size colonies, and lower rates of decline in presence of harsh conditions and catastrophic events. For these species, higher abundance of recruits appears to lead directly to higher abundance of juveniles and adults. A third group is characterized by species displaying high aptitudes to preempt space and resources in optimal environments through faster individual growth and asexual propagation by fragmentation. This group, referred to as competitive, is illustrated by some Acroporidae species with high proportions of clonality and high susceptibility to disturbances (Kayal et al. 2012, 2015). For this group, the preponderance of recruitment or early-stage mortality in population maintenance is still unclear.

3.4 Perspectives

Understanding the relationships between recruitment and population structure is challenging in many marine systems where propagules have the potential to travel long distances and populations are structured through a diversity of pre- and post-settlement events (Caley et al. 1996; Cowen et al. 2000; Cowen and Sponaugle 2009). For corals, this area of research is relatively recent, and further studies are clearly necessary to elucidate the relative importance of larval supply and settlement and early post-settlement mortality in shaping juvenile and ultimately, adult coral assemblages. Future lines of research should clarify the contradictory role of herbivores and grazers on post-settlement survivorships of recruits and juveniles. This is a critical point as many management actions focus on reducing fishing pressures, which generally induce an increase in the densities of herbivores and grazers. Another critical step is to integrate spatiotemporal variation in coral fecundity and density-dependent interactions to adequately test the mechanisms of population regulation. Future studies would also be more effective by taking into account the size-structure of adult colonies within populations which better reflects fecundity than simply adult colony densities. At present, the great majority of coral health monitoring programs focus mainly on the interannual variability of coral cover. Integrating all the critical phases of recruitment processes (pre- and post-settlement events) in classical monitoring programs clearly represents a challenge and requires considerable sampling effort with the development of simple techniques to monitor various processes such as coral fecundity. This is clearly the most effective way to increase our knowledge on regulation of coral populations and their replenishment capacities after disturbances.

4 Recruitment, Recovery, and Resilience

Coral reefs throughout the world are increasingly threatened by a combination of various large-scale disturbances and local stressors that are exceeding their capacity for resilience. The resulting global trajectory of declining reef ecosystems is calling for the need for practical tools to estimate coral persistence. In this context, coral recruitment represents an adequate, integrated, and effort-efficient indicator of the potential of populations to replenish. In this section, we describe how quantitative information on coral recruitment and recent modeling approaches can help estimate resilience of coral populations.

4.1 Recruitment Rate as Indicator of Resilience

A major goal in coral ecology and conservation is to identify early indicators of species performances that reflect their ability to persist. Such ecological indicators of resilience should be versatile in a way that can be implemented in diverse reef environments while remaining comparable between various systems. In addition, indicators of coral health need to be relatively simple to monitor and be both cost- and effort effective. Finally, a good indicator should integrate species success in multiple steps of their life cycle since diverse large-scale disturbances and local stressors affect corals not only during their adult sessile phase but also during other life stages (Harrison and Booth 2007; Anthony et al. 2015). The recruitment process plays a fundamental role in the maintenance of coral species as it drives both the continuous turnover of individuals within established populations and the episodic replenishment of populations following mass mortality events (Hughes and Tanner 2000; Hughes et al. 2000; Doropoulos et al. 2015). The larval phase and early recruitment represent the most critical periods in the coral's life, given the high rates of per capita mortality and sensitivity to alterations in their environment. Furthermore, adult corals surviving disturbance and stress often show reduced fecundity and growth given the higher needs for energy allocation to tissue reparation and colony maintenance, subsequently resulting in decreased reproductive outputs and recruitment rates (Anthony et al. 2015). Thus, coral recruitment represents an interesting indicator of population health and capacity for replenishment, as it integrates the effects of both acute disturbances and gradual deterioration of reef conditions on multiple life stages. However, efficiency of this indicator remains to be tested, as few studies have examined the impacts of large-scale disturbances or reef degradation on the interannual variability in coral recruitment.

4.2 The Importance of Recruitment for Recovery

Following major disturbances, recovery of coral populations is often based on a combination of newly settling larval recruits and growth and propagation of surviving corals (Harrison and Booth 2007). The relative importance of larval recruitment vs. growth and regeneration of remnant corals to reef recovery is however highly system specific, as it depends on the nature and intensity of disturbances, the species composition of the considered assemblage, and the level of connectivity with adjacent fecund populations (Hughes and Tanner 2000; Doropoulos et al. 2015). In theory, maintenance of isolated populations relies more on survival and regeneration of corals across mortality events, which is locally influenced by the ability of the species to resist and respond to disturbances and the availability of refuges (Baskett et al. 2010; Anthony et al. 2015). In contrast, populations exhibiting higher recruitment rates are more likely to show higher potential for recovery and resilience from intense mortality events and recurrent disturbances (Riegl and Purkis 2009; Muko et al. 2014). However, this theoretical relationship between recruitment rates and the capacity for recovery is far from simple (Gilmour et al. 2013). For example, despite showing relatively low recruitment rates compared to other regions (Adjeroud et al. 2007), coral assemblages around Mo'orea are among the few that have shown the ability to recover from severe and recurrent disturbances (Adjeroud et al. 2009). This outcome suggests that elevated recruitment rates are not necessarily a prerequisite for population maintenance and successful recovery of reefs. Additional empirical research from diverse reef systems is required to tear apart the importance of larval recruitment and growth of remnant corals in recovery trajectories following disturbances.

4.3 How Much Recruitment for Persistence?

Despite the obvious theoretical importance of recruitment in populations replenishing, it is actually difficult to evaluate the specific recruitment threshold that can guarantee persistence of a given population. This is mostly due to the complexity of the underlying machinery that drives population dynamics and the relatively long temporal scales at which demographic processes are playing (Kayal et al. 2015). Identifying the most critical stages in species life cycle, a prerequisite for effective species management, requires robust analytical tools to efficiently account for such complexity. This is particularly the case for species with clonal life histories like most corals, with numerous population processes that potentially contribute to population maintenance (see Fig. 4 step 1). Recent advancements in computational modeling have embraced a new line of research for population studies that aim to evaluate the importance of different population processes in species dynamics and persistence. Two different types of data-based models can be distinguished, descriptive and simulative. Descriptive models transcribe ecological observations into mathematical equations, allowing estimation of patterns and testing hypothesis from empirical data (Fig. 4 step 2). Such models are commonly used to evaluate trajectories of coral populations and variability in coral performance in different population processes across time, space, taxa, and development stages and to link observed dynamics with environmental drivers. For example, patterns of coral recruitment have recently been related to the density of local populations in different reef systems (Hughes et al. 2000; Doropoulos et al. 2015; Kayal et al. 2015). Simulative models allow projecting beyond observations to test for consequences of hypothetic scenarios on future trends (Fig. 4 step 3). Such models typically use in situ observations on species dynamics and estimations of species performance in different population processes calculated from descriptive models on empirical data. Three major types of simulative models have been developed on coral population dynamics: transition matrix models (Hughes and Tanner 2000; Baskett et al. 2010; Doropoulos et al. 2015), individual-based models (Riegl and Purkis 2009; Muko et al. 2014), and integral projection models (Madin et al. 2012). These simulative approaches have notably allowed comparing the projected trajectory of coral populations with differing levels of recruitment and post-settlement regulation. In particular, sensitivity analyses constitute interesting components of simulative models, as they allow evaluating quantitatively the importance of each or any given variable in the modeled outcome. As such, implementation of sensitivity analysis in data-based models has evaluated the relative importance of recruitment, versus survival and growth at different life stages, in specific coral populations (Riegl and Purkis 2009; Muko et al. 2014; Doropoulos et al. 2015). By comparing

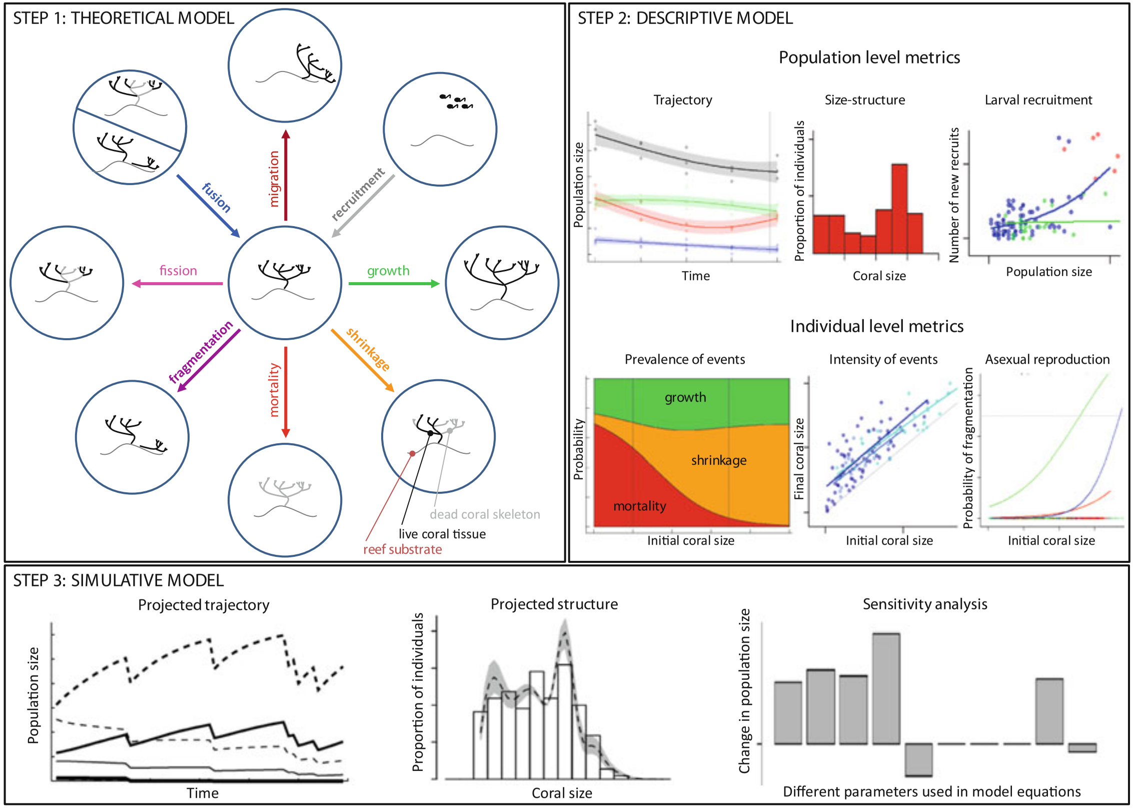


Fig. 4 Schematic illustration showing the different steps involved in quantifying the importance of recruitment and other demographic processes in coral population maintenance and future trends. The example of the construction of an integral projection model is shown here where individual coral dynamics are

observed patterns of recruitment with the estimated thresholds required for population maintenance, these approaches may greatly help to estimate resilience capacities of coral communities. Broadening the application of such models across various reefs will greatly help to identify, locally, the most critical life stages in species maintenance and the most vulnerable populations. Additionally, it will provide a more extensive understanding of how the relative importance of recruitment compared to post-recruitment processes varies with differing environments and future scenarios. However, building such population models necessitates a huge sampling effort for gathering the required amount of data on the different demographic processes and their variability (Fig. 4), which is currently only implementable in a few study systems.

4.4 Perspectives

In the present context of increasing disturbance regimes and reef degradation, quantitative knowledge on recruitment patterns can provide information on the recovery capacity of coral populations and can benefit conservation (Harrison and Booth 2007; Anthony et al. 2015). Increasing empirical data on coral recruitment in diverse reef systems will provide additional material to assess how recruitment varies across multiple disturbance events and changes in assemblage composition and reef environment. Increasing amount of quantitative data on corals is being available throughout the planet from long-term monitoring programs to short-term studies. Computational modeling is providing increasingly powerful tools that can more realistically transcribe complex ecological data and processes into powerful descriptive and simulative models (Baskett et al. 2010; Madin et al. 2012; Kayal et al. 2015). Management of coral reef ecosystems will particularly benefit from adaptive learning approaches to coral dynamics at multiple scales, from that of local assemblages to planetary dynamics (Anthony et al. 2015). Furthermore, population genetics investigations that quantify the dispersal, connectivity, and degree of openness of coral populations can greatly improve population models. Such models can be used to identify critical steps in species life cycles and develop finer indicators

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Fig. 4 (continued) quantified and related to the size of the colonies constituting the population. The theoretical model in step 1 identifies the different demographic processes that contribute to coral dynamics. The complexity of this theoretical model varies with life history of the considered species. Descriptive models in step 2 are used to transcribe observed dynamics into mathematical metrics and to estimate the prevalence and intensity of each of the demographic processes as a function of individual or population size. The representativeness of this approach depends on the sampling effort, as increasing observations on individual corals allow better estimates of natural variability as captured across time, space, and development stages. Simulative models in step 3 use estimations from the descriptive models to project coral dynamics under different scenarios. Sensitivity analysis performed on these simulations allows quantifying the importance of each of the demographic processes in the dynamics of populations. Steps 1 and 2 adapted from Kayal et al. (2015), step 3 from Riegl and Purkis (2009) and Madin et al. (2012)

of population health and resilience. Moreover, resilience capacities can be better characterized through holistic multidisciplinary approaches that consider reef ecosystems in their entirety, not as simplistic single-population systems. Similarly, the dynamics of both ubiquitous and rare species needs be considered to identify ecological keystone species and to avoid system collapses and erosion of biodiversity.

5 Conclusions

Our knowledge of coral recruitment processes has greatly improved in the last three decades. However, as other complex ecological mechanisms involving a variety of intrinsic and extrinsic controlling factors acting at various scales, our understanding in this area of research is far from being sufficient in correctly addressing conservation and management issues. For several reefs and coral taxa, consistent data on the spatiotemporal patterns of recruitment rates and some of their controlling factors are now available. But this type of information should now be collected for those several coral taxa lacking data to avoid oversimplifications of mechanisms of population maintenance. Moreover, the spatial origin of locally recruiting corals is unknown, and no consistent data are available to estimate the relative contribution of auto- vs. allorecruitment in the maintenance of local populations. Similarly, the link between variation in fecundity, larval supply, and successful recruitment has been poorly addressed. Therefore, even if we intuitively feel that recruitment is an important aspect in the recovery and resilience of coral assemblages after disturbance, the underlying mechanisms remain hypothetical. Additional empirical research coupled with modeling approaches are clearly necessary to determine the importance of recruitment processes in the persistence of coral assemblages under various scenarios of future environmental changes.

By increasing our knowledge on some key phases of coral recruitment processes, more effective conservation and management actions could be implemented. For example, by determining the spatiotemporal patterns of recruitment and by identifying potential “source” and “sink” reefs, managers could identify the most effective areas to protect and the critical periods during which potential stressors should be minimized. Moreover, additional information on the contradictory role of herbivores and grazers on survivorship of recruits will also clarify the expected cascading effects of fishery management. Coral recruitment is an interesting indicator of coral reef health and resilience and should be more widely considered in monitoring surveys. This is clearly a challenging task, but given the vulnerability of coral reefs to future changes, it becomes a necessary goal for successfully managing these marine animal forests.

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6 Cross-References

- ► Caribbean Coral Reefs: Past, Present, and Insights into the Future
- ► Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998

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21

Reproductive Strategies in Marine Invertebrates and the Structuring of Marine Animal Forests

Owen S. Wangensteen, Xavier Turon, and Creu Palacín

Abstract

Competition, predation, and facilitation mechanisms are the major drivers of biodiversity and community structure in marine benthic ecosystems. Habitat complexity is a determining factor of faunal richness and biodiversity in these communities. The structure of marine animal forests is originated by living three-dimensional aggregations of modular animals. The persistence of these systems through time relies on the growth of existing individuals and the recruitment of new ones. Therefore, the present and future health of these valuable ecosystems may depend on the reproductive success of a few vulnerable species which might often be accomplished only under strict or very narrow conditions. Reproductive patterns of ecosystem engineers play a crucial role in determining the structure, function, and distribution of all kinds of marine animal forests at different scales. The reproductive strategies of these habitat-forming species may vary considerably. Though most ecosystem-engineering species are, to some extent, able to reproduce asexually, their sexual reproductive strategies are diverse. Dispersal ability strategies are selected as an adaptation to spatial heterogeneity and habitat stability and are important factors for the resilience of the ecosystems. Dispersal traits are essential for both small-scale population structuring and connectivity

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among distant populations. Disturbed habitats may be promptly recolonized by species with long-distance dispersal capability, but recolonization by species with low dispersal capacity might limit the full restoration of a disturbed ecosystem, especially in fragmented habitats with reduced connectivity between patches. Due to the lack of knowledge on the reproductive cycles of many marine invertebrates, the response of animal forest ecosystems to global change is, in general, unpredictable.

Keywords
Benthic communities • Dispersal • Engineering species • Habitat complexity • Marine invertebrates • Reproductive ecology • Resilience

Contents

1 Introduction

Marine animal forests (Rossi 2013) are living three-dimensional structures resulting from the action of benthic ecosystem-engineer species (Jones et al. 1994) such as cnidarians, sponges, mollusks, bryozoans, annelids, or ascidians. The relevance of these biostructures as hosts for unique ecosystems is highlighted by the high degree of taxonomic and functional diversity allowed by the complex physical structures built by the engineering species over time (Sebens 1991; Buhl-Mortensen et al. 2010). The more mature and structured the animal forest is, the higher its capacity to alter the current flow and to retain in their surroundings particles and bigger bodies transported by seawater (e.g., zooplankton, eggs, larvae, adult organisms, or fragments) (Gili and Coma 1998), which may become both sources of food for benthic feeders or reproductive propagules for different species. Therefore, mature animal forests are crucial for driving energy and matter flows from plankton to benthos, acting as carbon sinks by sequestering primary and secondary productivity (Rossi et al. 2008). The biodiversity and functional patterns that characterize animal forests are mainly driven by the habitat heterogeneity originated by the interplay of two factors: first, the living community of benthic invertebrates, with their recruitment, growth, and mortality patterns; second, a set of abiotic factors which determine the suitability for the establishment and maintenance of the animal forest, such as light, currents, geomorphology, nutrient input, climatic or seasonal patterns, level of disturbance, or recurrence of catastrophic events.

2 Negative and Positive Interactions as Drivers of Habitat Complexity and Biodiversity

Mature animal forests are characterized by high complexity and biodiversity. How can such a high biodiversity originate? Ecological models based on the struggle for existence paradigm have traditionally focused on negative interactions (competition or predation) as the main biotic drivers that create and maintain biodiversity in natural ecosystems (Tilman 1982). This may be true to some extent. Competition for trophic resources may ultimately lead to radiations of trophic specialist species, competition for space is a key factor promoting morphological novelty among sessile organisms of benthic communities, and the arms race between predators and preys brings about lots of adaptive feedbacks. Nevertheless, the existence of diverse mechanisms based on positive interspecific interactions (facilitation) has been more recently recognized as another main driver of biodiversity (McIntire and Fajardo 2014). Countless examples of patent mutualistic symbiotic relationships are well known in marine benthic ecosystems. But facilitation mechanisms by means of which the presence of a given species promotes the existence of others may be often more subtle: structural support, abiotic stress amelioration, refuge formation, service sharing, predator release, or a combination of these (Fig. 1). In fact, in mature benthic ecosystems, the presence of organisms itself increases the number of ecological niches available for other organisms by promoting habitat complexity, through an ever-increasingly complex network of negative and positive interspecific interactions.

The importance of facilitating relationships in relation to trophic behavior or defense mechanisms in marine invertebrates is well known, but the key role that these positive interactions play in reproductive strategies has been often overlooked. Synchronous spawning events are probably the most outstanding example. Mass hetero-specific simultaneous spawning events are well documented in corals from the Great Barrier Reef (Harrison et al. 1984) (but not for coral species from the Red Sea, Caribbean, Central Pacific, or Southern Japan; Shlesinger and Loya 1985; Richmond and Hunter 1990). This behavior has also been observed in colder regions

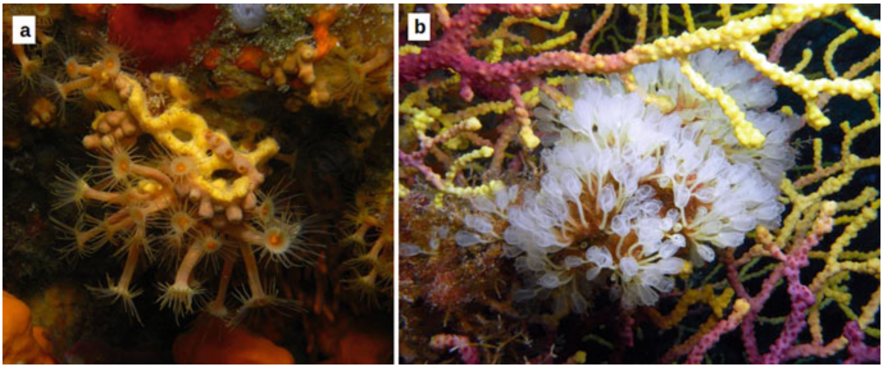

Fig. 1 Examples of reproductive facilitation in animal forest ecosystems. Although the zoantharid *Parazoanthus axinellae* (**a**) and the stolonial ascidian *Pycnoclavella communis* (**b**) are both able to dwell on bare rock substrates, their physical condition is improved and their asexual reproduction is facilitated when settled on the supportive species *Axinella damicornis* (**a**) and *Paramuricea clavata* (**b**), respectively (Photo credits: O. S. Wangensteen)

involving other groups such as echinoderms in British Columbia (Pearse et al. 1988). The species participating in these events often belong to different phyla and show otherwise unpredictable or irregular spawning patterns (Babcock et al. 2011). However, the most relevant facilitating reproductive interaction for the ecology of marine animal forests (though often overlooked) is the use of complex biogenic habitats as shelters, nesting sites, or nurseries by macro-invertebrates or fishes, during several crucial steps of their reproductive cycle, such as gamete release and fertilization, embryonic development, or postsettlement (Sale 1971; García-Charton and Pérez-Ruzafa 1998; Kroon et al. 2000; Hereu et al. 2005; Adams et al. 2006). Some species-specific instances of such interactions have been well documented, such as the Antarctic hexactinellid sponge *Rossella* and its crucial role as a substrate for the reproduction of several species of notothenioid fishes and comatulid crinoids (Barthel 2014, Gutt et al. in this same volume).

Thus, the high degree of diversity and habitat complexity of marine animal forests allows for the existence of successful complex reproductive interactions, which in turn contributes to a higher degree of entanglement and diversity, in a virtuous circle of ecological complexity. This complex interdependence in life cycles of marine species is crucial to understand resilience patterns of benthic ecosystems (Bianchi et al. in this same volume).

3 The Diversity of Invertebrate Reproductive Strategies

Of all biological processes, reproduction is the most fundamental. Reproduction allows the continuity of species and ecosystems over time and is the key process on which evolution by natural selection acts. The ecology of a species and the evolution of a genetic lineage are both direct results of their reproductive strategies. Marine

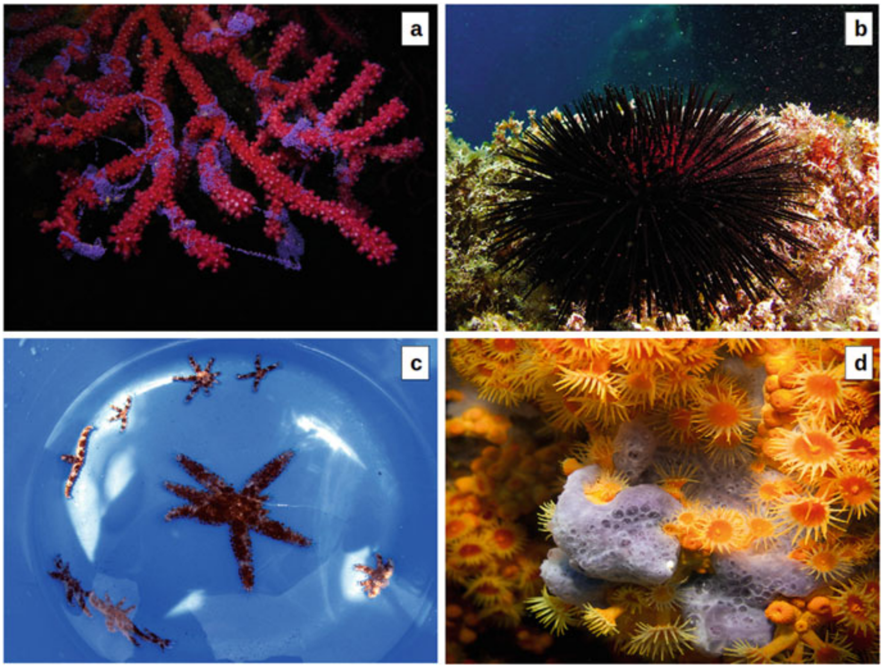

Fig. 2 Some examples of diverse reproductive strategies in marine invertebrates. (**a**) Surface brooding in *Paramuricea clavata*, the developing embryos (*purple spheres*) remain attached to their mother colony by a mucous exudate. (**b**) Broadcast spawning of oocytes in a female of the sea urchin *Arbacia lixula*. (**c**) Asexual reproduction by fission in the starfish *Coscinasterias tenuispina*. (**d**) Growth and fragmentation in the zoantharid *Parazoanthus axinellae* and the poecilosclerid sponge *Phorbas tenacior* (Photo credits: C. Palacín)

invertebrates display a remarkably high variety of reproductive strategies (Fig. 2), the most important division being between asexual and sexual mechanisms.

3.1 Asexual Reproduction

Many marine benthic taxa (and probably all colonial and modular invertebrates) are able to perform both types of reproduction: sexual and asexual. In many cases, alternating between both strategies is necessary for completing the whole life cycle. Strictly asexual reproduction is rare in marine taxa, and all major lineages of Metazoa known to be obligate asexual, such as Bdelloid rotifers or Darwinulid ostracods, live in freshwater (Welch et al. 2004; Schön et al. 2012). However, obligate asexual marine lineages are known, such as several species of clams in the genus *Lasaea* (O Foighil and Smith 1996) or some asteroid species such as *Stephanasterias albula* (Mladenov et al. 1986). Many examples of exclusively asexual geographic populations are commonly found alive and thriving in members of different phyla, including some strictly monoclonal populations (García-Cisneros et al. 2017).

There have been many discussions about the advantages or adaptive significance of sexual reproduction for maintaining a high degree of genetic diversity in natural populations and accelerating the selection of advantageous genotypes (Crow and Kimura 1965; Maynard Smith 1968, 1971). Given the almost universal presence of sexual reproduction among marine lineages, it seems obvious that the evolutionary rewards of sex must be widespread in most marine environments. On the other hand, asexual reproduction may be considered as an adaptation to both unfavorable local environmental conditions and relatively stable habitats (Foster et al. 2007). Clonal propagation allows a population to persist when it is unable to complete its sexual reproductive cycle and it enables well-adapted genotypes to become dominant in the absence of disturbances. The balance between sexual and asexual reproduction for a given species may be influenced by a series of biotic and abiotic factors. In marine environments, disturbance may dramatically alter the contribution of asexual reproduction to recruitment (Le Goff-Vitry et al. 2004; Rasheed 2004). Asexual reproduction is of crucial importance in shallow coral reefs forced by disturbances, and it becomes the dominant strategy whenever the time period between favorable conditions for sexual reproduction is prolonged (Foster et al. 2013), a situation that may usually occur in the extremes of the geographical range of the species.

In modular sessile invertebrates with indeterminate growth, there is a thin, fuzzy line between growth mechanisms and asexual reproduction. These organisms can grow, shrink, divide, and suffer partial mortality without dying or even showing signs of senescence. They can reproduce asexually by fragmentation, a process tightly linked to growth. The growth rates and asexual fragmentation patterns of modular invertebrates are influenced by environmental conditions (Lirman 2000) and interactions with boring symbionts (Highsmith 1982), as well as by genetic internal factors (Willis and Ayre 1985). Natural selection acts in the long term on the genetic individuals (genets) and not on the spatially isolated clones (ramets) (Sebens 1987). Since somatic and germ cellular lines are not separated in modular animals, cellular senescence mechanisms, which are common in organisms with determinate growth, must be relaxed or disappear, so that modular organisms could be considered, in practice, as potentially immortal (Hughes 2007).

Marine invertebrates use different methods of asexual reproduction, though all strategies can be effectively reduced at the cellular level to just two principal mechanisms, (1) subdivision of an existing body into two or more multicellular parts (fragmentation, fission, budding) or (2) production of diploid eggs (parthenogenesis) from which asexual larvae or propagules will develop. Fission is common in soft-bodied phyla, such as Porifera, Cnidaria, Platyhelminthes, Nemertea, or Annelida and in the Echinodermata, while it is unknown in nonmodular animals with a hard exoskeleton. Fission, fragmentation, and budding are common strategies among Porifera. In many Cnidaria (Hydrozoa and Scyphozoa), asexual proliferation by budding is a part of the regular life cycle, alternating with sexual reproduction stages. In Anthozoa, fragmentation, fission, and budding mechanisms are also widespread. Some colonial ascidians are also able to reproduce by fission or by budding (Turon 2005). In nonmodular organisms such as Platyhelminthes, Nemertea, Annelida, and Echinodermata, regeneration of whole individuals after fission probably evolved first as a mechanism of defense, and it does not constitute a principal strategy for reproduction, though some lineages exist (e.g., in echinoderms) in which fissiparity has become the dominant reproductive strategy. The transition to asexuality as a proliferation mechanism remarkably evolved in most parasitic lineages of Platyhelminthes and other phyla. On the other hand, there seems to be an evolutionary link between internal brooding and the origin of parthenogenesis, since this reproductive strategy has been mostly reported in lineages of brooding invertebrates (Lively and Johnson 1994). Parthenogenesis is the only asexual reproduction mechanism known in Mollusca and Arthropoda.

3.2 Sexual Reproduction

The strategies for sexual reproduction are strikingly diverse among marine invertebrates. They may be classified depending on different characteristics: (1) mode of reproduction – broadcast spawning with external fertilization, internal fertilization with brooding, internal or external fertilization with surface brooding; (2) sexual expression – gonochoristic, simultaneous hermaphroditic, sequential hermaphroditic (protandrous or protogynous); (3) number of reproductive events throughout the individual lifespan – semelparous, iteroparous; (4) number of yearly reproductive events – seasonal, continuous; (5) larval development (in indirect life cycles) – planktotrophic, lecithotrophic, mixed, poecilogonic. Most of these categories are far from being absolute, and many examples of mixed behaviors are frequently found. Despite all this diversity, Barnes et al. (2009) distinguished between two main opposite ecological groups of traits that are frequently found together in marine invertebrates and that are directly related to dispersal capacity. Group I includes broadcast spawners with external fertilization which release a big number of small eggs in a single yearly event, with planktotrophic larvae of long pelagic duration and high dispersal capacity. Most echinoderms and many polychaetes belong to this group I, although sessile animals like petrosiid or clionid sponges and anthozoans such as pennatulaceans (Fig. 2a) or many actinians can also be included in this group. Conversely, group II typically includes brooding species which incubate a small number of embryos within the female body or on its surface, in a continuous manner along the year. Their eggs are big, containing a high quantity of yolk, and may produce viviparous juveniles or (more commonly) lecithotrophic larvae of short pelagic duration which settle at a small distance from their parents. Many gastropods and small benthic crustaceans can be included in group II, jointly with some gorgonians and soft corals, calcareous sponges, colonial ascidians, and most cheilostome bryozoans (Fig. 3b).

The broadcast spawning strategy (group I) is typical of large-bodied invertebrates, whereas smaller and interstitial forms are more often internal brooders (group II). This follows from the fact that mass spawning requires the capacity to store a great quantity of gametes in a cavity within the body, in order to be able to release them all

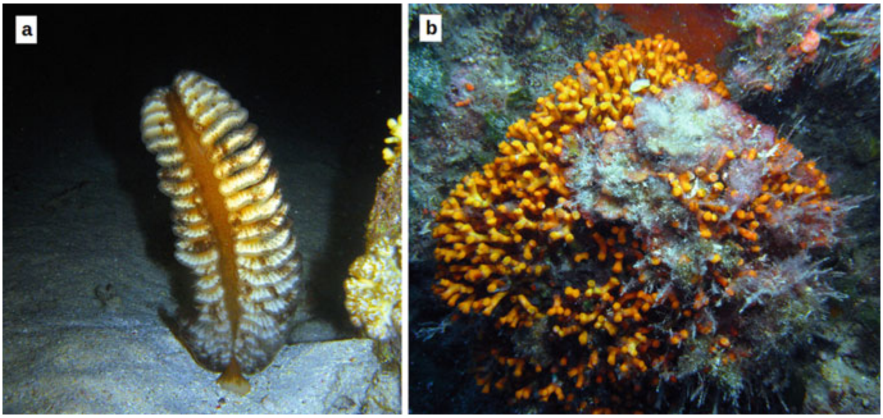

Fig. 3 Examples of benthic invertebrates with reproductive strategies belonging to group I (high dispersal capacity) and group II (low dispersal capacity). All pennatulaceans, like this *Pteroeides* sp. from the Red Sea (**a**), are broadcast spawners whose oocytes produce long-lived larvae after fertilization. Conversely, most derived cheilostome bryozoans like *Myriapora truncata* (**b**) brood their larvae in brooding chambers called ovicells. Their developed lecithotrophic larvae usually settle not far from the parental colonies within few hours after release (Photo credits: O. S. Wangensteen)

together in a synchronous (often annual) spawning event. Moreover, the gametes require of a more or less prolonged period of time to mature from gametocytes to mature gametes (gametogenesis). This period can last several months, during which the reproductive tissues of the individual can grow considerably so that they can eventually occupy a high proportion of the internal volume and the mass of the animal. The gametogenesis process is often longer for females than for males, since females usually require to transfer a high quantity of reserves (yolk) to the developing oocytes, which will be used by the developing embryo during the first stages of development (in planktotrophic larvae) or throughout the whole developmental period (lecithotrophic larvae). The reserves to be allocated in the yolk may come primarily from nutrients previously stored within the female body tissues (capital breeders) or may come directly from the food (income breeders). The use of one of these two strategies has important implications in the trophic behavior of both females and males and in the timing of gametogenesis. One extreme example of capital breeding is semelparity, where the capital of reserves stored throughout the whole animal lifespan is massively invested into a single reproductive event by both males and females, which is followed by the genetically determined death of the individuals. Polychaetes of the family Nereidae and cephalopod mollusks (except Nautiloidea) are well-known examples of semelparous invertebrates. Conversely, virtually all species of modular invertebrates, which are ecosystem engineers of marine animal forests, are iteroparous and have the potential to reproduce many times along their usually long (and sometimes extremely long) lifespans. In these species, the spawning events are usually followed by a period of latency or recovery, before the next gametogenic cycle starts.

In contrast with the often low energy requirements needed for asexual reproduction, sexual reproduction usually requires the investment of huge amounts of energy and resources. The development of the ability to generate gametes requires a minimum size and a minimum maturation period. This is also true for colonial and modular animals, whose maturation periods may be, in some cases, considerably long. For example, in shallow reef-building tropical corals, there appears to be a prereproductive period of 8–10 years until sexual maturation is attained. Often, males and females show different maturation periods; e.g., in *Corallium rubrum*, males become sexually mature at a minimum age of 6 years, whereas females need 10 years to reach maturation (Gallmetzer et al. 2010). Patterns of variability of minimum age for maturation are unknown for most marine invertebrates.

3.3 Diversity in Life Cycles, Distribution of Resources, and Habitat Stability

Most species of all marine metazoan phyla exhibit a benthic-pelagic life cycle belonging to the ecological group I previously described, with broadcast spawning, external fertilization and pelagic, long-lived planktotrophic larvae. An estimated 70% of all marine invertebrates in temperate zones exhibit this reproductive behavior, indicating that this pattern of reproduction has advantages in most ecological situations (with the exception of Polar latitudes, see Sect. 4.4 below). However, all the phyla with species having benthic-pelagic life cycles have also some, or many, species which present benthic larvae, internal fertilization, brooding of the embryos, or direct development, classifiable in ecological group II. Moreover, closely related species (frequently within the same genus) exhibit contrasting modes of development, indicating the high degree of plasticity and the adaptive value of reproductive strategies.

The transition from benthic-pelagic to holobenthic life cycles may be regarded as a trade-off between survival rate of the offspring and the need for colonizing new habitats by dispersal. Thus, species that require specific conditions as adults, conditions which are rarely met on the benthos at a regional level due to the rarity or heterogeneous concentration of the needed resources, may be expected to evolve a strategy of brooding their offspring so that the settlement of juveniles occurs at a short distance from the areas already occupied by the adults (which have been positively tested as suitable areas for adult success). Conversely, generalist species able to colonize diverse habitats which rely on resources that are widespread and evenly distributed across wide geographical areas may have more reproductive success when investing in long-distance larval dispersal, in order to extend their distribution area, decrease intra-specific competition, and optimize resource allocation. Thus, selection pressures towards long-lived pelagic larvae with great dispersal capacity are directly related to habitat spatial heterogeneity and distribution of resources.

Level of disturbance (in other words, habitat instability) is the other main factor to consider as an evolutionary driver of dispersal strategies. When disturbances are

Table 1 Dispersal strategies under diverse degrees of spatial heterogeneity and stability

	Low disturbance	**Intense disturbance**
Low spatial heterogeneity	Dispersal	Dispersal
High spatial heterogeneity	No dispersal	Mixed strategy

Modified from Poulin and Feral (1996)

intense, leading to ephemeral habitats, then dispersal of the offspring to colonize new habitats is an urgent need. Conversely, stable undisturbed habitats would lead to the selection of short-lived propagules which would settle close to their parental populations. In habitats that are both submitted to intense disturbances and have a high degree of spatial heterogeneity, long dispersal would not be the optimal strategy, since the odds of finding suitable conditions would be probably lower as the larvae get farther away from parental populations. Thus, a mixed strategy would probably be most favored, giving the chance to colonize new habitats, but not very far from parental populations. The optimal dispersal strategies under varying conditions of habitat heterogeneity and stability are summarized in Table 1.

3.4 Pelagic Larval Development

Depending on their ability to feed, marine invertebrate larvae have been traditionally classified as either planktotrophic or lecithotrophic. Planktotrophic larvae feed on other planktonic organisms (usually phytoplankton) and typically display long pelagic larval duration. Conversely, lecithotrophic larvae do not feed, but depend upon their lipid reserves to accomplish their development, which makes their pelagic duration typically shorter. However, the distinction between both feeding strategies is not as clear as it might seem. Some lecithotrophic species may actually turn into planktotrophy if their larval period is extended (Kempf and Hadfield 1985; Strömberg 2016) and some larvae have the ability to feed directly by uptaking dissolved amino acids from seawater, despite lacking any developed feeding structures, an uptake which could account for 40–70% of their total energy needs (Jaeckle and Manahan 1989). This would allow lecithotrophic larvae to outlive the energy reserves stored in the egg, granting them longer pelagic duration and enhanced dispersal capacity. This feeding by direct uptake could be a dominant strategy for planktonic larvae with low yolk reserves from deep-sea organisms, where phytoplankton is absent, but dissolved organic matter may be abundant.

3.5 Dispersal of Brooding Species

Though the general rule is that brooding species release short-lived larvae which settle at short distances from their parental colonies, not all the brooded larvae have short pelagic duration. For example, despite its brooding character, lecithotrophic larvae of the coral *Pocillopora damicornis* can survive and remain competent to settle after 100 days (Richmond 1987). This could enable this brooding species (and other brooders such as *Acropora cuneata* or *Acropora palifera*) to maintain high levels of gene flow and to form vast, effectively panmictic populations across the Great Barrier Reef, comparable to those formed by typical broadcast spawning species (Ayre and Hughes 2000) However, other brooding species such as *Seriatopora hystrix* or *Stylophora pistillata* show weak connectivity between populations, as expected from the short pelagic duration of their larvae. This indicates that the main determinant for connectivity among distant localities is not the mode of reproduction but the pelagic larval duration.

Moreover, many species from shallow waters with brooding behavior and short-lived larvae with low dispersal capacity may be still able to maintain panmictic populations across wide geographic areas. This could be explained by another dispersal mechanism which is often overlooked. Settlers and adult individuals of shallow benthic organisms might expand their dispersal range by rafting (Jokiel 1990). This mechanism of passive dispersal might account for the lack of correlation between pelagic larval duration and dispersal capacity predicted by the larval dispersal alone. Some brooding species have been described which present a wider geographic distribution range than the broadcasting sibling species (Johannesson 1988). This would imply that even though the transport of benthic stages by rafting or other adult dispersal mechanisms happens very rarely, it may still be more influential for long-term connectivity than larval dispersal over long distances.

4 Reproductive Ecology of Different Types of Animal Forests

Despite the astounding diversity in strategies and the thousands of possible exceptions to the rules among benthic invertebrate species, we will try to describe some general patterns that can be found in the dominant reproductive strategies in some of the diverse ecosystems considered as marine animal forests.

4.1 Tropical Coral Reefs

The reproductive ecology of coral reefs is undoubtedly the most thoroughly studied among the different instances of animal forests (Szmant 1986; Richmond and Hunter 1990; Richmond 1997; Baird et al. 2009; Darling et al. 2012). Tropical hermatypic corals display the full range of sexual strategies, with the majority of species studied so far being simultaneous hermaphrodites, a few species being sequential hermaphrodites and others gonochoristic. Both modes of reproduction (broadcast spawning and brooding) are present. Most tropical coral species (approximately 85%) are broadcast spawners, while brooders represent ca. 15% of the species. The mode of reproduction influences many aspects of the ecology of the species, including transfer of symbiotic algae to larvae, duration of pelagic period, dispersal capacity, spatial structure of populations, biogeographic distribution patterns, and genetic variability. Both hermaphroditic and gonochoristic broadcasters correlate with large colony sizes and short spawning periods, whereas hermaphroditic and gonochoristic brooders correlate with small colony sizes, multiple larval release cycles per year (or continuous reproduction), and occupation of unstable habitats.

The uneven distribution of instability in shallow tropical habitats has probably been the major force behind the evolution of brooding species, with high rates of local recruitment in habitats where adult mortality is high due to recurring intense disturbance events and thus colony sizes tend to be small (Szmant 1986). Conversely, big-sized coral species which live in more stable shallow tropical habitats would benefit from the wide geographical distribution of such habitats by evolving long-dispersal strategies. Sexual reproduction is the primary reproductive strategy for most coral species within the core of their distribution range, whereas asexual strategies may be dominant for the same species in the limits of their ranges, where conditions for success of reproductive events may be less favorable (Kawecki 2008; García-Cisneros et al. 2017).

4.2 Temperate Shallow Communities

Animal forest ecosystems from temperate shallow waters (0–100 m depth) are usually dominated by octocorals. The most studied reproduction patterns of temperate animal forests are those from Western Mediterranean (Coma et al. 1996; Gori et al. 2007; Rossi and Gili 2009; Fiorillo et al. 2012; Ambroso et al. 2013; Quintanilla et al. 2013). In this geographic area, the mode of reproduction of octocorals is also correlated with the stability of the habitat, but in the opposite way than the behavior of tropical hexacorals. Thus, species living in less stable habitats, but with low spatial heterogeneity, such as sandy or detritic bottoms (e.g., *Leptogorgia sarmentosa* or *Alcyonium palmatum*) are broadcast spawners whose populations are formed by scattered colonies, whereas species living in more stable rocky habitats with steady dominant currents (e.g., *Corallium rubrum*, *Paramuricea clavata*, *Eunicella singularis*, or *Alcyonium acaule*) are internal or surface brooders, with short-lived larvae and high rates of local recruitment. This suggests that spatial heterogeneity in resource distribution, and not habitat instability, could be the main driver of reproduction mode in these communities (see Sect. 3.3 and Table 1). All these species are gonochoristic and most of them show marked seasonality, with typically an annual reproductive event, which is coherent with the marked seasonality observed in the shallow Mediterranean waters. The release of larvae in internal or surface brooders occurs typically during late spring or early summer (May-July), whereas the broadcast spawners living in detritic habitats usually release their gametes during the late summer or early autumn (August–October). The sexual reproduction is dominant in all these Mediterranean species, where asexual propagation has just a marginal role.

4.3 Cold-Water Corals

The reproductive biology of deep-water scleractinian corals is much less known than that of their counterparts from shallower waters (Waller 2005; Roberts et al. 2006; Brooke and Järnegren 2013; Larsson et al. 2014). Although the reproductive strategies of very few deep-coral species have been studied, some patterns may still be found, and the differences with shallow water corals are striking. While most tropical shallow-water scleractinian corals are hermaphroditic, most deep-coral species are gonochoristic and the only three species found to be hermaphroditic (all in the genus *Caryophyllia*) are solitary corals which show a novel type of hermaphroditism (cyclical sexuality; Waller 2005). Although the rarity of suitable habitats in the deep-sea and the supposed stability of these ecosystems would point to brooding as a convenient strategy, actually only three species of deep-sea scleractinian corals (all of them in the genus *Flabellum*) have been reported to brood their embryos, and they all live at relatively shallow depths (500 m) in Antarctic waters (so, different ecological considerations may apply, see Sect. 4.4 below). All the other species of deep-sea corals whose reproduction have been described are broadcast spawners. Unlike the typical seasonality of shallow water corals, the gamete releasing processes of deep-sea corals may be continuous or semicontinuous, with very few species (e.g., *Lophelia pertusa* and *Oculina varicosa*) showing some kind of seasonality. The seasonality in deep water is not to be found in temperature, since most of these habitats are well below the permanent thermocline. However, there is some seasonal fluctuation in the input of phytodetritus from shallower to deep waters (Rice et al. 1986), coupled with surface primary productivity and delivered by tidal downwelling (Davies et al. 2009), which would act as a seasonal trigger for the reproduction of invertebrates such as echinoderms or bivalves (and maybe hexacorals). Most larvae of deep-sea corals are presumably lecithotrophic. Although the pelagic duration is generally unknown, the wide distribution range of most species of deep-sea corals suggests long pelagic time spans, generally longer than their shallow water counterparts. The slow metabolism associated with the low temperatures prevailing in the deep-sea and the ability to uptake dissolved organic matter from seawater might account for this prolonged larval duration. Moreover, a mixed trophic behavior has been recently discovered in larvae of *Lophelia pertusa*, which develop a mouth after 20 days of development and turn to planktotrophy, which would enable them for a prolonged pelagic duration, explaining the widespread distribution of this species (Strömberg 2016).

Asexual reproduction may be important for the continuity of deep scleractinian coral reefs. For example, reefs created by *Lophelia pertusa* are composed of a low number of genetically different individuals which can be several thousands of years old (Dahl 2013). The growth pattern of the colonies (where the outer parts are exposed to the current flow and alive, whereas the inner parts eventually die due to the reduced water flow) shapes the whole reef. The base of the dead branches is weakened over time by bioeroding animals, so some fragments may eventually fall off and create new ramets. This is yet another example of how interspecific interactions may facilitate the reproduction (in this case, asexual) of ecosystem-engineering species.

On the other hand, the reproduction patterns of octocorals from the deep-sea seem to be closer to those of their shallow-water relatives (Watling et al. 2011), with some particularities. Most deep octocoral species adjust to the general pattern of gonochorism, continual reproduction, larval brooding, and lecithotrophic larvae which is generally observed for deep-sea invertebrates (Gage and Tyler 1991). Like scleractinians, most deep octorals are gonochoristic, and only one genus (*Drifa*) is known to include hermaphroditic species (Sun et al. 2010). All deep-sea pens (pennatulaceans) are exclusively broadcast spawners, just like their shallow relatives. Deep alcyonaceans, again like their shallow counterparts, exhibit a variety of brooding and broadcasting strategies, with the difference that many species show continuous instead of seasonal reproduction (Kahng et al. 2011). In some cases, the gametogenesis may be extended beyond a year (Orejas et al. 2007). This extended time might be required for producing large yolky eggs in nutrient-depleted environments, so to increase survival of the lecithotrophic larvae.

Remarkably, asexual reproduction seems to be nearly absent in deep octocoral species. Asexual mechanisms which frequently occur in shallow alcyonaceans are yet to be observed in deep octocoral species (Watling et al. 2011).

4.4 Antarctic Benthic Ecosystems

In the realm of Antarctic benthos, a prevalence of brooding behavior can be found in benthic invertebrates (Thorson 1950; but see evidences against Thorson’s Rule in Clarke 1992; Pearse 1994), although broadcast spawners are not uncommon, most of them with nonfeeding lecithotrophic larvae and a few with planktotrophic larvae (Pearse et al. 1991). Temperatures in the Southern Ocean are the most stable in the world, ranging from −2 °C to +2 °C and this range has probably remained stable during the last 14 million years. Thus, well-adapted reproductive processes are expected to have evolved among Antarctic invertebrates. Physical constraints to developmental rates in cold temperatures make larval development a slow process requiring long periods of time for completion. Despite the narrow temperature range, Antarctic seas are among the most seasonal habitats in the world, with high primary productivity in mid-summer and low or null production from late autumn to early spring. Planktotrophic species take advantage of this productivity by adjusting their reproductive cycles so that larvae are produced in summer. However, some species, such as the abundant starfish *Odontaster validus*, release their planktotrophic larvae during the Antarctic winter (Stanwell-Smith and Peck 1998). Some of these larvae have so low metabolic rates that they might not have to feed at all during their development (Hoegh-Guldberg and Manahan 1995). Other larvae are known to rely on alternative nutrition sources, such as dissolved organic matter or bacteria, for their survival (Rivkin et al. 1986; Bosch et al. 1991).

It is important to note the remarkable differences in stability between shallower and deeper coastal ecosystems in the Southern Ocean. The shallow benthos around the Austral continent is probably the most unstable and physically disrupted marine habitat known. The shore-bond ice and shallow icebergs plow up the bottoms down to depths of 20–30 m, ultimately removing any form of long-lived macrobenthos and leaving only ephemeral communities of opportunistic organisms able to quickly colonize open spaces (Teixidó et al. 2004). In these harsh, unpredictable conditions, brooding and nonpelagic development which would bind the offspring to a threatened area and prevent the colonization of new open habitats will not be favored, whereas uncertainty in the timing of disturbances would not favor seasonal release of planktotrophic larvae as a good strategy. Conversely, the development by means of long-lived lecithotrophic pelagic larvae would become the most successful strategy. In clear contrast, relatively deeper Antarctic benthic communities from depths below 20–30 m might be among the most stable marine benthic habitats in the world. In these communities, biological interactions, rather than disturbances, may determine community structure and well-established mature communities of big-sized, long-lived benthic sessile animals with little population turnover can be found. In these conditions, organisms are expected to invest in larvae with little dispersal capacity, which would settle at a short distance from the parents. This high degree of stability would explain why brooding and nonpelagic development became the dominant strategy.

5 Structuring of Animal Forests at Small Scales

It is clear that the spatial structure of benthic invertebrate populations is directly related to their dispersal ability. In species which rely exclusively on sexual reproduction, the resulting spatial structure of populations is tightly correlated to their reproduction mode and pelagic larval duration. For example, the soft coral *Alcyonium acaule* is a surface brooder whose larvae show rapid settlement behavior. Its populations form dense patches of aggregated individuals, which shape the structure of some Mediterranean coralligenous outcrops. Conversely, the closely related *Alcyonium palmatum* is a broadcast spawner which is found as scattered colonies (Ambroso et al. 2013) in sandy and detritic bottoms (Fig. 4).

This determination of spatial structure by dispersal ability of the larvae is not exclusive of sessile animals. Mobile, nonmodular animals also show different distribution patterns, highly influenced by their mode of reproduction. For example, the North Atlantic nudibranch *Onchidoris proxima* has short-lived lecithotrophic larvae, behaviorally adapted to avoid dispersal in the water column. This species usually forms dense patches of locally abundant individuals in the shallow subtidal, feeding on bryozoans encrusted among seaweeds. Conversely, *Goniodoris nodosa* is a sympatric relative of *Onchidoris proxima*, with roughly the same size and which feeds also on bryozoans (when juveniles, since adult individuals feed on colonial ascidians), but it develops through planktotrophic larvae with a long pelagic duration of up to three months. It is considered a common species, widely distributed from intertidal up to 120 m depth. And it can be commonly found as solitary individuals which aggregate mainly for reproduction (Todd et al. 1998).

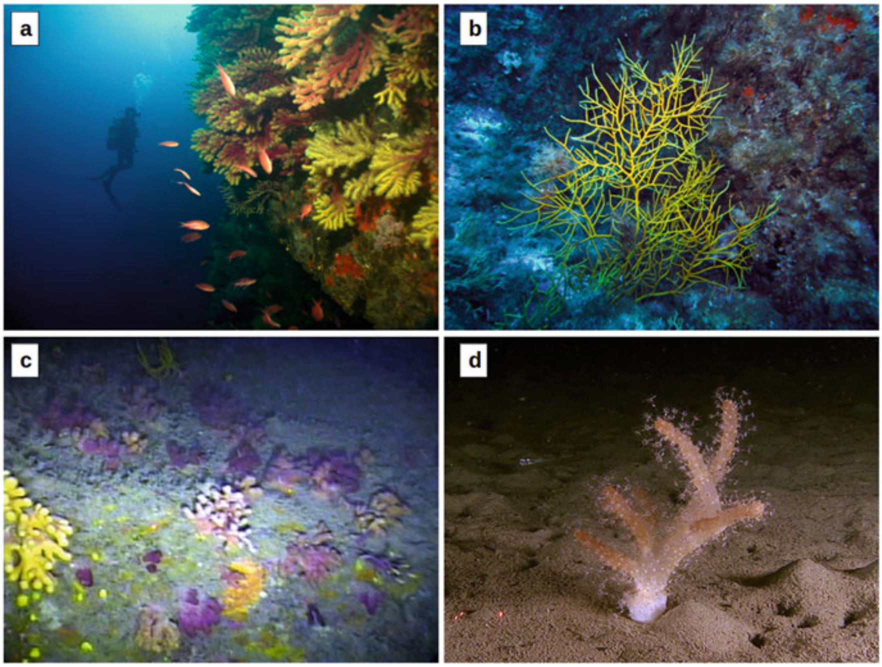

Fig. 4 The reproduction mode greatly influences the small-scale structuring of populations. The octocorals *Paramuricea clavata* (**a**) and *Alcyonium acaule* (**c**) are surface brooders with short-lived pelagic larvae, whose populations usually form dense aggregates. Conversely, *Leptogorgia sarmentosa* (**b**) and *Alcyonium palmatum* (**d**) are broadcast spawners with long-dispersal larvae, which are usually found as isolated colonies (Photo credits: (**a**) C. Palacín, (**b**) O. S. Wangensteen, (**c**) S. Rossi/ICM-CSIC and (**d**) G. Newman/ICM-CSIC)

The dispersal mechanisms that structure the spatial distribution of populations do not exclusively depend on the larvae and may occur at different life cycle stages. In many cases, the dispersal of adults may be also quantitatively important, even for sessile invertebrates, whose benthic stages may disperse by rafting mechanisms. Furthermore, the relationships between sexual reproduction mode and spatial structure is not always so clear in species able to reproduce and disperse by both asexual an sexual means, which may often disperse farther by the asexual strategy than by sexual propagules (Jackson 1986; Thomson et al. 2015).

6 What Genes Can Tell: Gene Flow, Connectivity, and Clonality

The relationship between pelagic larval duration and the geographic scales of genetic structure has been shown in the case of noncolonial species with mainly sexual reproduction, such as starfish and sea urchins, where brooding species with nonpelagic development show marked differentiation between populations at scales of just tens of km, whereas short-lived lecithotrophic pelagic larvae (e.g., 4 days pelagic duration) lead to genetic structuring in the range of hundreds of km, and the longest-living larvae lead to scales of differentiation over thousands of km (Poulin and Feral 1996). However, there are many exceptions to this rule (e.g., Kyle and Boulding 2000; Fernández et al. 2015). These relationships are not so clear for other benthic organisms, especially for modular long-lived ecosystem engineers (Jones et al. 2009). For brooding tropical hexacorals, all the possible scales of connectivity have been found, unlinked to the reproduction mode, from wide panmixia over 7000 km in the brooding coral *Stylophora pistillata* (Takabayashi et al. 2003) to differentiation at small scales of 2–60 km in the equally brooding coral *Seriatopora hystrix* (Underwood et al. 2007). Adult dispersal might partly be responsible of this uncoupling. For example, the high levels of gene flow reported for the brooding, solitary hexacoral *Balanophyllia elegans* along the American West coast, despite the reduced dispersal capacity of its crawling larvae, can be explained if we consider the rafting behavior of the adult individuals attached to kelp or other floating materials (Hellberg 1994).

Other nonbiotic factors, such as the presence of geographical barriers to gene flow, may alter considerably the genetic structure of populations. For example, the populations of *Lophelia pertusa* living inside the Scandinavian fjords are clearly differentiated from their counterparts living in the North Atlantic (Le Goff-Vitry et al. 2004), probably due to the reduced gene flow between the fjords and the outer waters in the case of deep-sea larvae, whereas individuals of the same species from the Mediterranean and the Barents Sea were virtually indistinguishable genetically (Flot et al. 2013). Genetic differentiation related to depth is also commonly found. For example, populations of the surface-brooder gorgonian *Paramuricea clavata* from shallow waters (5–35 m depth) were found to be genetically distinct from those living at the head of nearby submarine canyons (50–70 m depth) (Pérez-Portela et al. 2016).

Genetic structure studies can also uncover the clonal structure of the populations. Indeed, the use of genetic tools is, in most cases, the only practical way to assess the relative role of sexual and asexual reproduction in the make-up of populations of modular organisms. These studies have in general revealed the important contribution that asexual reproduction plays in the maintenance of the populations of landscape-dominant invertebrates (Calderón et al. 2007; Adjeroud et al. 2014).

In summary, the genetic structure and connectivity among populations of a given benthic species depend on the dispersal capacity of the species (at different life cycle stages) and its capacity for asexually colonizing the substrate, but it is strongly modulated by abiotic factors such as physical, oceanographic, and geographical constraints.

7 Persistence of Animal Forests in Time

Although the structures generated by ecosystem-engineering species may outlive the individuals that created them, the persistence of its functionality and ability to maintain a diverse community of organisms depends on the health of the living populations of the key engineering species responsible of originating the animal forest ecosystem. This health depends mainly on two complementary processes: growth of the existing individuals and recruitment of new ones. The growth of the existing individuals is related to asexual reproduction by fragmentation, which is able to originate new ramets of existing genetic individuals, whereas the recruitment of new genets, with unique genetic endowments, is tightly dependent of the ability of the existing individuals for successfully complete at least four sequential reproductive processes: gametogenesis, fertilization, larval development, and settlement.

Theory of conservation genetics shows that the maintenance of a minimum degree of genetic diversity is crucial for the long-term survival of populations (Shaffer 1981). In the case of ecosystem engineers, the survival of populations is tightly linked to the long-term survival of the whole ecosystem created and maintained by them. Thus, a minimum degree of successful sexual reproduction is necessary for the persistence of these ecosystems over time. Monoclonal populations maintained exclusively by asexual mechanisms may be considered ephemeral, however vastly distributed in the space they are, since different kinds of threats, such as pathogen outbreaks or changing environmental conditions, could eventually cause their extinction in relatively short times.

7.1 Recolonization and Recovery

Restoration of an animal forest ecosystem after it has been damaged by a disturbance may require long times. The capacity to regenerate following disturbances depends on sources of resilience that operate at multiple scales (Hughes et al. 2005). Initial recolonization depends on two factors: the degree of mortality caused by the disturbance and the availability of a larval supply (Connell 1973; Connell et al. 1997). If a minimum number of colonies survive within the destroyed area, they may continue to grow and produce new larvae which may recolonize the surrounding available habitats. However, if most colonies of a given species die off, leaving the remnant survivors below a critical threshold, then self-recolonization will be impossible and new colonies will have to be funded by propagules produced outside the damaged region. Thus, the distance to the source of larvae, the pelagic larval duration of the species, and the relevant current patterns are critical for the recovery of the population. In pristine systems, connectivity among the different patches or areas where the species is present may allow for the recolonization of the damaged area, but in disturbed systems, habitat fragmentation will decrease the connectivity between areas, and some patches may become isolated from other sources of propagules, which could lead to local extinctions when intense disturbances eventually arrive. This is especially true for species with low dispersal capabilities. Thus, the recovery of the fragmented habitats and the restoration of connectivity among patches should be considered a priority in conservation measurements.

The ability to achieve the full recovery of ecosystem function depends on the recolonizing capacity of the whole array of different species that have been lost due to the disturbance and the complexity of the interactions among them. Species with diverging life histories will need different timing for the recovery of their populations. For long-lived species (such as most marine ecosystem engineers) the recovery is necessarily slow. Alternate ecological states and regime shifts can temporarily occur as the ecological succession evolves, depending on the interactions among the species already present. Density-dependent mortality (due to altered predator-prey ratios) or density-dependent reproduction (due to the occurrence of density thresholds for reproductive success) will modulate the rates of recolonization and recovery. Due to the prevalence of these complex interaction networks, tipping points and thresholds, hysteresis may occur, meaning that the ecosystem may never recover to its pristine state (Scheffer et al. 2001) and is then doomed to remain in an alternative stable degraded state.

7.2 Resilience and Vulnerability of Reproductive Cycles

As we have seen, response to disturbances has been a major determinant in the selection of reproductive strategies of marine invertebrates. Thus, the recovery ability of an ecosystem after an anthropogenic disturbance will be highly dependent upon the previous degree of natural disturbance prevailing in the ecosystem in which they have adapted.

The reproductive strategies of organisms living in habitats with low degree of natural disturbance, such as Antarctic mid-depth benthos, Mediterranean shallow octocoral communities, or deep cold coral communities, have been selected for a low degree of instability and are likely to show a low recovery capability in response to intense human disturbances such as commercial trawling. The reproductive cycles of the species which have evolved in such ecosystems are expected to be successful only under narrow or strict conditions, and any change of sufficient magnitude could affect significantly their reproductive output. The natural resilience of these communities is then expected to be low, and they should be considered as highly vulnerable ecosystems.

Conversely, communities which are adapted to highly disturbed natural ecosystems, such as sandy or detritic bottoms or shallow coastal communities, have generally evolved reproductive strategies capable to cope with such local disturbances and are likely to show higher levels of resilience and a better response to impacts. Nevertheless, some extremely long-living species dwell in these habitats (e.g., bamboo corals, Isididae) which could be extremely impacted by disturbances such as bottom trawling (Roark et al. 2005).

In addition, the reproductive cycles of marine invertebrates may show different degrees of resilience in front of global changes in physical parameters such as water temperature or pH. Species adapted to ecosystems with marked seasonality and high interannual variation in physical factors will probably be more resilient to such changes (Hazan et al. 2014), whereas organisms living in mostly stable habitats might suffer intense disruptions of their reproductive cycles. Considering the complex interplay between physical and biotic factors, the response of the reproductive output for a particular species to global change may be unpredictable (Wangensteen et al. 2013). For example, small changes in the coupling between temperature and photoperiod might have dramatic consequences for broadcast spawners with planktotrophic larvae, if the spawning events are triggered by temperature, while phytoplankton productivity is still coupled with photoperiod. Ocean acidification driven by increased CO_2 concentration is also expected to have serious effects on the reproduction of organisms with calcifying larvae, such as echinoderms or mollusks (Dupont et al. 2010).

Given the little detailed knowledge that we currently have about the reproductive cycles of most marine invertebrates and the uncertainties in the effects of the multiple physical and biotic factors which may modulate them, the global response of marine ecosystems in general, and of animal forest ecosystems in particular, to such global changes will be, in general, unpredictable.

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Growth Patterns in Long-Lived Coral Species

22

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Abstract

The knowledge on the growth patterns of organisms constructing complex three-dimensional structures can help in understanding their role as engineering species. Growth and form of several sessile organisms are characterized by different properties; one of those is modularity. Trees in terrestrial habitats and corals in

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marine environments are sessile modular organisms where growth is regulated by similar processes. Part of forestry's theoretical and practical framework on the study of growth can then be applied to the marine environment. The aim of this chapter is to present an overview of the different growth patterns of corals by applying some of the techniques developed for trees (e.g., annual growth ring count).

As growth can be influenced by environmental conditions, understanding the mechanisms and rates of growth can give precious insights on the effects of climate change and anthropogenic disturbances. Annual growth rings of several species of corals act as climatic archive in a similar manner as it happens in trees. Corals grow in winter and summer, but the density of the calcium carbonate depositions in the coral skeleton is different due to seasonal changes in ocean temperature, pH, availability of nutrients, and differences in light irradiance.

Examples of different coral species living in different environments (from cold-water corals to tropical coral reef species) will be discussed in order to shed light on the mechanism of formation and development of the so-called animal forests.

Field- and laboratory-based knowledge can be integrated within numerical models describing the basic mechanisms of growth and fine-tuned by using observed data. Models are particularly useful as they assess effects that are almost impossible to observe in real time, due to the long life span of some species, as well as impractical experimental setups.

Keywords
Growth • Modular organism • Scleractinia • Octocorallia • Antipatharia • Cold-water corals • Environmental factors

Contents

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1 Growth in Modular Organisms

By definition, growth is the increase in cell size and number that takes place during the life history of an organism. Growth occurs according to a plan that eventually determines the size and shape of the individual. Thus, growth is a complex phenomenon, which involves changes in metabolism (energetic investment) and allometric scaling (Gould 1971).

From an evolutionary point of view, growth is a positively selected characteristic, as it is correlated with several fitness traits such as fecundity, offspring quality, mating success, and longevity (Stearns 1997). One of the most evident advantages of size increase is linked to predation risk: a larger size reduces the predator interaction and success. For instance, adult blue whales (*Balaenoptera musculus*), the largest living animals, do not have predators due to their large size. Another trait linked to size is fecundity: larger animals (clonal or individual) have higher energy inputs and can then invest more energy in offspring (the fecundity advantage model; Trivers 1972; Stearns 1997).

The advantages of an increase in body size are evident in modular organisms. Modular organisms, such as trees and corals, grow by the addition of modules (i.e., more polyps or leafs) which can result in extremely long life spans (Roark et al. 2009). Some unitary organisms can have very long life spans as well, such as the *Arctica islandica* (a boreal clam) and *Neopycnodonte zibrowii* (a deep-sea oyster) which can live for more than 500 years (Wisshak et al. 2009). However, the life span of modular organisms can be an order of magnitude greater; according to a radiocarbon-dating study published in 2009 by Roark and coworkers, the black coral *Gerardia* sp. can live up to 2,742 years and *Leiopathes* sp. can have a life span even longer, living up to 4,265 years (see Sect. 5 for further details on black coral growth). These extremely long life spans are linked to modularity, as each module can also reproduce asexually (cloning), which potentially produces “virtual immortality.” While unitary organisms are characterized by determinate growth, the growth of modular organisms can be indeterminate, as size increase is a consequence of an increase in the number of modules. It is worth to note that an increase in size in a modular organism can also be the result of fusion.

Unitary organisms often exhibit a well-defined age, with the typical cycle of birth, senescence, and death. However, in the case of long-lived modular organisms such as trees and corals, senescence could be less important as there is a generation of new modules which coexist with the older ones (e.g., in a coral colony old modules and young ones coexist in the same individual). In modular organisms, when an individual produces new modules, the increase in dimensions is directly proportional to the size of the colony. This makes indeterminate growth only limited by physical constraints, implying that even the largest individuals can continue growing. Modular growth can be modeled based on replication, growth, and mortality of the modules. Possible modules may be leaves, tillers, polyps, zooids, or branches, among many others. The individuals can be a single, physiologically discrete entity such as an oak tree or coral head or a more ambiguous entity such as strawberry plants, which are linked by runners or *Ranunculus* sp. bunches that are linked by stolons, in which the degree of integration changes markedly with time.

Once growth of single module and entire organisms is described, a better understanding of life histories of the modular organism can be achieved. Population structure (size class frequency) and fecundity are linked to modular growth and are considered important life history traits for the demography of populations (see by Bramanti et al., ▶ Chap. 19, "Demography of Animal Forests: The Example of Mediterranean Gorgonians" this same volume).

Generally, in modular organisms, the modules remain connected for most of the organism's life span, but in several marine invertebrates, modules have the capability to grow after being detached from the parental individual. Besides asexual reproduction, modular organisms also reproduce sexually, leading to complex population dynamics from a spatial and temporal point of view. This involves a number of processes that may act at the genet, individual, or population level, irrespective of their genetic identity.

Modular growth evolved both in terrestrial plants and colonial aquatic invertebrates, and it is linked to the ability to exploit resources such as light, space, and the translocation of energy from the site of production (source) to the site of consumption (sink). In plants, it has been demonstrated that a defined relationship between resource allocation and carbon budgets determines the rate and pattern of translocation of assimilated materials. Moreover, plants can redistribute resources between different modules. In invertebrates with modular growth pattern, responses to stress due to predation or competitive interactions (i.e., contacts and overgrowth) can be localized in specific regions of the colony where the interaction occurs.

Sessile modular organisms with large three-dimensional structures and long life spans are able to modify the environment (as ecosystem engineers; Jones et al. 1994), facilitating the presence of other species. In terrestrial habitats, trees are the typical ecosystem engineers. In marine environments, modular organisms with treelike three-dimensional structures may be algae (kelp forests), phanerogams (sea grass meadows), or animals (corals, sponges, polychaetes, and bryozoans). This chapter will focus on corals, as they form some of the most conspicuous three-dimensional structure of marine animal forests.

2 Methodologies for the Study of Growth in Corals

Corals have complex three-dimensional structures, which makes an accurate measure of growth difficult. Over the last few decades, significant research efforts have been dedicated to the characterization of coral growth patterns, mainly for age estimations, and to forecast reef resilience considering the environmental and/or anthropogenic perturbations. A range of methodologies have been utilized to gauge growth rates, including direct measures of colony size (linear growth or surface extensions), polyp addition rate, and the estimation of calcification rates (e.g., using alkalinity anomaly or the buoyant weight technique).

Surface extension and linear growth of a colony can be measured by using images or videos taken directly from the sea bottom, provided that a scale was used (e.g., lasers). This method has a low impact on corals, as they are not removed from their habitat. Measurements commonly correspond to the estimation of the diameter and the extension away from a defined point (base of the colony, substrate, etc.) (Coma et al. 1998; Larcom et al. 2014). However, this method is more appropriate for long-term surveys or faster-growing species.

The polyp addition rate, which is the amount or percentage of new polyps budded, is more appropriate for corals that produce large polyps and for species whose colony extension is primarily driven by polyp formation (e.g., reef-forming cold-water corals such as *Lophelia pertusa*) (Lartaud et al. 2014).

The buoyant weight method is based on the principle of Archimedes. Commonly used in experimental studies on isolated branch tips, it involves weighing corals underwater, calculating the weight of the skeleton by changes in density (Davies 1989).

Calcification rates inferred from alkalinity anomalies consist of measuring the change of total alkalinity in seawater, considering that the precipitation of 1 mol of $CaCO_3$ reduces the total alkalinity by a two molar equivalent (Chisholm and Gattuso 1991).

Other methods (sclerochronology or sclerochemistry) have drawback to be destructive but allow an accurate view of the growth in space and/or time. Sclerochronological methods analyze periodic growth increments. Depending on the species, analyses are performed on sections of the skeleton under optic microscopy, scanning electron microscopy (SEM), or X-ray fluorescence. A large number of coral species generate their skeleton by calcium deposition (and other components depending on the species), which form annual growth bands. The chronological scale in growth band formation is established by mark and recapture techniques, particularly using calcein or alizarin staining (Cohen et al. 2004; Marschal et al. 2004; Lartaud et al. 2013). An example of the application of sclerochronological techniques is given in Sect. 4.1 of this chapter.

Sclerochemistry is the analysis of geochemical proxies (e.g., stable isotopes or trace metals) along a growth profile to determine growth patterns when increments are not visible, and it is commonly used for calcareous shallow-water corals

(Pätzold 1984); however, its use is restricted in cold-water environments. Metabolic impacts, also called vital effects, induced by the uptake of respired CO_2 in the skeleton were shown to create an offset in the isotopic equilibrium (Adkins et al. 2003), associated with the combination of different factors (temperature, pH, calcification rate) that control the incorporation of metals (Raddatz et al. 2013). Radiogenic isotopes are thus promoted to determine the life span of long-lived species when ring counting is not possible. To study age and growth at multi-decennial scales, the main techniques used are ^{14}C (Roark et al. 2006), particularly to determine the growth of deep-sea octocorals and antipatharians, U-Th (Cheng et al. 2000), and ^{210}Pb-^{226}Ra dating (Sabatier et al. 2012).

3 Growth in Scleractinian Corals: Cold-Water Corals as a Case Study

The scleractinian corals (sometimes called “stony corals”) mineralize a hard calcium carbonate skeleton, allowing some species to have the capability to form complex three-dimensional reef structures that provide niches and nursery grounds for a variety of species (Roberts et al. 2009). Contrary to octocorals, which mineralize a mix of proteinaceous and calcareous skeleton that decays with diagenesis, the structures formed by scleractinian corals are perennial after their death (i.e., carbonate mound) and support biodiversity on the scale of centuries to millennia (the oldest *Lophelia* reefs in Norwegian waters were estimated at 8,600 years; Hovland and Mortensen 1999).

The reef-building scleractinians are ubiquitous, colonizing all ocean waters. They can be classified into two categories according to their distinct ecological features and geographic distribution: (1) the tropical and subtropical corals, restricted to warm and shallow waters, and (2) the cold-water corals (CWCs), more widespread but living in waters mostly below 15 °C at different depth ranges (presently discovered from 40 to deeper than 3,000 m depth). The main difference between these two groups is the absence of *Symbiodinium* in CWC tissues. While the energy demand of tropical corals is mainly derived from the symbiosis with symbiodinium, suspension feeding is the only strategy that supports CWCs. The absence of the symbiotic relationship between coral and *Symbiodinium* sp. does not prevent the ability for CWCs to build comparable reef structures (e.g., *Lophelia* reef off Røst in Norway reaches 35 km long and 3 km wide; Thorsnes et al. 2004). Another key difference between these two groups of corals is the size of their polyps, which are large for CWCs and generally smaller (but with some exceptions) for tropical reef-building corals (particularly branching forms), where colonies are packed with a myriad of tiny polyps.

Although they build reef structures (Fig. 1a, d, g), tropical and cold-water corals show overall different growth patterns. The small-scale morphology of branching tropical corals is more similar to octocorals than CWCs: a branch of an octocoral or a tropical scleractinian is covered by tens to hundreds of polyps, with a lateral continuity (Fig. 1b, e), whereas a branch of CWC is formed by the addition of polyps growing on top of each other (Fig. 1h). All polyps display the same anatomy, being the polyps linked by the coenosarc tissue (Allemand et al. 2004), but the size of the polyps seems to play an important role in the growth of the colony. In tropical corals and octocorals, the skeleton is primarily formed at the base of the calyx and poorly at the walls, while for CWCs skeleton growth is mostly defined by the extension of the walls of the large polyps (e.g., 5 mm polyp diameter for *Madrepora oculata* and 15 mm polyp diameter for *Lophelia pertusa*), which overstate the linear extension compared to the thickening of the branches (as growth is primarily driven by polyp turnover; Gass and Roberts 2011). Additionally, the remaining great imbalance between the length and width of the branches contributes to the creation of more fragile structures in CWC reefs than in the tropical ones. Another key feature is the role of symbiotic worms living within the branches of the CWCs. Aquarium experiments have shown that *L. pertusa* calcification increases in the presence of the polychaete *Eunice norvegica* (Mueller et al. 2013). The parchment-like tubes produced by the worms along coral branches are later calcified by its coral hosts, strengthening the reef framework by thickening and connecting coral branches (Roberts 2005).

Cold-water corals produce carbonate growth increments, but in radial sections (usually considered for sclerochronological investigations), their growth patterns differ when compared to gorgonians and tropical corals. Indeed tropical branched corals and gorgonian colonies revealed treelike growth bands in radial sections, growing from the center to the periphery of the skeleton (Buddemeier and Kinzie 1976; Marschal et al. 2004) (Fig. 1c–f). The radial section of a branch of a CWC often corresponds to the radial section of a single polyp (Fig. 1h) and would therefore only reflect a short part of the growth history of the coral. Additionally, staining experiments have shown that there are two growth centers: one on the outer edge of the calyx and another one on the inner edge near the septa (Brooke and Young 2009; Lartaud et al. 2013). Consequently, a single polyp produces growth increments both inside and outside the calyx, leading to complex bidirectional structures, which make difficult the chronological calibration of growth (Fig. 1i).

The annual growth rings produced by tropical corals are commonly used as chronological archive. Based on the growth processes described above, those corals exhibit a continuous record in each branch, allowing high-resolution studies at decade to centennial scales. Such long-term chronological continuity is not possible for branching CWCs due to the difficulties in time calibration of growth and merging of different polyps along a same branch. Estimation of seasonal trends can be made using a single polyp, and long-term paleoclimate reconstructions (based on geochemical tracers) are restricted to an average of the entire colony and comparison of different colonies throughout centennial to thousands of years (e.g., during the Holocene).

Similar growth increments to those found in tropical corals are observed in the CWC skeleton, but the description of their periodicity is still in its infancy. Opaque and translucent bands are revealed by transmitting light through thin sections of the calyx of *L. pertusa* (Wainwright 1964), but they are not associated with a clear rhythmicity (Gass and Roberts 2011). Microscale layers (<10 μm) have also been

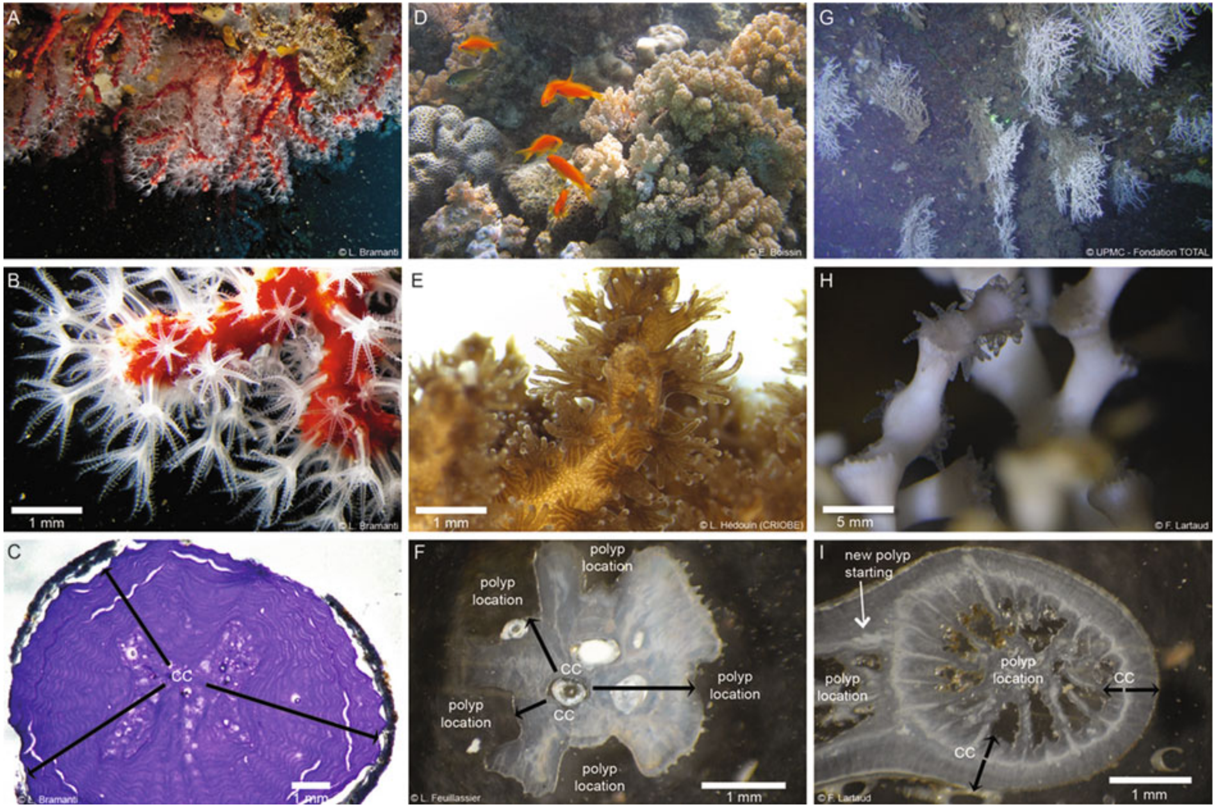

Fig. 1 Image of colonies, detail of polyps and radial sections of (**a**, **b**, **c**) a gorgonian (*Corallium rubrum*), (**d**, **e**, **f**) a tropical scleractinian (*Pocillopora damicornis*), and (**g**, **h**, **i**) a cold-water scleractinian (*Madrepora oculata*). (CC) is the center of calcification and the *black arrow* highlights the direction of growth

observed in the cup coral *Desmophyllum dianthus*, a solitary coral species (Cheng et al. 2000), but were associated with intrinsic timekeeping mechanisms (i.e., biological clocks). However, the merging or pinching out of some layers prevents their use as chronological markers. More recently, thin micro-layers (20–100 μm) in *L. pertusa* skeleton from North Atlantic canyons were described under SEM analysis after acid attack treatments and were associated with monthly lunar cycles and believed to be related to bottom-current changes (Mouchi et al. 2014). Strontium concentration fluctuations, which are also concomitant to these lunar growth rhythms, interestingly revealed the potential for use as a growth proxy for CWCs.

The sclerochronological analysis of CWC reveals a huge difference in growth rates between young (<1 year) and older polyps (Lartaud et al. 2013). Combined with a high rate of new polyp formation, the growth of the colony is primarily driven by new polyp addition. Asexual formation of new polyps at the distal part of CWC branches increases the spatial extension of the colony in three dimensions. This in turn increases the complexity of the living reef areas, whereas the death of coral polyps increases and modifies the proportion of dead coral framework (Fig. 2). The resulting segmentation of the colony between dead and living parts, as well as the diversity of morphologies produced during growth, explains the high diversity in CWC habitats; however, this is only supported by one species.

Another key parameter for habitat builders is the life span of the colony, but this feature is poorly known for scleractinian CWCs. The maximum age of a single polyp was estimated below 20 years (Freiwald et al. 2004); however, real data for most colonial species is still lacking. *Desmophyllum dianthus* polyps, a non-colonial CWC species belonging to the Caryophylliidae as *L. pertusa*, can live >200 years (Risk et al. 2002). Radioisotope measurements reveal that the age of a 40 cm long *L. pertusa* colony from the NE Atlantic can reach up to 250 years (Pons-Branchu et al. 2005), whereas a *M. oculata* colony of similar size from mid-Norway was estimated to be ~40 years old (Sabatier et al. 2012).

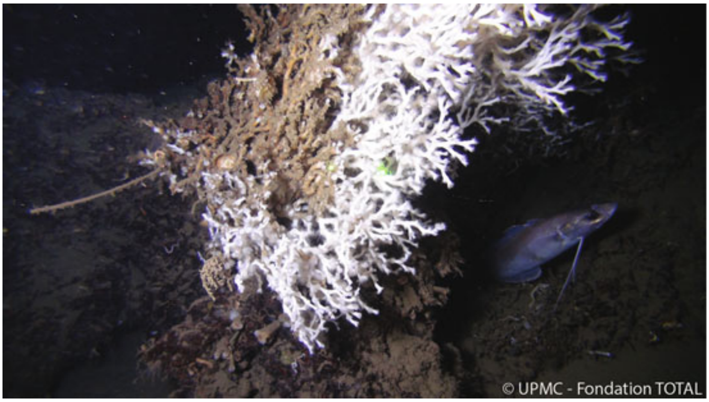
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Fig. 2 Colony of *Lophelia pertusa* showing the living (*white*) and dead (*brown*) polyps below. Space between the two *green* laser pointers is 6 cm

During the last decade, there was an increase in interest on the study of growth and quantification of CWC, based on both in situ and *in aquaria* experiments (Lartaud et al. 2014 and references therein). Although the comparison of growth measurements between studies can be difficult due to the use of different methods, the results show a high range of growth rates depending on the type of environment (see for a review Roberts et al. 2009). For instance, the growth rates for *L. pertusa*, the main deep-sea reef-building species, vary from a minimum of 2 mm year^{-1}in the Gulf of Mexico (using in situ mark and recapture of stained coral fragments; Brooke and Young 2009) to a maximum of 34 mm year^{-1}in the North Sea (observations of colonies from man-made structure; Gass and Roberts 2006). The growth rates of *M. oculata*, which forms smaller colonies, range from a minimum of 3.5 mm year^{-1}in the Mediterranean Sea (in situ mark and recapture of stained coral fragments; Lartaud et al. 2013) to a maximum of 14 mm year^{-1}in the North Sea (Pb-Ra dating; Sabatier et al. 2012). These values are clearly lower than the growth rates of branching tropical corals (100–300 mm year^{-1}; Buddemeier and Kinzie 1976), although there are exceptions. An aquaria study measuring growth rates by means of the buoyant weight technique showed that the tropical species *Galaxea fascicularis* has similar growth rates as *M. oculata* (Orejas et al. 2011).

According to the high variability in growth rates for CWCs, the linear extension of the colonies is very variable and reflects different environmental (i.e., food supply, turbidity, temperature, hydrography, and seawater chemistry), ecological, and competitive conditions (Roberts et al. 2009). Moreover, a large variability in size and form among individuals in the same ecosystem has also been detected (Vertino et al. 2010), being linked to environmental microscale differences (e.g., local topography, current flow exposition) and/or possible interindividual changes between different clones. The environmental influence on growth rates has also been observed for *L. pertusa* on artificial substrates (Larcom et al. 2014): colonies growing on man-made structures with small surfaces (e.g., spar or tension leg) displayed lower growth rates (up to 11 mm year^{-1}) than colonies growing on massive artificial substrates (up to 32 mm year^{-1} on subsea installation).

Additionally to changes detected in growth rates at different geographic scales (between geographic provinces or inside a same area), recent studies have shown changes in growth at seasonal scales (Lartaud et al. 2014). This is the case for *M. oculata* in the Lacaze-Duthiers submarine canyon (northwestern Mediterranean); this coral exhibits seasonal fluctuation in the formation of new polyps, this rate being higher during the winter-spring seasons compared to summer. This behavior can be attributed to the environmental dynamic at the study location, as this area is subjected to winter-dense shelf water cascades (Canals et al. 2006), providing an increase in the organic particle supply and carbon recirculation. However, growth responses differ among species, given that *L. pertusa* collected in the same location does not exhibit seasonal changes. This species-specific effect between two species living in the same habitat has also been reported for other biological processes in CWCs, such as reproduction (Waller and Tyler 2005) and feeding strategies (Kiriakoulakis et al. 2005). These results suggest the need to adapt species-specific management strategies or determine “good sentinel” species for conservation purposes.

Although CWCs display low growth rates at the all colony scales, at smaller scales a high recovery potential was observed both in aquaria (Maier 2008) and in situ (Lartaud et al. 2013), due to fast coral regeneration after fragmentation. This suggests a growth limitation for the colony, probably by frequent break of branches. Natural breakages are commonly observed on colonies due to current velocity changes (e.g., storm or intense cascading events) and predation or megafauna crossing, leading to frequent reparation of damaged tissues and recovery. Sustaining a rapid recovery should however impact other biological and physiological processes, such as reproduction, immune response, and protein synthesis, as this was observed in bivalves submitted to low pH conditions (Gazeau et al. 2013). Time of rapid recovery is thus probably limited to preserve colony health status. The differences in growth rate over time should also be taken into account for estimations of coral response to anthropogenic disturbances as CWCs seem to show relative short recovery rates at short timescales (branches) but higher values over the life span (colony).

4 Growth in Octocorals: The Mediterranean Red Coral (*Corallium rubrum*) Case Study

The subclass Octocorallia is divided into three orders (Helioporacea, Pennatulacea, and Gorgonacea) and it comprises about 3,500 species. The Mediterranean red coral (*Corallium rubrum*, L. 1758) is a slow-growing and long-lived gorgonian (order Gorgonacea) associated with rocky bottoms (Fig. 3). It is a modular suspension feeder with a treelike structure that can reach about 50 cm in height, with a life span that can exceed 100 years. Distributed throughout the Mediterranean Sea and adjacent Atlantic coasts, this commercially valuable species has been harvested for

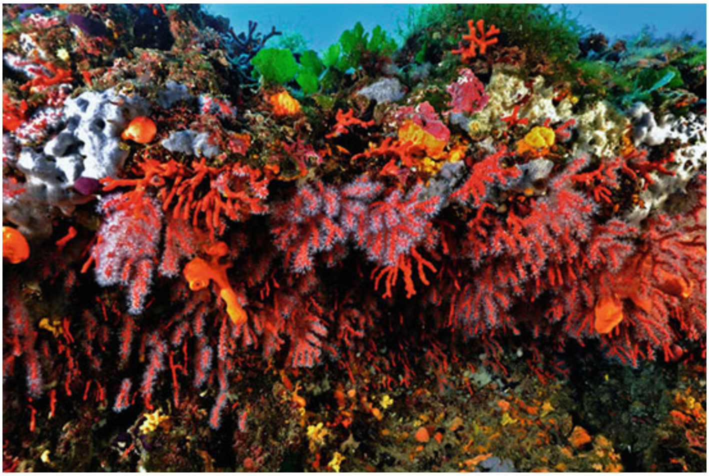


Fig. 3 *Corallium rubrum* patch in the Cap de Creus (Spain) at 25 m depth. Photo A. Ferrucci

more than two thousand years for its hard, red skeleton, which is commonly carved to produce jewels, talismans, and art (Tsounis et al. 2010) (see also ▶ Chap. 23 by Orejas and Jiménez, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume). Although this species has been overharvested, currently it is not considered at risk of ecological extinction due to its wide bathymetric range (found between 15 and 800 m; Costantini et al. 2010) and wide geographic distribution along the entire Mediterranean Sea (Zibrowius et al. 1984).

A large difference in colony size and density has been observed along bathymetric gradients in different locations. Shallow populations (less than 50 m) are characterized by small colony size (<10 mm basal diameter) and high density (>40 colonies m^{-2}), while deep populations (greater than 50 m) are mainly composed of large-sized colonies (>10 mm basal diameter) and low density (<40 colonies m^{-2}; Rossi et al. 2008; Bramanti et al. 2009; Cau et al. 2016). These differences are believed to be caused by higher fishing pressure in shallow compared to deep populations (Bramanti et al. 2009; Cau et al. 2016). The deepest populations have been found living down to 800 m depth and are characterized by sparse and small colonies. However, the majority of scientific studies on *C. rubrum* have focused on shallow populations because they are easily accessible by scuba divers (Santangelo et al. 2007). Only recently the introduction of remotely operated vehicle (ROV) devices has allowed the study of deeper populations (Rossi et al. 2008; Cau et al. 2016).

4.1 Colony Age Assessment

The internal carbonate ($CaCO_3$) skeleton of red coral colonies is coated by coenosarc, in which gastrodermal channels that connect polyps are embedded. A colony grows every year by adding one growth layer correspondingly (in the section orthogonal to the axial skeleton) to a growth ring made up of a dark and a light band. During the first 4 years, rings are not formed because the skeleton grows by the fusion of sclerites; therefore, a central core is formed instead (Fig. 4a). The size of the growth rings is similar among colonies from different depth ranges and geographic areas (Marschal et al. 2004; Gallmetzer et al. 2010).

In *C. rubrum*, colony age is determined by staining and counting the growth rings on thin sections (50 μm). For this purpose, the organic matrix staining (OMS) method, validated by Marschal et al. (2004), is used. Thin sections of the colony base are decalcified and stained making the annual growth rings visible. As some colonies can be affected by boring sponges, which prevent correctly reading the growth rings (Fig. 4b), this method can be applied only on unaffected colonies.

A protocol for growth ring counting was developed by Priori et al. (2013). The method was developed for *C. rubrum* but can also be applied to other octocorals. It consists in using the average of different ring counts, performed by different but experienced observers (see details in Priori et al. 2013). A power curve with a positive exponent >1 describes the correlation between age (i.e., number of growth

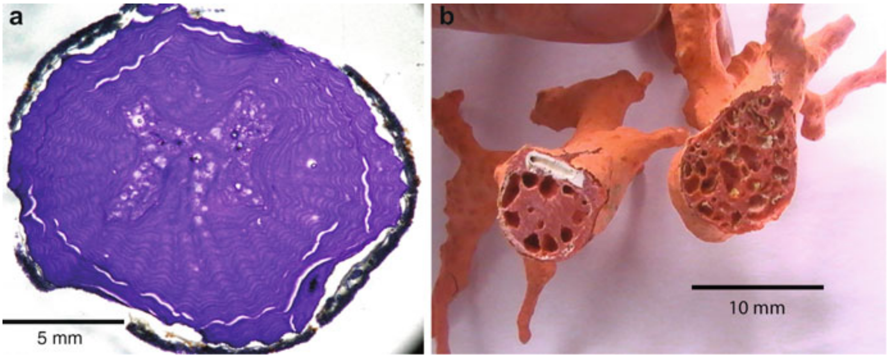
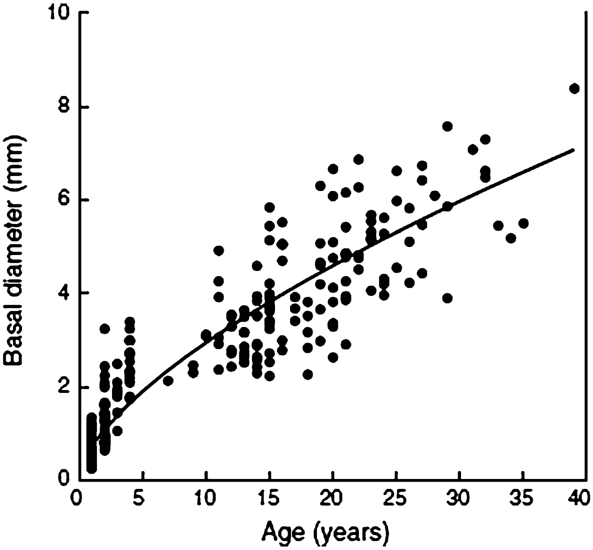


Fig. 4 (**a**) Thin section of a colony base of *Corallium rubrum* where growth rings are visible. The age of the colony is determined by counting growth rings plus the addition of 4 years. (**b**) Two *C. rubrum* colonies with the basal part affected by boring sponges

Fig. 5 Relationship between colony age (determined by annual growth ring counts) and basal diameter (Modified after Bramanti et al. (2014), with kind permission from Springer Science and Business Media)



rings) and mean diameter of colonies (Fig. 5; Bramanti et al. 2014). These findings suggest that estimations of age using colony size can be inaccurate, because small variations in colony diameter could lead to high differences in age determination for large/old colonies.

Although colony height, weight, and branching order can also be used as a size descriptor of colonies, basal diameter is preferred because it has been demonstrated that this measure is better correlated with age, while height (maximum distance between basis and tip) is highly variable between colonies of the same age. Weight increases with colony size according to a power curve with an exponent >1, but it can be determined only on entire colonies, which reduces the number of samples measurable due to their fragility. Moreover, large/old colonies are rare and the use of weight as a colony descriptor is considered a very destructive procedure. The branching order, on the other hand, is poorly correlated with age, but it is an indicator of the colony complexity: the maximum value found has been IV in shallow populations and VII in deep ones (Priori et al. 2013).

4.2 Colony Growth Rate

The annual growth rate can be defined as the ratio between the mean diameter and the age of a colony. In *C. rubrum* shallow populations, growth rate was found to decrease with colony age according to a monotonic curve with a negative exponent, a result that is similar to findings in deep *C. rubrum* populations (Fig. 6; Priori et al. 2013) as well as in some tree species (Bowman et al. 2013). Shallow *C. rubrum* populations showed a mean growth rate of 0.24 mm year^{-1} (Bramanti et al. 2014). As the growth rate in the first years cannot be measured by the OMS method, ad hoc studies have been carried out with the use of artificial substrates (see details in Bramanti et al. 2005) showing a threefold faster growth rate during the first 4 years (0.62 mm year^{-1}; Bramanti et al. 2005).

Although there has been considerable effort throughout the last decades to improve age determination techniques for *C. rubrum*, the differential growth of the distal part of a branch (the 1 cm tip; hereafter called apexes) is an almost unaddressed issue. Such research becomes particularly relevant as recent studies have highlighted morphological adaptation processes to the local environment, including branching patterns, differential (faster) recovery from fishing pressure, and accidental damage when colonies are not completely extirpated (Montero-Serra et al. 2015). The study of differential growth on apexes should answer the following

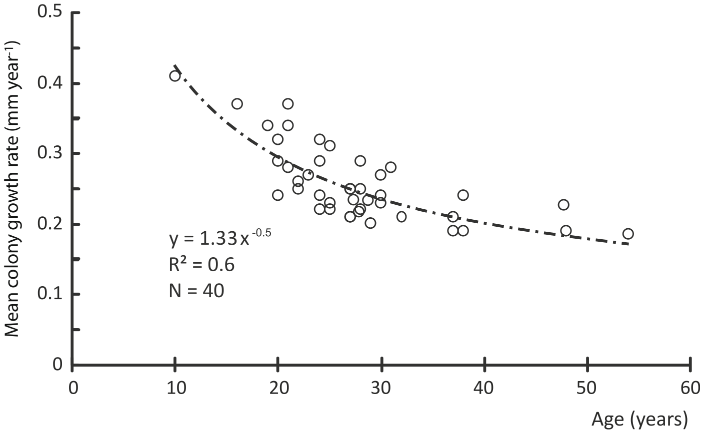


Fig. 6 Trend of colony growth rate with age (Reprinted from Priori et al. (2013), Copyright (2013), with permission from Elsevier)

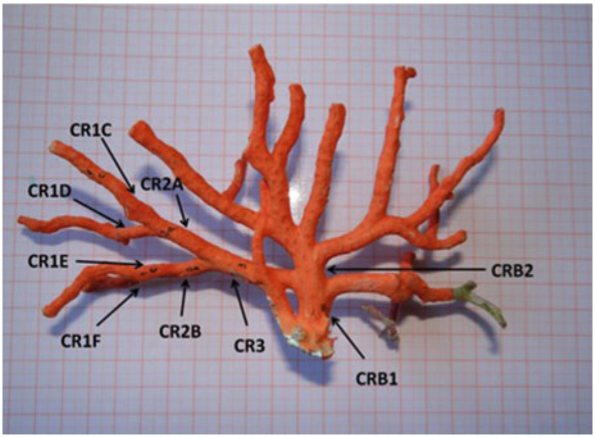


Fig. 7 *Corallium rubrum* colony used for the investigation on differential growth and age pattern. *CRB* base, *CR1* first-order branches, *CR2* second-order branches, *CR3* third-order branches

questions: (1) Do newly developed apexes have the same growth rate as estimated for the base? (2) What is the difference in age among different order of branches? (3) Is it possible to use branching patterns to estimate demographic features of the population?

A pilot study on the differential age and growth in different orders of branches in *C. rubrum* colonies is currently in progress (Benedetti et al. 2016), and samples are being processed using the OMS age determination protocol proposed by Marschal et al. (2004). Preliminary results obtained through the analysis of a few colonies have shown that, on average, new apexes (first-order branches) grow faster than the base of the colony. Sometimes these growth rates were 30% higher, which correspond to the growth rates of the first 10–15 years of the colony's life span. Similar results were found in cold-water corals (see Sect. 3).

Considering the modular growth of *C. rubrum*, it would be interesting to test if the same asymptotic growth pattern also takes place in branches of other orders. A major technical difficulty in this type of experimentation relies in the weak consistency of $CaCO_3$ deposited by the new first-order apexes (Fig. 7, branches labeled as "CR1"), which in some cases makes the cut and smoothing procedure extremely difficult and the age determination almost impossible. Experimental trials resulted in less than 50% of success in age determination of first-order branches, while the use of this technique in second- and third-order branches (currently under process) does not present any problems.

5 Growth in Antipatharia: The Millennial Black Corals of the Genus *Leiopathes* Case Study

Similar to the oldest terrestrial forests, some species of hexacorals have life cycles of thousands of years; this is the case of black corals of the order Antipatharia (phylum Cnidaria, class Anthozoa, subclass Hexacorallia), which comprises 7 families, 42 genera, and 230 species.

Despite the relatively reduced number of species, black corals are spread throughout all oceans of the world, from tropical and subtropical areas to temperate and polar regions. Black corals can be found over a wide bathymetric range: from an upper threshold of ca. 5–10 m depth in tropical regions (50 m in temperate/polar areas) down to ca. 500 m depth, where they dwell on hard substrates such as seamounts, canyons, rocky outcrops, and ledges (Opresko and Sánchez 2005; Bo et al. 2015).

Black coral forests are direct targets for professional precious coral harvesting (i.e., jewelry market; Grigg 2002) and are affected by fishing activities, which target commercially relevant species that occupy the same habitats. These practices severely damage the living portion of the colonies through the entanglement with lines or fishing gear in general, which leads to progressive necrosis.

Within the subclass Hexacorallia, the Antipatharia order comprises some of the longest-living marine organisms, which belong to the family Leiopathidae. The genus *Leiopathes* include eight species; four have been reported from the Indian Ocean (*Leiopathes secunda,* Opresko, 1998; *L. bullosa,* Opresko, 1998, and *L. acanthophora,* Opresko, 1998; and *L. valdiviae*, Pax, 1915), three are found exclusively in the North Atlantic Ocean (*L. montana*, Molodtsova, 2011; *L. expansa*, Johnson, 1899; *L. grimaldii,* Roule, 1902), while *L. glaberrima* is the only one reported, so far, in both the North Atlantic Ocean (Macaronesian archipelago and Bay of Biscay) and the Mediterranean Basin (Bo et al. 2015; Cau et al. 2015).

The skeleton of black corals is cylindrical, with a central canal surrounded by a series of concentric layers of deposited organic material. These micro-layers are responsible for the growth rings visible in transversal sections, actually used to infer colony age and growth rate (see Sect. 4.1).

In the genus *Leiopathes* the skeleton is proteinic (antipathin) which is a combination of chitin (a polysaccharide that also makes up the cuticle of insects and crustaceans) and a nonfibrous scleroprotein. No carbonate elements such as sclerites are present, which makes the skeleton extremely flexible and able to bend with the current.

Leiopathes specimens are the oldest skeletal-accreting marine organisms, with the slowest growth rates observed in species that have the greatest life spans (Carreiro-Silva et al. 2013). The extreme longevity of these organisms has triggered the use of isotopic studies on *Leiopathes* spp. as paleoclimatic archives (e.g., superficial and deep-water temperatures; Williams et al. 2006). *Leiopathes* spp. are suitable bioindicators for the availability of anthropogenic carbon and trace elements in the environment (e.g., Cd, Cr, Ni, Se, and Pb; Williams et al. 2007; Raimundo et al. 2013). Moreover, their presence within coral forests has been used as tool to detect non-disturbed ecosystems (Bo et al. 2015).

However, a considerable intraspecific variability in growth rates of black corals has been documented in the last decade, with some studies recording fast initial growth rates (13 μm year^{-1}) that tend to progressively slow down (5 μm year^{-1}; Roark et al. 2009; Carreiro-Silva et al. 2013), while others found slow initial and final growth rates (~4–5 μm year^{-1}) separated by a period of more rapid growth

(20 µm year^{-1}; Carreiro-Silva et al. 2013). An interesting exception was found for specimens from the Gulf of Mexico, which showed a linear growth trend (Prouty et al. 2011). Thus, growth rates appear not to be related to the colony height or basal diameter, but vary among specimens in accordance to other environmental and biological parameters (Roark et al. 2009).

6 Modeling Coral Growth

One of the big challenges in the study of animal forests species is to provide reliable estimates of their ecological response under current and future anthropogenic pressures, such as climate change and the introduction of invasive species.

Growth rate, form, and size are proxies to evaluate the species at the organism level, and as such, they provide metrics to assess species performance under different environmental conditions. However, in the case of corals, colony development can take decades, making most of the potential experimental approaches almost impossible to implement. At the same time routinely measured vital parameters such as growth rates are usually (as already seen in previous sections of this chapter) not constant over the entire life span, frequently changing with organism size and/or age. Consequently, the extrapolation of growth rates, experimentally obtained on colony fragments, to whole colonies or even reefs must be carefully considered.

Numerical simulation techniques provide diverse frameworks for addressing these issues. Application scales vary widely, ranging from small-scale physiological processes (e.g., ion transport across tissues; see Sect. 6.3) to whole ecosystem dynamics. The choice of the appropriate scale is a matter of the study aims and knowledge available for the targeted species. However, for conservation purposes, population and ecosystem approaches need to be considered. In some cases it is convenient to study simpler and smaller-scale systems in order to understand their basic functioning and scale up to higher, more complex levels. Coral growth lends itself particularly well to this approach, as colonies, which are characterized by their modular architecture, are a good example of a whole organism that results from the iteration of a single, potentially autonomous and relatively invariant unit, the polyp.

In this section we will outline the basics of some modeling applications that we believe are relevant for the studies dealing with coral growth, as well as present some examples of related literature and own contributions. Emphasis will be made on published studies that have already provided knowledge on growth processes, as well as on existing gaps and promising research perspectives.

6.1 Organism and Population Growth Models

From a modeling perspective, a living organism (either a coral or another living being) can be considered an open system that maintains high levels of internal organization by a continuous flux of energy through its boundary. Classical growth models are the so-called bioenergetic models whose history dates back to the first half of the twentieth century (von Bertalanffy 1938; see Kooijman 2010 for an extensive treatise). Such class of models describes growth as the evolution of a quantity (usually energy, biomass, or mass of a specific compound) over time through the balance of input and output fluxes, through the system boundary, and between compartments within the system.

The simplest possible formula (as a differential equation) of a bioenergetic growth model considers one single compartment for biomass (or energy), one input, and one output flux that depends on the system biomass/energy according to power laws (also termed allometric laws; see Glazier 2005 for a review):

$$\frac{dY}{dt} = IN - OUT = aY^{\alpha} - bY^{\beta} \tag{1}$$

where Y is mass or energy, t is time, a and b are specific rates of Y flow (e.g., per unit mass or surface), and α, β are the allometric scaling coefficients (typically ≤ 1).

Positive growth can continue only if the inputs exceed the outputs; therefore, if $\beta > \alpha$, eventually a value of Y is reached at which the two terms on the right-hand side are equal, stopping growth. This explains growth patterns observed in the majority of known species, including fast growth early in life and the existence of a maximal size (Fig. 8).

Bioenergetic models are particularly interesting because they are based on first principles (mass/energy conservation) and can be applied to any species (of course with species-specific formulations), offering a wide array of applications. While the bioenergetic modeling framework has been successfully applied to a variety of species, both terrestrial and marine, colonial and modular architectures (as found in corals, sponges, and seaweeds) entail some issues that must be properly addressed.

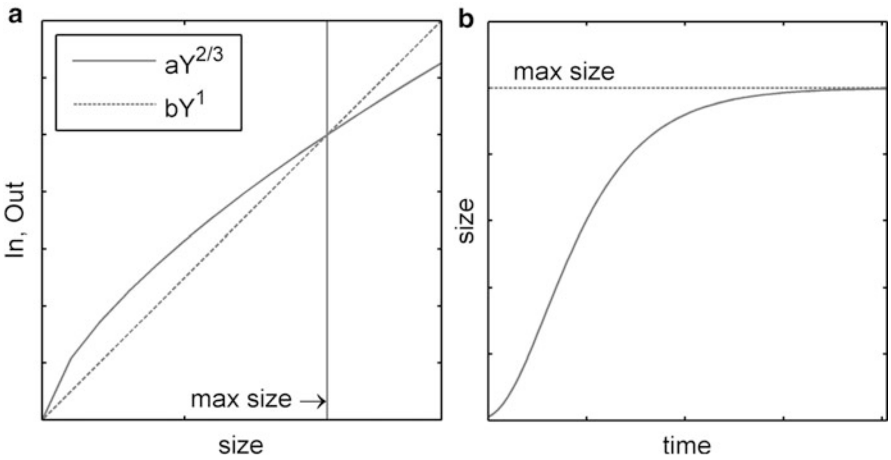


Fig. 8 (**a**) In and out fluxes from Eq. 1 as a function of organism size with Y, organism size, a, b, constant coefficients; (**b**) growth curve resulting from Eq. 1, characterized by the existence of an asymptotic maximal size

For instance, the values of allometric scaling coefficients (in Eq. 1) that are typically observed in solitary organisms may not be valid for colonies (Sebens 1987), possibly resulting in indeterminate growth.

When modeling the growth of a modular organism, it must be considered whether the colony will be described as a single organism or as a result of the coexistence of single modules. If a colony is described as a "population" of polyps, colony growth, measured as the increment of polyp number (N over time), results from the two processes of (1) new polyps being originated by division ("births") and (if applicable) (2) polyp death. The population's birth and death rates are usually considered to be dependent on population size. As an example, the famous Verhulst equation describing self-limiting growth of a population can be written as

$$\frac{dN}{dt} = \text{Births} - \text{Deaths} = rN - \frac{r}{K}N^2 \tag{2}$$

where r is the population's specific growth rate, K is the environment's carrying capacity, and the term $(r/K)N$ represents the specific mortality rate (assumed to depend linearly on population size N). Population dynamics may then be coupled with a single polyp growth model (of the kind described in Eq. 1) by making population growth and mortality rate functions of polyp biomass. Polyps indeed seem to undergo fission only if some threshold size is attained (Sebens 1980; Kooijman 2010), and they will arguably die if their biomass falls below a minimal value. The available information on these matters is however surprisingly scarce.

6.2 Growth Indeterminacy, Trophic Shading, and Bioenergetic Implications of Shape

One of the properties generally attributed to modular organisms is growth indeterminacy. For example, colonies may escape the constraints that limit maximal size of the single module if colony resource acquisition were to scale linearly with the number of modules (Sebens 1982, 1987). At present, it is unclear whether modular architecture ensures growth indeterminacy; in fact alternative theories have been proposed. For solitary organisms, it may seem trivial to infer they have a maximal attainable size (size being defined as metabolically active biomass). However, in corals the parameter size is elusive compared to other individual animals whose total mass is mostly metabolically active (instead of mostly calcium carbonate) and that can be readily weighted or their weight inferred from parameters like length or height (e.g., fish). Whereas coenosarc weight would qualify as an informative measure of metabolically active biomass, the skeleton, that is metabolically inactive, is more often measured. Also, as corals do not have defined body plans, parameters such as length, height, or diameter are usually scarcely informative for corals.

Models offer a valid alternative to test existing hypotheses. Kim and Lasker (1998) investigated the potential limits of modular growth with a bioenergetic model where colony resource acquisition does not scale linearly with the number of modules. The cornerstone of their reasoning was that polyps in a coral colony compete for resource acquisition; therefore, as the number of modules increases, the availability of food per module decreases. This process is known as *trophic shading* (analogous to *self-shading* in trees), as the authors demonstrated that it may effectively limit the maximal size of a colony that would otherwise exhibit indeterminate growth.

A simple process-based model of resource acquisition incorporating the phenomenon of trophic shading can be constructed as follows. Let us consider a colony surrounded by a conveniently chosen control volume, V, of water that is considered, for the sake of simplicity, well mixed. Polyp-specific consumption rate (assumed to be a non-photosynthesizing organism) is assumed to have a Michaelis-Menten type of dependence on food concentration, F, in the control volume. This kind of functional response is generally considered realistic and, in fact, is extensively found in literature, where different kinds of relations (e.g., linear, Holling type III) do not change the results substantially.

Assuming that colony resource acquisition, A, scales linearly with colony surface, S, then it can be written as

$$A = a_{\max} \frac{F}{k_F + F} S \tag{3}$$

where $a_{\max}$ is the maximum resource acquisition rate per unit of surface and k_F is the semi-saturation constant. If Q is the water flow through the control volume and F_b the bulk food concentration, then the variation of the mass of food, M, in the control volume over time is

$$\frac{dM}{dt} = QF_b - QF - a_{\max} \frac{F}{k_F + F} S \tag{4}$$

Assuming stationary conditions (the right side of the equation equals zero) and solving for F give a second-order polynomial in F:

$$F^2 + F\left(k_F - F_b + \frac{a_{\max} S}{Q}\right) - k_F F_b = 0 \tag{5}$$

This admits just one positive solution dependent on the values of S and Q.

This formalization is rather general and can be used to study the variation of F (hence of resource acquisition) with colony size once the relationship between flow and colony surface is established. It is possible to further specify the value of Q if we let the control volume V be cubic so that the area of a side is $A_S = V^{2/3}$, and let the flow be oriented normally to two faces so that $Q = v \cdot A_S = v \cdot V^{2/3}$, where v is flow speed.

We distinguish now two ideal cases, one in which the colony is spherical, the other in which it grows according to a space-filling pattern so that the surface area contained per unit of volume is constant at all sizes. The second case approximates branching and fractal geometries typical of many marine sessile species. In the spherical geometry case, we have $S = \pi \cdot V^{2/3}$, while for space-filling growth, the relation reads $S = k \cdot V$, with k constant. By substituting the relations for S and Q in Eq. 5, we obtain

$$F^2 + F \cdot \left(k_F - F_b + \frac{a_{\max} \cdot \pi}{v}\right) - k_F \cdot F_b = 0 \tag{6}$$

and

$$F^2 + F \cdot \left(\frac{k_F - F_b + a_{\max} \cdot k \cdot V^{1/3}}{v}\right) - k_F \cdot F_b = 0 \tag{7}$$

for spherical and space-filling geometries, respectively. It is readily noted that the value of F for the spherical case is constant and independent on colony size, while in the space-filling case, the result is related to the size of the control volume; therefore, the size of the colony is to the power of 1/3. By plotting the solutions of Eqs. 6 and 7 with respect to a measure of colony size (Fig. 9), it is evident that space-filling growth-specific resource acquisition diminishes with colony size, while this doesn't happen in the spherical case.

The presented model uses a number of simplifications, above all the assumption of a well-mixed volume of water around the coral and ideal geometries. Nonetheless, the results indicate that the process of trophic shading is mediated by the geometry of resource acquisition. This has consequences also for the size of the polyps: in branching morphotypes, the polyps will be less and less fed as the colony grows; as a consequence they will lose weight, resulting in an inverse relationship between

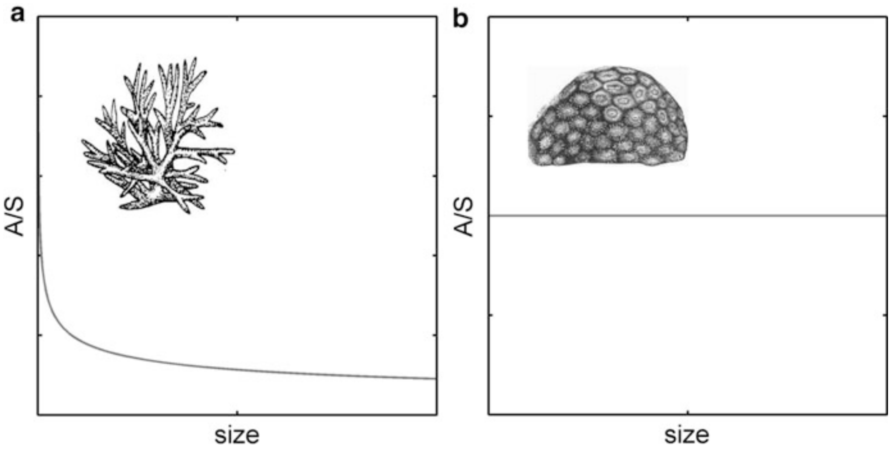


Fig. 9 Model of the specific resource acquisition rate (per unit surface area) according to the size of the control volume for space-filling (**a**) and spherical (**b**) colony shape

colony size and polyp size (Kim and Lasker 1998; see Sect. 6.4). On the other hand massive forms, for which food availability does not depend on colony size, would be characterized by polyps of relatively invariant size; massive forms would also generally feature larger polyps than branching forms. Furthermore, if one accepts that polyp division rate is mediated by polyp size (i.e., only polyps which are large enough can undergo fission; Sebens 1980), polyps in branching forms will eventually get too thin to undergo fission and colony growth will stop, i.e., trophic shading may effectively limit polyp number, hence maximal colony size. Spherical forms on the other hand would be characterized by indeterminate growth (see later in this chapter for a case study application). These conclusions are derived for idealized geometries; however, it is reasonable to predict that real growth forms will fall somewhere between the two extremes.

6.3 Growth of Calcified Structures and Skeletal Ring Formation

In classical bioenergetic models, the distinction between living biomass and skeleton is usually neglected; however, this is an important issue to deal with when attempting to describe the growth of organisms that have a high-proportion calcium carbonate. A general quantitative theory linking biogenic carbonate formation to organism metabolism is currently lacking (Allemand et al. 2011). In particular, it is unclear which part of coral energy budgets are devoted to skeleton formation (but see Anthony et al. 2002), how much $CaCO_3$ is yielded per amount of energy invested (Palmer 1992; Anthony et al. 2002), and how those quantities are affected by the external environment and organism status.

Some calcification models exploit the rather well-known inorganic chemistry of carbonates and calcium carbonates in seawater. Hohn and Merico (2012) developed a model of single-coral polyp calcification based on the transcalcification concept that describes the path of the chemical species relevant for inorganic $CaCO_3$ deposition from seawater to the calcification site. Nakamura et al. (2013) further expanded this model by incorporating a link between active ion transport and the rate of zooxanthellae photosynthesis.

The aim of these models is to provide a mechanistic understanding of the physiological-scale processes that are involved in the deposition of the skeleton. Colony growth is not resolved; however, a general framework is developed that could be fruitfully scaled up to describe whole organism accretion.

Anthony et al. (2002) dealt with the comparative analysis of energy allocation to tissue and skeletal growth in corals by using a bioenergetic growth model based on colony/branch geometry (branching or hemispherical). Results were consistent with the observed weak correlation between calcified and organic tissue growth across environmental conditions, suggesting that tissue properties (e.g., biomass, energetic content), rather than skeletal growth, are a better proxy for health or stress in corals. Furthermore, the authors found the existence of threshold dimensions (quantified as the radius of the colony/branch) below which energy investment is tissue dominated and above which most of the organism’s budget is devoted to the skeleton. Since these threshold radii are small (on the order of centimeters), the authors conclude that the energy investment of most branching corals is tissue dominated, while massive forms are skeleton dominated for most of their life history.

Skeleton deposition and accretion ring patterns can be linked to organism metabolism and environmental conditions (modeled in a bioenergetic framework) as demonstrated in Fablet et al. (2011) and Pecquerie et al. (2012) for fish otoliths. The authors recognized that carbonate deposition is decoupled from living tissue growth as the two processes originate from separate metabolic pathways; also, two distinct pathways are identified accounting for the organic and inorganic fractions of the skeleton. As such pathways are differently affected by the organism's status and external variables (temperature, food, etc.), the ratio between $CaCO_3$ and organic matter flow follows a seasonal cycle. Such studies demonstrate how it is possible to infer one of the three variables, ring appearance, thermal history, and feeding history, if two of them are known.

This kind of reasoning is not species specific and can be applied to corals as well. Galli et al. (unpublished data) developed a model for the Mediterranean octocoral *Corallium rubrum* where the growth of the organic component is an energetic cost linked to food assimilation and influenced by seasonality in food availability and temperature, whereas the growth of the inorganic component is an energetic cost which does not depend directly on food (rather depending on past feeding history), but does vary with temperature, although with a different kinetic. The differences between organic and inorganic component dynamics give rise to accretion rings (Fig. 10) whose aspect and timing match the already published observations. For example, Marschal et al. (2004) showed that yearly patterns observed for *C. rubrum* consist of thin rings rich in organic matter, which alternate with thick rings with low organic matter (OM) content. The thickness of rings is related to high or low inorganic matter deposition. Thick rings are laid down during summer when

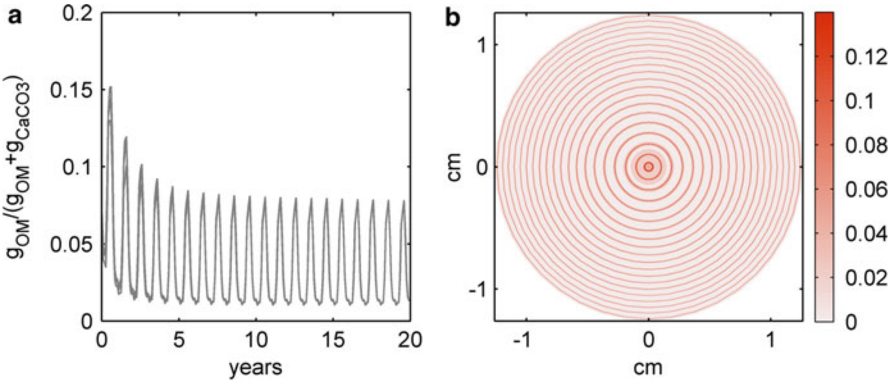


Fig. 10 (**a**) Model of the time dynamics of skeleton chemical composition expressed as mass of organic matter over total skeleton mass. (**b**) Same data as in panel a, but with a different graphic representation that makes seasonal accretion bands apparent; color bar values are organic matter mass over total skeletal mass as in (**a**)

temperatures are relatively high and food levels are low, while thin rings are deposited in winter when temperatures are low and food availability is high.

6.4 An Application of a Growth Model to the Case Study of *Corallium rubrum*

Possible applications for some of the concepts described above are featured in a recently developed model for *Corallium rubrum* (Galli et al. unpublished data) and are reported here. The model consists of two coupled modules: one accounting for single-polyp growth dynamics, including both soft tissue and calcified structures, and the other for population dynamics of polyps within the colony, considering the polyps as individuals and the colony as a population. Trophic shading is implemented as described above for the space-filling case, as *C. rubrum* is characterized by a branching morphology. Polyp division rate is assumed to depend on polyp biomass according to a sigmoid function, and no mortality term was considered because there is no conclusive evidence for polyps dying before the colony for this species (but see Vielzeuf et al. 2008). Skeletal growth is described above in the accretion ring formation section. The model uses monthly total organic carbon (TOC) concentrations from the NW Mediterranean (Rossi and Gili 2005) and uses it as a proxy for food concentration. In order to fit the model, colony weight and polyp number used to determine age were considered (Santangelo et al. 2003; Priori et al. 2013). As no clear correlation has been found between polyp number and age, nor between colony weight and age, we tested the model's performance against both weight and polyp number at the same time. This resulted in a 3D space (weight, polyp number, and age) in which, instead of a growth curve, we have a growth surface representing all possible combinations of weight, polyp number, and age. Growth surface is generated in the model by multiple growth trajectories obtained by varying the sole water flow speed parameter in the trophic shading module. This choice is intended to mimic the high variability in local hydrodynamic conditions that colonies experience and that are dictated by small-scale patch morphology and water flow.

In Fig. 11, some results of the model are displayed. Model results show good adherence with the experimental sets from Santangelo et al. (2003) and Priori et al. (2013). The trophic shading module has the effect of limiting maximal polyp number (Fig. 11a) and total polyp mass (Fig. 11d), effectively resulting in determinate growth of soft tissue and polyp "population." These effects arise because polyp size diminishes with polyp number (Fig. 11c). $CaCO_3$ mass (Fig. 11b) on the other hand shows unlimited growth due to the absence of maintenance costs for the skeleton.

6.5 Morphogenesis Models

The modeling applications that have been mentioned so far describe growth as a zero-dimensional process (i.e., spatial dimensions are only implicitly considered or

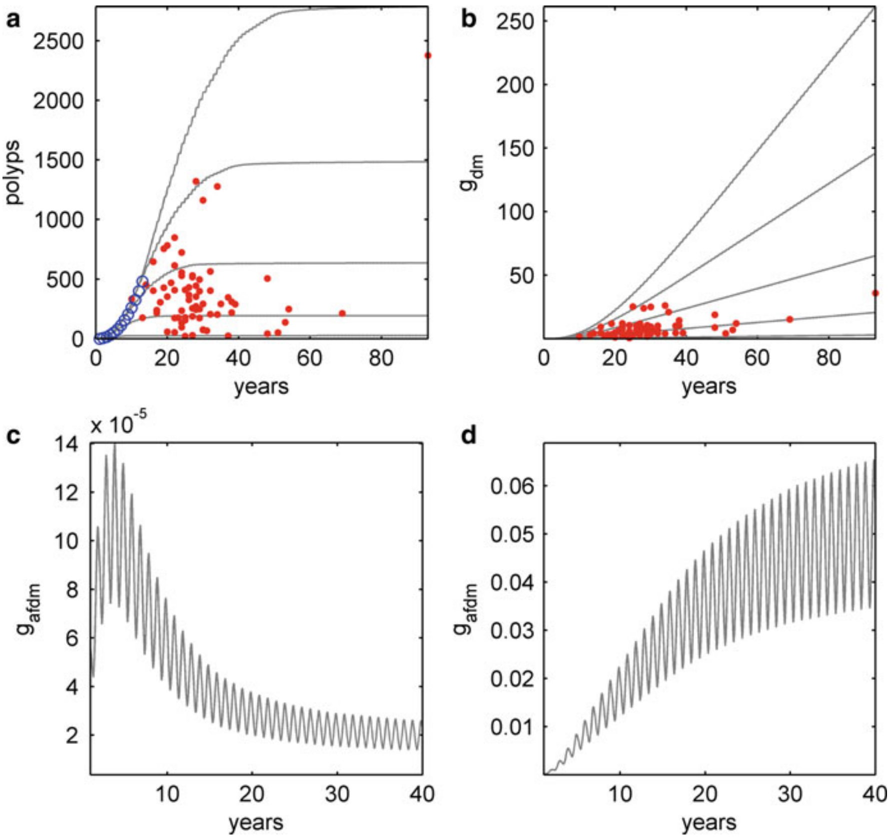


Fig. 11 (**a**) Model of the polyp number over time under different flow rates and experimental data points. (**b**) Total colony mass under different flow rates and experimental data points. (**c**, **d**) Single polyp mass (ash-free dry weight) and total polyp mass (ash-free dry weight) over time at a single flow regime. In plots **a**, **b**, *solid lines* are simulated growth trajectories under different flow regimes; filled dots in all plots are data included in Priori et al. (2013, Copyright (2013), with permission from Elsevier); empty dots are results included in Santangelo et al. (2003)

not at all). Whereas coral polyps are relatively similar among different species (at least from a body plan perspective), coral growth forms (branching, encrusting, massive, etc.) are widely different among species and even within the same species.

Morphological plasticity is interpreted as an adaptation of sessile growth that allows an organism to exploit, at best, the microenvironment of the patch where it once settled and from where it is very unlikely to ever move (Bradshaw 1965). Although some part of morphological variability is arguably mediated by genetics, a considerable part of it is believed to be determined by environmental conditions.

As mentioned before, at small trophic scales and in photosynthesizing species, light shading affects each module differentially. Exposed modules, such as those in apical branches, have more scope for growth and reproduction than sheltered ones.

This in turn determines differential growth rates for different portions of the colony and, ultimately, growth form (Kaandorp 1999).

Based on these premises, tridimensional coral morphogenesis models were developed by Kaandorp and coworkers (see Kaandorp 1999; Kaandorp et al. 2011 for an introduction). Such models work by coupling polyp-oriented models of coral growth with hydrodynamic simulations. Colony growth forms are not known a priori nor defined by the user, but rather emerge from the interplay between flow regime and processes of resource acquisition and shading among modules. Simulations show that under high flow conditions, the diffusive boundary layer around the coral surface is thin with short residence times; hence, the variability in food particle concentration is relatively small among different portions of the colony. This determines similar growth potential for all polyps that in turn results in massive growth forms. On the other hand, branching forms, which are characterized by high surface to volume ratio and a thick boundary layer, arise in low flow conditions with high diffusive boundary layer residence times. These effects increase the variability of resource allocation for different portions of the colony, producing unequal growth and the emergence of branching patterns. It is important to note that these results are strictly valid only within the same species (same vital parameters) and with all environmental conditions (different from flow speed) being equal; the terms “branching“ and “massive” are thus to be interpreted relative to the range of growth forms in a species.

The growth forms that can be obtained by these means bear a striking similarity with their real-life counterparts. Moreover the models are developed with a remarkably low number of species-specific parameters and, due to the ubiquity of the processes involved, can be applied to a wide variety of species including sponges and seaweeds.

7 Conclusions and Perspectives

The knowledge on growth rate patterns in long-living animals is essential for determining age, which allows to classify populations in size/age classes. On the basis of the age structure of a population, it is possible to make inferences on population trends by applying demographic models (see ▶ Chap. 19, “Demography of Animal Forests: The Example of Mediterranean Gorgonians” by Bramanti et al., this volume). However, size is generally regarded as a better descriptor of vital coral parameters and population structure than age alone, and demographic models based on size rather than age are considered more realistic. Age determination is nonetheless necessary to set the temporal dynamics of the model, as the time necessary to grow to the next size class represents a meaningful time step for the iteration of size-structured population models. This in turn can be applied to forecast population trends over time under different environmental scenarios, for both in the present and in the future.

The study of growth patterns for long-living sessile marine species constituting the so-called animal forest is still in its infancy, yet it is crucial to understand the basic rules driving this process. Forestry studies focused on the growth patterns of trees are already well developed, and in order to fill the gap between terrestrial and marine environments, a cross-disciplinary approach with forestry scientists is required. A parallel development of underwater exploration technologies will be necessary, in order to overcome the logistical constraints linked to the deep environments where some animal forests dwell, which is the case for CWC reefs.

Due to these logistical constraints and to the long life cycle of several corals, the modeling approach for the study of growth patterns is another promising field of study, complementary to experimental approaches. The fast increase in computing power allows a more precise description of growth pattern mechanisms and more accurate projections. These advances will allow forecasting the reciprocal influence of animal forests and current regimes at small spatial scales as well as at the landscape level.

8 Cross-References

- ▶ Activity Rhythm Measurement in Suspension Feeders
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Framework-Forming Scleractinian Cold-Water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998

Glossary

Allometry The scaling relationship between parts of an organism and its whole.

Arborescent Treelike in shape, generally aboveground or substratum.

Asexual reproduction When fusion of gametes is not involved. Production of new individuals by any nonsexual method, e.g., binary fission, budding, schizogony, etc.

Asymbiotic When symbiosis (mainly with symbiodinium) is absent.

Axial polyp The longest and terminal polyp of a group of polyps.

Calcite A form of calcium carbonate, crystallized in rhombohedric form.

Colonial organism A collection of genetically identical units which live together in a closely connected fashion.

Convenient choice In mathematical jargon, something you are allowed to choose arbitrarily, so you choose it in a way that makes your calculations easier.

Fecundity The number of eggs, seeds, or offspring of the first stage in a life cycle produced by an individual organism.

Gemmation A form of asexual reproduction or budding.

Genet A group of genetically identical individuals that have grown in a given location, all originating asexually from a single ancestor.

Indeterminate growth A type of growth for an organism or its part that does not terminate. By contrast determinate growth stops once a genetically predetermined structure has completed its formation.

Modular organisms Organisms that grow by iterative growth of parts, e.g., leaves, shoots, and branches of a plant, or the polyps of a coral or bryozoan.

Module A repeated unit of multicellular structure, normally arranged in a branch system.

Sclerochronology The study of periodicities stored in accreted hard parts and skeletons. The range of periodicity can vary from circa-daily to annual scales providing potentially long records of historical variations (from years to centuries). Annual periodicity can give information on age and growth rates. Sclerochronology is analogous to the study of annual growth rings in trees, termed dendrochronology.

Sessile Organisms that do not move and are fixed to the substrate.

Symbiotic The close association between different biological species that benefit from each other.

Solitary Corals that grow as a single polyp with a surrounding skeleton.

Unitary organism Organisms that start their development in a determinate fashion and eventually reach a definite adult form.

Zooxanthellae Photosynthetic algae that live in the tissue of most reef-building corals and have a mutualistic relationship with the coral.

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The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep

23

Covadonga Orejas and Carlos Jiménez

Abstract

At any scale, corals are live buildings. Their carbonate skeletons constitute three-dimensional frameworks allowing the delicate coral polyp to emerge from the sea bottom and populate vast areas of the ocean. These constructions, reminders of the structural complexity found in the forest, are found everywhere in the Earth's oceans, from the polar regions to the tropics and from the tidal pools to the dark abyssal plains. They can be found as solitary or in modest aggregations of a few centimeters in size or gargantuan colonies of mythological proportions; when many, they can create the largest nonhuman structures built by organisms. Life and death of the coral "trees" are influenced by the mineral architecture and the presence of bioeroders. Shape and size facilitate or restrict their access to food and light and influence structural strength tested by currents and swells. The role that corals play in the oceans defies any attempt at simplification since it transcends the life span of the small polyp, geological time, and ecological space. Long after the polyps are gone, coral skeletons continue to harbor numerous organisms of disparate nature by overgrowing, drilling, and dissolving the carbonates. These chapters are a personal journey into the coral forest of the world's oceans, with stations along singular aspects of their present and past. Our point of departure is the ecosystem engineering of the coral polyp through the construction of its skeleton, followed by selected examples of human interactions with the "stone

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from the sea" (see ▶ Chap. 24, "The Builders of the Oceans – Part II: Corals from the Past to the Present (The Stone from the Sea)").

Keywords
Architects • Structural role • Complexity • Biodiversity

Contents

1 A Journey Across the Marine Animal Forest

1.1 Animal Trees and Bushes of the Seascape over the World

Gravity forces us to live, as terrestrial animals, as humans, attached to the floor. However, life around us develops in three dimensions, and beside the perception of natural life in the aerial realm (e.g., flying insects or birds) and of our own manufactures (e.g., planes), a simple look to the sky during a walk in a forest displays in front of us this magnificent three-dimensional framework: Trees that elevate their branches and leaves as high as 115 m or more, such is the case for the giant sequoias (*Sequoia sempervirens*), which inhabit the wet mountain habitats of California and Oregon, or more humble species, for example, small herbs whereby their delicate blades in their size range of centimeters offer small-scale three-dimensional spaces found elsewhere on the planet. All living organisms spend their lives in this 3D space, as the natural architects that trees and bushes are offer shelter and a space to rest, to hunt, to reproduce, and to grow their offspring to many animal and plant species, from microscopic to large ones, and so do also the fragile blades of herbs to other organisms. If humans were able to walk in the most common habitat in the planet, the one which covers more than 70% of the Earth, they would also discover in many areas similarly impressive scenarios and landscapes (in this case seascapes). This "large habitat," which occupies the majority of our planet, is the sea. Hidden on the deep seafloor below the surface waters, that without the help of expensive technology is unavailable to most humans, there is a world of submarine mountains, valleys, canyons, sand, and mud deserts, which, as the terrestrial habitats do, change through the latitudes and depths offering a vast palette of impressive and colorful natural seascapes (Fig. 1).

In the shallow areas of the oceans, where the sunlight penetrates with all its intensity, a submarine vegetal forest composed by seaweeds or phanerogams (flowering marine plants) grow and play the same functional role of primary producers as terrestrial plants do. Impressive submerged plant ecosystems, such as kelp forests or sea grass meadows, supply secondary consumers with food and transform the sun energy into nutrients and

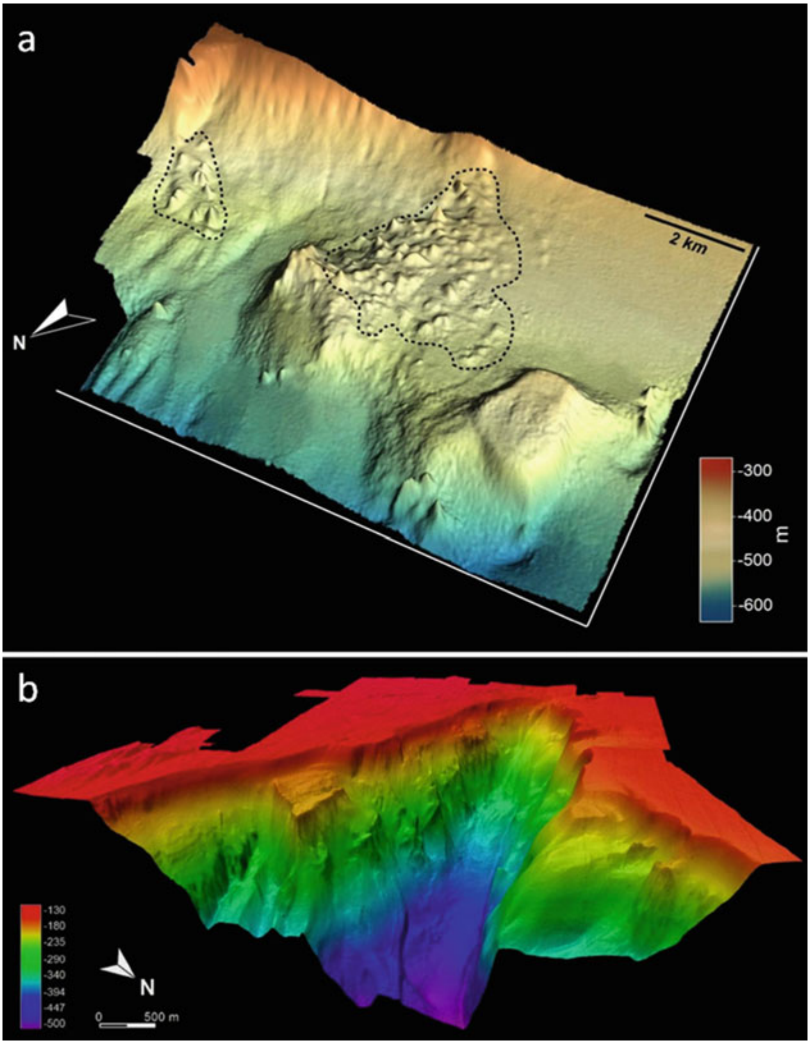


Fig. 1 Two examples of three-dimensional images of seabed topographical features obtained by sonar technology. (**a**) Sea mountains of the Melilla mounds, Alboran Sea (modified from Lo Iacono et al. 2014); (**b**) submarine canyon of Cap de Creus, northwestern Mediterranean (modified from Orejas et al. 2009)

eventually into structure. But in these shallow areas, another type of "hybrid forest" also develops. This is the one composed by animals, which nevertheless play an important role in the primary production: the so-called mixotrophic corals. These corals through the symbiotic relationship with microscopic algae (zooxanthellate) display the duality to be an animal but in close relationship with the kingdom of plants. Breaking this symbiotic "contract" usually leads corals to death. The zooxanthellate coral species are responsible for the world's largest bio-constructions, the shallow coral reefs. However, down to the deep shelves and slopes of the continents where the sunlight barely penetrates, a vast diversity of life forms develops, among them the deepwater coral reefs. At these depths, other organisms occupy the structural role of plants and hermatypic corals (reef-forming corals that contain symbiotic algae within the polyps) compared to the shallow-water marine systems. These structuring animal species of the deep do not play any role as primary producers, but similar to trees, bushes, and herbs, they offer three-dimensional structures providing a room supplying food, home, refuge, or nursery to a myriad of associated species.

This chapter intends to be a virtual journey throughout this submerged animal forest; the chapter will focus on the structural aspects of corals, the constructions they build, and the diversity harbored by these structuring species from the equator to the poles, from the shallow to the deep. In a second part (see ▶ Chap. 24, "The Builders of the Oceans – Part II: Corals from the Past to the Present (The Stone from the Sea)" by Jiménez and Orejas in this volume), this virtual journey will also travel, along the historical path where coral and mankind have interacted.

1.2 Life in the Coral Animal Forest

The simultaneous vision of a terrestrial forest or a scrubland and a marine ecosystem dominated by corals (*sensu lato*) is enough to intuitively understand the structural and morphological similarities between both systems, being branching trees and branching corals an example of convergent evolution (Fig. 2). As branches in a tree, the skeleton of a large group of coral species grow in different directions branching out and acquiring different shapes, lengths, and thickness and so occupying different volumes in the space. The growth direction depends on the synergy of many factors; the most important ones are currents and light. Coral habitats developing in areas with highly directional currents reveal stony corals and gorgonians which display the typical fan-shape morphology, whereas areas with multidirectional currents lead to corals with bottlebrush morphologies, sometimes producing an entangled mesh of branches.

Numerous structures increase the available surface area necessary to capture energy (branches and leaves in plants, branches and polyps in corals). The space within branches contains a large biodiversity and allows a multitude of species to take advantage of the protection offered by the corals, as well as the possibility to live in a "second floor" when using the top of the branches as "watchtower" (Fig. 3). Indeed, Wilson (1987) found in a single tree in the Peruvian Amazon 13 species of ants, and Erwin (1982) documented more than 1,000 kinds of beetles on 19 individual trees of a single species: the "guácimo colorado" (*Luehea seemannii*), in a seasonal lowland forest in Panamá. Regarding marine ecosystems, to our best knowledge such an approach does not exist for a single "coral tree" or "gorgonian tree," but changing the scale, several studies estimated that the Great Barrier Reef contains over 1,500 fish species swimming between more than 350 species of reef-building corals. This without mentioning the many species of other groups, such as mollusks, sponges, algae, soft corals, or sea pens, which also thrive in the Great

Fig. 2 (**a**) Black coral *Leiopathes* sp. in the Chella Bank seamount (Alboran Sea, ca. 230 m depth); (**b**) another *Leiopathes* sp. specimen in the same area, displaying several fishes swimming around and within the coral branches; (**c**) Beech tree (*Fagus sylvatica*) in a forest of Central Germany. The orange leaves and the darkness of the stem resemble the structure of black coral "trees." Credits: **a**, **b** (OCEANA); **c** (E. Isbert)

Barrier Reef. Living over the seafloor, even if just a couple of centimeters and protected by the coral branches, offers quite a lot of advantages for many species, among them a better accessibility to food particles in the water column, avoidance of sediment loads, and also protection from predators.

A walk across the benthic marine biome makes it necessary to point out that the journey will not always be a path between magnificent "green trees" (huge gorgonian fans, black coral trees, or stony coral reefs) but a road that includes deserts, tundra, steppes, scrublands, etc. displaying an ecosystem of "animal marine trees, bushes, and herbs" with different dominances and canopies (Fig. 4). Octocorals (soft corals) and scleractinians (stony corals) are among the tallest members of the canopy. Large gorgonians (octocorals), as it is the case of the impressive *Paragorgia arborea* (Fig. 5), are frequent elements of the cold-water coral (CWC) ecosystems in the Norwegian fjords and the Canadian coast of Newfoundland. These animal trees can be six meters tall and their stems display diameters up to 10 cm. Close to the images of bushes in terrestrial ecosystems are other gorgonian species, as the ones who populate many Mediterranean coastal areas (e.g., *Eunicella singularis* or *Paramuricea clavata*), as well as soft corals like several Alcyonacea species, or in deeper zones stony corals, such as *Madrepora oculata*, which apparently does not succeed building "true" reefs in Mediterranean waters. In the category that can be compared to herbal plants, organisms like hydroids, sea pens, or stoloniferan corals (Fig. 4g, h) would play a similar structural role offering a "dwarfed" 3D space.

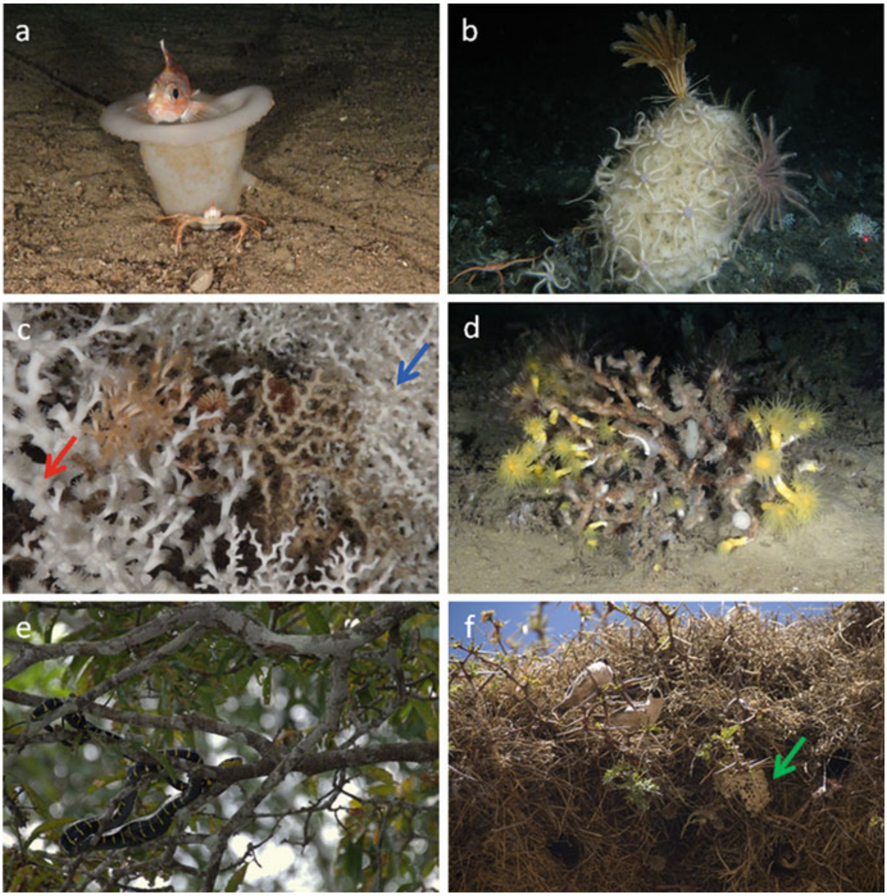


Fig. 3 Examples of the structural role of mega-benthic organisms and trees. (**a**) Deepwater sponge *Asconema setubalenses* (290 m depth, Cabliers seamount, Alboran Sea); the sponge offers shelter and an elevated position from the substrate to the fish *Helicolenus dactylopterus* and two different crabs (*Munida* sp.); (**b**) specimen of the sponge *Rosell*a cf. *villosa* (150 m depth, southern part of the Larsen Sea, western Weddell Sea, Antarctica), covered by many ophiuroids and some crinoids; (**c**) details of a *Lophelia pertusa* (red arrow) and *Madrepora oculata* (blue arrow) reef (Cabliers seamount, Alboran Sea, at 320 m depth). Note hydroids and a solitary coral (visible in the middle of the image) on the coral skeletons; (**d**) isolated colony of *Dendrophyllia cornigera* (Catifas seamount, ca. 400 m depth, Alboran Sea). Living and dead parts of the coral harbor several benthic-associated species; (**e**) mangrove snake resting on the branches of a tree in a forest in Borneo (Indonesia). This elevated position allows the snake to have a large vision field to detect potential prey and scape from possible predators; (**f**) entangled branches of an acacia tree in South Africa where social birds (weavers) and insects (wasps, *green arrow*) construct their nests. Credits: **a**, **c**, **d** (OCEANA); **b** (T. Lundälv, University of Gothenburg, AWI); **e**, **f** (J. González-Solís)

This journey will focus on the structural features of corals (*sensu lato*), starting in the paradigmatic coral reef forests located in the tropic of Capricorn, in the so-called Coral Triangle, together with the "Mesoamerican Reef." After this, the path will lead to other communities, located in the Mid-Atlantic Ridge: they will illustrate how magnificent are the deep, marine animal forest of the seamounts of the Azores Archipelago, where there are plenty of delicate black corals. Before moving to the highest latitudes, a short visit to several CWC reefs in the NE Atlantic and other areas is worthy to discover its gargantuan dimensions. The journey will finish with a brief visit to the animal forest of the Arctic and Antarctic regions, two of the most remote areas on earth.

1.3 A Journey Through the Coral Animal Forest of the Underwater World

Corals reefs (sensu stricto) occupy less than 0.2% of the ocean's surface (Knowlton and Jackson 2001). Notwithstanding the small area occupied by these ecosystems, this contrasts with the enormous productivity and diversity they harbor. Tropical coral reef ecosystems are highly productive, thanks to the associated photosynthetic production, from 5 to 20 g m^{-2} of organic carbon per day (Sorokin 1994), which is very high considering that kelp forests reach values from 0.8 to 6.8 g C m^{-2} d^{-1} (Valiela 1995). Although this chapter will deal mostly with the structural role of corals, it is important to mention these numbers to emphasize the paramount functional role of these animals, which is directly associated to the three-dimensional (3D) structure they have. They are also responsible for the high associated diversity; this high productivity affects not only the reef but also the surrounding waters as reefs export organic matter and nitrogen enhancing thus productivity.

Coral reefs are the major producers of carbonates, contributing to around 50% of the total amount in shallow waters. Fundamental to reef construction are growth and calcification processes, mostly performed by the basic units of the reef structure, the polyps of hermatypic corals with their massive aragonite skeletons. However, it is important to remember that reef accretion over geological time scales rely on several factors, such as high rate of accumulation of terrigenous sediment among others. Reef-forming corals are represented mostly by the order Scleractinia (subclass Hexacorallia), but also species belonging to other orders (e.g., Corallimorpharia, Antipatharia, and Ceriantharia) that contribute to the production of carbonate.

While coral skeletons extend the reef surface throughout carbonate accretion and cementation, several biological and physical agents lead to the erosion of the upper carbonate framework. The balance between constructive and destructive processes determines the ability of the reef surface to grow through net carbonate accretion. Currently, little is known about the rate of loss of topographical complexity associated with a negative reef carbonate budget, where the intricacy of the reef habitat mostly results from its topography (Perry et al. 2012; Bozec et al. 2015 and references therein). The complexity is also provided by foundation taxa which highly influence the ecosystem structure, function, and stability, which similarly occurs in terrestrial forests. Different coral taxa have differential influences in the architecture of reefs as hard scleractinian corals are a taxonomically and morphologically diverse group. Importantly throughout the Caribbean, the loss of some of

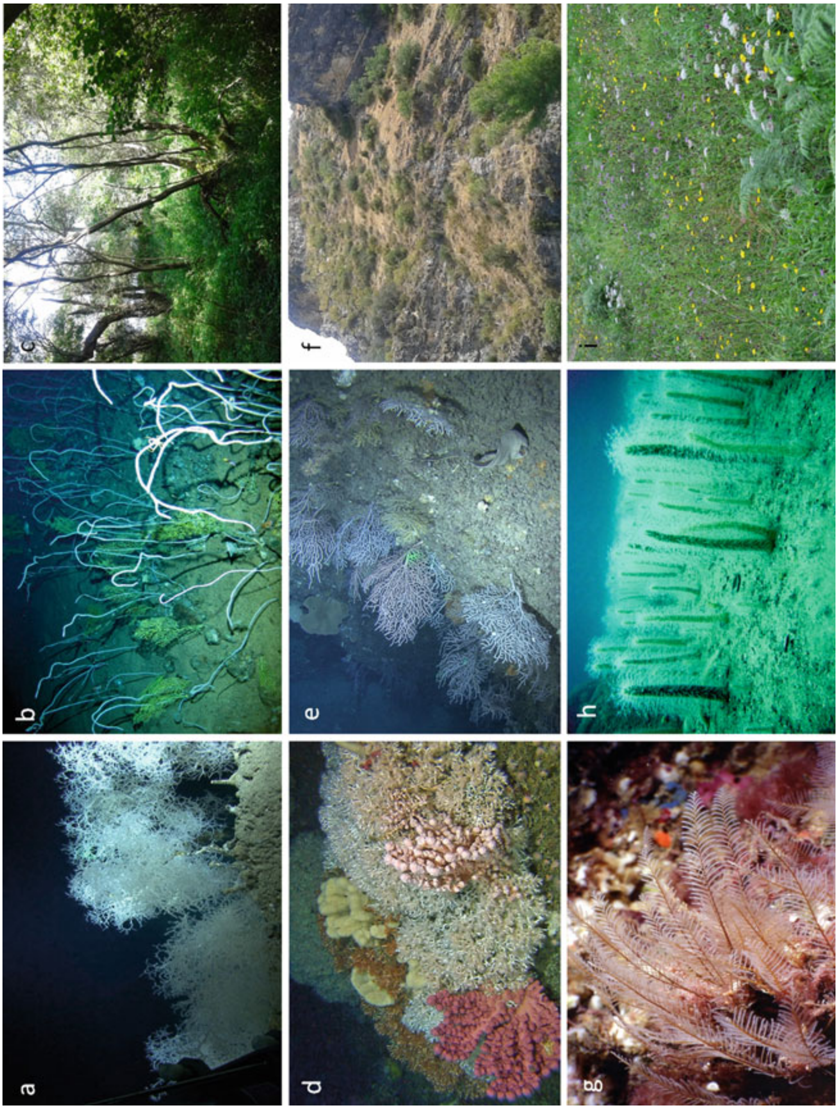


Fig. 4 (continued)

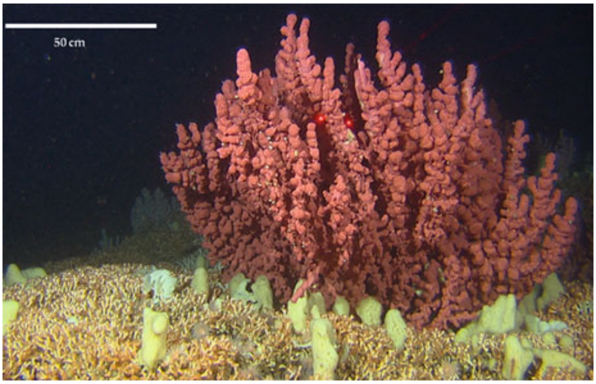


Fig. 5 A colony of *Paragorgia arborea* emerging from a thick *Lophelia pertusa* reef framework in Norway, at 310 m depth; the associated sponge *Mycale lingua* can be seen (*yellow*). Credits: P. Buhl-Mortensen (IMR, Norway)

the main reef-forming coral species (*Acropora* and *Orbicella*) has been accompanied by an increase in the relative abundance (frequently leading to eventual dominance) of stress-tolerant, early-colonizing corals that form smaller and less architecturally complex colonies, such as *Porites* and *Agaricia* (see review in Steneck et al. 2009 and references therein). The same authors indicate that this shift toward weedy coral species may constrain reefs to a state of lower potential architectural complexity even if overall coral cover remains stable or even higher than before (Álvarez-Filip et al. 2013; Jiménez and Cortés, pers. comm.). Recent findings suggest that the type and dominance of foundation species can be as important as their overall abundance in providing architectural complexity to the ecosystems (Álvarez-Filip et al. 2011b). In Caribbean reefs, these authors observed that the most architecturally complex sites are dominated by only a few coral species (and morpho-functional groups), and the characteristics (type and dominance) of these corals largely explain the differences in the architecture of these sites.

Fig. 4 Some examples of marine animal – and terrestrial vegetal forest, shrubs, and grasslands. (**a**) Black coral "forest" of the species *Leiopathes glaberrima* (240 m depth, Menorca Channel, Western Mediterranean); (**b**) gorgonian-dominated forest of the species *Dentomuricea meteor* and *Viminella flagellum* (summit of Condor seamount, ca. 200 m deep, Mid-Atlantic); (**c**) mature and well-developed alder (*Alnus glutinosa*) forest (Asturias, Spain). Different canopy levels can be appreciated here (**c**) as well as in (**b**); (**d**) seascape of a Norwegian cold-water coral reef with "bushes" of *Lophelia pertusa* and small gorgonians (*Paragorgia arborea*, 240 m depth); (**e**) gorgonian field of *Eunicella* sp. (150 m depth, Menorca Channel); (**f**) Mediterranean shrub-like landscape (Guadalajara, Spain), dominated by the species *Quercus coccifera*, *Juniperus phoenicea*, *J. oxycedrus*, and *Rosmarinus officinalis*. The community display a moderate canopy and a patchy distribution, very similar to the submarine shrub-like seascape display in (**d**) and (**e**); (**g**) detail of a hydroid (*Aglaophenia* sp.) in shallow Mediterranean waters; (**h**) field of a sea pen (*Veretillum* sp., 26 m depth, Arousa Ria, NE Atlantic); (**i**) grassland landscape (Asturias, Spain) comparable in canopy and density to the seascapes presented in (**g**) and (**h**). Credits: **a**, **e** (ICM-CSIC / IFM-GEOMAR); **b** (ImagDOP/EMAM); **d** (P. Buhl-Mortensen, IMR, Norway); **g** (J.M. Gili); **h** (J.M. Aldrey Vázquez, Grupo de Estudo do Medio Mariño, GEMM); **c**, **f**, **i** (J. Bartolomé Zofío)

Besides scleractinians, other organisms play an important role in the framework consolidation in different ways. This is largely notable in sponges that play an important role as physical support (see Fig. 3a, b) but also attaching loose carbonates restricting the mobility of the carbonate rubble and contributing to the consolidation of the fragments (Rützler 2004 and references therein).

Modern coral reefs have their origins in the Triassic and over the last 65 million years have flourished and declined due to a variety of extrinsic factors, such as sea level and climate changes (Richmond and Wolanski 2011). The total area occupied by modern reefs considering all oceans is estimated in 248×10^3 km^2, which is not evenly distributed (15% in the Atlantic Ocean, 53% in southeastern Asia, 19% in the Pacific, and 9% in the Red Sea), and only the Great Barrier Reef occupies 215×10^3 km^2 (Sorokin 1994). There are several factors controlling the current distribution of reefs, which can be summarized in (1) physical parameters (e.g., waves, currents, tides, nutrient concentration, light intensity, and turbidity), (2) intra- and inter-organism relationships (e.g., formation of monospecific, interspecific, or reproductive groups; commensalism; antagonism; symbiosis; and predation), (3) stochastic events (e.g., hurricanes and floods), and (4) anthropogenic influence. Zonation of environmental conditions define in a high degree the structure of the coral community. Changes among zones can be detected in the coral species composition, size and age of the colonies, morphotypes, and associated biodiversity, among others.

The modular nature of corals offers the possibility of constructing a large variety of phenotypes, which, for instance, enable the same coral species to colonize various biotopes under different environmental conditions. A comprehensive review on the morphological plasticity in corals and the influence of the environment can be found in Todd (2008). The two dominant parameters influencing morphological plasticity in hermatypic corals are water movement and light intensity. Other parameters closely linked to water movement are the supply of food and sedimentation; the latter can highly influence the availability of light, aerial exposure, and competition. Furthermore, a variety of invertebrates can modify the skeletal architecture of reef structural taxa, including scleractinian and milleporid corals, octocorals, sponges, and polychaetes, among others.

The formation of branching corals is related to the increase in surface area in order to capture a higher amount of light, but there are also other evolutionary reasons: branching and also the so-called “cribose” corals are constructed from less calcareous skeletal material, compared with massive corals (Sorokin 1994). This enables them to have a higher growth rate with the same calcification rate, overgrow massive corals, and better avoid sedimentation thanks to the branching shape (Vosburgh 1982 and references therein). Additionally, branching corals present a higher ability to capture zooplankton (Sebens et al. 1996) and to disperse by fragmentation (asexual reproduction), which may be advantageous in a system where the competition for substrate is very high. However, survivorship of fragments depends on their size and energy regime. Small fragments in a high-energy environment tend to have high mortality rates. Branching (also called “ramose”) corals are the most typical form in deeper biotopes. They can build flattened colonies, in which most branches grow laterally, perpendicular to the penetration of light. In this morphotype, energy resources are used to support growth only in one plane, which maintains generally low calcification rates, inhibited in deep reef zones by a deficiency of such light energy penetration. Lateral-form colony avoids the self-shadowing of branches which is important in light-deficient environments. Other morphotypes, such as the flat forms, are ideal for poorly illuminated environments, because they allow corals to have a larger surface in order to collect the light, expending minimal resources; massive and branching species can also show this morphology. Massive round and columnar morphotypes are successful in the upper reef zones, as these morphologies allow the species to better cope with waves, grazing, overgrowth, and siltation. In high turbulent or high water circulation environments, such as reef flats, flattened forms are also common.

The architectural complexity of ecosystems often underpins the biodiversity that they support. It is widely accepted that tropical coral reefs support the highest biodiversity of all marine ecosystems (Knowlton and Jackson 2001), and invertebrates contribute dominantly to this condition (see for a review Glynn and Enochs 2011). Species diversity is considered a fundamental feature of ecosystem structure, function, and resilience in coral reefs; higher species diversity might be expected to increase reef complexity due to the large variety of coral forms and shapes. However, positive relationships between the number of coral species and architectural complication may, in fact, be a consequence of the positive relationship between coral cover and architecture, as species diversity can also be positively associated with the extent of coral cover (e.g., Álvarez-Filip et al. 2011a). Conversely, declines in reef architectural complexity may result in lower species richness and potential long-term consequences for large-bodied species (Graham et al. 2007). More complex reefs tend to have greater numbers of individuals, biomass, or richness of reef-associated fishes and invertebrates. In line with this, Álvarez-Filip et al. (2011c) suggest that assemblages with dominant reef-forming species such as *Orbicella* spp. would be expected to facilitate more diverse and functionally important coral reefs in the Caribbean.

Structuring species in coral reefs have been also called “habitat providers,” as they offer structure or substrate where other species can live in or on, respectively. The habitat provider confers a variety of benefits to its associates including physical shelter from predation, camouflage, stability, range expansion, and/or advantageous positioning (Glynn and Enochs 2011). Habitat architecture is known to deeply influence the abundance and diversity of species through the provision of niches and diverse ways of exploiting environmental resources. Hence, morphology of coral taxa strongly affects the abundance and number of species associated. Gorgonian corals have also been observed to have abundant associated fauna (Goh et al. 1999); their three-dimensional structure (frequently tree-like), together with the often unpalatable tissue, which makes it unattractive for fish, contributes to protect the associated species. One of the most conspicuous examples is the association between basket stars and gorgonians, and the most well known is the association

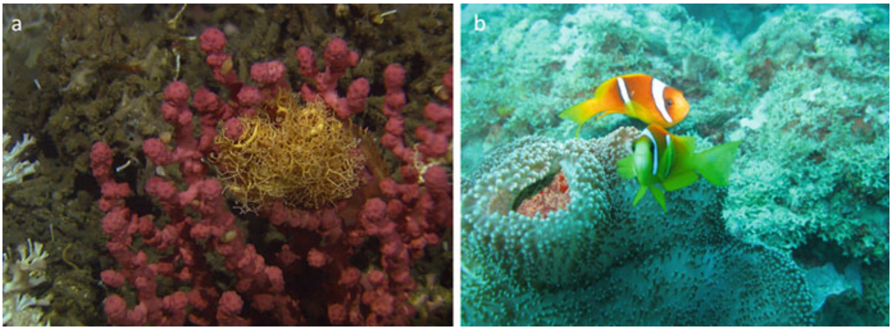


Fig. 6 Examples of species interactions. (**a**) Basket star *Gorgonocephalus* sp. entangled on the branches of *Paragorgia arborea* octocoral (reef "Korallen," north of Sørøya, NE Atlantic ca. 200 m depth); (**b**) Anemone with two clown fish (Bunaken National Marine Park, NW Pacific Ocean). Credits: **a** (P. Buhl-Mortensen, IFMR, Norway); **b** (J. González-Solís)

between anemones and clown fish species (Fig. 6). There are numerous association types between cnidarians and other species, some of which will be mentioned later on. Other structuring species and their obligated – or not – accompanying fauna will be presented in other chapters (e.g., polychaetes, Milazzo et al. ▶ Chap. 12, "Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean" in this volume). Even though the main focus of this chapter is coral structuring species, it is useful to note that other organisms also play an important role as habitat provider in coral reef systems. A common example would be sponges, which can form complex habitats and a shelter from predation for organisms living within their extensive canal network; the pioneer study by Pearse (1932) pointed out the high biodiversity and abundance of organisms associated to sponges, documenting the impressive number of 17,128 specimens, belonging to 22 different species, in a single specimen of the sponge *Speciospongia vesparium*. The role of sponges as structuring species will be extensively discussed in ▶ Chap. 5, "Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns" by Maldonado et al. in this volume.

The high species diversity in a reef is enhanced by the high variety of ecological niches offered, allowing the coexistence of different trophic strategies, harboring numerous morphological adaptations and substrate preferences. Besides benthic species, planktonic invertebrates have been observed to undergo diel vertical migration into and out of the coral framework. Large fish communities associated with the reef (Fig. 7) also profit from the available trophic resources as well as the 3D structure and, in turn, play an important role in the regeneration of nutrients and in bioerosional processes. This high fish density is reflected in the high biomass values, which can reach 500–1,000 g m^{-2} in protected reefs in contrast to 200–400 g m^{-2} in non-protected reefs (Aburto-Oropeza et al. 2011).

The fish community associated to the reef is also highly diverse: around 8,000 associated species have been described (Bellwood et al. 2012). This corresponds to

Fig. 7 Submarine animal forests and terrestrial forests harbor a high diversity of associated species, and number of individuals can be very high. (**a**) Tropical coral reef with large schools of fish (Bunaken National Marine Park, NW Pacific Ocean). (**b**) Orangutan rummaging in a wasp nest on a tree branch (Tanjung Puting National Park, Borneo, NW Pacific Ocean). Credits: J. González-Solís

less than a third of the total species of marine fish described, which has been calculated as 16,764 by Eschmeyer et al. (2010), displaying also a high variety of trophic guilds. Additionally, reefs with high architectural complexity support fish assemblages with larger numbers of individuals in the smallest size classes and longer food chains, highlighting the significant consequences that complexity could have for the structure and function of fish assemblages (Álvarez-Filip et al. 2011c). In tropical coral reefs at spatial scales smaller than 1 km, the recruitment of fish larvae partially depends on the availability of shelter; post-settlement movements of fish recruits are greatly influenced by the availability of microhabitat structures (Johnson 2007 and references therein). Also, in juvenile and adult fishes, aspects such as competition or predation can also be influenced by the structural complexity of reef habitats: generally more complex habitats may reduce competition by providing more diverse and a larger number of resources, as well as reduce predation by offering more refuges or decrease the number of encounter rates predator-prey (Álvarez-Filip et al. 2011c and references therein).

So far, this chapter has discussed the important role that coral architectural complexity plays in terms of taxonomical and functional biodiversity; however, there is a special feature of these systems which needs to be mentioned. In contrast to other ecosystems where degradation normally implies reductions in habitat area (e.g., deforestation), decreases in live coral cover on coral reefs do not immediately result in loss of available habitat because the reef framework, in the absence or reduced numbers of bioeroders, can persist long after the death of corals (Fig. 8). Particular cases have been documented in the eastern Pacific where the structural framework was destroyed within a few years (4–10 years) after mass mortality of corals (Glynn 1994; Pratchett et al. 2008). High bioerosion activity by sea urchins, low presence of sponges and calcareous algae, and low marine lithification that could otherwise maintain the integrity of the framework led to the destruction of hundreds

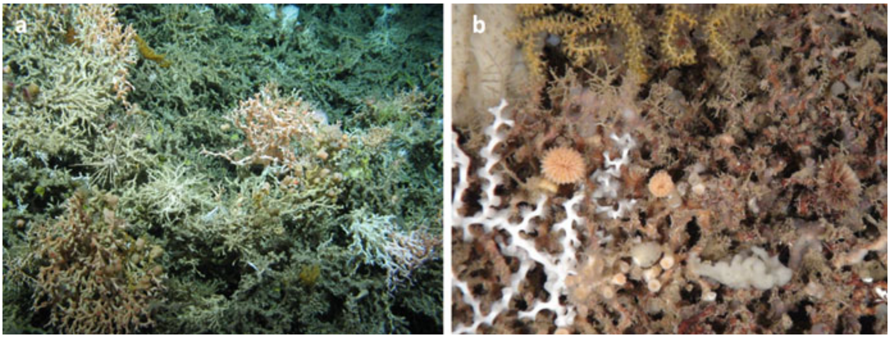


Fig. 8 Coral communities with live and dead corals. (**a**) Accumulation of scleractinian coral skeletons (Logachev mounds, NE Atlantic, ca. 600 m depth) with living colonies on top, including gorgonians and, among the mobile fauna, sea urchins; (**b**) close-up of coral skeletons (from Catifas, Alboran Sea, at 385 m depth), with solitary corals (probably *Desmophyllum* specimens) growing on the branches, as well as a gorgonian, sponges, and hydrozoans. Credits: **a** (J.M. Roberts, Changing Ocean Expedition, Heriot-Watt University); **b** (OCEANA)

of square meters of reef framework. Nevertheless, general declines in biodiversity are frequently associated with the loss of architectural complexity, which highly influences habitat specialists, and at the end of the line endangered fisheries' productivity due to increasing post-settlement mortality (e.g., Graham et al. 2007). The role of reef architecture is also crucial for humans, as this leads to coastal protection through the dissipation of wave energy transmitted over the reefs. Within the reef system, the physical barrier made of calcium carbonate acts as a wall that protects seagrass meadows, mangroves, and the shore from the fury of the sea when storms are roaring offshore; ▶ Chap. 42, "The Animal Forest and Its Socio-Ecological Connections to Land and Coastal Ecosystems" by Arias in this volume deals with this connection of the animal forests with land ecosystems, focusing on mangroves.

At local scales, mass coral mortality is associated with the loss of architectural complexity and "reef flattening" after direct and catastrophic impacts, such as hurricanes, by producing extensive breakage or detachment and displacement of coral colonies. The Caribbean is one of the regions more affected by the decline in reef complexity, especially over the last 40 years (Álvarez-Filip et al. 2009 and references therein) and, in general, is one of the most heavily impacted marine ecosystems (e.g., Halpern et al. 2008; Jackson et al. 2014 and references therein). Structurally complex reefs have been virtually lost from the entire region. Today, the flattest reefs comprise approximately 75% of the total area compared with approximately 20% in the 1970s, where most of the increase in the proportion of flattest reefs occurring in the 2000s (Álvarez-Filip et al. 2009). In the Caribbean, the greatest impacts on biodiversity are expected to occur with the breakdown of the "reef matrix" because even if there are no fish species that feed exclusively on live coral, many reef-associated species depend highly on rugose substrata to feed, recruit, and hide. Effects of long-term loss of structure (following coral bleaching events) have been documented by major changes in fish community composition in Indo-Pacific reefs (Pratchett et al. 2008 and references therein). There are many documented cases indicating that live cover of reef-forming corals is influenced by large-scale drivers, such as changing climate and the increasing human development (e.g., Knowlton and Jackson 2008; Schutte et al. 2010), as well as changes in reef architecture that may be more sensitive to local reef conditions than previously thought (e.g., rates of erosion and hurricane impacts) (Álvarez-Filip et al. 2011b). These findings are of high importance: the reduction of impacts on coral reefs by overarching processes (e.g., climate change) requires international agreements and regulations (frequently a complicated and long process). However, protection of reef architecture at local scale can be achieved by limiting or regulating activities which damage the reef by physical impact, as it is the case for destructive fishing practices or anchoring.

Reef-associated diversity includes many life forms, from bacteria to fish, thriving in different realms: from planktonic to benthonic ones. The total number of taxa living the reefs approaches 800 (Sorokin 1994), and the total number of described species occurring in coral reefs (considered globally) was estimated around 95,000 (Reaka-Kudla 2005), but the same authors argued that the expected species richness of these ecosystems (considering they are as diverse as tropical forests) should be around 950,000. Also Roberts et al. (2001) identify tropical reefs as marine biodiversity hotspots analyzing the geographic range of distribution of coral and associated species, concluding that the ten richest centers of endemism cover 15.8% of the coral reefs over the world (a small part of the oceans: 0.012%), containing 44.8–54.2% of species with a restricted range of distribution. Regarding the "structuring" species, most of them belonging to the scleractinian fauna, they vary among geographical regions. The most diverse reefs are the ones located in the regions of Indonesia-Philippines-North Australia; for example, there are 120 massive coral species in Australia's Great Barrier Reef, while the Caribbean harbors < 25 (Bellwood et al. 2004). "Massive" is used following the classification in Bellwood et al. (2004), where massive, bushy, platelike, columnar, unattached, encrusting, staghorn, and bottlebrush morphotypes are considered separately. Further information on the complexity and diversity of the Caribbean reefs and the diversity and evolution of octocoral animal forest in the tropical America can be found in the chapter by Sánchez, ▶ Chap. 4, "Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America," respectively, in this volume. Besides the scleractinian reef builders, reef benthic fauna is very rich and diverse (estimated in 250–500 species), as the reef structure provides for plenty of space for non-sessile organisms to hide, allowing them to escape from predators, and a large extension of substratum for sessile invertebrates (Sorokin 1994). Indeed, the numbers referred to above are undoubtedly gross underestimations since cryptofauna is not included, even though they constitute a significant portion of the reef benthic-associated fauna, in amounts greater than the visible reef surface. General estimations of the proportion of cryptic reef volume in several areas revealed values around 75–90%

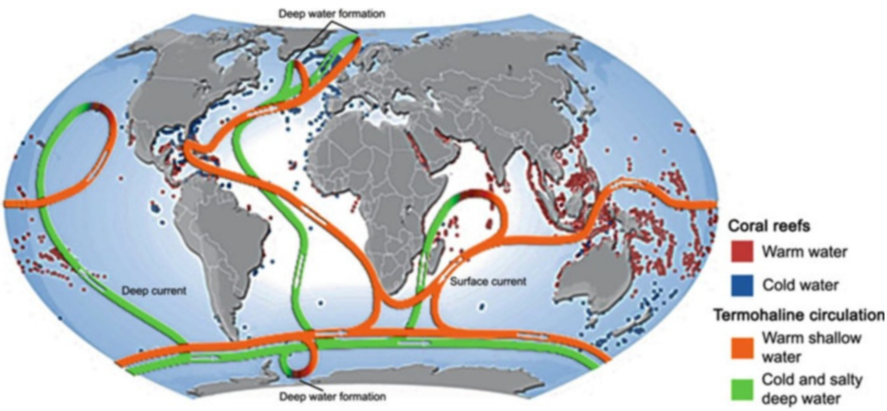


Fig. 9 Global distribution of warm and cold-water corals and path of the thermohaline circulation. Credits: map (Hugo Ahlenius, UNEP/GRID-Arendal), thermohaline circulation (wikicommons). Credits: Image composition by A. López-Sanz (*Sources*: Robert Simmon, NASA. Minor modifications by Robert A. Rohde, public domain NASA Earth Observatory and Hugo Ahlenius, UNEP/GRID-Arendal)

(Ginsburg 1983). These cryptic habitats have also been divided into subcategories, taking into consideration the intra-skeletal and inter-skeletal cavities as well as borings and inter-particle cavities. These hidden niches may offer higher environmental stability in contrast to the changing physical and chemical conditions on the reef surface which is more exposed to the environmental variations. This environment receives significantly less visible light than exposed reef surfaces, which affects the associated faunal community favoring heterotrophic invertebrates. Cryptic environments also offer a refuge to hide from predators, where predation pressure is probably lower (Jackson and Buss 1975); however, this seems to be a controversial aspect as certain predators present higher abundances in cryptic environments, such in the case for some cryptic fish populations in the Uva Reef in Panamá, which revealed a high percentage of carnivores (Glynn 2006).

On planet Earth, there are no isolated ecosystems as the Gaia theory (Lovelock 1979) nicely explains. This is also true for marine ecosystems, and the thermohaline circulation controls the connectivity between water masses and hence whole ecosystems (Fig. 9). Water masses move from the tropical areas (throughout the Gulf Stream), where warm coral reefs develop, to the next stop of this journey in the middle of the North Atlantic: the Mid-Atlantic Ridge. This visit will focus in the Azores Archipelago, which displays an underwater seascape dotted with numerous seamount-like features of different size, morphology, and depth (Morato et al. 2008). The Azores represents the transition between subtropical and temperate climates, displaying a high diversity of corals species (around 150) when compared to other studied areas in the Northeast Atlantic, located within shallow waters (25 m) down to more than 3,000 m depth. Studies on the islands' coral fauna are still in its infancy, and a recent publication (Braga-Henriques et al. 2013 and references therein) presents the discovery of the so-called coral gardens, as well as other coral-dominated

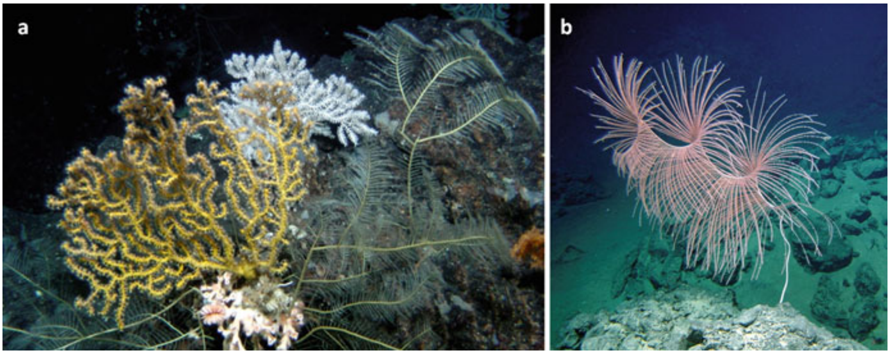


Fig. 10 Cold-water coral communities of the Azores Archipelago. (**a**) CWC diversity near the Menez Gwen hydrothermal field (ca. 850 m depth); (**b**) *Iridogorgia* sp. (antipatharian) at Saldanha Hill (ca. 1,000 m depth). Credits: SEHAMA

habitats abundant at the seamounts with highly dense populations in some places, such as the Condor Terra seamount, one of the most studied seamounts of the area (Fig. 10). It is known that seamounts are among the most suitable habitats for the establishment and development of CWC as they experienced strong current regimes with nutrient-rich upwelling and topographic features that retain particles and zooplankton. Coral distribution in the archipelago is mainly clustered around insular slopes and on the edges and summits of the seamounts. The characteristics of these seabed features fulfill the requirements for the development of this type of communities (summarized in Roberts et al. 2009), such as hard substrates, high topographic relief, low sedimentation levels, enhanced current flow, and high food supply. Coral assemblages found in the Azores display high taxonomic richness, which appear to be higher than in other Macaronesian archipelagos (e.g., up to 51 coral species in a single seamount, Braga-Henriques et al. 2013), and have been recognized as key indicators of vulnerable marine ecosystems (VMEs). The Azores seamount coral fauna do not respond to the patterns observed in other seamounts where endemism seems to be the rule. Indeed, Azores seamount megafauna is characterized by species with broad geographical distributions and few endemic species as also demonstrated in other seamounts: for instance, the Davidson seamount (off San Francisco Bay, USA; McClain et al. 2009). The results by Braga-Henriques et al. (2013) show a coral fauna with only 14% of apparently endemic species, whereas 71% of the species is shared with the Lusitanian–Mediterranean zoogeographic region, also presenting common components with the western North Atlantic (33%), the Canary and Cape Verde islands (30%), and the seamounts located south of the Azores and between mainland Portugal and Madeira (28%). These results are in line with previous studies in other geographic regions that demonstrated high similarities between seamount faunas and those from the nearest continental margin (Rowden et al. 2010 and references therein). The current knowledge on the coral fauna (community composition and geographical distribution) of the Azores is partially

Fig. 11 (**a**) Large *Leiopathes* sp. colony caught as bycatch by long-line fishing in the Azores seamounts; (**b**) basal section of the stem of another *Leiopathes* specimen from a private collection. Credits: **a** (Íris Sampaio / ImagDOP); **b** (F. Porteiro)

based on bycatch records. Corals collected are mostly dominated by specimens that display a three-dimensional morphology (78.5%), and branched corals were much more abundant (72.7%) than other morphotypes (Sampaio et al. 2012). Black corals (e.g., *Leiopathes* spp. Fig. 11) and gorgonians (e.g., *Callogorgia verticillata*, *Acanthogorgia armata*, *Paracalyptrophora josephinae*, and *Viminella flagellum*, Fig. 10) were among the most frequent bycatch organisms; most of them are known as habitat builders in the region and important components of bathyal "coral gardens." The role of the Azores' "coral gardens" as habitat providers seems to be highly relevant for the fish community, as it has been documented for the Condor seamount where some fish species (*Callanthias ruber*, *Anthias anthias*, and *Lappanella fasciata*) demonstrate a clear affinity to coral habitats (Porteiro et al. 2013).

Understanding the current biogeographical patterns requires knowledge on dispersal of the species, which in benthic sessile invertebrates occurs through larval stages. Reproductive processes and larval development strategies are relatively well known in shallow ecosystems, whereas almost nothing is known on these aspects for communities below the scuba diving depths (~50 m). Indeed, for the animal forests constituted by CWCs, to our best knowledge only two studies on larval development have been published, devoted to the scleractinians *Lophelia pertusa* and *Oculina varicosa* (Larsson et al. 2014; Brooke and Young 2005, respectively). In spite of poor knowledge on the dispersal capabilities of CWCs, it can be said that the Mid-Atlantic Ridge does not constitute a bathymetric biogeographic barrier for these organisms in Azores but could be instead an obstacle to east–west dispersal, especially in lower bathyal and abyssal fauna. The coral fauna display a mixture of steno- and eurybathic species with partially overlapping distributions; this pattern suggests that a combination of factors is involved in the establishment of depth ranges, such as food availability, temperature, pressure, and stratification of water masses, as well as biological interactions and processes such as competition, predation, and dispersal (reviewed by Carney 2005). Bathymetrical distribution in the coral fauna of the Azores seamounts suggests there are trends that agree with previous observations. The proportion of amphi-Atlantic and cosmopolitan species increases with depth, possibly as a result of more constant environmental conditions (e.g., Allen and Sanders 1996); high-latitude species increase with depth, whereas low-latitude species diminish. This pattern is consistent with the depth of the permanent thermocline in the NE Atlantic (600–1,000 m) and the predominance beneath its lower boundary of deepwater masses formed at high latitudes (i.e., the Subarctic Intermediate Water and the Labrador Sea Water). The higher latitudes will be the focus of the next part of the chapter.

Our attention remains in the regions corresponding to the deep ocean margins, the continental shelves and slopes, focusing mostly in one of the most emblematic CWCs of the world: the *Lophelia* reefs of the Norwegian waters. Since ▶ Chap. 32, "Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems" by Buhl-Mortensen et al. in this volume discusses several functional aspects of these ecosystems, the focus here will be mostly on the structural role that these organisms play, focusing on mega-benthic organisms rising from several centimeters to some meters above the seafloor.

Shelf-slope areas, located in the depth range of 150–400 m, seem to be some of the most suitable locations for the development of reef-forming communities of organisms such as CWCs. The combination of suitable substrate, strong tidal currents, wave energy, and seasonal temperature changes leads to the creation of large and complex structures by reef-forming organisms, which significantly increase habitat heterogeneity. The Norwegian shelves harbor not only the impressive *Lophelia* reefs but also sponge fields (e.g., the ones dominated by *Geodia* species; Fig. 12) and "coral gardens," mostly dominated by gorgonians. Even deeper in the upper bathyal zone (500–1500 m), there are some regions where the margins are intersected by submarine canyons (it cannot be forgotten that 95% of the seafloor is located under 130 m depth). In these settings, large, biogenic structures formed by reef-forming organisms are also found in the upper range, where sea pens and gorgonians are among the larger organisms responsible for creating complex biotic habitats even in deeper zones (Mortensen et al. 2008). However, CWCs are found elsewhere, most commonly in the depth range of 200–1,500 m. Nevertheless, very shallow, upper depth limits (up to 40 m) of CWCs in Norway, New Zealand, Chile, and British Columbia demonstrate that it is not the depth *per se* but the distribution of intermediate and deepwater masses (and hence also temperature) that controls the bathymetric distribution of these corals (Buhl-Mortensen et al. 2010). As described for tropical corals at the beginning of this chapter, CWCs also provide microhabitats which are under different current speeds, food sources, and substrates. Indeed, the branching tree-like morphology adopted by most CWCs allows these organisms to be elevated from the substrate (where the currents on the boundary layer are relatively slow) and take advantage of the faster flowing rates that supply food. *Lophelia* CWC reefs in the Norwegian shelf typically have a circular or elongated ("cigar-like") shape, reaching maximum lengths of approximately 1,000 m (Buhl-Mortensen et al. 2010), whereas

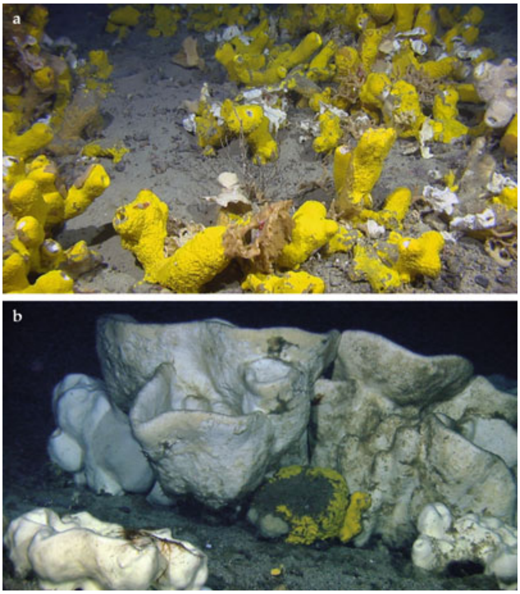


Fig. 12 Sponge fields in Norway. (**a**) *Aplysilla sulfurea* overgrowing *Stryphnus ponderosus* at 440 m depth (north of Sørøya); (**b**) field of *Geodia atlantica* at 150 m depth. Credits: **a** (P. Buhl-Mortensen, IMR, Norway); **b** (P. Buhl-Mortensen, IMR, MAREANO)

in other areas, as it is the case for the Mingulay Reef complex (Hebrides Sea off Scotland), the reefs are composed by cauliflower-like individual colonies creating a discontinuous framework. A different situation can be observed in the Logachev mounds (SE of Rockall Bank, off Ireland), where the living reef occupies a thin layer and a massive dead framework is highly populated by associated fauna (Fig. 13). At the Norwegian continental shelf, it is estimated that there are around 6,000 *Lophelia* reefs (Mortensen et al. 2001), many are several 100 m long and occur in clusters (reef complexes, as also mentioned for Mingulay) up to 35 km long (Fosså et al. 2005). Next to the reef-forming CWCs, gorgonians are also an important component of the CWC communities. They are also habitat providers within colonies as well as between colonies, when they occur in groups. Gorgonian patches display higher density values for smaller species rather than for larger species, as was recorded in populations from the Northeast Channel (Nova Scotia, Canada) where maximum densities of 199 colonies/100 m^2 were recorded for the small gorgonian *Acanthogorgia armata*, whereas the large *Paragorgia arborea* occurred with a maximum of 49 colonies/100 m^2 (Buhl-Mortensen et al. 2010). Coming back to the comparison with terrestrial groves, some oak forests in Mexico, display a density value of 1,246 trees/ha, whereas the shrubs associated to the oaks display higher densities reaching 2,544 trees/ha (Martínez-Cruz et al. 2009). Among the deep-sea gorgonians, it is important to mention two emblematic species: *Primnoa resedaeformis* and *Paragorgia arborea* (Fig. 5), which are among the most abundant and widely distributed large gorgonians in the North Atlantic (Mortensen and Buhl-Mortensen 2004 and references therein). These fantastic animal trees can form "coral forests" and are among the largest deep-sea gorgonian corals, reaching heights of 50–250 cm (Buhl-Mortensen et al. 2010). As microhabitat providers for

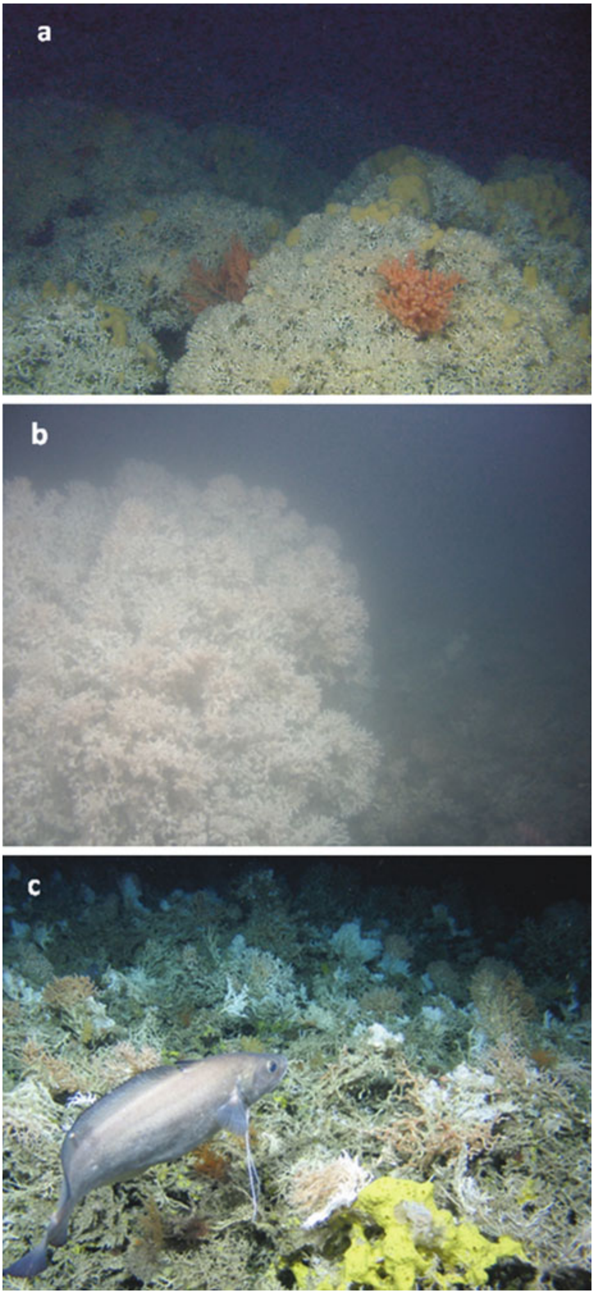


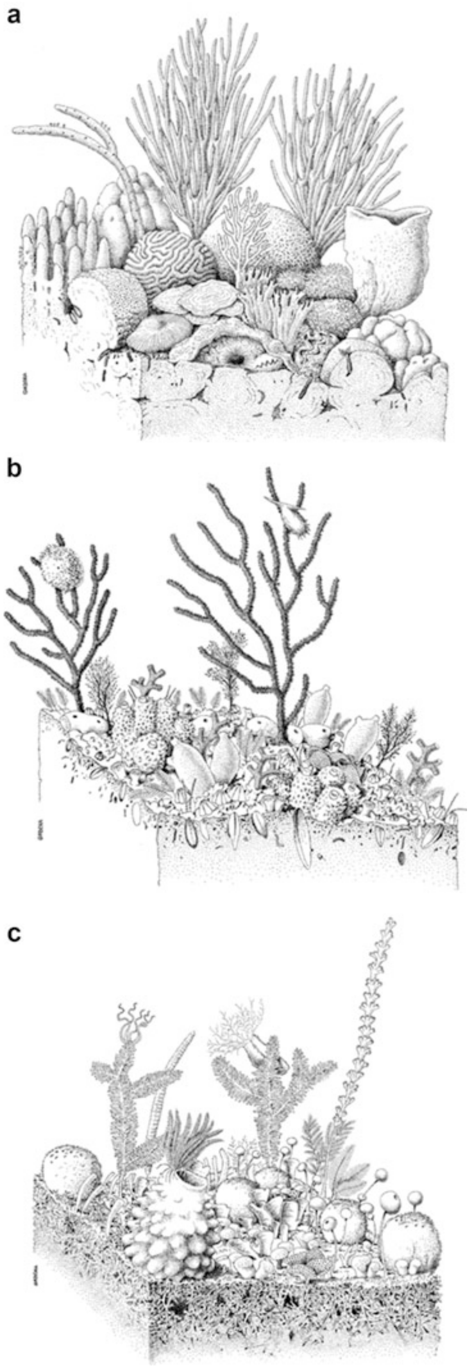
Fig. 13 Three different *Lophelia* reef communities from the NE Atlantic. (**a**) *Lophelia* reefs from Norway (Korallen, north of Sørøya, ca 200 m depth); (**b**) typical cauliflower-like *Lophelia* specimens in the Mingulay Reef (ca 130 m depth); (**c**) aspect of the *Lophelia* framework in the Logachev mounds (ca. 600 m depth). Credits: **a** (P. Buhl-Mortensen, IMR, Norway), **b,c** (J.M. Roberts, Changing Ocean Expedition, HW University)

associated species, they offer the living surface of coral tissue in the younger parts of the colony and the pockets of detritus and exposed skeleton in the older parts of the colonies (Buhl-Mortensen et al. 2010).

Would a coral larva from a female coral in the deep waters of the tropics or the Mid-Atlantic Ridge be able to reach the Antarctic or the Arctic realms transported by the currents? Undoubtedly, it won't happen in a single event, but it could indeed be feasible in repetitive steps throughout generations and, of course, under environmental favorable conditions. Nevertheless, this would be almost impossible in the particular case of the Antarctic continent, as nowadays the Antarctic is quite isolated due to the presence of the so-called Antarctic convergence, a fairly circular current that keeps the Antarctic continent isolated from the surrounding water masses. The polar regions are the last stop in this imaginary journey. It was only in the 1960s when the benthic polar seascapes displayed their beauty to human eyes for the first time, as it was in these years when the initial research cruises using underwater photography and video produced images from under the freezing cold polar waters. And so, the traditionally considered inhospitable places to host life that human fantasy imagined as deserts revealed a variety of habitats and life forms that no one had expected to find. The benthic Antarctic seafloor is populated by such well-developed three-dimensional structures that they are comparable indeed in complexity (Fig. 14) and biomass to other mega-benthic communities in the tropics and in the temperate seas (Thomas et al. 2008). The two polar environments, the Arctic and the Antarctic, display many differences (as well as similarities), due to different geographic features. The Arctic is close to other land masses and is highly influenced by continental waters and consists of several pieces of land similar to an "Archipelago"; conversely the Antarctic is a true continent, strongly isolated from the others, and with no influence of continental water. Although the extension of the pack ice is of the same order in both poles, in the Arctic, it is mostly multiyear ice covering the benthos year around, whereas in the Antarctic, most of the ice melts each year. This difference is very important for the benthic communities living below the ice. Hence, these radical different physical features lead to differences in the biological characteristics of the benthic communities in both poles. Some of the traditionally accepted ideas on the polar systems have been partially corroborated or completely rejected due to these new findings, an example is the low endemism and faunistic affinity of the Arctic benthic assemblages and the North Atlantic ones (see review by Piepenburg 2005).

As it is the case for other benthic communities, regarding either the Arctic or the Antarctic, it cannot be spoken of single "typical" Arctic or Antarctic benthic assemblages since both occupy large extensions. Both polar realms display a high diversity of biotopes including great bathymetrical differences, due to the vast extensions covered by the Arctic and the Antarctic, both included largely distant geographical locations which also suggest different environmental and biological features. For instance, different water currents and advection regimes can be documented in both realms, as well as freshwater supply via river runoff – in the case of the Arctic – which is also present in the Antarctic in some areas of the Antarctic Peninsula, but absent in the so-called high Antarctica. Differences in seasonal ice dynamics and coverage are also very different in both poles, as well as the features of the seafloor (different geological histories and origins) and food

Fig. 14 Ideal representations of (**a**) a tropical coral community; (**b**) a Mediterranean one and (**c**) a benthic Antarctic community. Drawings by J. Corbera



supply for the benthic communities. Both polar regions have very different biogeographic histories, which also mark differences in the composition of the benthic assemblages (Piepenburg 2005).

Intermediate species richness seems to characterize the biogeography diversity of both Arctic and Antarctic benthic assemblages (Thomas et al. 2008). However, to our best knowledge, no comparative studies exist only considering the mega epibenthic communities. Nevertheless, based on what is known, it can be said that the Southern Ocean benthos is more diverse than the Arctic, though this conclusion carries the caveat that to date, relatively few locations have been analyzed in a truly comparative fashion (for a comprehensive revision on these topics, see Thomas et al. 2008). Comparisons with other areas are limited by the general lack of marine species richness data comparable with that now available for Antarctica, but for a cross section of major macro invertebrate groups, the species richness of the Antarctic continental shelf is comparable with the shelf faunas of Hawaii or northwest Europe (Clarke 2008). The recent published field guide of Antarctic marine macrobenthos by Rauschert & Arntz (2015), nicely display with fantastic photographs and close ups of organisms, the colourful and richness of the benthic diversity of the South pole.

In this part of the chapter dedicated to the polar benthos, there is no specific focus on coral communities as the Arctic displays a scarce representation of this group and no specific studies on cnidarians have been published. Specifically for Antarctica, most published studies are on taxonomy, very few deals with cnidarian ecology (but see Orejas et al. 2003; Rodríguez et al. 2013 and references therein). Nevertheless, communities dominated by cnidarians are abundant and diverse with different dominant taxa. ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" by Gutt in this volume deals also with these cnidarians communities, including spectacular images of the highly reach Antarctic benthos.

Although the first descriptions of the polar benthic fauna in the 1970s described the Arctic as much poorer in species richness than Antarctica, recent studies revealed that the former is not as low as previously thought, concluding that the number of macrozoobenthic species for the Antarctic is only slightly higher than in the Arctic (Piepenburg 2005). Nevertheless, the real architects in the Arctic sea are the macroalgae communities, especially the calcareous algae called rhodolites (found in extensive maerl fields) which play a relevant role in the dim depths where the fleshy macroalgal communities cannot develop. The dominant animal benthic communities on shelves and slopes are characterized by brittle stars, followed by bivalves and polychaetes, but these communities do not reach the paramount structuring role played by maerl.

The low disturbance level experienced by Antarctic benthic ecosystems seems to be one of the main reasons for the remarkably developed and diverse three-dimensional mega-benthic assemblages and the abundant associated fauna. Having said this, one must not forget that iceberg scouring is one of the five most important disturbance agents at ecosystem level (Gutt and Starmans 2001). Iceberg scouring display a different impact on shallow and deep areas (being the impact frequency higher in shallow areas) (e.g., Smale et al. 2007), and it has been recently documented an increase in the frequency in the last decades due to climate change (e.g., Barnes and Souster 2011). During the last two decades, it has been found that the role of this natural disturbance can be more relevant than previously thought, similarly to the role of other natural hazards in terrestrial ecosystems, such as forest fires, tree falls, or hurricanes. Indeed, iceberg scouring seems to be an important element in the functionality of the entire Antarctic shelf ecosystem, and the destructive effect of the impact has, at medium- to long-term, positive effects on biodiversity (Gutt and Piepenburg 2003).

As there are several comprehensive reviews on polar benthos, it is not the aim of this section to deal with such a complex subject. Considering that this journey started in shallow waters and continued into deeper realms, this last section on the Antarctic benthos will present some aspects concerning the communities inhabiting the so-called high Antarctica, where the continental shelf starts at depths around 200 m and beyond. Sponges play a key role in these areas, structuring the deep benthic communities with an important role in their dynamics. Antarctic sponge fields can form heterogeneous habitats supporting some of the richest benthic communities in the region, as is the case for the Weddell Sea, Ross Sea, East Antarctica, and the West Antarctic Peninsula. The three-dimensional structures can cover up to 55% of the substrate, providing heterogeneous and complex habitats, nurseries, and substrate for a vast array of marine organisms. As mentioned at the beginning of this chapter for the tropical corals, the sponge structure provides microhabitat for many endo- and epibiotic species, and large sponges provide habitat for mobile species, such as echinoderms and holothurians, often using the sponge as a raised platform for filter feeding, as well as playing an important role in several fish life cycles. The high biomass of the sponge communities (up to 3 kg m^{-2}, Thomas et al. 2008) constitutes an important food source for numerous organisms, such as amphipods, sea stars, and nudibranchs. Sessile benthic Antarctic communities include Porifera, (Demospongiae, Hexactinellida, Calcarea), Cnidaria (Gorgonaria, Pennatularia, Alcyonaria, Stolonifera, Hydrozoa, Actiniaria), Bryozoa, Brachiopoda, Polychaeta, and Ascidiacea. To give an insight to the dimensions of these communities, among the most prominent structuring species are *Rossella nuda* and *Scolymastra joubini*, both known as "white volcano sponges," individual colonies can be up to 2 m tall and 1.5 m in diameter (Thomas et al. 2008).

Local dominance of some sessile taxa takes place, with more presence in some areas of sponges, cnidarians, and bryozoans due to their three dimensionality and high canopy in some cases (see figures in Gutt's, ▶ Chap. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems" in this volume). Mobile invertebrates co-occur with these sessile fauna and in particular places may be the predominant group in the community. Commonly occurring taxa include Echinodermata and Peracarida, both of which are very successful in Antarctica and can exhibit high abundances or dominance of particular species. Many of these are symbionts and use sessile invertebrates as habitat, including specialized predators such as nudibranchs, asteroids, and gastropods (Clark et al. 2015). Further, some taxa, such as pycnogonids, amphipod, and isopods, display gigantism, reaching larger sizes than related taxa in non polar regions, which seem to be due to the high oxygen availability in the deep benthic Antarctic ecosystems (Chapelle and Peck 1999).

This short walk through the polar underwater forests has hopefully shown how these harsh environments (as it happens in glaciers or deserts on terrestrial systems) also harbor myriads of life forms perfectly adapted to these extreme environmental conditions, including structuring species as corals and sponges.

The authors hope that this imaginary journey through some of the hidden deep ecosystem of the planet was successful presenting the richness, structural complexity and functionality, and magnificence of these submerged animal forests.

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2 Cross-References

- ▶ Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems
- ▶ Diversity and Evolution of Octocoral Animal Forests at Both Sides of Tropical America
- ▶ Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean
- ▶ Evolution of the Marine Animal Forest: EvoDevo of Corals, Sea Anemones, and Jellyfishes
- ▶ Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems

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The Builders of the Oceans – Part II: Corals from the Past to the Present (The Stone from the Sea)

24

Carlos Jiménez and Covadonga Orejas

Abstract

At any scale, corals are live buildings. Their carbonate skeletons constitute three-dimensional frameworks allowing the delicate coral polyp to emerge from the sea bottom and populate vast areas of the ocean. The role that corals play in the oceans defies any attempt at simplification since it transcends the life span of the small polyp, geological time, and ecological space. Long after the polyps are gone, coral skeletons continue to play an important ecological role by hosting assemblages of disparate species utilizing the calcareous remains. However, the skeleton is one of the reasons coral has a privileged position in human culture. Coral has been regarded as mystic object and unique material of lapidary medical and apotropaic properties, this in great part due to the architecture and arrangement of the skeleton, growth morphologies, and color. Human history has been carved in chalk-white coral tombstones, on effigies, and on painted coral skeletons. Coral eyes of basaltic sentinels on Easter Island contemplate a plethora of coral artifacts scattered along the footpath of mankind: mortuary offerings, statues of pagan goddesses, helmets of Celtic warriors, military fortifications, and insular mosques shared the dream of the stone, when life seemed to depart from the mineral limbo, in the figure of the humble coral polyp. This chapter is the continuation of a personal journey into the coral forest of the world's oceans (see ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep"). A selection of examples

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of human interactions with the “stone from the sea” will illustrate this complex and fascinating relationship with coral.

Keywords
Coral • Amulet • Apotropaic medicine • History • Folklore • Mythology • Fossil • Archaeology • Myth • Superstition

Contents

1 Historical Coral

This review is a personal journey into the intricate and fascinating story of coral use throughout human history. There is always a risk to repeat information exhaustively treated in other important reviews (e.g., Morel et al. 2000, Bowen 2015, among others). Here is a selection of a few eclectic aspects of the history of use that we consider worth of discussion. However, for a more specific analysis, the reader is encouraged to consult the sources of information (and the references therein) given in the bibliography.

It is deemed futile to try an exhaustive search in the literature regarding corals through history, mythology, folklore, and religion. It is a lifetime endeavor to sound properly all sources of information, even though the digital area has made available hidden and, more often than not, forgotten literary, papyrical, and epigraphical treasures overlooked by academic reviews. One common complication is that original documents are frequently mistranslated, and more seriously, misquoted, and by constant repetition of such mistakes eventually they became engrained in the technical literature. It should not be strange to find coral where it may have not been mentioned as such, or perhaps it was wrongly considered as rock, shell, deteriorated nacre, bone, ivory, plant, and material of fantastic origins. Only to trained eyes, or to advanced technologies (e.g., Schrickel et al. 2011), coral is properly identified, and this applies to the old compilers of information, such as naturalists, alchemists, practitioners, pharmacists, and even coral traders.

Corals have been regarded as unique materials, mystic objects, and strange organisms throughout human history in great part due to the architecture and arrangement of the coral skeleton, growth morphologies, and colors. In the particular case of the red coral (*Corallium rubrum*), it resembles a leafless tree, a primordial and miniature botanical wonder with tormented branches; red-blood as our most precious body fluid, the same one offered (voluntarily or not) in the ultimate sacrifice to the gods. It is a mythical plant brought up from the mysterious and daunting depths of the ocean, directly from the gardens of sea monsters and deities and from the depths of legend, superstition, and awe. It is not unusual to find evidence of corals traded from their native seas toward faraway destinations. Coral was collected by fishermen with their nets and by early divers, either freemen or slaves, but it was also gathered after stormy seas when brought out to the beach. These curios or virtuous objects were transported on foot by itinerant traders or by organized caravans, later on canoes, galleons, and by armies. Whatever the means of transport, coral found its way as a funerary and votive offering, a commodity, and medicine or protective charm.

The following is a collection of notes gathered during the last three decades dedicated to coral reef research; they are stories to illustrate the historical use of coral. Not considered here are references and documents where the term coral is ambiguously used, most probably assigned to other materials or marine organisms (e.g., bryozoans, calcareous algae). This nuisance is rather common, for example, in European sources from the sixteenth to the eighteenth centuries where coral meant “bead,” which could have been made from many different materials. Even more recently, at the beginning of the twentieth century, semiprecious stones in Ghana were commonly referred in English by the locals as “coral.” Similarly, coral and pearl were terms used interchangeably and discussed intensively in academic circles of the time (e.g., Mingana 1925). In the technical literature of the last 50–60 years, in the discipline of archeology, for example, coral not always is properly recognized as such, and when it is, it can be found as “white,” “colored,” “red,” “tubular,” “branching,” or simply as “coral.” This lack of precision renders difficult to identify the real historical record for any particular coral species or group. In consequence, “coral” in the present essay may refer to several kinds (red, pink, white, black, etc.) and categories (e.g., branching, massive, foliose) except when specified otherwise. Date labels are referred to as before present (BP), before common era (BCE), and common era (CE). Centuries are in numerals and, if not indicated otherwise, correspond to the CE.

2 Since the Beginning

Starting from the Paleolithic archeological record, coral is present in many distant places suggesting a network of communication and trade more elaborated than previously thought. While fragments of red and white coral were found in Egyptian Paleolithic middens hinting on an incipient trade in nonutilitarian objects along the

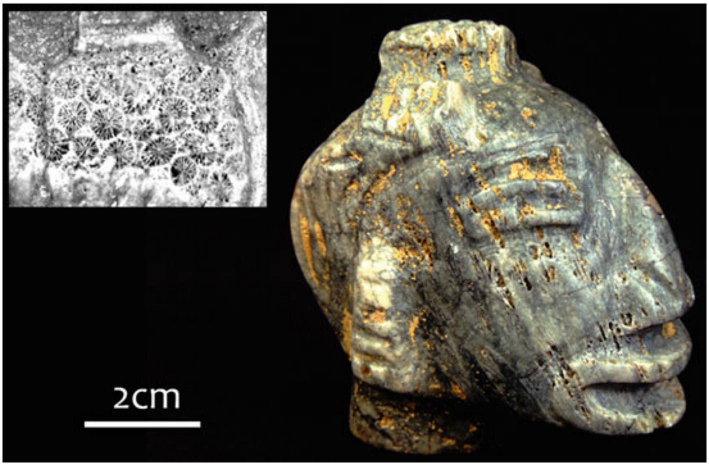


Fig. 1 Archeological fake of a head carved on fossil coral *Antiguastrea cellulosa*; polyps visible in the back (*insert*), Costa Rica (Credits: C. Jimenez)

Nile, at the Roc-aux-Sorciers (Vienne, France), an Upper Paleolithic rock shelter (ca. 12,000 BP), several carved fossil corals, resembling human heads, were found. It is not known if the fossilized material was particularly selected for this purpose or if it was opportunistically used, such as flint axes made of fossil coral found elsewhere. In any case, fossilized coral of different species was a common material to produce personal adornments. Other Paleolithic shelters in France (e.g., Grotte de la Mairie, 16,000–9000 BP) and Russia (e.g., Kostenki, 34,000 BP) have yielded worked coral remains (Trupp 2007). On a side note on the use of fossil coral, in the late 1980s and early 1990s, singular archeological forgeries mysteriously appeared in the illegal trade of antiquities in Central America. In Costa Rica, statuettes of idols, warriors' heads, and other "ceremonial" objects were crudely carved on beautiful fossilized coral (Fig. 1). The forgeries were claimed to be from the Paleo-Indian period (10,000–3500 BCE) of the Mesoamerican history of human occupation. Archaeologists reacted fast and the scam uncovered. Even though fossil coral was used throughout history, it was not as popular as other fossilized remains of organisms that were widely sought after and sold as medicine or amulets.

Coral beads and pieces of branches, possibly part of necklaces or pendants, were found in Neolithic (sixth to fifth millennium BCE) archeological sites in Italy, Spain, France, Alpine areas (e.g., Switzerland), Mediterranean Islands (e.g., Sardinia), Balkans, Central Asia, Egypt, and Southern Arabian Gulf. In archeological records from those areas, red and white corals are reported in different contexts, quantities, and degrees of modification. Fragments and small branches of raw (unworked) coral are found in several Italian shelters (e.g., Grotta dei Piccioni). Also in Italy, coral fragments show traces of limited processing (e.g., incisions). One pendant found in Pavia (De Grossi and Rugge 2009) was produced from the base of a colony and shows scarring left by epibionts (serpulid polychaetes). Cylindrical beads were manufactured by selectively choosing thin branches or distal sections that may have facilitated the shaping. Coral ornaments were often associated with other decorative elements such as shells, fossils of other marine organisms, and minerals in apparently well-though combinations of colors. These chromatic arrangements suggest coral was part of the symbolic meaning of colors since early periods, achieving a particular significance during the Middle Ages with the association of the holy blood and resurrection in the Christian tradition (more on this later).

At the spectacular and very well-preserved Neolithic settlement of Çatalhöyük (or Çatal Hüyük, Turkey, 7400–6200 BCE), corals (mostly fossilized) were found in several burials including those of children and fashioned as beads for necklaces, bracelets, anklets, and armlets (Mellaart 1964). The significant amount of beads suggests coral played an important role as ornament if not as amulet in Çatalhöyük. Around the same time period, Red Sea coral found its way to the early Neolithic settlement of Basta (Jordan), more than 100 km away from the sea, through a widespread network of trade that branched to other contemporary sites in Jordan and the Sinai Peninsula. In Jordan, as well as in Israel (e.g., Nahal Hemar cave), raw coral was used to some degree during the pre-ceramic period but only came to be common as beads and pendants during the Early Pottery Neolithic (ca. 6000 BCE; Al-Nahar 2014). Through similar Neolithic pathways, coral reached the Arabian Peninsula and islands and even India. In Upper Egypt (El-Badari and Naqada), during the fifth and fourth millennium BCE, coral (mostly white) from the Red Sea is found in funerary context of wealthy individuals, never in burials of commoners (Meeks 2000 in Morel et al. 2000).

However, in comparison to other materials, coral is not a common artifact in Neolithic archeological context. When present, beads of coral are the most abundant vestiges. Scant supply of coral has been suggested as the most probable reason for its relative low archeological record (Borrello et al. 2012). Later on, the archeological record for coral increases significantly. For example, during the Copper Age (ca. 3500–2300 BCE), coral was used for ornaments found mainly in deposits with human remains. There is evidence that small quantities of white coral were imported in the Alps. Bronze Age (ca. 3200–600 BCE) had its vogue on coral together with shell ornaments from living and fossil specimens. In any case, an early long-distance trade of symbolic (magic) coral ornaments seems to predate the ceremonial and gift (mundane) exchange of coral-made objects. Together with other exotic and fascinating objects called at one time “submarines” (Camel and Cuninghame 1702–1703), coral from the Mediterranean, Red and Arabian Seas was exported to the Mesopotamian region. As uncut or unworked material, coral was found in Mesopotamian archeological sites (e.g., Tell Al-'Ubaid, ca. 6500 to 3800 BCE; collection British Museum; reg. 1919,1011.5211); another find is a coral hammerstone (collection British Museum; reg. 1919,1011.1312). Expansionist Assyrians imported coral and large *Spondylus* and *Dentalium* shells probably for their magic or medicinal procedures or for more banal purposes, such as satisfying curiosity or fashion. It has been suggested that calcium carbonate in the Mesopotamian ancient history was intended mainly for medicine against diseases, and coral was one source of it; ostrich egg shells, however, were the primary source (During 1986). In predynastic Egypt (before 3000 BCE), small quantities of several types of coral were frequently deposited in tombs of the nobility (Meeks 2000 in Morel et al. 2000). These were small beads and unworked fragments of Mediterranean and, in lesser quantities, Red Sea coral. It is only later, during Pharaonic times, that funerary caches of corals are documented and have been associated with the cult of Hathor, the cow goddess. Votive offerings of Red Sea corals in several temples dedicated to this multifaceted and very popular goddess may have been tokens ensuring to the recently dead a safe passage and rebirth in the afterlife. Coral was a symbol of birth, rebirth, and fertility, attributes associated with Hathor. It is during the New Kingdom (between sixteenth and eleventh century BCE) that the Mediterranean Sea played an important role in Egypt's sphere of influence. Not surprisingly, the archeological record of coral (mostly Red Sea material) is enriched during that period with corals from the Mediterranean. Branching corals were valued by dynastic elites and are abundant in votive deposits of the time. Enter the red coral ca. seventh century BCE, with the arrival in Egypt of Greek traders and settlers. Fragments or worked red coral were found at temples and shrines associated with the Greco-Egyptian netherworld. For example, directly from the vowels of the earth, one of the manifestations of Hathor had its cult places associated with mines and caves; coral was among the offerings found there (Meeks 2000 in Morel et al. 2000). Serapis is another of such deities with attributes to the netherworld and whose cult intentionally syncretized Greek and Egyptian communities at the beginning of the Ptolemaic Kingdom (fourth to first century BCE). In the British Museum collection (reg. 1814,0704.1123), there is a wonderful miniature bust from the first to second century CE representing Serapis. The bust is remarkable since on Serapis' shoulder, there are two small feet belonging to a smaller figure now lost (a subordinate individual or an alter ego?). However, the nature of the material is contested and until definitive negative results are published, the bust is still considered made from red coral.

During the early Iron Age (ca. 750–250 BCE) of Central, Eastern, and Western Europe, Mediterranean coral was imported as beads (some shaped as small vases and amphorae) and as raw pieces (Ugolini et al. 2000 in Morel et al. 2000). There is also evidence in continental and insular localities (e.g., England) of reworking the coral, which was inlaid into brooches and other objects (including metal) found in tombs of different social stratification. Early studies associated the presence of coral only with the wealthiest individuals. There is a remarkable cache of metal objects decorated with coral found in a chariot burial of a woman in England (Wetwang, between 210–160 BCE). According to the British Museum description of finds (accessible through the museum's website), the great quantity of coral used for some of those objects was unusual for the British Iron Age. Also in England, the Arras culture (fifth to fourth century BCE, East Yorkshire) received coral and possibly glass from the Mediterranean area. The discovery of Celtic tomb in 2014 of an important individual in Lavau (France) illustrates how coral and other socially important "gifts" may have traveled altogether more often than suspected. In the tomb located below a 40 m diameter tumulus, a bronze wine cauldron (Fig. 2), of Greek or Roman manufacture, was found among the funerary cache. Such an important and exotic object indicates the interest on Mediterranean wine of Celtic high local aristocracy, which was rapidly and avidly developing a taste for it judging from other similar artifacts

Fig. 2 The royal Celtic tomb of Lavau (France). (**a**) Bronze cauldron to store wine, (**b**) bone remains of the individual who was buried wearing garment with iron and coral clasps (Credits: **a**, **b** (© Denis Gliksman, INRAP))

(Perrin 2000 in Morel et al. 2000). Together with other imported wine vessels (e.g., amphorae for wine), coral-made garment hooks and unworked branches confirm the existence of a constant Mediterranean link that contributed to develop a "coral fashion" among individuals at the top of social position. Therefore, not long ago a "Coral Age" was proposed as a new Nord-Alpine protohistoric period (Reinach 1899 cited by Perrin 2000 in Morel et al. 2000).

In the Mediterranean area, coral has been found associated with ancient towns, city-states, cemeteries, temples, and shrines. At the Minoan Palace of Malia (Crete), coral fragments were found in strata corresponding to the second millennium BCE (Hermary 2000 in Morel et al. 2000). The Golasecca culture (ninth to fourth century BCE) in Northern Italy used coral as ornament and inlays for fibulae and metal objects, such as weapons. Coral remains are still identifiable in some cases in the cremated remains of individuals and their garments (De Marinis 2000 in Morel et al. 2000). It is possible that the Celts learned from the Golasecca culture to inlaid coral in metal objects and developed further the technique until it became to be one of the iconic symbols of Gaul. Elsewhere in the Mediterranean, what seem to be votive offerings of coral are reported from more than a dozen ancient sanctuaries, spanning from the seventh century BCE to late Roman time. These ex-votos were found as unworked branches (predominantly during the Archaic period), fragments, and polished objects, the latter in the context of Classical and Imperial periods (Quercia 2008). Also the powerful Punic city-state of Carthage (ninth to second century BCE, modern Tunisia) was hungry for coral. In the necropolis and habitational quarters of Carthage, red, white, and pink coral beads, cylinders, figurines, and unworked fragments were used as ornaments and, undoubtedly, amulets (Morel 2000 in

Morel et al. 2000). After the fall of Carthage, during the Roman occupation, coral seems to have been crafted in local workshops as suggested by the large quantities of fragments found in what appears to be waste deposits of ateliers. Noteworthy is the find at the Punic necropolis of Predio Ibba (Sardinia) of a white coral fragment; it was identified as the shallow water scleractinian *Cladocora caespitosa* (Taramelli 1912). Other corals found in Punic-Phoenician archeological sites were shaped as amulets to be carried either in necklaces or as pendants. There is one example, also from Sardinia, of a red coral amulet with a *uraeus* (Morel 2000 in Morel et al. 2000), the emblematic sacred serpent from Egypt. During the period of the Roman occupation of this island, soon after the first Punic War 264–241 BCE, remains of red, pink, and white coral increase in the archeological record. For example, in the city of ancient Tharros, a sizeable deposit was found of what is considered discarded coral from ateliers (e.g., poor-quality fragments damaged by bioerosion or by manufacturing; Morel 2000 in Morel et al. 2000).

Even though corals were known to ancient Greeks in classical times (fifth century BCE), they were not widely used (neither by the Romans) in contrast to other cultures. Amber and shells from the Red Sea seem to have been more popular even though coral was regarded as a surrogate, or better alternative, to ephemeral plants in the "gardens of Adonis." It was used at temples dedicated to this deity in Northern Africa and the Levant but only after the beginning of the Roman imperial period (first century BCE). Gaul (Western Europe) was an avid importer of corals for decoration and inlaying till, weapons, helmets, shields, and garments as Pliny the Elder (23–79 CE) wrote in his *Natural History*. At one point in time, according to Pliny, coral became scarce due to exportations to India, China, and even to Sri Lanka through Massilia (modern Marseilles) and Alexandria. In publications from the late 1890s, *Natural History* and *Periplus maris Erythraei* (first century CE) are the sources identifying Gaul as the main supplier of coral for such a large market, inevitably producing a shortage. It is mentioned as well that Gaul responded to the shortage by supplying enamel. This information requires a measure of caution first because Gaul (southern territories) aside from producing coral also imported from other parts of the Mediterranean and from the Red Sea. A shortage may have occurred but the trade network could have always supplied coral. Second, available translations of *Natural History* and *Periplus* do not mention red enamel as substitute nor that was used to deceive the market. Interestingly enough, Egypt's archeological record of this period does not have any trace at all of this "flourishing" export of coral. However, coral in Egypt may have been outcompeted by the local production of the immensely popular, and with similar apotropaic properties, carnelian stone. In any case, important trade of coral from Hyeres (France) to Gaul took place around 300 BCE through Massilia. Why Gaul was so voracious importing coral? Perhaps because the emerging Celtic chieftains were in the process of consolidating position and acquisition of certain exotic artifacts, as the aforementioned wine cauldron and coral were considered symbolic elements of power. As proposed elsewhere, the Celtic fondness for coral may have been the reason why Romans were not. As a note to illustrate how appealing coral commerce was more than a millennium later, between the thirteenth and sixteenth century, shipments to the east of Mediterranean coral reached the impressive level of several tonnes per year (Bresc 2000 in Morel et al. 2000).

3 The Eye of the Idol and the Arrow of the Dead

From locations out of the Mediterranean region, there are several historical examples of coral's important position in folklore, mythology, as well as medicinal tradition, and of its more "banal use" in tool making and construction (with and without coral magical protection). In this section, there are some examples of the magical coral and its iconic representations.

In the tale of island building by the legendary god Uta-matua at the Kapingamarangi Atoll (Polynesia), the insular god threw a stone on a coral and created thus an islet (Elbert 1949). In the same myth, a "floating" coral boulder was relocated into a lagoon as a result of a contest between an antagonistic god and a "magic man." The magician created storms and tsunamis and could not move the coral, while the god hero of the story succeeded only with a humble spring. Local inhabitants still showed to visitors during the 1940s the famous coral boulder. Coral with political and religious symbolism is found in protohistoric Hawaii where large cairns with corals demarked territory between communities and functioned as shrines. Abundant layers of broken coral colonies in the cairns suggest their use as religious votive offerings. On Maui and Moloka Islands, offerings to agricultural gods included branching coral colonies (Kirch and Sharp 2005). Since the skeletal elements and features are very well preserved and devoid most of them of abrasion and erosion, it is assumed that the corals were collected alive before being used as offerings. Other coral species, boulder corals, for example, were mostly used as tools for rubbing or filing and for building structures.

The preferential use of branching corals for ceremonial purposes in Hawaii contrast to the use in the Caribbean and Micronesia of brain corals. Brain corals are commonly regarded as magical or with affinity to the underworld. Is it the resemblance with our brain that makes these species magic doppelgängers? Idols of uncertain antiquity were carved on brain coral in the Pacific and Caribbean regions (Fig. 3a). Coral colonies and small patch reefs with brain corals are known in Micronesia to host spirits or have the potential to produce harm by black magic arts. Several interesting examples can be mentioned from this coral region. Black magic enabled stone drafts made of corals to take a wizard out of danger and transport him to Ifaluk Island (Beauclair 1963). At the New Hebrides Islands, on another twist of the magical predisposition of brain corals, poisoned arrows are made from human bone (there is an important detail; the bone must be from a recently unearthed corpse!), broken into splinters, and rubbed to shape on a brain coral (Codrington 1890). Poison from different plant extracts, crab dung, or soil is later applied to the arrow; alternatively, the arrow can be left marinating in the poison, as it was described to a horrified cleric by a native islander in the late 1800s. More on poisoned arrows will be discussed later when the apotropaic properties of coral will be described.

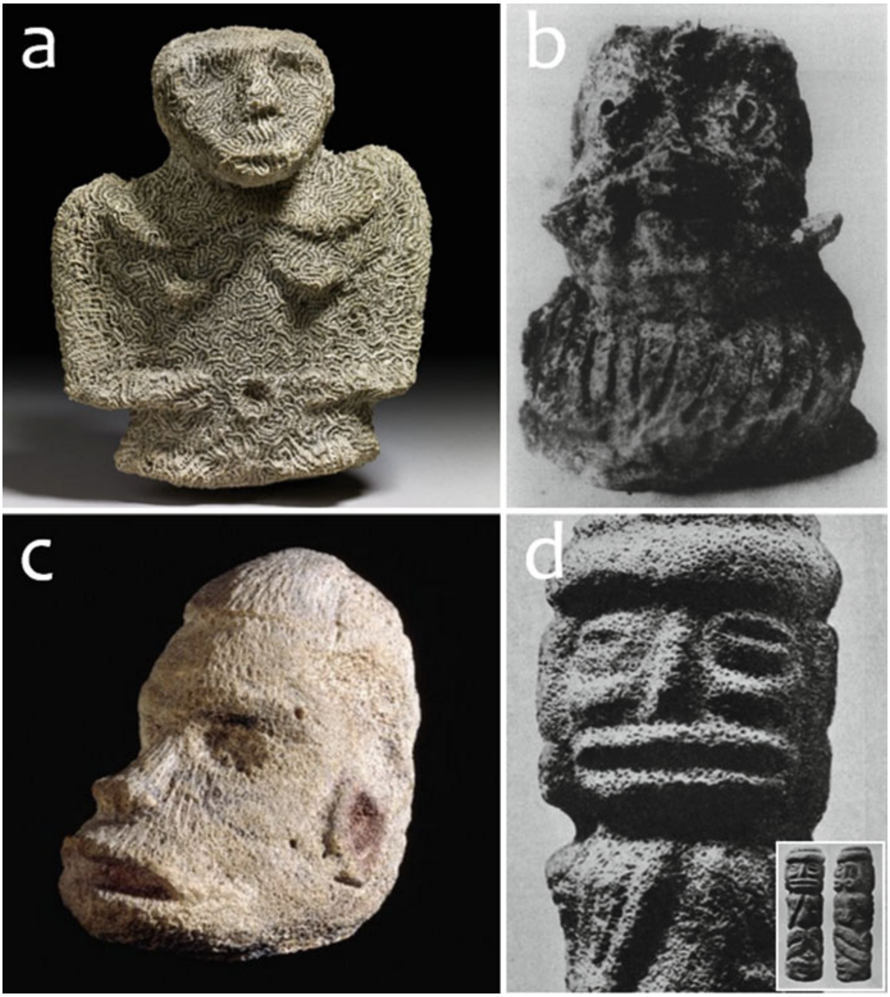


Fig. 3 Anthropomorphic and zoomorphic coral figures. (**a**) Mer Island (Torres Strait), 23 cm height, British Museum; (**b**) Androth Island (Lakshadweep, India), ca. 125 cm height; (**c**) Makira (Solomon Islands), 12.2 cm height, British Museum; (**d**) Cueva de Boruga (Baracoa, Cuba), Santiago Museum (Credits: **a**, **c** (© Trustees of the British Museum), **b** (with permission from Tripati 1999, Antiquity, 73:827–835), **d** (with permission modified from Fewkes 1904, American Anthropologist, 6: 585–598))

At the Lakshadweep Islands (off Indian southwestern coast), archeological excavations have uncovered numerous heads and torsos carved on coral (Tripati 1999). They represent Buddha, other individuals, and, possibly, nature spirits (Yaksha). One representation of such demons is an impressive head with protruding canines and tongue (Fig. 3b). Several sculptures were made by carving the head or torso on the coral and applying after a coral-based plaster in which the fine details (e.g., curly hair) were sculptured. Remains of Buddhist buildings (fifth to sixth century CE) on the island suggest the common use of coral as building material.

A "curiosity" found in the nineteenth century at the Solomon Islands is a figurine of one human head carved in coral, which has kept traces of pigments (Fig. 3c). The coloring of the base material inevitably reminds us the case of the ancient white marbles of classical antiquity. The traditional view was that they were "elegantly" white. Surprise came when an avalanche of evidence proved that the romantic view of and *Hellenistic* white was no more than an idealized concept. Most of the ancient marbles, including friezes, statuary, and other figures, were colorfully painted, like the coral figure of Solomon Islands. Similar effigies to the painted coral head are found elsewhere around the coral biogeographical regions. There are mute idols of polyp-pocketed faces that seem to represent a ceremony where the skin of the effigy is a lesson in sclerochronology. Growth bands, radial corallites, and punctuated calyxes are flesh, skin, or fur of arrogant anthropomorphic and zoomorphic deities. Large idols made of coral by the Ciboney culture (twelfth to thirteenth century CE) in Cuba are eloquent examples of these metamorphic transgressions of the coral skeleton. One particular idol found inside a cave (Cueva de Boruga; Fewkes 1904) is pockmarked by hundredths of remarkably preserved corallites (Fig. 3d), creating thus an eerie effect that may have inspired awe and perhaps reverence.

Other effigies carved on coral, found in the late ninteenth century at the Pitcairn Islands (Brown 1900), resemble the famous Easter Island (Rapa Nui) statues. The eye sockets of these colossal statues (Moai) of Easter Island, which were produced between 1100 and 1600 CE, were presumed to be empty (since at least 1869 when one statue was removed and shipped to Europe). It was until recently in 2003 that evidence was found that the sockets were actually inlaid with red stone and white coral (Beck et al. 2003).

4 A Prayer Made of Coral

The votive context in which coral has been frequently found in the archeological and historical records can be further illustrated with the following examples. Fragments of coral colonies of what is believed to be *Dendrophyllia cornigera* were found at the Phoenician temple of Tas-Silg (2500 BCE to 850 CE) in Malta (Quercia 2008). This is an interesting record for this species since no other similar find is reported in any other archeological context. It may have been an important offering (fragments found in the temple were up to 20 cm in length) dedicated to the "successors" of the Punic goddess Asthar: Tanis, Hera, and, during the late Roman period, Juno. The goddess Juno, and its Greek equivalent Hera, had strong association to coral in other sanctuaries of the Mediterranean (Hermary 2000 in Morel et al. 2000, Theodoropoulou 2013). For example, at the sanctuary of Hera Limenia (eighth century BCE, Greece), coral figurines and pendants were found. Hera was protector of navigators and corals were accredited with the same ability. It is in the late

Fig. 4 Coral iconography associated with deities, the "cephalic" coral. (**a**) Oceanus' mosaic (Themetra, Tunisia), Sousse Museum; (**b**) the rape of Europe (detail) by Luca Giordano (1634–1705); (**c**) the birth of Venus (detail) by Giorgio Vasari (1511–1574) (Credits: **a**–**c** (commons.wikimedia.org))

Hellenistic and Roman periods of Tas-Silg in Malta that *D. cornigera* was offered to Hera or Juno. Local variations in the attributes and roles of deities occurred throughout the ancient Mediterranean; several other sources have Athena bestowing coral with protective virtues for those traveling by sea, including protection against piracy. Whole branches of broken colonies are notorious offerings at insular temples (e.g., Kythnos, Cyclades Islands; Theodoropoulou 2013). White coral votive offers have been found, not surprisingly, at the archaic sanctuary of Poseidon in Isthmia (mainland Greece). In iconography, Poseidon and the more ancient and primeval deity Oceanus are represented with coral branches or lobster/crab appendages sprouting from the head. One of such representations (Fig. 4a) was originally located at the Roman baths of Themetra (Tunisia), near the pre-Carthage Phoenician colony of Hadrumetum (ninth century BCE). Interestingly, significant quantities of coral fragments were also found at Hadrumetum, higher than in any other Phoenician archeological site (Morel 2000 in Morel et al. 2000). In relation to Poseidon and Oceanus "cephalic" coral, branching stony corals as well as octocorals were often considered integral parts of minor deities in the European artistic tradition (Fig. 4b, c). Coral (most probably an antipatharian species) was at one point called the *hair of Isis*, as well as the *beautiful eyebrows* or *eyelids* of the Three Graces (Charites), depending on the translation (see, e.g., During 1986). The *hair of Isis* is associated by Plutarch in his general digressions on *Moralia* (*On the Face Which Appears in the Orb of the Moon*, ca. first century CE) to marine plants growing underwater in the Red Sea, stimulating modern authors to associate corals with Isis-Hathor-Selene in the lunatic's realm of demons. Coral ex-votos are also found in ancient temples dedicated to other female divinities, such as Demeter, Persephone, Artemis, and Aphrodite (Hermary 2000; Perrin 2000 both in Morel et al. 2000).

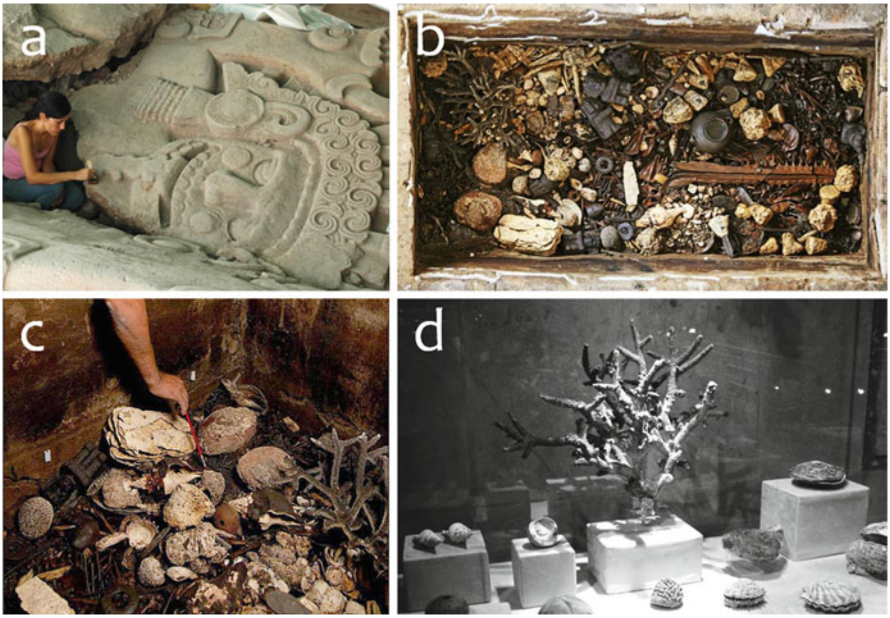


Fig. 5 Votive corals at the Aztec Templo Mayor (Mexico D.F.). (**a**) Monolithic representation of the goddess Tlaltecuhtli that covered the stone niche with the offering; (**b**) exposed stone niche with votive objects; (**c**) assemblage of marine organisms and other objects in the upper layer of the offering; (**d**) coral colonies, shells, and echinoderm skeletons on display at the Templo Mayor Museum (Credits: **a**–**c** (courtesy of Proyecto Templo Mayor), **d** (courtesy of Bertrand Lobjois/ Mexique Ancien))

A world apart, a spectacular cache, the first of its kind, of votive offerings to a female deity was found in the Aztec Templo Mayor in Mexico (López et al. 2012). Underneath a 4-ton monolithic representation of the monstrous goddess Tlaltecuhtli (Fig. 5a), an offering of about 4000 biological remains of diverse nature and provenance (plus other objects such as statuettes and knives) was deposited inside a stone niche (Fig. 5b) during the late fifteenth or early sixteenth century CE (a few years before the contact with the European conquistadores). Most of the offerings are shells but also intact coral colonies of branching (*Acropora cervicornis*) and massive (*Diploria strigosa*) scleractinian species (Fig. 5c, d), as well as octocorals (e.g., *Gorgonia* spp.). The excellent condition and preservation of the corals suggest that they may have been collected alive. Noteworthy is the fact that most species in the cache were considered to possess ritual significance. Coral was one of the symbolic elements of the Aztec netherworld.

One last comment is needed in relation to the symbolic female nature of coral. During the early period of Northern Italy’s Golasecca culture (mentioned earlier), coral was exclusively associated with the burial tradition to female individuals, particularly unmarried or without children or who died while giving birth

(De Marinis 2000 in Morel et al. 2000). Perhaps this is one of the earliest clear examples of the association of coral with blood and the death-birth cycle that later culminated in the apotropaic tradition with rebirth. It is until later periods in pre-Celtic Golasecca that coral was associated with masculine symbols and individuals.

5 Pass the Coral, I Mean the Hammer

There are instances were coral is considered no more than a convenient material to be used as a tool to rasp, grind, or "smash someone's fingers" as simply put by a Garifuna artisanal boat maker in the 1990s at the Bay Islands (Honduras). Worked and shaped to produce imaginative tools, coral has a wide range of uses in the hardware repertoire. However, the simplest way is to use it raw or unworked; at least until the late 1990s, sieves were made from the gridded skeletons of octocorals, such as *Gorgonia* spp. (pers. observation), in the Caribbean. After being rinsed in freshwater and air-dried, the octocoral sieves were used to prepare soup and coconut milk. In the recent historical past, fragments or small colonies of scleractinian corals were purposely used to roughen outside surfaces of fresh clay pots in the Lesser Antilles (e.g., Saint Kitts and Nevis). Middens' refuse in the Antilles, as well as in Central America, contains fragments of corals worn out by rubbing. In general, corals were good for filing, rasping, and smoothing wooden objects (e.g., in boat making) and perhaps shell and bone, in many islands of the Antilles, Central America, and Polynesia (Tikopia). In Polynesia, coral is still used by wood-carvers to rub down smooth figures representing sacred symbols. Until recently, human migrations and first settlements in Polynesia were difficult to date with precision. Ingenously, coral tools made by the first settlers were used for high-resolution dating (Burley et al. 2012). Coral abraders (files) from the Kingdom of Tonga (Nukuleka) were produced from live or recently dead corals during the first human landfall in the islands. Similar tools were found at Easter Island (not in association to the Moai's coral eyes), more than 6500 km east. Other examples are the elaborated pestles, in the shape of idols, produced from at least three different coral species. One pestle from Cuba (Loma del Cayuco; Fewkes 1904) is of anthropomorphic shape; the excellent preservation of the corallites suggests the pestle was not used at all and perhaps this was never the intention. The coral pestle was probably a ceremonial or funeral ex-votos. Ancient potters in the volcanic Mono Island (Solomon Islands) added to the clay-making process fragmented and pulverized coral as a tempering material, resulting in a noticeably grainy surface of the vessels.

Not always corals were the best available material to produce tools. Corals were commonly used until stronger tools (made of materials harder than usual) were available. The case of iron on remote and isolated islands of the Western and Central Pacific illustrates how coral was not the best option, even though it was abundant. The arrival and dispersal of iron among those insular communities has all the fantastic elements for a marooned story in the literary field. Starting probably in the sixteenth century CE or earlier, drift iron in the form of nails, bands, hoops, and other items attached to planks, beams, and other kinds of fragmentary wood detached from ships arrived to different islands (Rickard 1934). This fantastic flotsam, wreckage from unknown sources, must have made an impression on the inhabitants of those islands; they started to use opportunistically the metal objects without modifying their shape at the beginning. We may assume that in order to shape the objects into tools according to the need (e.g., carpentry in boat construction), trials were made to hammer or whet the iron using corals, the only hard-enough available material. It can be further speculated that corals proved to be of limited use due to the hardness of iron. The solution came as well from the sea. One navigator, Otto von Kotzebue, observed in 1817 how the islanders priced the "hard stones" that came entangled within the roots of drift trees, another exotic source of fantastic flotsam. The stones were enthusiastically used for whetting the iron. Both drifting materials, the iron and the stones, were exclusive property of the chiefs.

6 Give Me a Coral and I Will Build...a City

Corals as building materials were commonly used by masons throughout history and all around the coral regions of the world. Civilian, administrative, and military structures made almost entirely of "stone from the sea" can be found from the rain forests of tropical Mesoamerica and the Isthmus of Panama to the arid Arabian Peninsula and in the middle of the Pacific.

Starting with Africa, the first example is from Egypt. At the ancient seaport of Ptolemaic Berenice (Berenike), Southern Egypt's Red Sea, only the permanent buildings of the annual market were said to have been built with "fragile" coral from the coast. Archeological excavations in Berenice's late Roman port and surroundings uncovered walls made of fossilized coral heads, which were uncut and placed without mortar. Temples and walls were also made using coral. At one particular temple, a double wall was built using whole, massive coral colonies (heads) and stone blocks. Floor pavements inside the temple and other buildings had a high percentage of coral material. Also along the Egyptian Red Sea coast, corals were used as building material, although to a lesser extent, at Mersa Shuni (medieval Islamic period).

Other examples are from the Solomon Islands where an ancient and large coral wall was built to delimitate territory at the Sikaiana Atoll. At the ancient capital of Leluh on the remote island of Kosrae (Central Pacific), truncated pyramidal royal tombs (Fig. 6a, b) and even roads (Fig. 6c) were made using corals (Richards et al. 2015); corals were collected alive when the structures were built between 1250 and 1850. Coral platforms in Timor-laut, also in the shape of small pyramids consisting of coral blocks or large colonies, were still used during the late 1800s as resting place for palm stem-wrapped bodies, as reported by academics busily discussing the orientation of the dead on the coral platforms (Forbes 1906). In Moorea, live corals were collected from reefs and used to dress platforms at monumental ritual sites as well as for sculptures. Staking of branching and massive coral species was common. Also at the Ascension Islands, corals were used for paving floors (Gulick 1859).

Fig. 6 Coral as building material at Leluh, Island of Kosrae (Central Pacific). (**a**) Researcher on top of a funerary structure made with coral, (**b**) detail of one of the royal tombs, (**c**) coral-made pavements between basaltic structures (Credits: **a** (courtesy of Paul Hobbs), **b**–**c** (courtesy of Zoe Richards))

Coral was used in Mayan cities of the Yucatan Peninsula. The impressive walled city of coastal Tulum (ca. 500–1600 CE) and the majestic Chichen Itza (ca. 600–1200 CE) exhibit corals in their ruined walls and pavements. Fossil colonies of boulder species were cut into rough blocks and laid between slabs of limestone. At the city-state of Chichen Itza, a burial was found with a wooden disk encrusted with coral, shell, and turquoise (collection Musée du quai Branly, France). In the Coastal Maya in Southern Belize (Port Honduras), massive quantities of finger coral (*Porites* spp.) were used to lay the foundations of buildings (McKillop et al. 2004). The modern use of this particular coral species still happens at the Caribbean coast of Panama. Observed in 1993 (Jimenez, unpublished data), the Kuna people of Acuatupu, a small island in the San Blas Archipelago, extracted about 130 m^3 of live and dead finger coral to build the foundation of a basketball court (Fig. 7a, b). The coral was extracted from the fringing reefs around the island (Fig. 7c) in spite of the opposition from a few members of the community who complained on the resulting low fishing catch during the coral extraction.

At the East African coast (Kenya), the ruins of Gedi contain splendid buildings made with coral blocks and entire colonies (Fig. 8a). Even though the town's origins go back to the twelfth century CE, it is during the fifteenth to sixteenth centuries that coral structures were erected (as of December 2015, Gedi is still in the UNESCO's World Heritage tentative list). The town's mosque was also built with coral. Coral

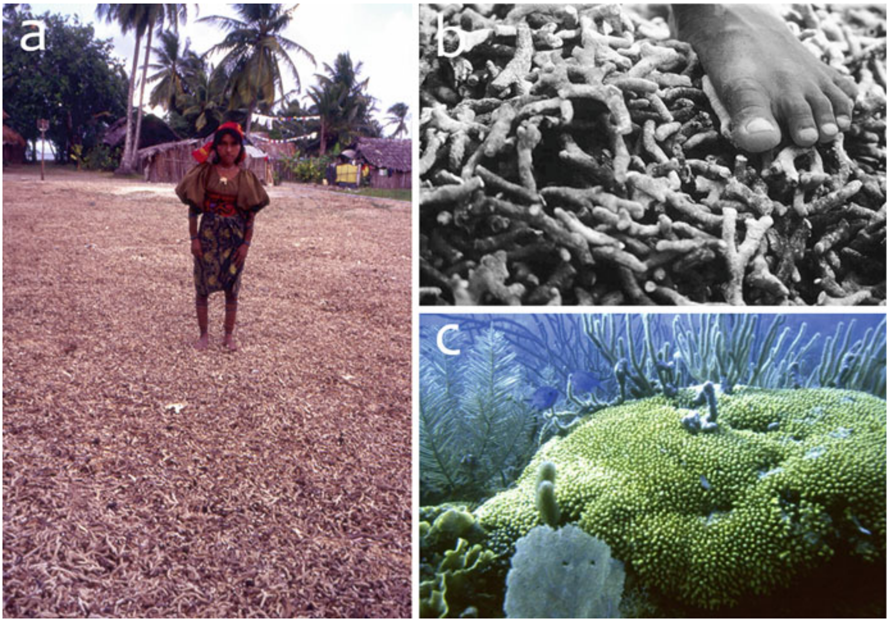


Fig. 7 Corals as building materials. (**a**) Foundation for a basketball court using *Porites* spp. Acuatupo Island (Kuna Yala Archipelago, Caribbean Panama), February 1993, (**b**) detail of the coral foundation, (**c**) the reef (−10 m) a year before the extraction (1992) (Credits: **a**–**c** (C. Jimenez))

Fig. 8 Coral as building material. (**a**) Ruins of Gedi (Kenya), walls of broken and whole (*insert*) coral colonies; (**b**) coral tombstones and Friday Mosque, Male Island (Maldives) (Credits: **a** (courtesy Louis Hadjioannou), **b** (dbimages/Alamy Stock Photo))

tools, such as grinders and mills (e.g., British Museum, reg. Af193,01.1), were also produced at Gedi. Some thousands of kilometers away, during the same period (late sixteenth and early seventeenth century), teams of slaves under the scrutiny of foremen were diving and quarrying corals from shallow coral reefs near the fortified colonial town of Portobelo, Caribbean coast of Panama. Overseers dully recorded the volume of corals extracted from the reefs and for which specific building the corals were intended to be used (Jimenez and Guzman, in prep.). The building process to fortify Portobelo, from the sixteenth to the eighteenth century, experienced several periods of destruction, restoration, and expansion of the colonial fortifications including administrative buildings. Coral was always a convenient material even though it became scarce as the time passed, and the building and expansion of the fortifications continued. Thousands of cubic meters of coral and reef framework were extracted during those few centuries. A nunnery, one monastery, and a hospital were partially made with coral blocks and colonies. Coral blocks can also be seen in colonial Castillo del Morro (Havana, Cuba; pers. obs.).

Other historical architectures in Mexico illustrate how resourceful and convenient it was to be in the vicinities of coral reefs. The town of Veracruz and the fort of San Juan de Ulua were built during and after the conquest of Mexico utilizing live and fossil coral (Carricart 1998). Alexander von Humboldt observed the corals in the buildings and wrote about it in 1891. The extraction of coral for these constructions was not limited to the surrounding reefs. Ancient walls from temples, most probably made of coral, at the near Island of Sacrificios, were dismantled between 1590 and 1599 to produce lime for the construction of the seawall and other buildings around the fort (Nuttall 1910). In addition, mining along the shore for dead coral hastened geomorphological changes in a few decades. Also from Sacrificios Island, a pre-European coral figurine, now in the British Museum (reg. Am1844,0720.896), suggests a ceremonial use of the coral.

An interesting historical case illustrates that even when coral is common in the surroundings, human ingenuity surprisingly not always chose the most abundant material. Ancient Nan Madol, a ruined city on a small island of the high volcanic Pohnpei Island (Federated States of Micronesia), was built from the tenth to the seventeenth century upon a coral reef flat. The builders utilized boulders and columnar lava, not coral, as the material of choice. However, the angular columns were stacked to build a frame which was later infilled with coral material to create elevated platforms. For a society without metal tools nor pulleys, columnar lava weighing several tons is not an easy choice. Abundant corals are found in the fringing reefs of the island and were utilized to produce tools, such as pounders. Elsewhere in the Maldives, coral and wood were the most durable building materials employed for centuries. Between the fifteenth and nineteenth centuries, numerous buildings were constructed utilizing coral, such as the case of the famous coral mosques of Male (Fig. 8b). Recent research found that from 51 original ancient mosques, only 40 survive and 18 are confirmed made of coral (among other materials). Four to six massive species were selectively targeted for the constructions. As of December 2015, these mosques are in the UNESCO's World Heritage tentative list. Coral is nowadays still used in the Maldives to build structures though under regulatory measures from the authorities. In Indonesia, a group of fishermen known as the “sea nomads” still use coral for different purposes, including temporal creation and expansion of ground around the islets and islands.

There are a few historical cases were coral material was used to plaster walls. One is found at the Mahabodhi Temple complex, Bodh Gaya (Bihar, Eastern India; second century CE). Inside a shrine containing a Buddha’s throne, the plaster lining the walls has a mixture of lime mortar with fragments and grains of coral, sapphire, ivory, and pearl (collection British Museum; reg. 1892,1103.70.a-b). It is not known the reason for such mixture other than contributing to the sacred nature of the shrine by building with precious substances. The other example is more recent and comes from wall decorations of the *Nymphaeum grotto* (eighteenth century), Argotti Gardens in Malta. The inside of the grotto was lined with mosaics of various materials including fragments of corals.

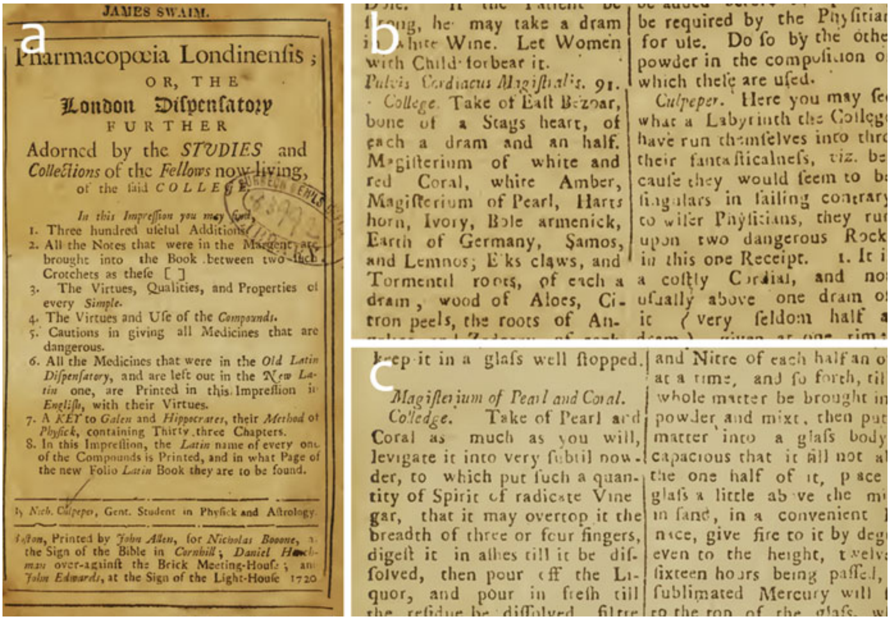
7 Do I Drink You or Should I Wear You?

At one point in time in the ancient world, coral started to be considered among the most powerful magic materials available. It was the magic-apotropaic “substance” per excellence. However, it was not a simple task to obtain the precious coral from the water; it was not only an endeavor enthralled with dangers but also one that required skilled approaches to avoid losing the coral “juices” and “blood” and, thus, its virtues given by the hidden secrets of nature. If the extraction was not properly done (e.g., not using the right tools), what remained was “terrestrial chaos without its true forme” (Maier 1617). Therein lay the difficulties associated with coral extraction. It will be presented in this section the characteristics that crowned coral on top of mankind’s *imaginarium*, making it the substance that could be ingested or carried as an amulet or charm with the consent of tradition and religion. On occasion the examples illustrate several forms of use preventing a clear separation in the narrative.

7.1 Take Two Corals and Call Me in the Morning

We have to start by asking why there is a need to consume unusual substances. For example, consumption of soil or blood has been explained by different reasons including mental or physiological disorders, religious beliefs, cultural traditions, adaptive evolutionary behavior, and senseless fashion, just to mention a few. An ancient example of coral ingestion with mystical results is found in Vedic legends (ca. 1750–500 BCE). Coral and four other precious “substances” (gold, silver, pearl, sapphire) were cast into the seas by Indra and consumed later by elephants, bears, snakes, and frogs, among other creatures (Beer 2003). Once ingested, these substances produced intestinal stones or bezoars to the animals. In consequence, precious and highly sought after in antiquity, bezoars had supposedly different medicinal and apotropaic properties transferred to them by the coral and the other substances. If coral was ingested by the animals with fantastic consequences, why not to do the same and obtain medicinal or magical effects? This example reminds of geophagia, a widespread behavior with medicinal implications exhibited by animals and people. However, coral is not found commonly referred to as medicine in ancient texts (see Magdelaine 2000 in Morel et al. 2000, and Harris 2009 for extensive discussion of the subject). For example, in the *Hippocratic Corpus* (fifth to fourth century BCE), which is the earliest surviving medical text from the Greco-Roman era, coral is surprisingly absent among the *Corpus'* pharmacopeia. Neither is coral mentioned in the Aristotelian manuscripts (fourth century BCE) that dealt with medicine. It is until Pedanius Dioscorides' *De Materia Medica* (first century CE) that curative coral (red and black) is mentioned for the first time and its properties enumerated, such as being cold and an astringent. Dioscorides' contemporary, Pliny, will also do it in his *Natura* (mentioned before). An important distinction made by Pliny is that coral was placed in the chapter of aquatic animals (even though its true nature couldn't be clear for him). Another significant omission of medicinal coral is found in the monumental work of Claudius Galenus, or Galen (*De simplicium medicamentorum temperamentis et facultatibus*, second century CE). It is important to emphasize that coral is indeed mentioned in ancient sources dealing with the magical properties of stones and other materials (Lapidary tradition) as capable to affect natural processes. It is only later that both apotropaic magic and medicine became an interesting "mixture" and had coral among the predilected substances. Why does coral have such a minor role in the pharmacological knowledge of Galenus' time and following centuries? In view of the popularity that coral gained during Early Middle Ages (seventh to eleventh century) and later with the incorporation of Arab medicine, this is an interesting question that still needs to be properly addressed.

In the collective mind, lapidary medicine and tradition provided the means, even though fantastic, to cope with the brutal reality of staying "healthy." Mixtures of red and white coral and pearls were added to other ingredients, pulverized, and taken with rosewater for diverse maladies and fevers (Fig. 9). We only need to browse *Rosa Anglica* from 1314 by John of Gaddesden (1929) to find blended traditions steaming from folklore, superstition, and "institutionalized religion" that produced preparations and concoctions that on occasions may have had real medicinal use, but most probably were useless and certainly of a horrible taste! A characteristic of the lapidary medicine was to cure through the use of jewelry or ornaments (discussed in the next section) and infusions of coral as one precious ingredient in the mix. In the lapidary literature, as well as the popular "manuals of healing," a series of preparatory steps were described before administering the infusion (e.g., ground, mix, and dissolve). These steps were not very difficult to follow. It is only later when more complicated steps were required, such as distillation and precipitation that a more professional apothecary was in charge of the preparation of coral (Harris 2009). Coral precipitates or *magisteries* (Fig. 9b, c), ground and dissolved in vinegar, had higher price than untreated material. Ingestion of powdered coral, particularly red coral was one of the most popular uses in late medieval lapidary medicine and early modern times. It is during early modern England that lapidaries specific for women and children started being printed (Magdelaine 2000 in Morel et al. 2000). They



JAMES SWAIM.

Pharmacopœia Londinenſis ;
OR, THE
London Diſpenſatory
FURTHER
Adorned by the *STUDIES* and
Collections of the *Fellows* now living,
of the ſaid *COLLEGE*.

In this Impreſſion you may find,
1. Three hundred uſeful Additions.
2. All the Notes that were in the Margent are brought into the Book between two ſuch Crotchets as theſe [ ]
3. The Virtues, Qualities, and Properties of every *Simple*.
4. The Virtues and Uſe of the *Compounds*.
5. Cautions in giving all Medicines that are dangerous.
6. All the Medicines that were in the *Old Latin Diſpenſatory*, and are left out in the *New Latin* one, are Printed in this Impreſſion in *Engliſh*, with their Virtues.
7. A *KEY* to *Galen* and *Hippocrates*, their *Method* of *Phyſick*, containing Thirty three Chapters.
8. In this Impreſſion, the *Latin* name of every one of the Compounds is Printed, and in what Page of the new Folio *Latin* Book they are to be found.

By *Nich. Culpeper*, Gent. Student in Phyſick and Aſtrology.

Boſton, Printed by *John Allen*, for *Nicholas Boone*, at the Sign of the Bible in *Cornhill*; *Daniel Henchman* over-againſt the Brick Meeting-Houſe; and *John Edwards*, at the Sign of the Light-Houſe 1720

ſtrong, he may take a dram in White Wine. Let Women with Child forbear it.

Pulvis Cordiacus Magiſtralis. 91.

College. Take of Eaſt Bezoar, bone of a Stags heart, of each a dram and an half. Magiſterium of white and red Coral, white Amber, Magiſterium of Pearl, Harts horn, Ivory, Bole armenick, Earth of Germany, Samos, and Lemnos; Elks claws, and Tormentil roots, of each a dram, wood of Aloes, Citron peels, the roots of An-

be required by the Phyſitian
for uſe. Do ſo by the othe
powder in the compoſition o
which theſe are uſed.
Culpeper. Here you may ſe
what a Labyrinth the College
have run themſelves into thro
their fantaſticalneſs, viz. be
cauſe they would ſeem to b
ſingulars in ſailing contrary
to wiſer Phyſicians, they ru
upon two dangerous Rock
in this one Receipt. 1. It i
a coſtly Cordial, and no
uſually above one dram o
it (very ſeldom half a

keep it in a glaſs well ſtopped.

Magiſterium of Pearl and Coral.

Colledge. Take of Pearl and Coral as much as you will, levigate it into very ſubtil powder, to which put ſuch a quantity of Spirit of radicate Vinegar, that it may overtop it the breadth of three or four fingers, digeſt it in aſhes till it be diſſolved, then pour off the Liquor, and pour in freſh till

and Nitre of each half an o
at a time, and ſo forth, til
whole matter be brought in
powder and mixt, then put
matter into a glaſs body
capacious that it fill not al
the one half of it, place
glaſs a little above the mi
in ſand, in a convenient
nace, give fire to it by deg
even to the height, twelve
ſixteen hours being paſſed,
ſublimated Mercury will

Fig. 9 Coral in medicinal publications. (**a**) Nicholas Culpeper (1720) Pharmacopoeia Londinensis; (**b**) description of a “magisterium” of white and red coral, detail from page 145; (**c**) preparation of “magisterium” of pearl and coral, detail from page 262 (Credits: **a**–**c** (scanned book available at https://archive.org/details/2548018R.nlm.nih.gov))

were immensely popular; one of them (*A Directory for Midvvives* by Nicholas Culpeper) had eleven editions in less than 50 years after its publication in 1651. Women’s “bleeding” and “children illness” were commonly treated by ingesting coral (e.g., in Culpeper’s 1720 edition). Undoubtedly, the wider these lapidary texts communicated the attributed virtues of red and white coral powder, the more they contributed to increase the use and demand for these coral-based remedies (one recipe to prevent stillbirth in 1698 required 25 “grains” of red coral).

Liniments or plasters, coats, and pastes made from ground coral or coral ashes, mixed with other ingredients (usually pearls), were used for singular and disparate diseases or symptoms: filling ulcerative wounds, smoothing scarring tissue, toothaches, soothing gums, and treatment of epilepsy. Seventeenth-century inventories of supplies of apothecaries in London (Harris 2009) provide a glimpse of the lapidary importance of coral. Coral is accounted in different grades of powder, coarse to fine. Interestingly enough, white and red coral were generally considered to possess different gender (female and male, respectively) and medicinal quality. The medicinal properties of ground coral (black or white) that came as traditional knowledge and superstition from the Netherland’s overseas territories were widely advertised in Amsterdam and other large cities.

Mixtures with coral were incredibly diverse as well as the quantities required of each ingredient. For example, white and red coral mixed with several other ground ingredients, such as pearls and antler of a hart, were prescribed as remedy for plague in Europe. At the Ambonese Islands in Indonesia, the ground tube shell of a *boorworm* or "lombrico maggiore," named *Solen arenarius* (despite this name, most probably it was a vermetid gastropod), was prescribed in the 1700s against food poisoning if taken together with coral (Rumphius 1750). Spines of sea urchins and flying squid were also mixed with ground *Accarbarium rubrum* coral (probably the octocoral *Melithaea ochracea*) and taken against bloody urine as well as food poisoning; in this case, the coral should be beforehand washed by rain and sun dried. Rumphius describes in his monumental work *Herbarium Amboinense* (1750) that even though several coral/octocoral species have the "virtues of coral," they are considered weaker and their main use was ornamental. Presumably is Bayer (1959) publication the only systematic effort to identify the coral species mentioned by Rumphius; the present review follows Bayer (1959) with updated taxonomical names. Rumphius' observations suggest a long historical process of trial and error in order to separate the apparently active (effective) coral species from the "weak" ones and also to identify the specific parts of the coral that are medicinal (e.g., outer crust, tips, longer/shorter branches). One particular example is from an octocoral species (Ellisellidae), which at the time of Rumphius' observations was considered a potent remedy for fever, gastroenteritis, and any kind of food poisoning. From this octocoral, only the freshly grinded powder was effective, and the active parts were the basal trunk and branches.

Not only fish is better when fresh. On occasions, medicinal properties of coral were considered superior or at its best if recently brought up to the surface by fishers or divers. This was the case of an extremely important coral species for its medicinal properties according to Rumphius. The *Calbahaar puti* in Ambonese language (corresponding perhaps to the bamboo coral *Isis hippuris*) was only used if fresh. This coral is nowadays famous because it produces anticancer chemicals. Between the seventeenth to eighteenth centuries, this species was held in the highest consideration and was the basic ingredient of any antidote made in the East Indies. So strong were considered the curative properties that this coral was used even against gonorrhea. Rumphius' amazing catalog of wonders includes a shallow-water sea pen (probably *Pteroeides* sp.), which was used to remove the poison from the wounds produced by poisoned arrows. An exemplar of this octocoral, Rumphius writes, was kept in a bamboo container to avoid "damage."

In most of the written sources about obtaining corals, medicinal or ornamental, diving activities are seldom described, only the finds made by fishermen when pulling up lines and nets or by beach combers (e.g., Targioni 1903). It is noteworthy that many coral species, particularly from the Indian Ocean, were kept without any particular value other than esthetic. Colonies were repeatedly washed in freshwater (e.g., rainwater), sun or air-dried, and kept as decorative curios. In Targioni (1903) comments on the Rumphius' collection of specimens, there is an entry about corals retrieved with fishing nets from deep waters (down to 180 m) in the Indian Ocean. He called the coral *accabario bianco marino* and described how it was highly prized by Hindu people who used it against fevers, poisonous foods, and choleric bouts.

The author remarks on the difficulties to export this coral to Europe due to the Hindu's local interest for it.

Antipatharian species (e.g., black coral) and octocorals in general were considered effective against a troupe of maladies, misfortunes, allures, and other "calamities." One particular species, referred to as *accarbario cenerino* (possibly *Viminella* sp.) by both Rumphius and Targioni, is described as being very expensive because it was rare, hard to find, and used only as medicine. Other black "accarbarios" more abundant in the trade had medicinal or apotropaic properties but were also used in the manufacture of handlers (knives, daggers, scepters), reaching high prices in the Indian market, even more than gold. Another important coral species referred to as black *acarbahar*, possibly *Rumphella antipathies* (a gorgonian species), was used to manufacture scepters. The species *R. antipathies* is a source of important active chemical compounds. It was used as an amulet against the common evil eye and magic spells, but also as a medicine against food poisoning (so many cases in these region of the world), small pox, and measles, and if mixed with white coral, it will be an effective laxative or emetic. One drawback was its bad taste and smell ("horn-like"), but who said medicines should taste good? This potent coral was used as an ointment to ease bites, stings, and ulcers, even though Rumphius recommends not to use it directly on open wounds. In relation to the latter application, one more example of coral as topical medicine is when it was used against headaches produced by insolation. The octocoral *accarbaar gabba gabba* (possibly *Subergorgia* sp.) was smeared upon the foreheads of the local inhabitants or European visitors caught unprepared by sunny days at the Ambonese Islands.

Black corals, but also octocorals, after removal of their crust, were often polished into ebony-looking bracelets and wore as protective charm and for its aphrodisiac properties. The latter attribute was a popular belief since at least Pliny's time. Between the fifteenth and seventeenth centuries, scepters of several species of black coral were used by dignitaries and royal figures in Europe and Indian Ocean (Targioni 1903), therefore the common name of King's coral for the species. Also in the Indian Sea, at one point in time, black coral was considered more precious than hard or stony coral. Some of the occult characteristics of black coral were explained by "its purposed ability to neutralize or repel threats", thus the name *Antipathes* (αντιπαΘες, to oppose). An example of the "complicated nature" of black coral is that not long ago, in Mediterranean countries, it was believed that when red coral came into contact with sulfuric emanations, it will turn black (Corswant 1956 cited by Meeks 2000, in Morel et al. 2000).

At the Cayos Cochinos Islands (Caribbean coast of Honduras), lobster fishers make use of the crust from black corals in a sad and very peculiar way. During the 1990s it was observed by one of us (CJ), how fishermen diving for lobster, stir fried fragments of the proteinaceous skeleton of black corals and then removed the crust and crushed it into fine powder. This powder was added to a mixture of ganja and tobacco and avidly smoked. If burning of the mixture was difficult, crushed heads of matches were added to facilitate combustion. These divers worked in deplorable safety conditions and the bends (divers' disease) is the "silent death" responsible for dozens of casualties and crippled survivors on the islands. The ingestion on the mixture with black coral is one way to cope with the extreme diving conditions of diving for lobsters. On a final note on ingestion of coral, fossil coral is nowadays taken in a mixture with other ingredients as a supplement for calcification.

7.2 The Metamorphic Coral

In another dimension of coral's world of apotropaic magic, the power to alter the elements and the metaphysical realm was also manifested in the coral object itself, therefore the symbolism of votive offerings as discussed before. Fortunately, the ingestion of coral prepared in not-so-nice flavored concoctions was not always necessary. Coral-made objects of power could be used instead. Religious ornaments and historical sacred representations were often made of coral, particularly red coral, or at least had attached small pieces of coral. Cameos made with coral with the images of holy, mythical, or classical figures were extremely popular during medieval period (Piquereddu 2004). For example, coral became a required ingredient of the popular *paternosters* (later known as rosaries), reaching upper social levels. Royal heirs in medieval and Renaissance Europe were not exempted to risk high infant mortality; their portraits usually show them holding branches or worked pieces of coral in rosaries, necklaces, or bracelets (Fig. 10a). Rosaries of polished,

Fig. 10 Red coral as amulet and teether. (**a**) Portrait of Anne of Austria (detail) by Juan Pantoja de la Cruz (1553–1608), (**b**) King Charles II of England (detail) by an unknown artist (1630), (**c**) multi-functional rattles (gold and silver) with whistle and teething coral, ca 16 cm length, mid-eighteenth century (Credits: **a** (commons.wikimedia.org), **b** (courtesy of National Portrait Gallery, London), **c** (courtesy of The Metropolitan Museum of Art-Open Access for Scholarly Content))

worked, or crude coral fragments have evidently an apotropaic value for the carrier but also for religious statuary. Effigies or other representations of religious themes were often adorned with coral rosaries and necklaces. A visit to Latin churches is an ideal way to corroborate the role of coral in religious iconography. Far away from Europe, in the Western Pacific, garlands of corals and shells adorned effigies of sea-gods in Madagascar by the Veso people.

Several "high-risk" activities, such as war, common piracy, navigation, and treachery, could also be affected by the powerful coral. Regarding to navigation, lapidary sources described in detail how coral, together with a fur of a seal (seals were among the powerful apotropaic animals), hung on top of the mast will protect against stormy weather and wreckage in general (Perea 2010). What an irony of life is the occurrence of ancient and historical shipwrecks with the almighty and protective coral included in the merchandise on board. Very bad news for the business of protective charms! There are two shipwrecks off Marseille from the sixth century CE with red coral fragments (Pomey 2000 in Morel et al. 2000). Another failure of the protective coral is an early medieval (twelfth to thirteenth century) shipwreck off Cape Galera (Sardinia; Galasso 2001). The ship sunk with no less than 10 kg of red coral as part of its cargo! The cause of failure will never be known (ineffective fur or coral?). However, it must be noted that the allegedly inherent powers of coral to ward off storms, or somehow modify weather, was not confined to the sea. In the *Orphei Lithica Kerygmata* lapidary (between second to fourth century CE), it is written that "crushed coral mixed with seeds" is planted in the fields to advert bad weather (hailstorms in this case). Noteworthy is the different translation or interpretation of the same original information. In other reference material (e.g., McCartney 1934), coral acts against "hot weather" (drought), not hail.

Coral was common in medieval paraphernalia as an amulet against an eclectic variety of maladies; frequently it was worn or carried as unpolished fragments in the fourteenth century Europe. Magical lore associated with substances "from the sea" is vast. Evil eye, a terrific and ever present threat to humans, demanded significant amounts of protective ingenuity from the potential victims and ineptitude, at the same time, from the dark forces. Red coral was selected as one of the most critical substances for protection. Lapidary corpus in Europe asserted repetitively the protective powers of coral against different manifestations of evil. With time, tradition evolved making the protective properties of coral irradiate to the surroundings, such as buildings and holy places in particular. This was thought to be possible by the consecration of coral no less than by God himself! Several medieval lapidaries and inventories mention coral necklaces to assist in childbirth (Forbes 1963) and red coral amulets held near the "privy parts" of pregnant women. Famous physicians in the early fourteenth century recommended to have a necklace with a coral amulet when drinking wine (Magdelaine 2000 in Morel et al. 2000); the coral in contact with the stomach will assist the bearer in case the libations went a bit out of hand.

Red coral was of particular interest in medieval society due to its association with the philosophers' stone. Even though alchemical texts describe how heated materials change into red stone, which was called blood and red coral, among other names, the nature and environment of the change were also considered important. *Atalanta*

Fugiens (1617), by the Renaissance alchemist Michael Maier, clearly states the similarity of coral and the stone of the philosophers. A major difference is recognized and is due to the process that hardens the material. While cold is what makes coral hard (by exposure to the air after the coral is brought up from the sea), heat is what produces the stone, which will dissolve if heating continues. The two terms were often interchanged as *philosophical corral* in alchemical texts (e.g., Maier 1617), but is clearly distinguished from common white coral.

The color of red coral amulets was thought to change according to the bearer's health; in European folklore and Indian tradition, it paled during illness. Red coral bracelets worn by girls in Spain, for example, turned yellow with the moon if the girl was going to be ill (Hildburgh 1919). However, in Burma, it was basically the opposite, the beads darkened in the presence of illness (Hildburgh 1909). Interestingly enough, the late nineteenth- and early twentieth-century texts mention corals losing their magic-apotropaic properties if iron tools were used during the production of amulets (Bellucci 1907). Iron was thought to repel and neutralize evil or underworldly creatures. How did the Christian tradition so openly tolerate the use of coral, a material with undisputed pagan influences which could be affected by iron? Not surprisingly, many profane elements were incorporated along the history of the church in Europe and elsewhere. In doing so, sacred and institutionalized symbols were reinforced with pagan elements and, hence, their powers amplified. However, breaking the coral amulet, intentionally or by accident, also compromised its properties exposing thus the bearer to wizardry or disease (Piquereddu 2004). One important object in the Christian symbolic resources is the rosary. Popularized by the Dominican order during the thirteenth century, the praying beads started to be made of red coral and, at least by one account, were named as rosaries (until the late 1400s, they were known as *Paternoster*). The origin of the name, however, is far from being properly resolved.

Romans regarded coral not only as a potent protection against evil eye but also with capabilities to protect animals. For example, hunting dogs wore collars with Maltese coral to prevent them from turning rabid (Manley 1959). Lapidary sources emphasized the capacity of coral amulets to influence atmospheric phenomena, such as whirlwinds and lightning, to restore damaged crops, and to protect buildings against crime. The prophylactic use of coral as amulets commonly wore by children and adults of diverse background and position in the society (Fig. 10a) suggests that the cultural practice of displaying red coral jewelry was a statement of "protection and good health" more than of wealth. Since overseas colonial powers were exposed to coral amulets and medicines with coral ingredients at the tropical territorial possessions, charms made of black coral were often worn by Dutch expats against rheumatism (During 1986). Sea trade by the Portuguese along Western Africa shores brought coral as ornament and amulet to the popular traditions.

Perforated corals and gems were used, and still are, as amulets to protect against witchcraft and evil eye in Europe, the Americas, and Africa. Since the seventeenth century, official royal dress in Benin is rich in coral beads and displayed during the annual coral festival, which drew considerable attention from the Europeans due to suspected sacrificial activities (Law 1985). Coral bead regalia are an essential element of Benin's royal court and art, and it is considered sacred. In Italy, pendants of perforated coral are considered important amulets to ward off negative influence; their mystical property lies in the perforation hole as well as in the coral itself (Elworthy 1903). In Mexico, strings of coral beads are given to children for protection against the *ojo*, a kind of fever produced by "overprotection from relatives" (Espinoza 1910). Local folklore, on occasion, may oppose tradition. In parts of Central America, for example, it is believed that shells and other marine life, corals in particular, bring misfortune (pers. obs.).

Another historical and popular use of red coral by children (both genders, infants and toddlers) was the multipurpose "teething sticks," toys to ease discomfort during that period and to ward off evil (Kelley 2014). Silver or gold rattles and bells and whistles with an attached piece of polished red coral as teething stick were strongly associated with childhood during several centuries. They can be found in classical paintings in major historical art galleries (Fig. 10b). Metal whistles with bells and corals (Fig. 10c) are recurrent symbols in the eighteenth-century British satires. Printed etchings colored by hand were the media to attack dignitaries, the royal family, celebrities, etc., portraying them as children. In the satiric illustrations, the targeted personalities are ridiculed by holding the children's symbol, the whistle with the coral.

In relation to iconographic records, the Passion narrative with the crucifixion and resurrection themes associated with red coral in the Catholic Christian tradition started around the eleventh century, and it was common in the leading Flemish, Spanish, and Italian artistic traditions. The metaphoric representation of such important concepts using red coral is perhaps a legacy from the "syncretization process" that started with Medusa's blood. The metaphoric symbols of coral can be found among the earliest Arabic papyrus (second half of the ninth century CE) describing the hair of celestial (angels) or human individuals (Abbot 1946). Red color functioned as a distraction and to repel evil eye and demonic spirits. It was associated with the Passion of the Christ. But it was the branching shape of the red coral, sometimes associated with the Christian iconic cross, which gave the power to ward off demonic manifestations on early medieval tradition (Bresc 2000 in Morel et al. 2000). Discussed elsewhere in the academic literature is the strong association of coral to the child, often portrayed with coral colonies, coral necklaces, and bracelets or charms (Fig. 11).

Historically, red coral found its way to the Americas through the colonial trade by the Spanish and by the English wanderers. Since then, coral has been incorporated in the Native American cultures into their regalia together with beads of shell and turquoise and in more fashionable items with silver (Stephen 1893). Protective charms made of coral are related to peyote (psychoactive cactus) meetings of Native Americans (Opler 1936). Occasionally, during these healing meetings, rivalry between powerful individuals leads to aggressive confrontations and "stealing of power." A piece of an unidentified coral provided effective protection. There is one particular charm in the British Museum collection that deserves to be mentioned here. It is a female torso and head carved from a brain coral colony, which was mentioned earlier (Fig. 3a), from the Torres Strait. Alfred C. Haddon reported in

Fig. 11 Religious iconography of red coral. (**a**) Madonna and Child (detail) by Francesco Traini (active 1321–1365), (**b**) The Brera Madonna by Piero della Francesca (ca. 1415–1492), (**c**) Madonna della Vittoria by Andrea Mantegna (ca. 1431–1506) with a hanging coral colony, (**d**) (Credits: **a** (© Museo Nacional del Prado), **b**–**c** (commons.wikimedia.org))

1889 (this entry can be seen in the museum website) that when people left their homes these figures were placed near fireplaces and a protective spirit (*Lamar*) would keep the fire alight.

There are charms to ward off influences but there are others whose function is precisely the opposite. Coral "love charms" were supposed not to protect, they were meant to attract. There is one entry in a late fifteenth century lapidary (*Peterborough*) of the use of coral as love charm and to enhance fertility (Harris 2009). The fertility effect was also extended to fruit trees from which coral was hung with the purpose to increase production (see next for an alternative explanation). In relation to this topic, a particular gorgonian coral, probably *Junceella juncea* from Ternate Island (Moluccan archipelago), was expected to help virility because it was the "male of white coral" (Rumphius 1750). Surprisingly, at other Moluccan islands, the same coral was disregarded as curative.

For a common eighteenth-century observer, the baskets made from weaved palm leaves commonly found in Ambonese households were no more than banal objects to store personal items. However, the observant Rumphius writes in his *Herbarium* that, not surprisingly, coral was an essential item in those baskets. One particular "red coral" or "false red coral" found in the baskets, when taken diluted in water, was considered effective against the usual food poisoning and the terrifying loss of blood when urinating or coughing. The fundamental curative mechanism of this coral was explained because it “dries and cools” and is an astringent, by the way. Other “false” red or pink corals (e.g., bryozoans, *Adarce*), which were thought to have formed from mineralizing solutions or “petrifying juices” in the sea (Agricola 1546), had common magical properties similar to coral; protection is one and they were hung from fruit trees to protect against thievery. In one source, it is explained that the fruits were protected because the superstitious inhabitants feared to be burnt by the protective amulet (Targioni 1903). Tree fruits were also protected by using amulets made of the organ-pipe coral (*Tubipora musica*), which may cause painful urination when in contact with the skin, but it would alleviate problematic urinating if it was ingested. This paradox is perhaps the result of a historical confusion when the same name and attributes were given to different organisms, one described as found along the Mediterranean shores (bryozoan) and the other only in the Pacific Ocean (*Tubipora*). Linnaeus contributed to such historical confusions when he named red coral *Isis nobilis*, ignoring that the genus was associated with other corals in lapidary tradition.

Going back to the European tradition, coral charms were, and still are, shaped as gesturing hands to ward off evil, but most commonly as simple horns (*corno portafortuna* in Italy). In this example, the coral was not the main reason for the popularity of such charms because they can be found made of other materials. Phallic coral amulets are known since antiquity. Surprisingly, coral tombstones with phallic symbolisms were produced in Africa (e.g., collection British Museum; reg. Af1936,0502.4). Other tombstones made of coral are found at the Maldives Islands (Fig. 8b). However, the confusing nature of coral (from the sea, resembling a rock, plant, or something in between) and the additional strangeness because of its color and shape all contributed to have coral in a “privileged position” in the lapidary medicine and folklore. The added value of the red color was because it had the principles of life and death, the power of blood (as mentioned earlier). Blood is the most intense corporal fluid. This red “vitality” incarnated in the coral suggested a mystical origin. This may have been one of the reasons that coral amulets had to be handled and treated in specific ways. Other amulets, in contrast, were very complex, requiring elaborated combination of materials. Metal ornaments and objects have been embellished with coral additions. Assyrian necklaces (Al-Mina, ca. seventh to fifth century BCE; British Museum collection) and European bracelets and fibulae, bronze, gold, and silver were elements combined with coral. Also bone was combined with coral; a fibula shaped as a dolphin with coral eyes (400–300 BCE) was found in Taranto (Ugolini et al. 2000 in Morel et al. 2000).

There are particular Italian amulets that had a central “magical substance” (e.g., silver) surrounded by several (up to 15) other powerful items of different typology, coral, for example. Triads of magic objects around a central medallion were common in seventeenth- to eigthteenth-century Europe. In an interesting variation, the central medallions had the number 13 engraved and were accompanied by that number of “reinforcements,” coral being one of the essential components (Piquereddu 2004). These multipurpose supplements acted simultaneously, in theory, against a cornucopia of threats, a kind of full combat kit. In consequence, charms of multi-elements were fashioned for the wealthy consumer of such talismans. If coral (black, red, and white) was not conspicuously exhibited, it would have been worn discretely as buttons, brooches, pins, and buckles. Coral amulets in China are worn suspended on one side of the body (Hildburgh 1919).

It is with the adoption of Buddhism that Mediterranean coral found its way into Japan (Kosuge et al. 2010). The ideal ruler (Chakravartin) in Buddhism and Jainism has a number of jewels or powerful royal insignia; a branch of red coral is one of them. Coral can be found in the Potala, the monastery palace of the Dalai Lamas in Tibet. When the last Dalai Lama died, followers from all over the world contributed with gifts, such as corals, to the ornamentation of his tomb (Chapman 1938). Tibetan nomads (pastoralist Amdo) display corals in their women's ornaments and in the scabbards and hilts of swords carried by chiefs. A particular kind of highly priced beads in Tibet, the gZi, is worn in necklaces with interspersed beads of red coral (Nebesky-Wojkowitz 1952). The gZi is considered one of the most powerful protective and medicinal amulets for the Buddhist. Marco Polo (or whoever gave him information for *The Description of the World*, published in the late thirteenth century) noted that coral was highly prized in Tibet to produce necklaces for women and idols.

The need to engrave coral with specific figures to amplify and better focus its power can be found in many ancient traditions. Engraved coral with particular figures, such as Medusa or the favorite animal of a deity, allows the fortunate owner of the amulet to be protected against wrath, for example (Perea 2010). In many of the ancient lapidaries, representations in coral of sea deities were recommended for protection and for a smooth sea voyage. These representations will evoke the deity's powers by "connecting" the mythological realm with this world though the coral as the "channel". Given that coral came from the mythical sea, and because its nature was not very clear (neither plant, animal, nor rock), these characteristics positioned engraved coral as one of the most powerful materials in the ancient seafaring tradition.

The charms fashioned as horns or *manufica* were also made of black coral; their magical properties were mostly to repel or neutralize sorcery. There is an interesting hypothesis concerning black corals (or octocorals) and the Sumerian poem *Gilgamesh and the Netherworld*. This epic is best known from a version that circulated in Babylonia and Assyria, more than 1500 years after it was originally conceived. Gilgamesh in his search for the *Tree of Life* went to what seems to be an island in the Persian Gulf to find a survivor of the flood. Gilgamesh, after being told at the island that the *Tree of Life* grew beneath the waves, "dove" (or sunk by tying heavy stones to his feet) to the bottom and retrieved a twig of the "thorny plant." Since black corals are known as "thorny corals" because of the spiny skeleton, they were postulated as candidates for the marine and thorny "plant" of the story (During 1983). However, other coral species (gorgonians) match as well with the description (During 1986). Even if the hypothesis that the mythical plant Gilgamesh found in the sea is wrong and is a gorgonian instead of an antipatharian coral, the tradition of the "mystic coral" was present in the region. Until recently, the head of the Gulf was considered as a restrictive environment to coral growth due to the siltation from the Euphrates and Tigris Rivers. However, corals and coral reefs are found there despite high sediment loads (Pohl et al. 2014). Gulf corals may have been well known in the past. During the "opening" of the Seleucid Empire (Hellenistic dynasty, 312–63 BCE), the traditions contained in the Babylonian lapidaries were accessible to Greek culture and later to Roman literate (e.g., Pliny) (Gordon and Simon 2010). It is precisely in the Greek lapidaries that coral magical properties are firstly described. Control of weather and human fate, healing and protection (e.g., deflection of weapons), metamorphosis, and changing sex as well were some of the impressive properties of coral. However, in one of the lapidaries, the kerygmata, it is clearly stated that coral must be first consecrated in order to have optimal, stronger properties.

Returning to the European use of coral for awkward necessities, we find an interesting case in a fascinating medieval-Renaissance object used to detect and neutralize poison in food and drinks, the *languier* (also known as *Natternzungenkredenz* and *credenzas*). These were table ornaments shaped like trees with hanging fossil teeth of sharks. Since antiquity fossil teeth of sharks were believed to be powerful objects (Zammit-Maempel 1975), and in some sources, they were considered fallouts from the sky during solar eclipses. Drinks were tested for poison by dipping the fossilized teeth and observing for changes in teeth's color or "sweating." It was expected the teeth will make the drink safe by removing the poison. Table etiquette required their use at least from the fifteenth to eighteenth centuries. Among the very few *languier* that survived to the present, there is a magnificent exemplar at the Schatzkammer und Museum in Vienna (Fig. 12a). The "tree" is actually a large red coral colony (ca. 20 cm height) mounted on a silver-gilded base and pedestal. The *languier* was commissioned at some time between 1400 and 1540 (Duffin 2012). From the "tree coral", 14 fossil teeth hang in an eerie fashion. Red coral was also believed to detect and neutralize poison and change its color accordingly. In any case, regardless of the effectivity, these were beautiful table ornaments. There is another surviving *languier* (sixteenth century) at the Cathedral Museum of Mdina, Malta. However, this one is "missing the teeth," no pun intended. An earlier example of the combined use of both elements, teeth of sharks and red coral, is a necklace from the Phoenician-Punic period of Sardinia (Morel 2000 in Morel et al. 2000). Shark teeth with alternating branches of red coral were found in a funerary context as elements of a necklace.

There are two examples of surreal ornamental figures with coral attached. The mid-sixteenth-century statuettes at the State Art Collections of Nuremberg and Dresden (Germany) represent the transformation of the nymph Daphne. The dramatism of these representations lies entirely on the red coral extruding like "branching bouts of energy" from the nymph's forearms and head (Fig. 12b), at the precise moment when she turned into a tree. The powerful effect of the coral metamorphic nature, between *naturalia* and *artificialia*, was certainly recognized at the workshop where the figures were conceived (Bowry 2014). Goldsmiths, particularly after the fifteenth century, fancied raw coral material for their imaginative work, sacred and profane, that endured into late medieval iconography together with coral material and other curiosities (fossil shark teeth, as mentioned above). Complex sceneries as miniaturized representations (dioramas) of the Crucifixion or the

Fig. 12 Red coral apotropaic and metamorphic nature. (**a**) Natternzungenkredenz with a large (ca. 20 cm length) red coral colony, (**b**) silver-gilded statuette and drink vessel of the nymph Daphne with "sprouting" red coral, ca. 68 cm height (Credits: **a** (commons.wikimedia.org), **b** (© bpk – Bildagentur für Kunst, Kultur und Geschichte, Berlin))

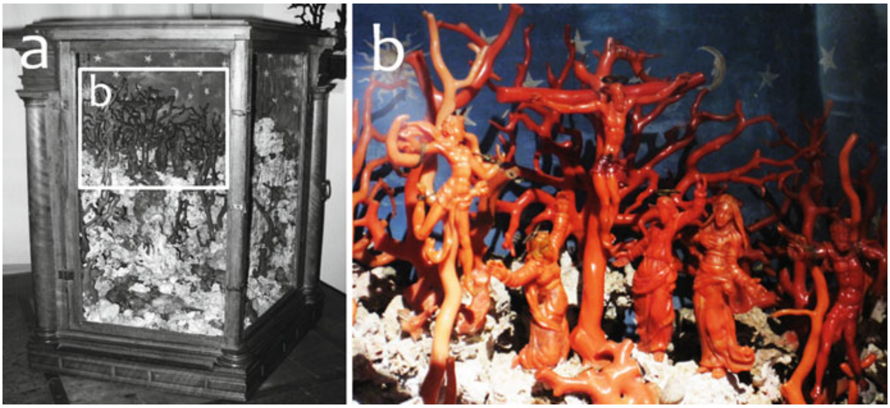


Fig. 13 Religious iconography of red coral. (**a**) Diorama of the Crucifixion in a Korallenkabinett, ca. 46 cm height, Schloss Ambras (Innsbruck, Austria); (**b**) detail of the figures carved from coral (Credits: **a**, **b** (commons.wikimedia.org))

Nativity were made using red coral. A spectacular example of the former is the *Korallenkabinett* in the collection of the Schloss Ambras Museum (Innsbruck, Austria). The cabinet contains a forest of coral branches representing crosses, trees, and the main characters of the stories (Fig. 13). Thick and particularly long coral branches carved as architectural elements, such as columns or porticoes, can also be seen in the sixteenth- to eighteenth-century Nativity cribs (*presepi*), such as the ones at the Museo Regionale Pepoli (Trapali) and Museo di San Marino (Naples). Large branches allowed the artisan to craft sizable figures of the crucified (see work attributed to Fra Matteo Bavera, ca. seventeenth century; Bresc 2000 in Morel et al. 2000). Loincloth folds, strained muscles, and contorted limbs were carved in almost photographic exactitude.

In our last example, esthetics overwhelmed practicality and functionality. Also in Dresden, there is a cutlery set with handles made of coral branches. The pieces of the set could not have been used without extorting strenuous finger contortions, and most probably they were never meant to be used. There are records of similar silverware indicating a moderate production to satisfy the wealthy patron acquiring them for their posh mansions (Hackenbroch 1981).

8 The Transitional Origins of Coral

The previous sections presented a few remarkable examples of how imaginative were the options to use coral as a medicinal element or to be used as a fantastic and magical object of hybrid nature. This final section contains a few selected cases in which imaginative origins of this "hybrid" were postulated, such as from the hair or blood of mythical creatures and deities or from the foam of the ocean, dew, air, earth's entrails, and, of course, as pranks or follies of nature or "imagination of the heavens." The reader is encouraged to consult Bowen's 2015 erudite and highly enjoyable review on how from "marine insects" the coral polyp was discovered and the "skeletal obstacles" to understand its nature were surmounted.

Perseus slaying Medusa is the classical myth explaining the origin of corals and their hard nature. Ovid (43 BCE - 17 CE), after celebrating the hero Perseus who cut off Medusa's head, describes how seaweeds hardened by contact with the monster's severed head. Later he adds *and even till this day the same nature has remained in corals so that they harden when exposed to air*. However, depending on the many versions (translations) of Ovid, not only the hardness of corals when taken out of the water can be linked to the killing of Medusa but the origin of corals, in this case red coral, is ingeniously explained by the ability of the fluids of the creature to metamorphose life. For example, in another variation of the myth, gushing blood from the monster's head came into contact with the sea, originating thus red corals. Joyful nymphs dispersed the hardened seaweeds throughout the seas. An almost cinematic depiction of this myth can be seen in Giorgio Vasari's painting (1570) currently exhibited at the Palazzo Vecchio, Florence (Fig. 14). As pointed out by Kelley (2014), it is somehow paradoxical that for some variants of classical myth, the origin of corals is tied to a monstrosity, and yet, it is considered a vessel that provides health and protection of many sorts against natural and supernatural threats. In this sense coral is not alone; in many traditions severed parts of monsters are powerful objects.

Another mythological origin of coral can be found in Hindu and Buddhist traditions of the fourth century CE (McLaughlin 2014). After deceiving a demon lord into a mock sacrifice, the primordial serpent king Vasuki slaughtered and

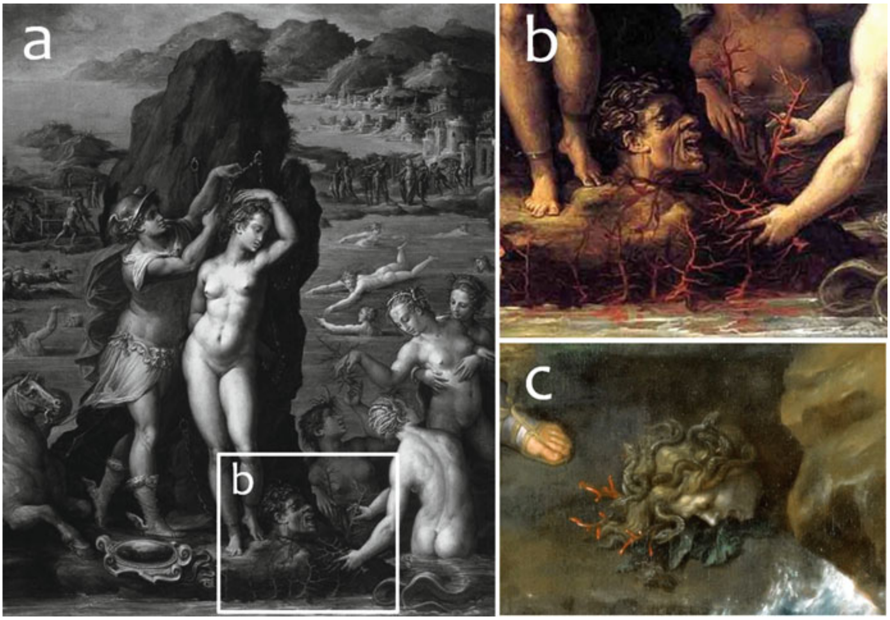


Fig. 14 Mythological origin of coral. (**a**) Perseus and Andromeda by Giorgio Vasari (1511–1574), (**b**) detail of Medusa's severed head from Vasari's painting, (**c**) Perseus and Medusa (detail) by Pierre Mignard (1612–1695), coral sprouts from Medusa's severed head in contact with plants (Credits: **a**–**c** (commons.wikimedia.org))

dismembered the victims' body. From the limbs and body parts, many gemstones and crystals originated, but it was from the entrails thrown into the seas that coral came to be. Fittingly enough, the *Roman country* is mentioned among the places of origin. In a Greco-Egyptian magical papyrus written between the second century BCE and the fifth century CE, coral (probably red) is considered a manifestation of Selene's *pneuma* (breath). In a mythical origin of colored birds, coral is endowed with power to affect permanently the birds' plumage. According to a tale recorded in the postwar Polynesia of the 1940s (Elbert 1949), a magical mixture of water and coral was considered the origin of the bridled tern whiteness.

Aside from fantastic and epic mythical origins, the historical lore on corals was rich on imaginative explanations about its ambiguous and sometimes obscure nature. Some of the explanations were the product of their time, when knowledge about geology, biology, and ecological processes in general were still "encased in dogma and metaphoric reasoning". But it was the marine provenance and conspicuous skeleton that gave coral its unusual character. Even though they were regarded as inert stones in most lapidary texts, ancient and medieval, they were said to "grow in the sea." Theophrastus (fourth century BCE), successor of Aristotle, approached the problematic nature of coral. Theophrastus is credited for having introduced the word *Kouralium*. However, the etymology of coral is yet a mystery to be fully resolved. For example, Pliny in his *Natura* and Isidore of

Sevilla (seventh century CE) in his *Etymologies* both claimed the derived from the iron tools used for the extraction. Aelius Herodianus (second century CE), the grammarian, attributes the name of coral to the ancient Greek adjective for marine. Other sources propose different Semitic origins for the word; for example, Sumerians had a word for a "petrified plant" (During 1983; Lipinski 2000 in Morel et al. 2000). Impervious to etymological debates, coral hard skeleton, considered a stone of biological origin, gave corals the "alive in death" nature, adding only to the confusion transmitted along centuries by the lapidary medicine, folklore, and tradition. Such was the ambiguity that the early seventeenth-century Florentine collectors in possession of a coral branch attached to a rock (Dobson 1908) claimed the stored coral still grew.

There is an all-time favorite example of such dilemma in *20,000 Leagues under the Seas* by Jules Verne (1869). In the story, Professor Pierre Arronax meditates on the seafloor communities and address corals and their skeletons from the prevailing view of the last thousands of years: *There is perhaps the real point where life rises obscurely from the sleep of a stone, without detaching itself from the rough point of departure*. The quest to explain the origin of the coral, particularly if it was of vegetable nature, was considered far from trivial or insignificant; it was deemed crucial in several documents, even if it was referred as the "famous question" (Bowen 2015). In the same way, fossilized corals posed, as other fossils did, a serious challenge to logic and called for ingenuous and sometimes passionate and dogmatic explanations. A few scholars considered fossils as a joke of time, not of nature. Alternatively, they were referred to as marine-like bodies unearthed from the bowels of the earth, "*Natives* of the earth" (e.g., Beaumont 1676). Fossil outcrops containing corals, shells, and other organisms were thought to have been somehow washed up during the flood. During the late sixteenth century, it was proposed that those "forms" were born in situ, from the earth, and later petrified (Palissy 1580 cited by Bowen 2015). Agricola (1546), mentioned earlier, had also a word on corals in his treatise on metals. He considered them to be plants that turned to stone by the action of a *petrifying sap* or *fluid.*

Astonished writers of the seventeenth century wrote about the presence of abundant forests made of stone flowers in the Red Sea and included in the discourse other fantastical curiosities like the coral flowers (polyps) that puzzled observers. How did the stone flowers get their nature? Like the coral flowers that "need seawater," the stone flowers needed clay as support and eventually hardened into the stony consistency (Beaumont 1676). The coagulation of dew (including dew from the sea) was poetically mentioned as the agent responsible for several of such hardening processes (Segal 1967), including the one of pearls. In synthesis, nature could produce stone flowers (corals) and shells in the sea as well as in mines or other terrestrial environments. The confusion regarding the mineral, plant, or animal nature of coral is best represented by the agonizing and enigmatic thoughts of Theophrastus who in the same work calls coral a plant and then animal and finish with the appalling mineral nature. Another alternative explanation for the mineral nature of the coral was found by comparing the formation of crystals and dripping forms in caves (Boccone 1673), resembling on occasions a coral because of the

Fig. 15 Corals as obligatory *mirabilia* in collections. (**a**) Cabinet of Curiosities by Domenico Remps (ca. 1620–1699) with black, white, and red coral among the items; (**b**) engraving from Dell'Historia Naturale (1599) by Ferrante Imperato, corals are on display in this early museum (Credits: **a**, **b** (commons.wikimedia.org))

branching patterns. The comparison of coral to small trees or plants is found almost everywhere, regardless of the observer's background. This generalization obviously does not apply to other coral morphologies. Brain coral species, as seen earlier, have a position of their own in myth and tradition. Mushroom corals (*Fungia* spp.) were thought to be mushrooms that fell in the sea and turned into stones (Bowen 2015).

In synthesis, coral and other curious *submarines* were sea creatures, stone plants, excretions, or coagulated fluids of nature and the gods; they exercised the fascination of early naturalists or anyone with the capacity to awe. Any of such mysterious specimens will draw attention and admiration, even sometimes gloomy thoughts, when displayed among other extraordinary objects of fantastic origins in the highly popular late medieval *scrittoi* or Renaissance *wunderkammern*, *musea*, and *cabinets of curiosities* (Fig. 15). With its medicinal and apotropaic properties, mythical aura, bizarre hybrid nature, and no less strange but beautiful architecture, coral was one of the essential items to display. These *mirabilia* did not lose easily their allurement with changes in the general knowledge and advances in the methodical and scientific thought; they always had a privileged place in the folklore and popular traditions and, of course, in the collections of wonders. Contrary to common belief, curiosity cabinets were not only property of elite or royal members of the society but also of apothecaries and physicians (Bowry 2014). Coral may have represented a difficult task to collectors when attempting to classify coral and coral-made objects for such cabinets.

9 Concluding Remarks

Enshrouded in time and imagination, the coral has a long tradition in human history. The oldest use for this remarkable *substance* was perhaps ornamental (Paleolithic beads), and only later (Neolithic of Italy) is found the oldest carved coral in the shape of an idol. World's religions have coral as a figurative characteristic, conceptual metaphor, or as an important object. Examples can be found among the earliest Arabic papyrus on celestial and human aspects. As of material importance, there are fragments, raw skeletal material inside ceramic containers deposited as votive objects in temples of ancient cultures. Coral was a powerful object to ward off or avert evil eye; these apotropaic magic properties are found in old traditions of different countries from distant geographical regions. What is more, coral was so magical and sublime that it had to be ingested. Many sacred or magical substances are taken orally; coral ingestion was in powdered form, diluted, or in a mixture of different coral species and more common with other inconceivable ingredients. In general, coral was invested with important properties that defined the mode of use and preparation. It was used to prevent (prophylactic) and cure (medicine), to avert (apotropaic) negative influences (e.g., evil, bad luck), to protect (amulets), to influence (magic) activities, to decorate (body and objects), and, of course, to build (e.g., blocks and mortar). It is futile to strictly classify uses according to these categories; there are a number of possible combinations. Even though the decorative appeal of coral may have overlapped its apotropaic properties, depending on the culture, geographical region, and time period, the societal changes blurred the original meaning and purpose of the use of coral. Coral objects became no more than jewelry. Fashion may have prevailed as the main purpose to have coral as body ornaments or part of garments and passementerie in general, satisfying thus status demands.

At this final stage, to conclude the present overview, it is necessary to remember Maier's lament in Atalanta Fugiens (1617) that echoes the millennium-old confusion with coral: *For who would ever have believed that a Stone should grow under waters or a plant there generated should become a Stone, unlesse Experience and the credible testimony of Writers had confirmed it?*

10 Epilogue

Most people are probably not aware that corals are present in our daily life more than imagined. Six years ago, the two authors of this chapter (CO and CJ) assisted the International Symposium of Reef Studies held in Wageningen (Netherlands). It was December; the wind was cold and it was snowing. The day after the symposium, while strolling through the beautiful but nearly frozen streets of Amsterdam, CO's careful steps to avoid slipping were halted by CJ when he suddenly said "Look at your feet!" and pointed his globed finger to the pavement's black stone slabs partially covered with snow. In response to CO's puzzled expression, CJ carefully cleared the snow and with a smile uttered one single word: Corals! Yes, black stones in the pavement entombed constellations of whitish, small corallites. This was a fantastic discovery even for someone studying coral and who never realized they are everywhere, even in the city. Millions of years of geological and evolutionary history of coral and other reef builders are hidden in these humble "tombstones" lining sidewalks and streets, on top of which we walk day after day. After this inspiring

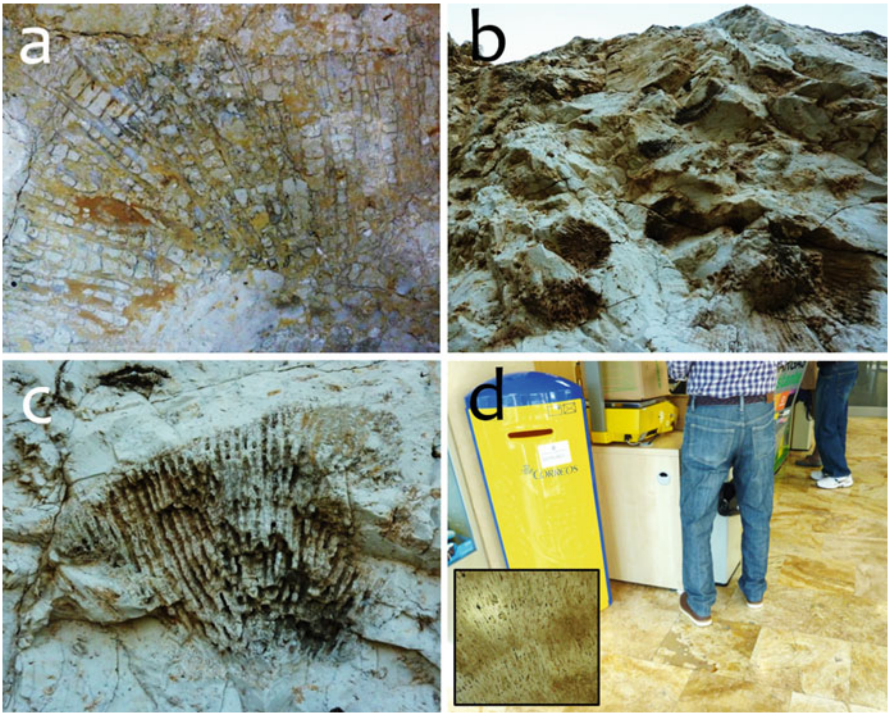


Fig. 16 Look at your feet. . .corals! (**a**) Coral floor tiles at Barajas (Madrid) Airport; (**b**) fossil coral outcrop, eastern coast of Cyprus (Cape Greco); (**c**) detail of a coral colony in the lower sections of the outcrop; (**d**) coral floor, Palma de Mallorca postal office (Credits: **a**–**d** (C. Orejas))

experience, the hunt for hidden reefs in the urbanized world was launched. Buildings are all frequently inhabited by these silent "observers" of the comings and goings of urbanites, since their dream at the quarries was disturbed. During a visit to Cyprus and while waiting to board the airplane, the "coral hunter" was again successful. Coral tiles were part of the floor of Madrid's new and fancy terminal 4 (Fig. 16a). After arriving in Cyprus, there was another stunning surprise: meter-high "walls" of ancient coral reefs in the middle of the shrubland (Fig. 16b, c). From similar outcrops, distant reminders of exuberant reef formations, quarried slabs of frozen ecology find their way into the urban maze of streets and buildings. One recent encounter with corals was 100 m away from home, when visiting the post office. The floor of such familiar building had wonderful corals too, some of the most beautiful fossil corals one can stumble upon on these urban reefs (Fig. 16d). It is clear that it is not always necessary to visit a paleontological museum to enjoy these treasures. Look around. Look at your feet!

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Framework-Forming Scleractinian Cold-Water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective

25

Claudia Wienberg and Jürgen Titschack

Abstract

Framework-forming scleractinian cold-water corals, with *Lophelia pertusa* and *Madrepora oculata* being the most common species, show an outstanding concentration in the North Atlantic Ocean. They are unique in their ability to provide habitats for other organisms ranging from micro- to mega-scale, and some species are even exceptional in their capability to shape the seafloor by forming large three-dimensional structures called coral mounds. Our understanding about the spatial and temporal distribution of cold-water corals and coral mounds and the environmental factors that control coral occurrence and influence mound development increased tremendously during the past 15 years. This synthesis highlights that: (i) species-specific environmental preferences and tolerances need to be considered when describing any coral distribution pattern; (ii) corals and coral mounds are linked to a complex set of multiple environmental variables that must work in concert as each variable might present a stimulator as well as a suppressor for coral occurrence and mound formation; (iii) environmental conditions for mound aggradation are more restrictive than those for coral occurrence; and (iv) the majority of environmental variables influencing the occurrence of corals and mound development are linked to distinct water masses whose characteristics vary with climatic fluctuations. Hence, regional coral distribution pattern and mound aggradation periods are in phase with these fluctuations, even though the specific environmental controls might vary from region to region. Nevertheless, certain data limitations and resulting constraints to generate generalized pattern

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regarding the climate-related spatiotemporal distribution of cold-water corals and coral mounds still exist and ask for more sophisticated future research strategies.

Keywords
Framework-forming scleractinian cold-water corals • North Atlantic • Distribution • Environmental control • Habitat • Coral mound • Mound aggradation • Dating • Data inventory

Contents

1 Framework-Forming Scleractinian Cold-Water Corals: A Brief Introduction

Cold-water corals occur in all seas occupying latitudes from the Barents Sea (71°N) in the north to the Ross Sea (75°S) in the Antarctic and water depths ranging from a few meters down to over 6,000 m (Roberts et al. 2009). They are nonsymbiotic (i.e., not bearing *Symbiodinium* sp.) and encompass more than 700 species of the order Scleractinia (stony corals), as well as species in the orders Octocorallia (e.g., gorgonians, sea pens, bamboo corals), Antipatharia (black corals), Zoanthidea (gold corals), and the family Stylasteridae (hydrocorals).

This synthesis exclusively focuses on the small group of framework-forming scleractinian species (also referred to as constructional, habitat-, reef-, or structure-forming corals; see Roberts et al. 2009) as they are the nuclei of one of the most important benthic ecosystems in the world's ocean and as most knowledge on cold-water corals has been obtained for this intriguing group. In particular, the North Atlantic, including the Gulf of Mexico, the Caribbean Sea, and the Mediterranean Sea, exhibits an outstanding concentration of framework-forming scleractinians with *Lophelia pertusa* and *Madrepora oculata*, and to a minor degree *Oculina varicosa*, *Solenosmilia variabilis*, and various dendrophylliid species (e.g., *Enallopsammia rostrata*, *Dendrophyllia cornigera*) being the most common species. They occur in a wide variety of marine benthic habitats (sensu Greene et al. 1999). But even more important is their outstanding ability to provide habitats themselves as they create, modify, and maintain a structural habitat, which forms a refuge for a large number of associated organisms (Henry and Roberts, ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume; Orejas and Jiménez, ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume). Hence this results in biodiversity hotspots in the upper bathyal once envisioned as a rather monotonous environment depleted in macrofaunal abundance (e.g., Marshall 1954). Technological achievements, such as the development of deep-diving remotely operated vehicles (ROV), manned research submersibles, autonomous underwater vehicles (AUV), landers, and high-resolution acoustic mapping devices, tremendously increased our knowledge of these formerly hidden marine animal forests of the deep and dark ocean during the last 15 years.

From a geological perspective, framework-forming scleractinian cold-water corals are of utmost importance due to two particular attributes. First, their skeletal remains might be preserved on the seafloor or in sedimentary sequences and thus are stored in the geological record. In addition, their aragonitic skeleton is suitable for various dating techniques allowing to trace the temporal occurrence of cold-water corals going thousands to even millions of years back in time (e.g., Kano et al. 2007; Frank et al. 2011). Second, some species (*L. pertusa*, *M. oculata*, and *O. varicosa*) are known to have the capability to form large and complex three-dimensional seabed structures, in the following referred to as coral mounds.[1] Coral mounds are composed of scleractinian coral remnants and other subordinate shells loosely embedded in fine sediments and are the result of complex interactions between biological (coral growth) and sedimentological processes (sediment input), which depend on specific environmental and hydrodynamic conditions. Compared to the adjacent seafloor, they experienced enhanced aggradation expressed in their positive seafloor relief and might even preserve sediment succession which are lacking in neighboring sedimentary records. Consequently, coral mounds provide valuable stratigraphic records as they display depositional cycles corresponding to successive periods of sustained coral proliferation and coral decline and thus are important environmental archives.

Based on a thorough evaluation of various available data sources dealing with framework-forming scleractinian cold-water corals (and coral mounds) in the North

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[1] Regarding the terminology of seabed structures formed by framework-forming scleractinian cold-water corals, Roberts et al. (2009) proposed the following classification: a "reef" comprises a continuously deposited sedimentary unit, while a "coral mound" comprises several successive reef units. However, this classification suffers from the limited knowledge of the temporal evolution of most coral reefs/mounds. This is exemplified by Norwegian reefs, which were believed to exhibit a continuous formation since the onset of the Holocene, but recent chronological studies revealed a discontinuous development for some of them (e.g., López Correa et al. 2012). To avoid this nomenclature pitfall, all three-dimensional structures formed by cold-water corals are termed in the following coral mounds referring exclusively to their geomorphological sculpture disregarding their internal organization.

Atlantic, this synthesis aims: (i) to summarize the current knowledge about their spatial distribution, (ii) to provide a comprehensive database on the temporal occurrence of corals and the development of mounds focusing on the last glacial and Holocene, and (iii) to discuss any spatiotemporal distribution pattern in the light of environmental boundary conditions identified for these corals in the modern ocean. Finally, any constraints regarding the existing data inventory are discussed and new systematic research, sampling and documentation strategies are proposed to overcome these limitations.

2 Modern North Atlantic-Wide Distribution

Most of the recent knowledge about the geographic distribution of framework-forming scleractinian cold-water corals results from intense research efforts in the frame of multiple international- and national-funded projects during the past 15 years. Reports of their widespread occurrence were incorporated into the cold-water coral global point dataset of the World Conservation Monitoring Centre of the United Nation Environmental Programme (UNEP-WCMC; Freiwald et al. 2005). Focusing on the North Atlantic Ocean and exclusively considering reports of framework-forming-scleractinian species, this dataset contains more than 2,900 records. Although the UNEP-WCMC dataset is not complete (similar to all other available datasets), as new discoveries of the past 9 years in particular from the Mediterranean Sea, Gulf of Mexico, Florida Straits, and African margin still need to be incorporated, it is used here to assess the North Atlantic-wide distribution of the most common framework-forming scleractinian cold-water coral species (Table 1).

Thirty-four percent of all records stored in the UNEP-WCMC dataset comprise occurrences of living specimens, 21% report exclusively dead/fossil specimens, and from 45% the vitality status was not documented (Table 1). Any habitat information of the records is virtually absent (only available from 2% of all North Atlantic records). The majority of the records (91%) are from the eastern North Atlantic, from the Barents Sea in the north to the Gulf of Guinea in the south (Fig. 1a). In addition, few records are available from the western North Atlantic (9% of all records; Table 1), where cold-water corals are documented from the south-eastern margin of the USA, the Gulf of Mexico, and around the Caribbean Sea (Fig. 1a).

Lophelia pertusa is the most abundant species (77%) of all reported living occurrences of framework-forming scleractinian cold-water corals in the North Atlantic (Table 1). This species is abundant between 70 and 50°N (highest abundance between 65 and 60°N; Fig. 1b) and exhibits an exceptional dominance in particular in the cold-temperate eastern North Atlantic (off Norway, south of Iceland, around the Faroe Islands, along the Irish-Celtic margin). *Madrepora oculata* (19% of all live records; Table 1) has frequently been reported together with *L. pertusa* but is less abundant in particular toward higher latitudes (see Fig. 1b). Compared to *L. pertusa*, it has its predominant occurrence further south and exhibits two maxima in distribution between 60 and 50°N, mainly corresponding to the Irish-Celtic

Table 1 Summary of reported occurrences of framework-forming scleractinian cold-water corals in the North Atlantic (n = 2,948). The reported records (*R*) are subdivided into living and dead/fossil occurrences; partly the vitality status of the corals is unknown. Records obtained for the western (*W*) and for the eastern (*E*) North Atlantic are given separately in brackets below the total record. The data are extracted from the global point dataset (version 2; 2006) compiled by the World Conservation Monitoring Centre of the United Nation Environmental Programme (UNEP-WCMC; Freiwald et al. 2005)

	Total (W/E)	% (W/E)	Live		Dead/fossil		Unknown	
			R	%	R	%	R	%
Lophelia pertusa	2,252 (114/2,138)	**76** (41/80)	778	**77**	439	72	1,035	78
Madrepora oculata	478 (56/422)	**16** (20/16)	196	**19**	155	25	127	10
Madrepora carolina	52 (52/0)	2 (19/0)	/	/	/	/	52	4
Oculina varicosa	25 (25/0)	1 (9/0)	24	2	/	/	1	<1
Solenosmilia variabilis	102 (25/77)	3 (9/3)	9	1	14	2	79	6
Dendrophylliids[a]	39 (6/33)	1 (2/1)	3	1	6	1	30	2
SUM	**2,948** (278/2,670)	100 **(9/91)**	1,010	**34**	614	**21**	1,324	**45**

[a] Comprising *Dendrophyllia cornigera*, *Enallopsammia* spp. *Eguchipsammia* spp.

margin (exceeding live *Lophelia* records by a factor of ~2; see Fig. 1b), and between 40 and 35°N, although less pronounced and mainly corresponding to the Mediterranean Sea and the Iberian and Northwest African margins (Fig. 1b).

For all other framework-forming scleractinian cold-water coral species, only few records are documented in the UNEP-WCMC database (<4% of all live records, Table 1; note: due to the low number of records, these species are not displayed in Fig. 1a–e). *Madrepora carolina* represents a further potentially important species of the genus *Madrepora*, which is only reported from sites in the western North Atlantic comprising the Florida Straits, the Gulf of Mexico, and the Caribbean (34–13°N; Cairns 1979). *Oculina varicosa* exclusively occurs in warm (22–26 °C) and shallow waters (<110 m water depth) of the western Atlantic with a concentration along the shelf edge off eastern Florida (~29–27°N; Reed 2002). *Solenosmilia variabilis* shows a scattered distribution and has predominantly been reported from the Mid-Atlantic Ridge and various seamounts (see Mortensen et al. 2008). Records of *Enallopsammia* spp. (comprising *E. rostrata*, *E. profundla*, *E. marenzelleri*) are only occasionally reported from seamounts in the western North Atlantic and from the Mid-Atlantic Ridge (e.g., Robinson et al. 2007; UNEP-WCMC database). The dendrophylliid species *D. cornigera* and *Eguchipsammia cornucopia* are endemic to the warm-temperate eastern North Atlantic (49–15°N) and the Mediterranean Sea (Gori et al. 2014; Vertino et al. 2014). For example, *D. cornigera* is abundant in the Bay of Biscay and the Mediterranean Sea and is the dominant coral species around the Canary Islands (Gori et al. 2014).

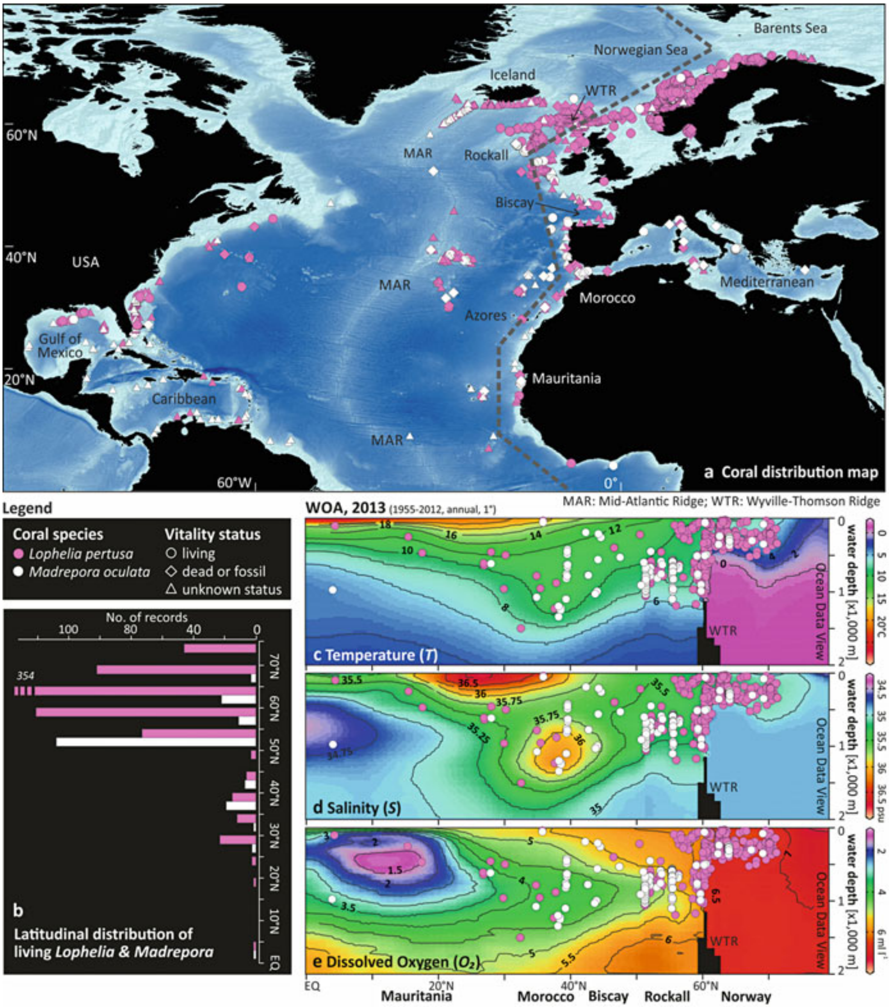

Fig. 1 Distribution map of cold-water corals. (**a**) Map of the North Atlantic showing the spatial distribution of *Lophelia pertusa* and *Madrepora oculata*. The data are extracted from the global point dataset (versions 2; 2006) compiled by the World Conservation Monitoring Centre of the United Nation Environmental Programme (UNEP-WCMC; Freiwald et al. 2005). The compilation of reported records comprise living (*dots*) and dead/fossil (*diamonds*) occurrences, partly the vitality status of the corals is unknown (*triangles*). (**b**) Latitudinal distribution of records of living *L. pertusa* and *M. oculata*. (**c**–**e**) Oceanographic parameters along a north–south transect in the eastern North Atlantic (indicated in A as *dashed bold line*) overlain by living occurrences of *L. pertusa* and *M. oculata*: (**c**) temperature, (**d**) salinity, and (**e**) dissolved oxygen concentration (data source: WOA Boyer et al. 2013 World Ocean Atlas, 2013; plotted using Ocean Data View vers. 4.6.5; http://odv.awi.de; Schlitzer 2014)

3 Environmental Controls

The ecology of framework-forming scleractinian cold-water corals prescribes the necessity of any kind of hard substrate for coral larvae settlement that might vary from extended outcropping hardgrounds (e.g., rocky escarpments, cliffs, scars, and overhangs) to even small-sized features like gravel, rocks, or shells (Wheeler et al. 2007). After initial coral larvae settlement and subsequent coral growth, the fossil coral remains act as settling ground for new coral generations, hence substrate availability is no more a limiting factor (Wilson 1979). As sessile suspension-feeder they prefer elevated positions where they profit from accelerated currents that deliver food to their tentacles and limit potential smothering by fine sediments (e.g., White et al. 2005). Although hard substrate is a prerequisite for coral larvae settlement, environmental factors eventually control their recent geographic distribution (e.g., Davies and Guinotte 2011) as well as their occurrence in the geological past (e.g., Frank et al. 2011). Various abiotic and biotic factors have been identified to directly impact on the proliferation of cold-water corals, which encompass distinct chemical and physical properties of the surrounding bottom water masses, the availability of sufficient food, and the local hydrodynamic regime.

Freiwald (2002) presented a first overview of the basic oceanographic boundary conditions (temperature ***T***: 4–12 °C, salinity ***S***: 33-37 psu, dissolved oxygen $\boldsymbol{O_2}$: 3–5 ml l^{-1}) for live occurrences of *L. pertusa* at selected sites in the eastern North Atlantic (64–37°N). Since this very first assessment, habitat-suitability models extended these preliminary defined thresholds for *L. pertusa* (*T*: −1.8 °C to 14.9 °C, *S*: 31.7–38.8 psu, O_2: 3–7.2 ml l^{-1}) by using global datasets (Davies et al. 2008; Davies and Guinotte 2011). In addition, the importance of further environmental variables has been emphasized comprising chemical and biological parameters (e.g., aragonite saturation, dissolved inorganic carbon, nitrate, phosphate, silicate, pH, particulate organic carbon, primary and export production) as well as hydrographic and topographic variables (e.g., current speed, water depth, slope) that are likely to influence the probability of the presence of *L. pertusa* and other important framework-forming scleractinian species (see Flögel et al. 2014 and references therein). According to Davies and Guinotte (2011), framework-forming scleractinian cold-water corals occur preferentially within high productivity areas in water depths shallower than 1,500 m that bath in water masses which are: (**i**) supersaturated with respect to aragonite, (**ii**) exhibit *T* between 5 °C and 10 °C with a limited *S* range of 34–37 psu, (**iii**) show low nutrient (e.g., nitrate, phosphate, silicate) concentrations, and (**iv**) O_2 concentrations of more than 4 ml l^{-1}.

However, wherever favorable oceanographic boundary conditions for the cold-water corals prevail, it is the availability of sufficient food that in the end controls their occurrence and proliferation (Mortensen et al., ▶ Chap. 32, “Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems” this volume). Food availability is controlled by the primary production in the surface ocean and by secondary food delivery processes, which are in turn related to various hydrodynamic phenomena providing a constant or periodic flow of water. The delivery of food to as well as the enrichment of food around the corals is reported to be steered by: (i) rapid downwelling and cascading, which drives fresh organic matter from surface waters toward cold-water corals occupying intermediate to deep water depths (Davies et al. 2009; Taviani et al. 2016); (ii) geostrophic currents and internal waves and tides, which pump food particles through the coral framework (e.g., White et al. 2005); (iii) the formation of intermediate and bottom nepheloid layers, in which food particles are enriched, thus forming an important pathway for the lateral delivery of fresh food particles (Mienis et al. 2007); and (iv) Taylor columns, which are anticyclonic, quasi-stationary eddies above the summit of a seafloor obstacle (e.g., seamount, submarine bank, coral mound), causing upwelling, and hence increasing the concentration of food (White et al. 2005). Regarding the dietary preference of cold-water corals, at least *L. pertusa* is rather opportunistic with respect to food source and composition as this species feeds on fresh phytodetritus and/or zooplankton as well as organic debris, and might additionally consume bacteria and dissolved organic matter (see Naumann et al. 2015 and references therein).

3.1 Species-Specific Requirements

To identify species-specific oceanographic boundary conditions, basic parameters such as water depth, T, S, O_2 (all data extracted from World Ocean Atlas 2013) and net primary production (*NPP*; source: http://data.guillaumemaze.org/ocean_productivity; Behrenfeld and Falkowski 1997) were reevaluated (Fig. 1c–e). Exclusively live occurrences of framework-forming scleractinian cold-water corals in the North Atlantic (including the Mediterranean Sea and the Gulf of Mexico) were considered (Fig. 2). However, only for the two main species *L. pertusa* and *M. oculata* a sufficient number of records within the UNEP-WCMC database was available for a direct comparison. Other species were omitted from analysis due to the paucity of records (Table 1).

The compiled data of *L. pertusa* exhibit two maxima in its depth distribution at 200–250 m and between 500 m and 900 m (Fig. 2) that depict two main areas of their recent occurrence: the Norwegian shelf and the Irish margin (Porcupine Seabight, Rockall Bank), respectively (Fig. 1a). In contrast, *M. oculata* seems to prefer slightly deeper water depths as most records are from water depths between 500 and 1,000 m (Fig. 2). With regard to their thermal tolerance, both species occur in temperatures of 1–14 °C. However, living *L. pertusa* occur more frequently in colder waters with a maximum between 6.5 °C and 8 °C, whereas living *M. oculata* occur preferentially in warmer waters between 8.5 °C and 10 °C (Fig. 2). Both species favor similar S of 35–35.75 psu, while they differ in their O_2 tolerance. Most records of *L. pertusa* cluster around 6.25 ml l^{-1}, while *M. oculata* has its maximum at considerably lower values of 5.25 ml l^{-1}. Nevertheless, *L. pertusa* seems to cope better with extremely low O_2 concentration as revealed by live occurrences coinciding with O_2 concentrations of down to

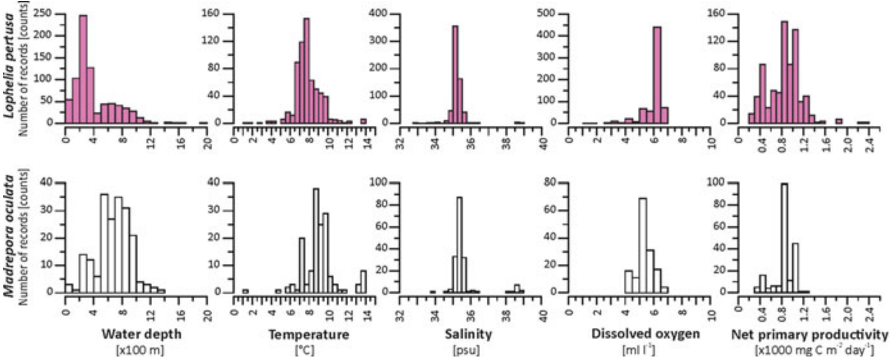

Fig. 2 Oceanographic boundary conditions. Oceanographic boundary conditions (water depth, temperature, salinity, dissolved oxygen concentrations, net primary production) for living occurrences of *Lophelia pertusa* and *Madrepora oculata* in the North Atlantic (data sources: UNEP-WCMC see Freiwald et al. 2005; WOA World Ocean Atlas 2013 see Boyer et al. 2013)

1.0 ml l^{-1} (as displayed in Fig. 2 representing occurrences off Mauritania). Annual mean *NPP* varies between 200 and 2,400 mg C m^{-2} day^{-1} in areas where living *L. pertusa* occur, whereas for *M. oculata* values range between 300 and 1,300 mg C m^{-2} day^{-1} (Fig. 2).

The apparent deviating environmental preferences identified for *L. pertusa* and *M. oculata*, in particular regarding their depth distribution and thermal preference, highlight the importance of a species-specific evaluation of their environmental tolerances. This finding is substantiated by multiple experimental studies. For example, *D. cornigera* maintains its physiological functions at water temperatures of 12–16 °C, which encompass or even exceed the upper thermal tolerance of *L. pertusa* and *M. oculata* (Gori et al. 2014), which is also expressed in its restriction to warmer environments within the eastern North Atlantic and the Mediterranean Sea. Moreover, distinct changes in environmental conditions, such as drastically reduced oxygen conditions or sudden drops in temperature, have a negative influence on the physiology (calcification, respiration, and metabolism) of cold-water corals. Thereby, some species seem to have higher acclimatization capabilities as others, and hence, respond differently to environmental changes, thus affecting their occurrence and local abundance (see Naumann et al. 2014 and references therein).

Consequently, generalized environmental boundary conditions used to explain the recent geographical distribution of the entire group of framework-forming scleractinian cold-water corals are to some extent problematic and should be avoided as already emphasized by Davies and Guinotte (2011). In addition, our understanding of the environmental controls and boundary conditions of the framework-forming scleractinian cold-water corals, in particular for distinct species, is still in its infancy as it suffers from: (**i**) the paucity of data for some species, (**ii**) the rarity of in situ measurements of environmental parameters, and (**iii**) a bias in exploration focusing on the eastern North Atlantic (Table 1, Fig. 1a).

4 Coral Habitats

Following Greene et al. (1999), marine benthic habitats can be classified by their size ranging from micro- to megahabitats. According to this classification scheme, (i) microhabitats represent seafloor features of a few centimeters and below, such as gravel, fissures, and macrofaunal remains; (ii) macrohabitats range in size from 1-10 m and include features such as rocky boulders, bedrock outcrop, sand dunes, and waves; (iii) mesohabitats having sizes from tens of meters to a kilometer comprise large submarine banks, cliffs, overhangs, gravel, and cobble fields; and (iv) megahabitats, which refer to large features that have dimensions from kilometers to tens of kilometers such as canyons, mud volcanoes, seamounts, and the Mid-Atlantic Ridge. Thereby, different types of small-scale habitats can also be part of superordinate habitat classes. For example, steep vertical cliffs and overhangs might be part of canyon walls and seamount flanks.

Framework-forming scleractinian cold-water corals occur in all these habitats (regardless of their dimension) as these habitats have in common that they provide hard substrate suitable for coral larval settlement and that they are exposed to accelerated currents allowing the corals to profit from potentially enhanced food supply. However, framework-forming scleractinian cold-water corals not just occur in various marine benthic habitats, they also have the outstanding ability to offer habitats to other organisms ranging from micro- to mega-scale, which is unique in the deep-sea realm (Orejas and Jiménez, ► Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep" this volume). In this context, already a single coral branch provides a microhabitat to (micro-) organisms (such as parasitic foraminifers, boring sponges), which use the skeleton as an attachment ground or as an invasion target (e.g., Beuck et al. 2007). At the other extreme, corals provide megahabitats for a highly diverse micro- to megafauna when forming coral mounds (Henry and Roberts, ► Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems" this volume). All habitats provided by framework-forming scleractinian cold-water corals might be classified into habitats in which the corals act exclusively as "habitat provider" and into habitats in which the corals additionally act as "seafloor modifier" as the principle backbone of coral mounds.

4.1 Corals as Habitat Provider

In the following, the most important North Atlantic megahabitats are (briefly) introduced, in which framework-forming scleractinian cold-water corals occur frequently as habitat providers, forming themselves micro- to mesohabitats but do not modify or shape the seafloor significantly.

4.1.1 Seamounts and the Mid-Atlantic Ridge

Framework-forming scleractinian cold-water corals are a prominent component of the faunal community of many seamounts in the North Atlantic

(Clark et al. 2006). Seamounts provide partly extended areas with hard substrate on their summits (mainly basaltic outcrops, boulders, fields with cobbles) and along their steep slopes they offer special hydrographic conditions with elevated current speeds (e.g., forming Taylor columns above their summits) both aspects being most favorable for cold-water corals. The majority of seamounts in the North Atlantic occur on the Mid-Atlantic Ridge, where *L. pertusa* is one of the most frequently observed species (Mortensen et al. 2008). Its occurrence is well documented along the Reykjanes Ridge south of Iceland and on Mid-Atlantic Ridge seamounts close to the Azores. Within these megahabitats, living *Lophelia* occur as relatively small-sized colonies (~0.5 m in diameter), while dead coral framework and coral rubble are far more abundant (Mortensen et al. 2008). Other reported framework-forming species comprise *M. oculata*, *S. variabilis*, and various dendrophylliid corals (Mortensen et al. 2008; UNEP-WCMC database). Also from seamounts with some distance from the Mid-Atlantic Ridge (comprising seamounts on the Madeira-Tore Rise, around the Canary and Madeira Islands, and east of the US margin), *L. pertusa*, *M. oculata*, *S. variabilis*, and dendrophylliid species have frequently been observed (e.g., Clark et al. 2006; Robinson et al. 2007; Somoza et al. 2014). Thereby, *D. cornigera* is restricted to warm-temperate latitudes in the eastern North Atlantic, while *E. profunda* and *E. rostrata* have solely been reported from the western North Atlantic (Robinson et al. 2007). Nevertheless, worldwide less than 300 seamounts of the estimated >100,000 seamounts (~4,400 seamounts in the North Atlantic; Yesson et al. 2011) have been surveyed or even sampled for their macrofaunal diversity so far, which is mainly related to their remote position. Thus, the real extent of cold-water corals associated to seamounts will presumably remain nebulous for decades.

4.1.2 Canyons

Submarine canyons incising the continental margin are impressive modern examples of cold-water coral occurrence. Along their flanks, canyons largely provide hard substrate for coral colonization but also a kind of refuge (i.e., natural protection against deep-sea trawling) as canyon surfaces are characterized by rugged areas, steep or near-vertical walls, overhangs, clefts, and caves. This steep and heterogeneous topography makes it rather difficult to assess the real extent and present-day status of these coral habitats by mapping, video observation, and sampling. Nevertheless, in recent years framework-forming scleractinian cold-water corals have been described from numerous canyons in the North Atlantic including the Gulf of Mexico and the Mediterranean Sea, where they predominantly occur as isolated colonies (e.g., Cordes et al. 2008; Mazzini et al. 2012; Gori et al. 2013; Brooke and Ross 2014; Sánchez et al. 2014). The only exception exists for the Whittard canyon in the Bay of Biscay, where extended occurrences of *Lophelia* with a faunal coverage of ~70% were observed along near-vertical to overhanging cliffs (Huvenne et al. 2011). Whereas the majority of North Atlantic canyons are dominated by *L. pertusa*, in the western Mediterranean Sea also few *Madrepora*-dominated canyons are described (e.g., Orejas et al. 2009).

4.1.3 Mud Volcanoes

An extraordinary example for the occurrence of framework-forming scleractinian cold-water corals are mud volcanoes, which are common seabed features along the Moroccan Atlantic margin (Gulf of Cádiz) and the western Mediterranean Sea (Alboran Sea). During periods of slow seepage activity or volcanic inactivity, partly extensive carbonate crusts may form on the surface of mud volcanoes, which offer a favorable hard substratum for corals. Indeed, cold-water coral communities have been reported from several mud volcanoes of these regions, which are dominated by patchy distributed *L. pertusa* and *M. oculata* (Wienberg et al. 2009; Margreth et al. 2011; Rueda et al. 2015). In the Gulf of Cádiz, also dendrophylliid species such as *D. alternata* and *E. cornucopia* have been observed (Wienberg et al. 2009). However, mud volcanoes just provide a temporary habitat for corals due to the periodic reactivation of mud volcanism, which leads to a burial of the carbonate crusts and/or the corals.

4.2 Corals as Seafloor Modifier

Framework-forming scleractinian cold-water corals can develop from individual colonies into extended occurrences as they become self-sufficient in terms of primary substrate with new generations of corals growing on dead framework or coral rubble, and scattered coral patches merging to larger structures (Wilson 1979; De Mol et al. 2005), eventually providing meso- to megahabitats for other organisms. Moreover, scleractinian cold-water corals have the capability to become seafloor modifier, meaning they significantly modify or shape the topography of the seafloor by forming large three-dimensional seafloor obstacles. In this context, the capacity of the coral framework to entrap (baffle) bypassing sediment plays a decisive role, as it significantly increases the sediment accumulation (e.g., Dorschel et al. 2005; Titschack et al. 2009, 2015). The contemporaneous input of "hemipelagic sediments" (defined as fine sediments deposited along continental margins mainly composed of foraminifers, coccolithophors, and fine terrigenous material) from vertically as well as laterally advected sediments stabilizes the biogenic construction. Hence, if favorable environmental conditions for corals persist over sufficiently long periods of time, and coral growth and sediment input stay in equilibrium, substantial meter-thick coral sediments can form. On geological timescales, such coral sediment deposits might eventually lead to the formation of coral mounds (Fig. 3), which as elevated seabed structures or seafloor obstacles influence their environment (e.g., bottom currents) when having reached a certain dimension. However, the transition from extended coral occurrences to a coral mound (sensu stricto) is fluent and difficult to discriminate. This is well exemplified by coral mound-like seabed structures found in the Santa Maria di Leuca coral province in the eastern Mediterranean Sea (Fig. 4). In this area, preexisting topographic heights (originating from Pleistocene mass wasting events) are covered by

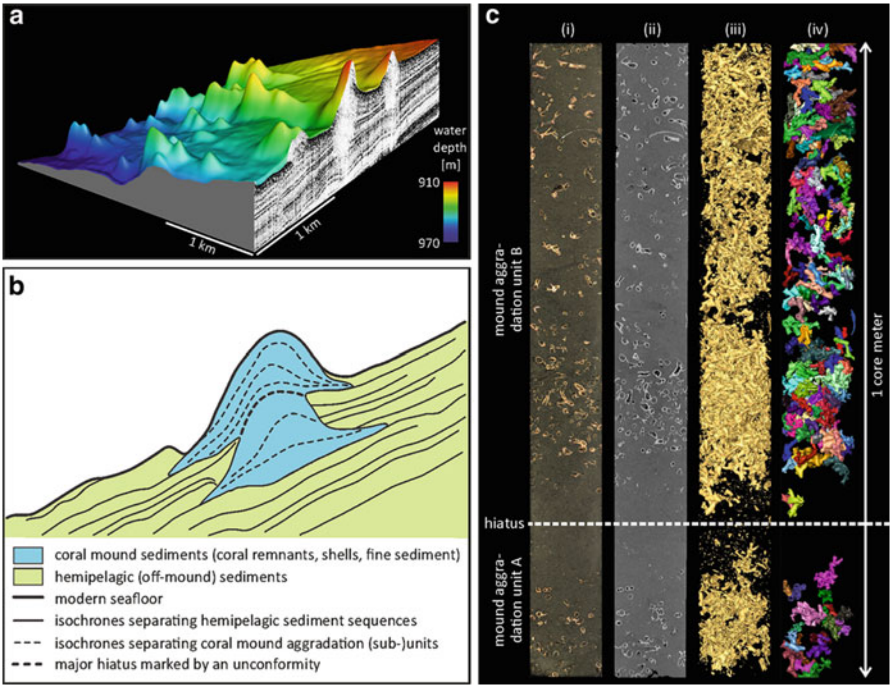

Fig. 3 Coral mound. (**a**) Multibeam bathymetry in combination with a sub-bottom reflection profile of a sector of the Moroccan coral mound province in the eastern North Atlantic (~35°N). (**b**) Idealized sketch of depositional sequences of a coral mound (vertical orientation has approximately ×10 exaggeration) and adjacent hemipelagic sediments. The hypothetical depositional history of the mound comprises two major aggradation units (additionally divided into subunits) which are separated by a major hiatus marked by a pronounced unconformity. (**c**) Cold-water coral-bearing sediment core collected from a coral mound. *i*) Photo scan of the surface of a halved one meter-long core section showing coral fragments (mainly *Lophelia*) embedded in hemipelagic sediments. (*ii*) – (*iv*) Computed tomography (*CT*) analysis of the same core section. (*ii*) Central CT-slice in x-z orientation. (*iii*) Coral-clast visualization by an isosurface. (*iv*) Visualization of coral clasts > 4 cm; colors mark individual clasts. *Note*: The internal organization of coral mounds is not deducible from sub-bottom reflection profiles due to their acoustic transparency (see **a**). Detailed information about mound aggradation and hiatuses can only be obtained from core analyses (ideally by a combination of CT analyses and dating of corals)

1–2 m-thick coral sediments which have been deposited since the last deglaciation (~13.4 kyr BP; Fink et al. 2012), and hence exhibit a long-lasting colonization by cold-water corals. However, these mound-like features still display the original morphology of the underlying seafloor and need to be distinguished from genuine coral mounds, which have developed their own characteristic morphology shaped by the interplay between coral growth, mound aggradation, and bottom currents regardless of the base on which they initiated.

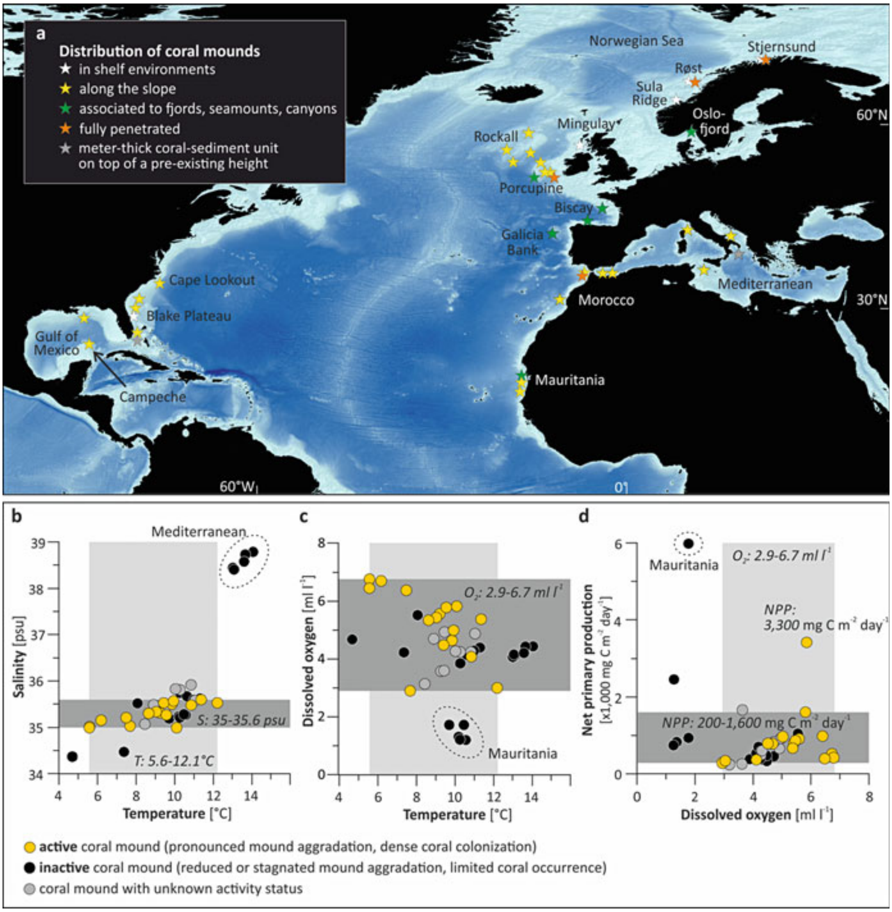

Fig. 4 Distribution of coral mounds. (**a**) North Atlantic-wide distribution of coral mounds comprising individual mounds as well as provinces containing hundreds to even thousands of mounds (verified by long coral-bearing core material and/or detailed high-resolution bathymetric and seismic data). Displayed are mound occurrences in shelf environments (*white stars*), on slopes (*yellow stars*), and in fjords, on seamounts and canyons (*green stars*). Preexisting heights covered by meter-thick coral-bearing sedimentary units are indicated as well (*gray stars*). So far, solely five coral mounds have been fully penetrated to their base (*orange stars*) including coral mounds off Norway (Stjernsund and Trænadjupet; López Correa et al. 2012), in the Porcupine Seabight (Challenger Mound; Kano et al. 2007), and along the Atlantic Moroccan margin (MeBo drilling during RV Maria S. Merian cruise MSM36, doi:10.2312/cr_msm36). (**b**–**d**) Coral mound provinces in the North Atlantic versus environmental boundary conditions (data for temperature, salinity, and dissolved oxygen concentration extracted from World Ocean Atlas 2013; source for net primary production: http://data.guillaumemaze.org/ocean_productivity; Behrenfeld and Falkowski 1997). Displayed are correlations between (**b**) salinity and temperature, (**c**) dissolved oxygen concentration and temperature, (**d**) net primary production and dissolved oxygen concentration. Coral mound provinces are subdivided into *actively* aggrading mounds (*yellow dots*) and *inactive* mounds (*black dots*), partly the activity/aggradation status is unknown (*gray dots*)

4.3 Coral Mounds

4.3.1 Mound Formation and Aggradation

Coral mounds are very specific and unique habitats created by framework-forming scleractinian cold-water corals. So far, solely *L. pertusa*, *M. oculata*, and *O. varicosa* have been identified being capable to form coral mounds in the North Atlantic (note: mounds formed by *O. varicosa* are exclusively known from sites off eastern Florida; Reed 2002). Although the development of coral mounds directly (and primary) depends on the proliferation of these coral species, coral mounds are eventually the result of a well-balanced interplay between coral growth and sediment input. This is also shown by the composition of coral mound sediments, which predominantly consist of hemipelagic sediments (>50%; Titschack et al. 2015) loosely interspersed by coral fragments and other shells (Fig. 3). A sufficiently high sediment supply being entrapped within the coral framework (as described above) guarantees the fast infilling of the coral framework, which has a stabilizing effect, but it also increases sediment accumulation, and thus mound aggradation. Moreover, even during periods of enhanced bottom current intensities, coral mounds might still aggregate and preserve sediment successions while the adjacent areas experience nondeposition or erosion (Titschack et al. 2009; Thierens et al. 2013).

Stratigraphic records obtained from coral mounds reveal that their temporal development and aggradation is discontinuous (Fig. 3; Eisele et al. 2008; López Correa et al. 2012; Stalder et al. 2015). Coral mounds exhibit several recurring periods of coral colonization, coral framework aggradation, coral demise, and renewed colonization. On this basis and regarding their modern distribution in the North Atlantic, coral mounds can be subdivided into: (i) mounds which are “active” by exhibiting a vivid coral community and a significant subrecent mound aggradation, and (ii) mounds which are “inactive” in terms of dense coral colonization and mound aggradation, and hence are exposed to substantial breakdown, (bio-) erosion, or even burial.

4.3.2 Topographic Variety of Coral Mounds

Coral mounds show highly diverse morphologies. Their heights mainly vary from a few meters (e.g., Moira mounds off Ireland; Wheeler et al. 2007) to tens of meters (e.g., Mauritanian mounds, Colman et al. 2005; Melilla mounds in the western Mediterranean Sea; Stalder et al. 2015). But they can even tower up to hundreds of meters as found for the Rockall Bank along the Irish margin (Mienis et al. 2007), where the worldwide largest examples of coral mounds exist. Laterally, coral mounds may reach dimensions of hundreds to thousands of meters in extent and exhibit a wide variety of appearances comprising conical, oval, elongated, ridge-like, or V-like shapes (Wheeler et al. 2007). They may occur as individual mounds but are abundantly arranged in clusters or provinces (Fig. 3) consisting of hundreds to even thousands of mounds (Mortensen et al. 2001; Glogowski et al. 2015). When arranged to provinces, coral mounds tend to be confined to certain depth intervals sometimes forming slope-parallel chains (e.g., off Ireland; Wheeler et al. 2007) or even being merged to very complex reticular structures extending over long (>100 km) marginal transects (off Mauritania; Colman et al. 2005).

As elevated seabed structures, coral mounds are well displayed by high-resolution bathymetric and seismic data, which can be used (to some extent) for their identification, in particular when the mounds are arranged in clusters or provinces (Fig. 3). Seismic data can even yield information about buried mound structures as they appear as transparent features (due to their chaotic internal structure; Fig. 3) surrounded by stratified sediments. So far, buried mounds have been identified from the Irish, Moroccan, and Mauritanian margins (Colman et al. 2005; Huvenne et al. 2007; Vandorpe et al. 2014). However, solely long sedimentary records collected from potential coral mounds (Fig. 3) provide reliable and ultimate evidence whether a genuine coral mound is present.

4.3.3 Geographical Distribution of Coral Mounds in the North Atlantic

The large variety of coral mounds regarding their appearance, their aggradation history, and the different oceanographic settings in which they occur, makes a direct in-depth comparison between different sites a challenge. In addition, even after 15 years of intense research and numerous recent discoveries of coral mound provinces, our knowledge of the North Atlantic-wide distribution of coral mounds is far from complete. This is mainly related to two aspects: (i) many regions in the North Atlantic (and other oceans) that potentially host coral mounds still need to be explored, and (ii) it is very time- and cost-consuming to verify the nature and origin of coral mound-like seabed features (as described above). Nevertheless, in the following an overview about the geographical distribution of coral mounds and mound provinces in the North Atlantic (including the Mediterranean Sea and the Gulf of Mexico; see Fig. 4) is provided, which will highlight the peculiarities of the different coral mound areas.

Coral mounds from rather shallow shelf environments (50–300 m water depths) have been reported from the eastern Florida shelf (solely formed by *O. varicosa*; Reed 2002) and the western Scottish shelf (Mingulay area being dominated by *L. pertusa*; e.g., Douarin et al. 2013) (Fig. 4). The most impressive coral mounds in shelf settings are known from the Norwegian shelf (e.g., in the Trænadjupet, Røst, Fugløy, and Sula ridge areas), where so far hundreds of mounds with an estimated spatial coverage of at least 500 km^2 have been discovered (Mortensen et al. 2001). The Norwegian mounds are dominated by *L. pertusa* and overall are colonized by the most vivid cold-water coral communities discovered so far (Mortensen et al. 2001; Fosså et al. 2005). In general, the elevation of coral mounds being developed in shelf environments seems to be restricted to maximum heights of 30–40 m.

Coral mounds on the upper- and mid-slopes of the continental margins (mainly confined to 500–1,000 m water depth) are far more abundant, occupy several regions of the North Atlantic (Fig. 4), and, in contrast to shelf mounds, exhibit a much larger range in height, lateral extension, and volume. The most prominent and best-studied sites are the Porcupine Seabight and the Rockall Bank along the Irish and UK margins

(Fig. 4; De Mol et al. 2002; Dorschel et al. 2005; Rüggeberg et al. 2007; Mienis et al. 2009; van der Land et al. 2014 and many more). Here, more than 1,000 coral mounds are reported between 57 and 51°N (Roberts et al. 2009), comprising some of the largest known examples with heights of up to 380 m at the southwestern Rockall Bank (Mienis et al. 2007). These mounds are confined to distinct provinces and are partly arranged as slope-parallel chains (e.g., Belgica mound province). The Irish mounds are largely colonized by *L. pertusa* and *M. oculata* (e.g., De Mol et al. 2002).

Several hundreds of rather small-sized coral mounds exist along the northern Moroccan margin (around 35°N; Fig. 4), which are partly arranged as clusters, and rarely exceed heights of 10–20 m (Wienberg et al. 2009). In contrast to the Norwegian and Irish mounds, the Moroccan coral mounds are today solely covered by fossil coral remnants (Wienberg et al. 2010). Another mound province along the Moroccan margin (Eugen Seibold mound province) has very recently been discovered north of the Agadir canyon (~31°N; Fig. 4), where an extensive area of 410 km^2 is densely covered by up to 12-m-high mounds, which are at least partly colonized by living *Lophelia* (Glogowski et al. 2015).

An example for coral mounds occurring in subtropical latitudes (20–17°N) is the Mauritanian margin, where mounds are arranged in slope-parallel chains or occur as complex composite structures, each having a length of several kilometers and heights of 60–100 m (Colman et al. 2005; Eisele et al. 2011). The Mauritanian mounds are today colonized by scattered small-sized colonies (~10–20 cm in diameter) of *M. oculata* and *L. pertusa*.

In the Mediterranean Sea, coral mounds have been detected in the Alboran Sea, Tyrrhenian Sea, Strait of Sicily, and southern Adriatic (Fig. 4; e.g., Freiwald et al. 2009; Fink et al. 2013). They vary in height from a few meters to tens of meters and occupy much shallower water depths (250–600 m) compared to examples from the Irish, Moroccan, and Mauritanian Atlantic margins. The Mediterranean mounds are frequently colonized by living cold-water corals although mainly exhibiting a rather scattered distribution. *Madrepora oculata* seems to be more frequent and occurs partly as dense, large colonies while the presence of *L. pertusa* comprises rather isolated colonies or small patches (Vertino et al. 2014; Fink et al. 2015 and references therein).

At the western side of the North Atlantic, coral mounds exist along the southeastern US margin (between North Carolina and Florida, e.g., Cape Lookout) and in the Florida Straits (Fig. 4, e.g., Paull et al. 2010; Correa et al. 2012; Matos et al. 2015). A new Coral mound provinces was recently discovered at the northeastern slope of the Campeche Bank in the southern Gulf of Mexico (Fig. 4), which consists of numerous 20–40 m-high elongated mounds that cover an area of >40 km^2. The living coral community is dominated by *L. pertusa* and *E. profunda*, which form today very dense coral thickets up to 60 cm in height (Hebbeln et al. 2014).

Although being mainly confined to the shelf, shelf edge, and continental slope, an increasing number of mounds have been reported from other settings (Fig. 4). Well-described examples originate from fjords/sunds (here developed on morainic sills in Scandinavian waters) as well as from the top of seamounts (e.g., Galicia Bank, Iberian margin), submarine cliffs (Pen Duick escarpment, Moroccan margin), and canyon flanks (Porcupine Bank, Irish margin; Bay of Biscay, Mauritanian margin) (e.g., Freiwald et al. 1997; Van Rooij et al. 2011; Mazzini et al. 2012; Sánchez et al. 2014; Somoza et al. 2014).

4.3.4 Environmental Controls of Mound Aggradation

The specific environmental conditions that trigger the temporal development of coral mounds are far less known than the environmental controls favoring cold-water coral occurrence. However, as coral mounds do not necessarily develop, even if environmental conditions are within the constraints for coral growth, it is likely that environmental controls triggering mound formation are far more restrictive. Moreover, the baffling capacity of coral framework and the sediment supply, both being critical for the formation and aggradation of coral mounds, are difficult to assess due to the lack of appropriate data.

As environmental conditions being important for cold-water coral occurrence should also be important for the development of coral mounds, a preliminary assessment of some oceanographic boundary conditions (T, S, O_2, and *NPP*) of over 35 North Atlantic coral mound provinces has been conducted (Fig. 4). Actively aggrading coral mounds occur in water masses with T between 5.6 °C and 12.1 °C (Fig. 4), which constitutes a much narrower range as that identified for living *L. pertusa* and *M. oculata* (1–14 °C; Fig. 2). This suggests that T presents a potentially crucial environmental factor for mound aggradation. In particular, very high temperatures above ~12 °C likely hamper mound aggradation today, as identified for mound provinces in the Mediterranean Sea (Stalder et al. 2015). Although framework-forming scleractinian cold-water corals can survive in or adapt to such warm waters, they seem not to be capable to form mounds anymore. In contrast, S seems to have no influence on mound aggradation. Mounds occur in water masses with S values between 35 psu and 35.6 psu (Fig. 4). This S range is largely similar for the occurrences of living *L. pertusa* and *M. oculata* (35–35.75 psu; see Fig. 2). Another important environmental control for mound aggradation might be O_2 concentrations. Actively aggrading mounds are found in waters with O_2 concentrations of 2.9–6.7 ml l^{-1}. In contrast, Mauritanian coral mounds, which are today bathed in oxygen-depleted waters of <2 ml l^{-1} (Fig. 4), ceased aggradation with the onset of the Holocene (Eisele et al. 2011) and exhibit today just a scattered coral colonization. Again emphasizing that cold-water corals may cope with such extreme environmental conditions, while mound aggradation is hampered. *NPP* is clearly one of the primary factors controlling coral occurrence, therefore should also be a prerequisite for mound aggradation. But high *NPP* alone does not provoke coral growth or mound formation, which is again clearly apparent for the Mauritanian coral mounds. Although they are today situated in an upwelling area with maximum annual mean *NPP* values of up to 6,000 mg C m^{-2} day^{-1} (Fig. 4), mound aggradation is hampered. As described above, this is likely related to the very low present-day O_2 concentrations providing extreme environmental conditions for cold-water corals (expressed in the low abundance of living corals). This clearly emphasizes the importance of a “balanced” interplay between the entire set of environmental variables being critical for coral growth and, thus, for mound development.

Overall, regarding our recent knowledge on coral mound formation and environmental controls, the following can be concluded. It is of utmost importance: (i) to differentiate environmental conditions being preferential for coral growth from conditions being preferential for mound aggradation, which seem to be much more constrained; (ii) to study the interplay of various environmental variables controlling mound development as each environmental factor (in particular T and O_2) might act as a stimulator as well as a suppressor; (iii) to collect in situ environmental data from coral mound provinces (considering any seasonal change); (iv) to examine the role of sediment input, which is likely a key factor for mound aggradation (in terms of stabilization) but so far not considered due to a lack of appropriate data of local sedimentation rates; and (v) to evaluate the recent “activity” status of coral mounds (mound aggradation vs. stagnation, which in fact can only be verified by dating sediment cores that were retrieved from coral mounds; see next section) to gain a comprehensive understanding of coral mound development over geological timescales.

5 Dating Cold-Water Corals: A Key to the Past, But How to Read It?

5.1 Data Inventory

Many efforts have been conducted in recent years to collect and date framework-forming scleractinian cold-water corals from various sites in the North Atlantic and to decipher their temporal occurrence going thousands to even millions of years back in time (Kano et al. 2007; Frank et al. 2011). The aragonitic skeleton of scleractinian corals is suitable for various dating methods to determine the age of a coral specimen or more precisely to determine the years since the coral died. The radiocarbon (^{14}C) method is applied for rather “young” material as its dating range extends only back to 40–50 kyr (depending on the contamination of the skeleton from modern carbon) and requires the consideration of the offset between the radiocarbon content of the atmosphere and the ocean (known as reservoir effect). The Uranium-series (U/Th) dating method relies on the decay of ^{234}U to ^{230}Th and allows accurate dating back to ~500 kyr. The strontium isotope dating method has been applied as well to date cold-water corals (Challenger mound, Porcupine Seabight, IODP Expedition 307; Kano et al. 2007), but is only reasonable for corals that are beyond the dating range of the radiogenic dating methods due to the rather high uncertainties of the determined age. Therefore, these ages are not considered for the following evaluation of the data inventory of North Atlantic coral ages.

During the last 30 years, more than 35 publications have been published presenting a total of 580 ^{14}C and U/Th coral ages obtained from North Atlantic framework-forming scleractinian cold-water corals (for references see Table 2). The herein presented coral age compilation derives from intense literature research as no database is available to date that provides a complete set of published cold-water coral dating. Besides the coral age itself, the following metadata were compiled (if available): (i) the coordinates and water depth of the coral sample, (ii) the coral species, (iii) the habitat type from which the coral was sampled (coral mound vs. other habitats), and (iv) the sampling type and sampling depth for samples that were retrieved from sediment cores (Table 2).

The majority of coral ages (92%) originates from the eastern side of the North Atlantic, where most dating records were obtained from coral sites off Norway, off Ireland and the UK, and along the Moroccan margin. In addition, a considerable number of coral ages has been published from Mediterranean coral sites, thereby >50% of the ages originate from the Alboran Sea (see also Fink et al. 2015). In contrast, from the western North Atlantic only few dating records exist from the Gulf of Mexico (Vioska knolls, West Florida slope), along the Blake Plateau off North and South Carolina (Florida-Hatteras slope, Cape Lookout) and from various seamounts (for references see Table 2; Fig. 5).

The majority of all published coral ages of framework-forming scleractinian species were obtained from *L. pertusa* (74%; Table 2), which simply mirrors the cosmopolitan occurrence and dominance of this species in many parts of the North Atlantic and its preferential selection for dating due to its thick massive theca easily providing sufficient uncontaminated material for analyses. Eighteen percent of all available coral ages were obtained from *M. oculata*, and very few ages exist for *S. variabilis* (~2%) and various dendrophylliid species (5%; Table 2). Seventy-five percent of all published coral ages derive from coral mound habitats and just 15% of all ages comprise corals sampled from habitats such as seamounts, canyons, and mud volcanoes. From 10% of all ages even no habitat information was available (Table 2). Just 34% of all dated corals originate from surface samples, whereas the majority of ages (66%) were obtained from corals collected by sediment cores (Table 2, Fig. 5). This is of particular importance as solely by coring (or drilling) several meters into the seabed, the possibility to obtain “old” coral material going far back in time is significantly enhanced. In this context, in particular, sediment cores retrieved from coral mounds (Fig. 3) are crucial to reconstruct recurring periods of sustained coral colonization on coral mounds and thus to identify periods of mound aggradation. Such mound-derived cores often exhibit discontinuous stratigraphic records marked by hiatuses (Fig. 3), representing intervals of stagnation, nondeposition, or erosion (e.g., Dorschel et al. 2005; Eisele et al. 2011; López Correa et al. 2012; Stalder et al. 2015).

Considering the temporal distribution of coral ages obtained from framework-forming scleractinian cold-water corals in the North Atlantic, 85% of all published dating coincide with the last 71 kyr (Fig. 5), hence encompassing the last glacial (lasting from 71-14.6 kyr BP), the last deglaciation (Bølling-Allerød: 14.6–12.9 kyr BP), the Younger Dryas (12.9–11.7 kyr BP), and the recent Holocene (lasting from 11.7 kyr BP until today). Just 15% of all available coral ages go beyond this time interval and originate mainly from cold-water coral sites within the Porcupine Seabight and along the Atlantic Moroccan margin (Fig. 5). This limited number of coral ages older than 71 kyr is likely attributed to the limited availability of long

Table 2 Metadata of coral ages obtained for framework-forming scleractinian cold-water corals collected in the eastern and western North Atlantic (including the Mediterranean Sea)

Coral site ID	Latitude range	Depth range	Coral ages[a]			Coral species					Habitat type			Sample type	
			Total	^{14}C	U/Th	Lp	Mo	Sv	D	NSI	CM	other	NHI	Core	Surface
	(°N)	(m)	(No.)			(No.)					(No.)			(No.)	
Eastern North Atlantic															
NOR	70.4–59.0	0–344	69	31	38	68	1	/	/	/	55	/	14	37	32
MIN	56.8	107–164	47	15	32	47	/	/	/	/	47	/	/	35	12
ROC	55.5	634–747	67	5	62	61	6	/	/	/	67	/	/	62	5
POR	52.3–51.3	610–1,005	82	4	78	75	3	/	/	4	81	1	/	75	7
BIS	46.9	286–866	8	0	8	8	/	/	/	/	2	6	/	0	8
MED	43.4–35.3	139–1,044	108	71	37	63	45	/	/	/	54°	15	39	43	65
eSMT	42.8–30.2	823–1,859	13	0	13	1	2	6	4	/	./.	13	/	0	13
MOR	36.6–35.0	356–897	116	25	91	62	44	/	10	/	85	31	/	89	27
MAU	17.7	444	21	0	21	21	/	/	/	/	21	/	/	21	0
Western North Atlantic															
wSMT	39.0–38.0	1,176–1,524	21	0	21	/	2	6	13	/	0	21	/	0	21
E-US	34.3–30.5	46–802	24	2	22	22	/	/	2	/	19	0	5	19	5
MEX	29.2–26.4	469–780	4	2	2	4	/	/		/	3	0	1	0	4
		SUM (No.)	**580**	**155**	**425**	**432**	**103**	**12**	**29**	**4**	**434**	**87**	**59**	**381**	**199**
		SUM (%)	**100**	**27**	**73**	**74**	**18**	**2**	**5**	**1**	**75**	**15**	**10**	**66**	**34**

Abbreviations: *NOR* Norway/Faroer, *MIN* Mingulay Reef, *ROC* Rockall Bank/Trough, *POR* Porcupine Seabight, *BIS* Bay of Biscay, *MED* Mediterranean Sea, *eSMT* NE Atlantic seamounts, *MOR* Moroccan margin, *MAU* Mauritanian margin, *wSMT* New England seamounts in the NW Atlantic, *E-US* eastern US margin, *MEX* Gulf of Mexico, *Lp Lophelia pertusa*, *Mo Madrepora oculata*, *Sv Solenosmilia variabilis*, *D* Dendrophylliid species (including *Enallopsammia profunda*, *Dendrophyllia alternata*, *Eguchipsammia cornucopia*), *NSI* unknown species, *CM* coral mound (note: for the Mediterranean Sea, coral ages obtained from the Santa Maria di Leuca coral province were considered as "coral mound" ages), *NHI* no habitat information

[a] Coral ages are originally published or compiled by Chen et al. (2015), De Mol et al. (2011), Dorschel et al. (2007), Douarin et al. (2013), Eisele et al. (2008, 2011), Fink et al. (2015), Frank et al. (2004, 2009, 2011), Matos et al. (2015), Mienis et al. (2009), Robinson et al. (2007), Schröder-Ritzrau et al. (2005), Stalder et al. (2015), Taviani et al. (1991), Titschack et al. (2015), van der Land et al. (2010, 2014), Wienberg et al. (2009, 2010)

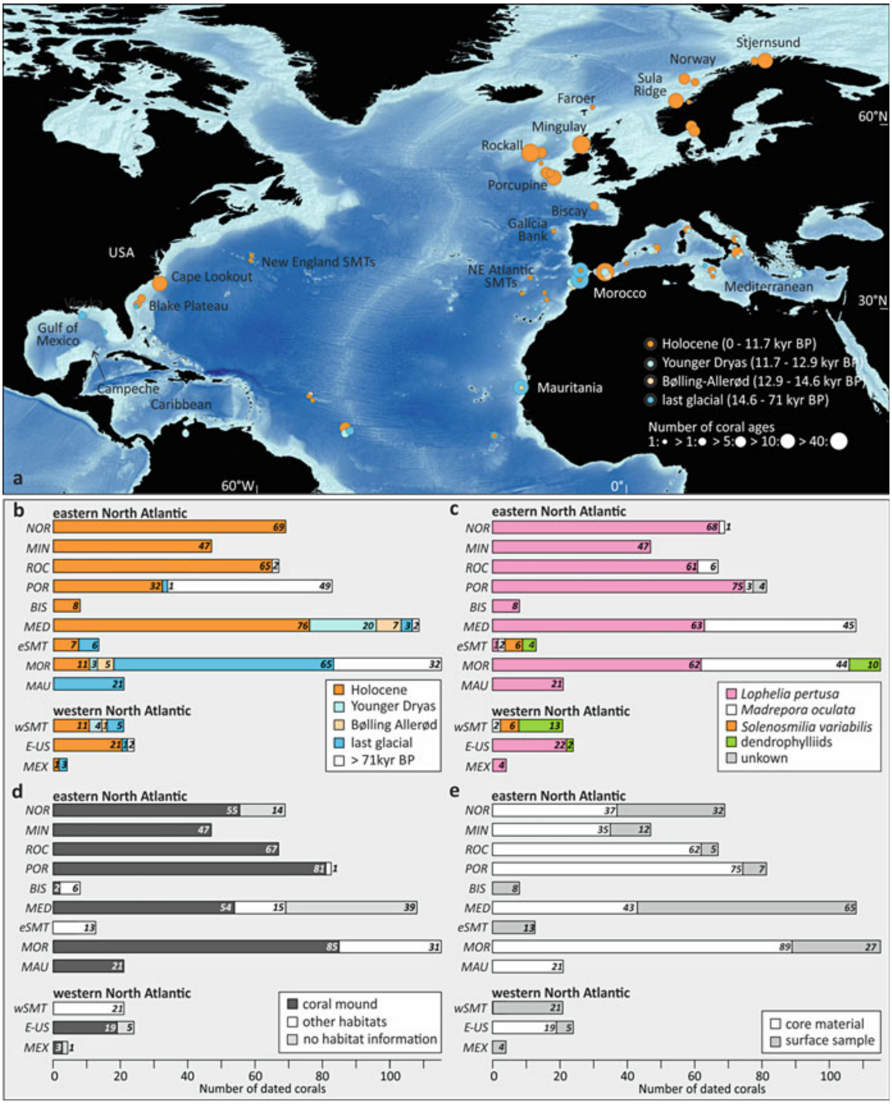

Fig. 5 Coral age distribution and metadata. (**a**) Map of the North Atlantic showing the spatial distribution of coral ages (comprising radiocarbon and Uranium-series dating) obtained from framework-forming scleractinian cold-water corals (mainly *Lophelia pertusa* and *Madrepora oculata*). coral ages are subdivided into climatic epochs and events (see legend for color code): Holocene (0–11.7 kyr BP), Younger Dryas (11.7–12.9 kyr BP), Bølling-Allerød (12.9–14.6 kyr BP), and the last glacial (14.6–71 kyr BP, comprising marine isotope stages MIS2-4). Size of circles represents amount of ages for a given coral site, varying between one and more than 40 coral ages. Radiocarbon and U-series dating (n = 580) obtained from framework-forming scleractinian cold-water corals (abbreviations for coral regions are given in Table 2) in relation to (**b**) the climate period in which the ages plot (Holocene, Younger Dryas, Bølling-Allerød, last glacial, and >71 kyr BP), (**c**) the dated coral species, (**d**) the habitat from which the coral samples originate (coral mound

sedimentary records. As coral mounds often exhibit lithification, conventional coring is limited to rather short records (<10 m). Consequently, the majority of the recent knowledge on coral mound chronology refers to the top sequence of most coral mounds. To overcome this sampling/dating bias in the future, the recovery of drill cores of several of tens of meters in length are needed, either drilled by ships (see Kano et al. 2007) or portable deployable drill rigs (such as the MARUM seafloor drill rig "MeBo"), to trace the temporal occurrence of corals and development of mounds going far beyond the last Glacial-interglacial cycle.

5.2 Spatiotemporal Distribution Pattern of North Atlantic Corals and Coral Mounds During the Last 71,000 Years

Dating framework-forming scleractinian cold-water corals yield the potential to provide valuable insights into: (i) the temporal occurrence of cold-water corals and (ii) the temporal development of coral mounds (if retrieved from coral mounds and combined with mound aggradation rates). Stratigraphic records obtained for the various coral (mound) sites in the North Atlantic (including the Mediterranean Sea) revealed very peculiar pattern with largely opposing regional chronologies. By comparing the observed spatiotemporal distribution pattern with environmental proxy data, regional environmental controls were identified, which are potentially linked to global oceanographic changes. This is best exemplified by the development of Challenger Mound (Porcupine Seabight, Irish margin), which was drilled down to its base during IODP Leg 307 (Kano et al. 2007). The initiation of this particular coral mound coincided with the onset of the northern hemisphere glaciation, while a major hiatus identified for the mound record corresponds to the mid-Pleistocene transition (Kano et al. 2007). However, numerous other examples are known, in particular, from the eastern North Atlantic that exhibit distinct regionally restricted time periods of coral mound aggradation.

During the last 71 kyr, the development of coral mounds encompassing the different mound provinces in the eastern North Atlantic exhibited a distinct latitudinal shift (Fig. 5). North of 50°N, comprising the Norwegian Sea and the Irish and UK margins, coral mounds experienced pronounced aggradation during the Holocene (Fig. 5). The formation of the Norwegian mounds is entirely restricted to the Holocene and started at ~11 kyr BP (Fig. 6), coinciding with the retreat of the Fennoscandian ice sheet beyond the present-day coastline (López Correa et al. 2012). The exceptional success of the Norwegian coral mounds is expressed in (short-term) maximum mound aggradation rates of ~600 cm kyr^{-1} to even 1,500 cm kyr^{-1}, which are the highest rates obtained so far (López Correa

Fig. 5 (continued) vs. other settings such as fjords, canyons, seamounts, mud volcanoes), and (**e**) the sample type (surface sample vs. sediment core). The data are separated between eastern and western North Atlantic and subdivided into the main coral regions

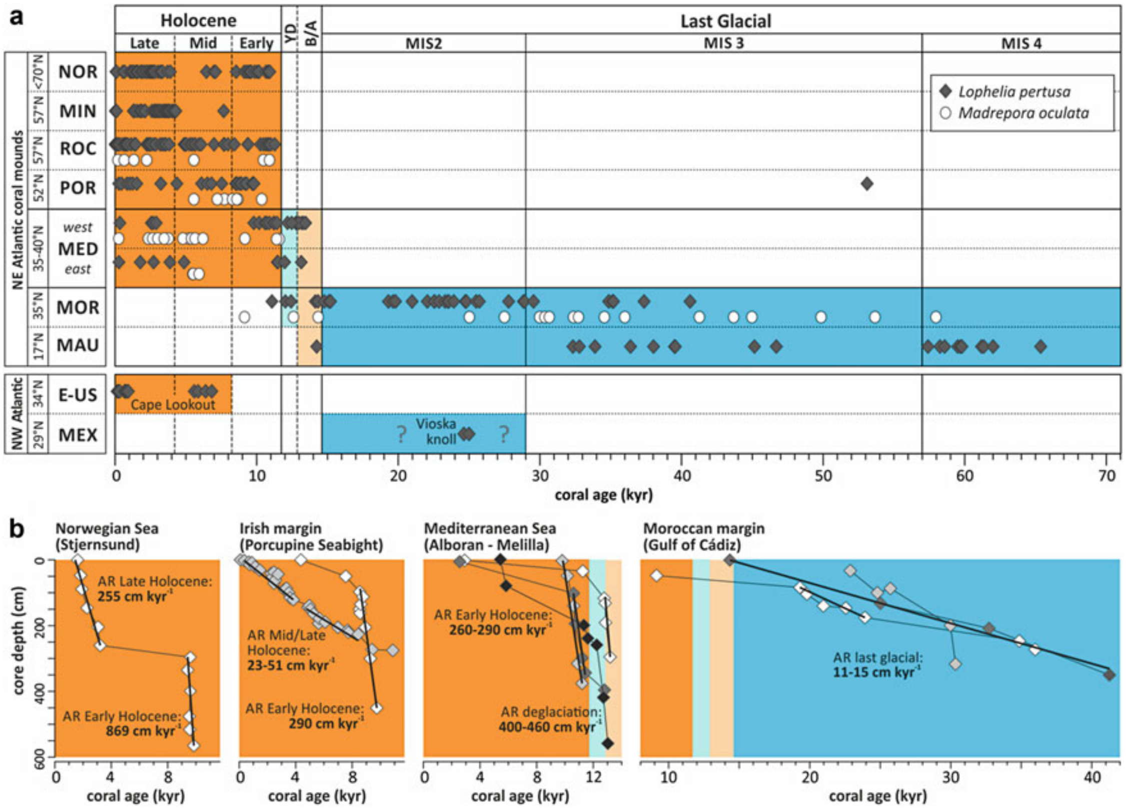

Fig. 6 Coral ages and mound aggradation. (**a**) Coral ages obtained from framework-forming scleractinian cold-water corals collected from various coral mounds in the North Atlantic (for references see Table 2). *YD* Younger Dryas, *B/A* Bølling-Allerød, *MIS* marine isotope stage. (**b**) Estimated mean coral mound

et al. 2012; Titschack et al. 2015). However, the aggradation of the Norwegian coral mounds also experienced distinct fluctuations, including stagnation during the Middle Holocene (Fig. 6), which are assumed to be linked to climatic/oceanographic changes (López Correa et al. 2012; Titschack et al. 2015). Coral mounds on the Scottish shelf started to develop during the Middle Holocene with maximum aggradation rates of 120 cm kyr^{-1} (Douarin et al. 2013), and the most recent mound aggradation phase identified for the large Irish coral mounds started at ~11 kyr BP, thereby maximum aggradation rates of up to ~220 cm kyr^{-1} have been estimated for individual mounds (Frank et al. 2009). In contrast, at coral sites south of 37°N, encompassing the Atlantic Moroccan and Mauritanian margins, mound aggradation was restricted to the last glacial and stagnated with the onset of the Holocene (Figs. 5 and 6; Wienberg et al. 2010; Eisele et al. 2011). Glacial mound aggradation rates for both southern areas vary between 1–53 and 28–45 cm kyr^{-1}, respectively, being significantly lower compared to the northern Holocene mounds (Fig. 6).

Another distinct pattern with opposing settings can be traced on a west–east transect when comparing the Atlantic Moroccan margin with the Mediterranean Sea. In contrast to the Moroccan mounds (see above), the few coral mound records from the western Mediterranean Sea (East Melilla coral province, Alboran Sea) revealed that mound aggradation was most pronounced during the Bølling-Allerød and the Early Holocene with very high mound aggradation rates of 260–460 cm kyr^{-1} (Fig. 6; Fink et al. 2013; Stalder et al. 2015). During the Younger Dryas and since the Middle Holocene, mound aggradation was significantly reduced or stagnated (Fig. 6). This pattern is additionally supported by the general occurrence of cold-water corals in the entire Mediterranean, which indicates a basin-wide occurrence of corals with the onset of the last deglaciation (at ~14 kyr BP; Fink et al. 2015) and their presence in the Mediterranean Sea until today.

In all regions described above, the proliferation of cold-water corals and periods of pronounced mound aggradation was interpreted to be triggered by specific environmental conditions; thereby the availability of food is of primary importance for these sessile organisms. Nevertheless, distinct key factors enhancing and delivering a sufficient amount of food were proposed for the different areas. Vigorous bottom current regimes were assumed to be of primary importance by enhancing the delivery of food particles for cold-water corals forming mounds along the Irish margin during the Holocene (Dorschel et al. 2005), and the increase in current

Fig. 6 (continued) aggradation rates (*AR*) obtained for selected sites in the eastern North Atlantic (off Norway, Ireland, and Morocco), and in the Mediterranean Sea. *Squares* represent coral ages obtained from coral fragments collected at different depth intervals of sediment cores. Different colors of squares used for one coral site represent different cores. Norwegian Sea, *white*: core STJ-POS325-472 (López Correa et al. 2012). Irish margin, *white*: core MD01-2459G, *light gray*: core MD01-2463G; (Frank et al. 2009). Mediterranean, *white*: GeoB13728-2, *light gray*: GeoB13729-1, *dark gray*: GeoB13730-1, *black*: TTR17-401G (Fink et al. 2013; Stalder et al. 2014). Moroccan margin: *white*: M2004-02, *light gray*: GeoB12102, *dark gray*: GeoB12740 (Wienberg et al. 2010) strength is assumed to be related to the reentrance of the Mediterranean Outflow Water in this northern coral area (De Mol et al. 2005). Increased primary production enhancing the availability of food for corals was assumed to control mound aggradation along the Atlantic Moroccan and Mauritanian margins during the last glacial (Wienberg et al. 2010; Eisele et al. 2011) as well as in the Mediterranean Sea during the Bølling-Allerød and the Early Holocene (Fink et al. 2015). For the Mediterranean, a close relationship to intermediate water masses (mainly Levantine Intermediate Water) is assumed, as since the last deglaciation corals were solely present during intensified intermediate water mass circulation (Fink et al. 2015). Furthermore, Fink et al. (2012) highlighted reduced O_2 concentrations, which prevailed during the Middle Holocene sapropel S1 event in the eastern Mediterranean, as a key factor that hampered cold-water coral growth and mound aggradation during this particular time interval.

The very low number of coral ages being available for the western North Atlantic (Table 2) causes a very high uncertainty in the so far observed temporal occurrence pattern from this region. However, a very first study dealing with coral mounds off North Carolina (Cape Lookout) showed that their development in this area seems to be restricted to interglacials. The youngest period of mound aggradation started (at least) at ~7 kyr BP (Figs. 5 and 6), when bottom current strength and bottom water temperatures increased, likely triggered by the influence of the Gulf Stream (Matos et al. 2015). Beside this study, the stratigraphic range of the NW Atlantic cold-water corals and mounds remains poorly constrained.

Overall, the statistical significance of any coral age dataset is a crucial factor and needs to be considered before interpretation. Statistically, most important are: (i) the total number of different sampling locations (spatial variability) for a given coral region from which coral ages were obtained to define periods of sustained coral growth on a regional scale and (ii) the total number of coral ages obtained for the different coral regions in the North Atlantic to define (paleo-) biogeographical margin- or even basin-wide patterns. For example, all published coral ages from the Mauritanian margin (n = 21) derive from one sediment core (Eisele et al. 2011), hence questioning if this age dataset is really representative for this region. And even for the Irish margin, from which a considerable number of coral ages originates (n = 149), all ages were obtained from just 13 coral mounds, which is a very low number compared to the >1,000 coral mounds being reported from this region (Roberts et al. 2009).

Nevertheless, despite any statistical constraints, the patterns described above provide some fundamental insights regarding the temporal occurrence of framework-forming scleractinian cold-water corals and the development of coral mounds in the North Atlantic during the last 71 kyr. In conclusion, a large variety of environmental variables has been identified, thereby key environmental controls were proposed to trigger coral growth and mound aggradation in the different Atlantic coral mound provinces. However, it is obvious that any temporal distribution pattern (regardless of the spatial scale) cannot be sufficiently explained by one (key) environmental parameter alone. It is rather the interplay of various environmental parameters, with each parameter acting as potential stimulator or suppressor, that controls coral proliferation as well as mound aggradation. As most environmental variables being relevant for framework-forming cold-water corals and coral mounds are strongly related to water masses, variations in water mass characteristics and ocean circulation induced by climate change likely explains the observed climate-related spatial shifts in the temporal occurrence of corals and mound aggradation within the North Atlantic. However, details about the regional mechanisms behind this linkage still largely need to be explored and might vary from region to region.

6 Future Directions

Much progress has been made in recent years to increase our understanding about the North Atlantic-wide spatiotemporal distribution of framework-forming scleractinian cold-water corals and related environmental controls. Nevertheless, the available datasets (used here for a thorough evaluation) also reveal some distinct limitations that may hamper a further in-depth understanding of these fascinating eco-/geo-systems in the North Atlantic. These mainly comprise: (i) a past bias in exploration focusing on the eastern North Atlantic and the difficulties to explore remote areas such as seamounts and the Mid-Atlantic Ridge; (ii) the paucity of data for some species and an often largely incomplete set of associated sampling metadata being important to evaluate any coral record; (iii) a clear differentiation between sites where the corals act as habitat provider and sites where they form coral mounds and thus additionally act as a seafloor modifier; (iv) the difficulties to identify the status of coral mounds (aggradation vs. stagnation) today and during the past; and (v) the limited understanding of the processes regulating the interplay between coral growth, formation of a coral framework with a high baffling capacity and sediment supply, which are prerequisites for coral mound formation.

To overcome these limitations, new research strategies need to be developed. First and foremost, a fast implementation of any newly discovered cold-water coral finding (including coral mounds) into public databases is indispensable. There is an urgent need to continuously update and maintain available databases or, even more promising, to agree on one single database (for example, by merging national or project-related databases), which is ideally well-known and broadly accepted in the international scientific community and guarantees a high quality of data maintenance and management. In addition, it is essential to complement each coral record by a full set of metadata including the primary sampling code, positioning data (coordinates, water depth), species information, and vitality status of the observed coral, and habitat information. To date, we rarely know whether any given record corresponds to an isolated occurrence or a more substantial coral mound formation. This additional information should always be provided when adding new coral records, as it is crucial in evaluating the North Atlantic basin-wide (and global) distribution of cold-water corals and coral mounds, and to examine environmental controls. In this context, comprehensive environmental datasets (bathymetry, temperature, salinity, etc.) in high spatial resolution supplemented by more in situ measurements (such as lander-based long-term measurements of physical and chemical bottom water mass properties) are urgently needed. Both will improve our understanding of environmental controls and ecological constraints, in particular for distinct coral species, and to examine the local environmental heterogeneity in detail.

The number of dating obtained from framework-forming scleractinian cold-water corals is still rather low, but will certainly significantly increase in the near future, consequently improving our understanding about the hypothesized climate-related regional shifts in coral occurrence and mound formation as observed for the eastern North Atlantic. This asks for the establishment of a comprehensive open access database for coral dating, which so far does not exist, to manage and maintain existing as well as upcoming dating. A future coral age database (preferably storing ages obtained from all relevant coral species comprising framework-forming and solitary scleractinians as well as octocorals and antipatharians) should contain beside the coral age itself: (i) a reliable taxonomy; (ii) a thorough documentation about the origin of each coral sample selected for dating including its positioning, water depth, sampling type, and sampling depth as well as habitat information; and (iii) all relevant information about the dating laboratory such as about mechanical and chemical cleaning procedures, settings and specifications of the dating machine, as well as the original analytical raw data (isotopes and isotope ratios) of the respective dating method. Only this information will allow for a recorrection or recalibration of dating with any new arising calibration approach/update and, thus, will ensure a future comparability of coral ages.

In addition to a reliable taxonomy, an in-depth biological and ecological knowledge about the cold-water coral species used for stratigraphic studies is of utmost importance due to two aspects. First, each species occupies a specific ecological niche expressed in species-specific environmental preferences and tolerances, which for the majority of species still need to be identified but already ask for a separate treatment for future studies. Second, regarding the scientific question that is envisaged to be solved it needs to be considered that solely framework-forming scleractinian corals provide suitable information about coral mound development and related environmental controls, while solitary corals rather have the potential to provide archives for paleo-oceanographic reconstruction and ecological studies (e.g., Thiagarajan et al. 2013). Regarding the development of coral mounds, increasing attention should be given to the modern mound formation processes (interplay between coral framework and sediment supply) and the reconstruction of mound aggradation rates. Only mound aggradation rates have the potential to provide detailed information about mound development varying between slow and fast aggradation, with the latter indicating most prolific periods for corals under optimal environmental conditions. In this context, detailed computed tomography analyses can improve the identification of various preservation stages and Hiatuses (Fig. 3), which can be used to optimize sampling strategies for dating corals from sediment cores retrieved from coral mounds (Titschack et al. 2015). However, also periods of mound growth stagnation and/or erosion provide some valuable information, as these periods point to environmental conditions, during which corals may still be present but suffer from unfavorable conditions and in the long term largely decline.

Consequently, future studies on coral mound records should follow a strategy, which concentrates on the entire set of potentially relevant environmental parameters instead of focusing on one key parameter to gain a comprehensive picture of the conditions stimulating or suppressing cold-water coral occurrence in general and coral mound development in particular. Thereby, species-specific aspects and their interplay with relevant environmental variables need to be considered. By facing these challenges, overcoming the current data limitations and merging the knowledge of different research disciplines (e.g., biology, geology, oceanography, climatology), our understanding of the fascinating world of framework-forming scleractinian cold-water corals will improve tremendously.

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7 Cross-References

- ▶ Global Biodiversity in Cold-Water Coral Reef Ecosystems
- ▶ The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep
- ▶ Trophic Ecology and Habitat Provision in Cold-water Coral Ecosystems

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Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles

26

Carme Huguet

Abstract

Seston refers to the organisms (bioseston) and nonliving matter (abioseston) swimming or floating in a water body. Bioseston includes plankton as well as nekton. The abioseston comprises mainly detritus as well as minerals. A classical approach is to correlate sedimentary organics to quantitative benthic fauna characteristics. This poses two main problems: (a) finding the most appropriate unit to assess organics in the sediment and (b) the nutritional process is complex encompassing ingestion, absorption, and assimilation and thus cannot be assessed linearly. For example, selectivity is associated to ingestion, but not everything ingested is digested and absorbed by the consumers, and incorporation is dependent on meeting specific nutritional requirements. Fate of particulate organic matter (POM) is influenced by benthic fauna through nutrition and bioturbation, and in turn POM influences benthic faunal biomass, reproductive output and abundance, making relationships between seston and benthic fauna bidirectional.

As nutrition results from processes which do not affect the whole sedimentary POM pool, there is little hope of linking benthic secondary production and biomass to bulk descriptors. This makes essential to identify and use more specific biochemical parameters. Quality of seston can be assessed through total organic matter, organic carbon, nitrogen content, total and available proteins (TPRT and APRT), carbohydrates, lipids, and total and enzymatically hydrolysable (available) amino acids (THAA and EHAA, respectively). Parameters such as digestibility and composition are key to understand seston nutritional value. So far, available amino acids and lipids have been shown to be the best descriptors of food nutritional value and they are associated to the most labile fraction of particular organic matter.

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Suspension feeders and other sessile and vagile organisms have adapted their feeding strategies to use both biotic and abiotic seston. These organisms compose a highly diverse benthic community, regardless of their original food source being similar or not. In this chapter, the relationship of animal forest components (benthos filter feeders) and seston quantity and quality are described and their relationships explored. Organisms may adapt to changes in seston though storage and then consumption at times of low seston presence. Notably, a lot of organisms change their activity either by feeding on different prey or by constraining activity to highly nutritious times. A clear example of the latter is the coupling between phytodetritus pulses and reproductive activity observed in many benthic communities.

Keywords

Seston • Biotic • Abiotic • Particulate organic matter (POM) • Benthic community • Ingestion • Digestability • Assimilation • Absorption • Phytoplankton bloom • Suspension feeding • Nutritional value • Available proteins • Lipids • (Enzymatically hydrolysable) amino acids

Contents

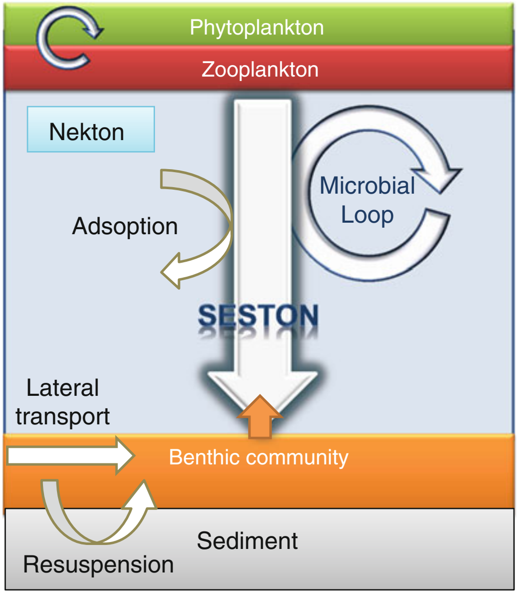
1 Introduction

Primary production is the synthesis of organic compounds from atmospheric or aqueous carbon dioxide. It occurs mainly through the process of photosynthesis (Eq. 1), which uses light as its source of energy, but it also occurs through chemosynthesis (e.g.,: Eq. 2), which uses the oxidation or reduction of chemical compounds as its source of energy.

$$CO_2 + H_2O + \mathbf{Light} \rightarrow CH_2O + O_2 \tag{1}$$

$$CO_2 + O_2 + \mathbf{4\,H_2S} \rightarrow CH_2O + 4S + 3H_2O \tag{2}$$

Fig. 1 Processes of seston production, transport, and degradation



In both cases, the end point is a polymer of reduced carbohydrate, $(CH_2O)n$ which can be used lately as a building block for more complex compounds such as lipids or proteins. Primary production can take place through the mediation of micro- and macroalgae, bacteria, and some dinoflagellates mainly in the photic zone of the oceans. The produced organic matter is then consumed by heterotrophs such as archaea, bacteria, zooplankton and nekton, which transfer these organic molecules (and the energy stored within them) up the food web. The complexity of the food web will depend on the environment and the stage of development of the ecosystem with nutrition-rich, older environments usually displaying the most complex organization. All heterotrophic organisms will produce organic particles that can then sink to the bottom (Fig. 1), autotrophic organisms will also form seston usually after death and clumping at the surface. Both heterotrophic and autotrophic origin organic matter will be essential to maintain the benthic sessile and vagile organism. As most of the activity takes place in the photic area of the water column, the amount and quality of seston reaching the bottom will depend mainly on production, but also consumption, lateral transport, degradation, particle size, and shape.

Particles from heterotrophic consumers are mainly produced by packaging in fecal pellets or by death of the heterotroph organisms, however, there is also some amount of material that is liberated due to messy eating. Messy eating means that some heterotrophic organisms may not efficiently capture or use all food that enters their mouth area; there may be some reflux, selective dumping, or loss of small parts of ingested organisms. This essentially results in the release of organic rich particles that can then be incorporated in seston. Once the particle is formed, further reworking may occur as it sinks down to the bottom. The particle reworking may have opposing effects: on the one hand, organic molecules may be stripped making the particle inorganically rich; on the other hand, it has also been reported an increase in nutritive characteristics through the action of bacteria (e.g., Azam and Long 2001; Rossi et al. 2003). Aggregation can also occur without mediation of heterotrophic organisms, through the action of: (a) mucilaginous substances or (b) mass falls of phytoplankton that sieve out material from the water column. It has been shown that particles may grow as they travel down the water column though surface sorption of smaller ones (Azam and Long 2001).

Seston's quality and quantity will be directly linked to biological production and consumption processes which will be explained in depth in Sect. 4.1 of this chapter. Both static and dynamic physical factors will influence the quantity and quality of the seston production that reaches the bottom. This will depend on transport distance and speed as well as timing. This point will be further elaborated in Sect. 4.2.

Particle sinking is an important process for the transportation of organic carbon from surface waters to the sea floor. It is estimated that only 3% of the surface production reaches the deep sea (below 2,500 m) but that percentage is higher in coastal areas. This organic matter (seston) supplies the complex benthic communities with a high quality material that fuels benthic production. The quantity and quality of the seston particles has been associated to benthic feeder's fitness parameters such as growth or reproduction success. Benthic suspension feeders will actively exploit seston particles and part of their organic carbon will be returned/ recycled through dissolved organic carbon (DOC), **fecal pellets,** and the release of meroplanktonic larvae (e.g., Ribes et al. 1991). Therefore the benthic activity will in turn contribute to the seston pool.

2 What Is Seston?

Seston is the particulate matter suspended in bodies of water such as lakes and seas. Seston is composed by organisms (bioseston) and nonliving matter (abioseston) swimming or floating in a water body. Bioseston includes plankton as well as nekton. The abioseston comprises mainly detritus but may also include mineral particles and fecal pellets. Abiotic components will range from small sand to clay sizes, while biotic ones can go from virus to macroplankton. Fecal pellets will fall in between these two categories as they may contain both abiotic and biotic components. In coastal areas, there will be a high contribution from primary producers such as phytoplankton while further away from the coast a substantial increase in heterotrophic organisms is observed (Gasol et al. 1997).

Typically a seston particle will be composed of abiotic and biotic components in different proportion (Fig. 2) depending on mineral input, type and amount of primary production, and energy of the system in the shape of currents, for example at a given location. Minerals and inorganic particles' average sizes range between 2 and 175 μm (Fig. 2). Small clay-organic complexes have also been described and are typically around the 100 μm size point. The biggest seston component is usually the marine snow which may also incorporate both organic and inorganic components

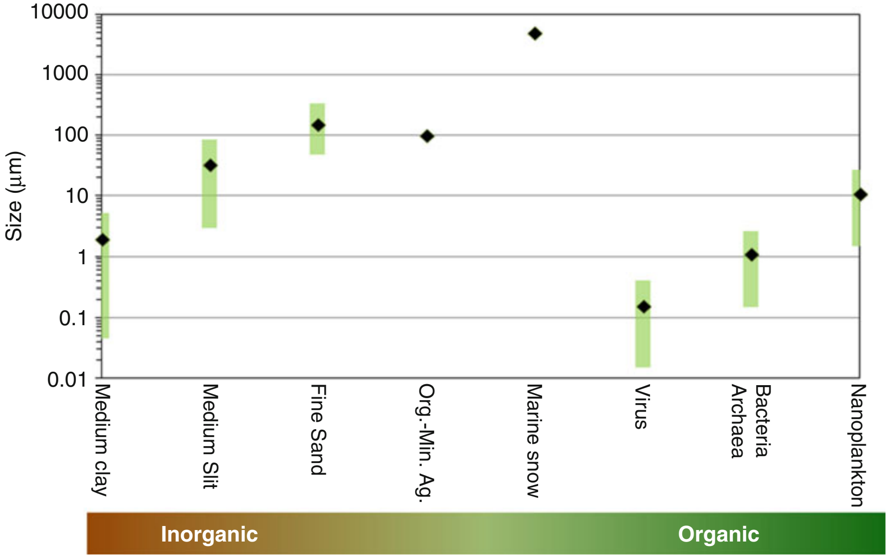


Fig. 2 Size fraction distribution of different seston particles. The approximate proportion of organic and inorganic components is shown in the *colored bar*

and whose size can be bigger than 500 µm (Fig. 2 and Table 1). The suspended particulate matter (seston) can also be subdivided in nanoparticles (<20 µm), microparticles (20–200 µm), and mesoparticles (200–1,000 µm). Generally, the smaller particles have the lowest nutritional value being mainly composed of inorganic matter (Díaz et al. 2007). While increased size is usually linked to an increment in the proportion of organic carbon in the particles.

Areas close to the coast will tend to be richer in minerals of bigger sizes specially if situated near a river or if they are subject to high resuspension (Shimeta and Jumars 1991). Seston or POM (particulate organic matter) comprises a wide range of sizes (Fig. 2), for the particles to sink and thus eventually reach benthic organisms they need to surpass the 0.7 µm threshold which is the critical size threshold above which particles can sink. Inorganic particles will be denser than organic ones and thus in this case may be able to sink at sizes below this critical threshold. In Table 1, we can see typical seston particles dimensions, density, and settling velocity. Sand will be the fastest to sink, followed by invertebrate nonmotile larvae (0.1 cm s^{-1}) and the marine snow (8.8×10^{-2} cm s^{-1}), being the slowest the medium clay (8.9×10^{-5} cm s^{-1}) and bacteria (2.7×10^{-6} cm s^{-1}). The settling speed will affect the nutritious quality of the particle reaching the benthic community. The slower the transit through the water column the higher the opportunity for the nutrients in the particle to be mineralized either through degradation or bacterial consumption. On the other hand, bacterial activity may enrich the nutrient value of certain particles (e.g., Rossi et al. 2003) and additionally a slow transit may allow a more efficient sorption of particles through the water column transit. A fast transit of the particle should in principle mean that fresh organic matter will reach the benthic community

Table 1 Typical seston particle dimensions, density (as calculated by density of particle minus density of water), and particle settling velocity (Modified from Shimeta and Jumars 1991)

Particle	Dimensions (μm)	Density p-density w (g cm^{-3})	Particle settling velocity (cm s^{-1})
Medium clay	1	1,630	8.9×10^{-5}
Medium silt	20	1,630	3.5×10^{-2}
Fine sand	150	1,630	2
Org.-min. aggregate	100	0.088	5.0×10^{-2}
Bacterium	0.1	0.050	2.7×10^{-6}
Small phytoplankton	10	0.069	3.4×10^{-4}
Large phytoplankton	100	0.009	5.0×10^{-3}
Invertebrate larvae	500	0.073	0.1
Marine snow	5,000	6.5×10^{-5}	8.8×10^{-2}

providing a better seston quality. However, particles with a higher inorganic content will sink faster and yet carry very little or no organic content.

Seston input is preferentially vertical but there is also a lateral transport component as well as resuspension (Figs. 1 and 3). The relative importance of each mechanism will depend on (a) production of the area and (b) physical factors such as currents or storms. The physical factors will be further examined in Sect. 4.2.

3 Where Is Seston Produced?

Seston entering a marine environment can have an autochthonous or allochthonous origin (Fig. 3). Allochthonous particles will be produced in terrestrial settings and transported to coastal areas by rivers, continental run-off, and wind. Particles of continental origin may have an organic component, but are mostly mineral rich. Particles carried by wind will be mainly within the clay and silt categories (~0.0002–0.06 mm). While they have been shown to have a great impact on phytoplankton communities (through iron fertilization), they are very small and will therefore not constitute a major seston source. Unless aided into aggregating to form bigger particles, for example, though presence of mucilaginous substances or flocculation (though salinity changes) most of the fine particles will remain in suspension. Surface runoff and river discharge, especially when coupled to storms, can carry much bigger particles that will also have a higher organic matter proportion and thus be very important seston components in certain coastal areas. Especially in the case of riverine discharge, colloids will come out of suspension in the form of flock or flake when fresh water mixes with the saltier marine water. Surface runoff due to enhanced precipitation and/or storms can also be the source of massive inputs of allochthonous-sourced organic matter. Other windfalls of organic matter may be caused by tsunamis, hurricanes, or a variety of extreme geo-climatic phenomenons.

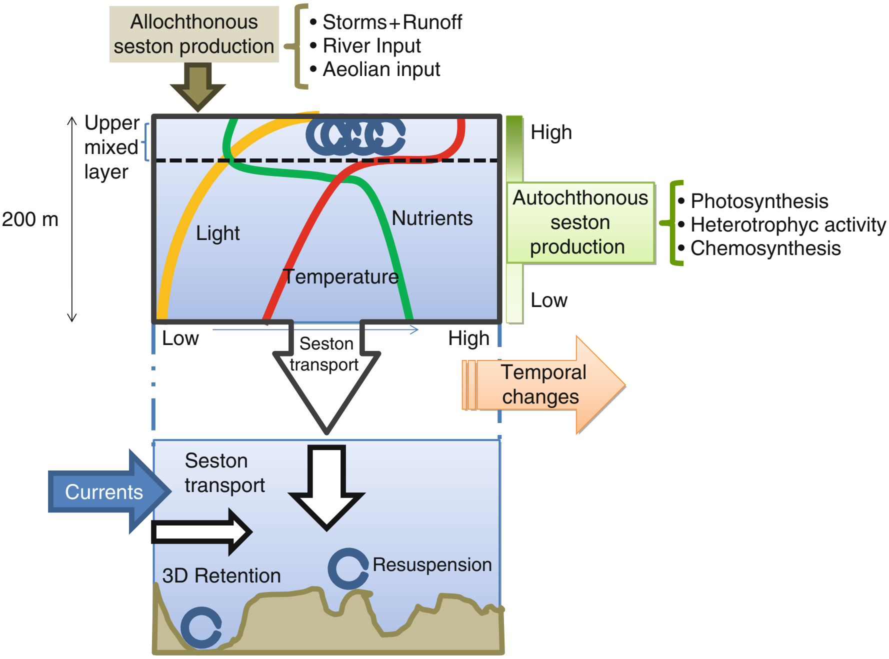


Fig. 3 Conceptual figure of factors affecting the quality and quantity of seston in the water column

Autochthonous seston formation will take place in ocean basins and either sink to the bottom below the production area or be laterally transported by currents. Production of seston takes place preferentially at the surface layers where light allows primary production. Light is key to perform photosynthesis thus primary production will be constrained to the first 200 m (Fig. 3). However, due to the nutrient and CO_2 concentrations being higher together with most wave lengths being mostly limited to the upper 30 m, most of the water column primary production will take place there. Coupled to that superficial primary production, a high density of food for heterotrophs and thus a high level of heterotrophic activity will also take place in this water column portion (Fig. 1). While other processes that are not light dependent such as bacterial chemotrophy can take place as the particle sinks down the water column, this will represent a very small portion of seston production compared to the surface processes.

Production can be controlled by factors such as nutrient supply and favorable environmental conditions but will also depend on the number, type, and interactions of the species present at a certain area. For example, areas with favorable conditions will foster higher productivity making it easier for some of that productivity to reach the bottom. As a general rule, coastal areas have higher nutrient levels and thus can sustain a stronger primary production and as a result a denser benthic community, while off the shore the heterotrophic activity will be relatively more important.

4 What Can Change Seston Quality or Quantity?

Particle flux studies in several shelf habitats indicate that 6–60% of the net annual primary production can reach the seafloor (Ivan Valiela 1995) but part of that may be inorganic. The properties of typical seston particles encountered in particle capture studies are shown in Table 1 (Shimeta and Jumars 1991). While benthic organisms will likely consume all seston, the higher the inorganic to organic ratio, the most costly will the feeding be, as no direct benefit will be obtained from the inorganic component. On the other hand, inorganic components will aid faster sinking and thus preserve the quality of the transported organic components, making the particles more nutritious.

The speed of transport will influence the quality of seston, especially bioseston reaching the benthic community: the faster the transport the fresher the material will be. Fresher material will generally be organic rich and provide better nutrition to effort ratio for the benthic organisms. Some organisms may possess ballast such as shells or other hard parts which will make them sink faster. For some species such as haptophytes microalgae, their carbonate skeleton will provide ballast and hence will help the organisms sink and reach the bottom once they die. In the case of haptophyte, diatoms, and other shelled organisms the shell will not only aid fast transport but also enhance preservation of the organic matter within the shell, making the material fresher and thus higher quality when reaching the benthos. However, the presence of shell may also make it more difficult for certain benthic organisms to access the remaining organic matter. While in some cases that high speed may be due to inorganic material acting as ballast and increase in the critical sinking mass can also be achieved through aggregation of organisms, a clear example of this are the mass falls detected in Antarctic waters (Elias-Piera 2014). Similarly, phytoplankton fallouts from the euphotic zone have been shown to reach deep water environments in temperate areas (Billet et al. 1983) and also in northeast Greenland (Ambrose and Renaud 1997).

Seston quality and quantity may vary over time and will be distinct at different locations, therefore we can describe this as a 3D variability incorporating a vertical, a lateral, and a temporal axis. For example, biogeochemical characteristics of surface sediment and POM have been shown to vary regionally and locally, for example the Mediterranean is clearly poorer than other oceans (Table 2; e.g., Isla et al. 2006). Regional changes between nutrient content and depth can also be seen in Table 2. Availability of seston may also vary in the temporal scale, for example, through enhanced primary production in the surface at certain times of the year (Ambrose and Renaud 1997; Billet et al. 1983; Elias-Piera 2014). Seasonality on storms and water currents will also affect seston quality and quantity and can in some cases present seasonal segregation. Additionally, the type of organisms will also affect seston quality. For example, changes in total seston quantity and quality were found to be associated to river discharges and marine circulation in the Bay of Biscay (Díaz et al. 2007).

Table 2 Comparative data of main biochemical contents in sediment and settling particulate organic matter (POM) in several regions of the world's ocean (Modified from Isla et al. 2006)

References	Area	Depth (m)	Proteins (mg g^{-1})	Lipids (mg g^{-1})	Carbohydrates (mg g^{-1})
Sea floor sediment					
Albertelli et al. (1999)	Mediterranean	135	0.35	0.35	1.6
	Mediterranean	90	0.27	0.24	1.7
Grémare et al. (2002)	Mediterranean	340		0.16	3.53
	Mediterranean	94	0.16	2.71	0.06
Danovaro et al. (2000)	Mediterranean	200	1.24	0.14	1.32
	Mediterranean	1,540	0.16	0.08	2.19
Relexans et al. (1996)	Tropical Atlantic	5,000	0.5	0.12	0.04
	Tropical Atlantic	3,500	0.7	0.19	0.07
Neira et al. (2001)	South Pacific	27	5.75	7.2	5.8
	South Pacific	34–120	6.34	3.16	3.23
Fabiano and Danovaro (1999)	Antarctica	560–580	2.37	0.37	0.78
	Antarctica	430–450	0.33	0.05	0.3
Isla et al. (2006)	Kapp Norvegia, Antarctica	295–421	4.81	2.99	2.25
	Four Seasons Bank Antarctica	63–107	3.94	1.1	2.13
	Austasen, Antarctica	209–480	2.29	1.73	1.64
Settling POM					
Grémare et al. (1997)	Mediterranean	30	15.5	7.2	36.5
Rossi et al. (2003)	Mediterranean	30	11.5	5.6	21.81
	Mediterranean	30	11.7	9.5	12.42

4.1 Biological Factors

The quantity of seston will be directly linked to the amount of primary production. More productive areas will generally present high seston levels while oligotrophic zones will yield a sparser distribution of the organisms (e.g., Isla et al. 2006). Areas where there is high terrestrial input, either through riverine or eolian paths, will generally present high production, while water masses further away from the coast will tend to be more oligotrophic as there are less nutrients and thus a smaller community of primary producers can be sustained (e.g., Díaz et al. 2007). Areas with higher production will produce more seston particles; for example, Mediterranean waters will present low particles while Antarctic ones will show higher seston density (e.g., Gili et al. 2006; Isla et al. 2006). Areas with higher species diversity will have longer food webs and more complex biological 3D structures. Areas with low phytoplankton production can still produce high particle counts but they will be preferentially of inorganic composition (e.g., Galimany et al. 2015).

Regarding the settling speed, in the case of bioseston vertical migration can also play a role as some organism will perform daily downward migrations to tap resources from deeper layers and/or hide from predation; this can then be easily reached by benthic organisms and thus consumed (Elias-Piera 2014; Gili et al. 2006). For example, in Antarctic waters the vertical migration of *Salpa thompsoni* looking for phytodetritus material from the spring-summer bloom accumulated in the bottom has been reported to aid opportunistic alcyonarian *Anthomastus bathyproctus* to cover its nutritional needs during the early autumn period (Gili et al. 2006). In temperate latitudes phytodetritus falloffs have been reported directly after surface blooms and fresh pigments can still be detected when reaching abyssal depth indicating fast movement through the water column (e.g., Billet et al. 1983; Graf et al. 1982). In this case, it is probably through aggregation of phytoplankton after death. Aggregation through mucilaginous substances has been reported to aid sinking or POM. Organisms such as Diatoms produce exogenic mucilaginous substances that will aggregate both organic and inorganic particles, this process will increase the size of particles and it will help create bigger seston particles and thus speed up sinking. When a peak of phytoplankton takes places, such as in upwelling zones or in cold areas during the protracted productive season, mass falls may occur. The enhanced phytoplankton population will eventually run out of nutrients in the surface waters and die, as many of the phytoplankton organisms have mucilaginous compounds they will aggregate creating mats of phytodetritus. This mats will eventually sink to the bottom sieving out material from the water column (e.g., Billet et al. 1983).

The type of production (primary or secondary) incorporated into the particles will also change their nutritious quality providing different nutrients to benthic organisms. Seston can contain both heterotrophic (bacteria + protozoa + mesoplankton) and autotrophic (algae) biomass. In this sense a ratio of heterotrophic over autotrophic (H:A) biomass can be calculated. The H:A ratio will not be constant but change according to primary production and phytoplankton biomass (Gasol et al. 1997) and thus it will depend on the study area but also on sampling seasonality (Fig. 4).

Observed patterns in primary production and carbon export from the euphotic zone suggest that the relative contribution of planktonic heterotrophs to community biomass decline along gradients of primary production and phytoplankton biomass (Gasol et al. 1997). The proportion of heterotrophs in the plankton of unproductive regions is very high resulting in inverted biomass pyramids, whereas the plankton of productive areas are characterized by a smaller contribution of heterotrophs to community biomass and a normal biomass pyramid with a broad autotrophic base (Fig. 4).

A difference is also observed between the type of area; while autotrophic biomass showed a similar range of variation, the open-ocean communities supported significantly more heterotrophic biomass in the upper layers than do coastal communities for a given autotrophic biomass (Fig. 3 and Table 2). These differences in the

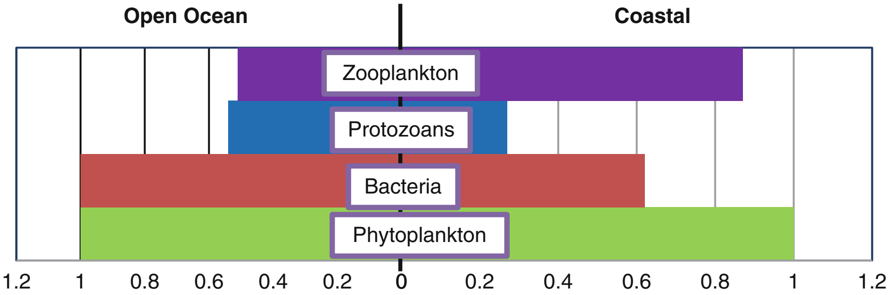


Fig. 4 Distribution of mean zooplankton, protozoan, and bacteria biomass relative to autotrophic biomass (Modified from Gasol et al. 1997)

biomass structure of the community could be explained by the changes in the biomass-specific rates of phytoplankton production that seem to occur from ultraoligotrophic to eutrophic marine regions, but other factors could also generate them. The patterns described suggest a rather systematic shift from consumer control of primary production and phytoplankton biomass in open ocean to resource control in upwelling and coastal areas (Gasol et al. 1997).

4.2 Physical Factors

Physical processes will influence phytoplankton distribution, especially at high-energy levels where community development is enhanced (e.g., Ribes et al. 1991). Physical factors can be subdivided into dynamic (e.g., currents, storms) and static (e.g., bottom topography) and will mainly affect the speed of transport and distribution of seston particles (Fig. 3). There are two main kinds of transport, vertical and lateral. Lateral transport is largely controlled by lateral current speed and direction, while resuspension will also be associated to the benthic topography both in terms of physical and biological structures. A clear example of a complex three-dimensional biological structure would be the animal forest (see ▶ Chap. 1, “Animal Forests of the World: an overview” of this book for further details). The benthic community will create a hydrodynamic environment which favors particle sedimentation, retention, and cycling. The vertical variation of physical factors such as temperature and salinity changes (Fig. 3) will clearly influence the abundance and possibly composition of planktonic-nektonic organisms. The existence of multiple sublayers separated by thermo- or haloclines allows habitat partitioning and hence enhances community diversity. In coastal areas, this vertical structure could become more homogeneous due to continuous mixing and in this case lateral heterogeneity rather than the vertical one may be more important to control production.

Apart from the vertical input, lateral transport is largely recognized as one of the main factors in controlling seston quantities both through lateral transport and resuspension. Lateral transport through currents, tides, and storms may bring organic matter to otherwise oligotrophic areas; however, the quality of the material provided will depend on the length of transport and quality of the original material being transported. In extreme cases of inorganic or even organic material settling in great quantities may even suffocate the benthic community. The resuspension of microphytobenthos (mainly benthic diatoms) and mud (<55-pm fraction) from tidal flats was studied in the Ems estuary (Netherlands/Germany), of which 50% is covered by intertidal areas. Mud and microphytobenthos were resuspended simultaneously as a linear function of effective wind speed (de Jonge and van Beukesom 1995). Tides are vital transport mechanisms carrying nutrients both in and out shore and they may be one of the important factors in the control of eutrophication in some coastal areas. The phytoplankton production in the Bay of Brest (France) is easily accessible to the benthos because of the relatively long water residence time and the high tidal current mixing. Spatial distribution of benthic populations was found to be related to the tidal currents in that particular mudflat (Hily 1991). Another study in a tidal flat of southern Chile demonstrated that the seston load in the water column was highly dependent on both seasonality and tidal resuspension (Navarro et al. 1993). Location trends linked to lateral transport were reported in the Mediterranean with higher lipid content in low resuspension environments versus more carbohydrates in higher energetic settings (Rossi et al. 2003).

Areas with abrupt bottom topography as well as steep slopes or canyons will present enhanced currents and thus higher lateral transport (Thomsen and van Weering 1998). Another article reports that megafaunal species richness was greater for-within the Scripps and La Jolla canyons than out. It was shown that canyons present currents and detrital flows that greatly increase species richness but excludes urchin populations (Vetter and Dayton 1999). Seston with a pigment composition similar to surface waters has been reported from deep locations in the Arctic when those were close to a canyon (Clough et al. 2005). In this sense, the bottom topography will also be crucial with abrupt areas like canyons having enhanced resuspension and lateral transport. However, resuspended material will be richer in inorganic material and will not be suitable for all suspension feeders. In fact, particles in suspension near the bed floor in coastal areas may be up to 40% inorganic (Rossi and Gili 2005). However, it has been shown that few bivalves simply encounter and engulf particulate matter; it seems that they rather rapidly sort them based on physical and chemical factors, with material of higher quality being ingested and digested preferentially over that of lower quality (Ward and Shumway 2004).

Nepheloid layers may also play an important role in providing particles for the benthic community. A nepheloid layer or zone is a stratum of water in the continental platform or deep-ocean basin, above the ocean floor, that contains significant amounts of suspended sediment. The particles in the layer may come from the upper ocean layers and from stripping the sediments from the ocean floor by currents.

In the high turbidity zone, suspended particulate matter had a low nutritional quality because the easily available organic fraction represented less than 15% of the overall particulate organic matter. The high turbidity will result in little phytoplankton growth due to light limitation and, therefore, restricted food availability, as well as difficulties in food selection by planktonic organisms as nonliving particles will dominate (Burdloff et al. 2000). It has been shown in Mediterranean red coral (passive suspension feeder) that the variability of hydrodynamic processes may have a higher influence on the feeding rate than seasonal changes in the seston composition (Tsounis et al. 2006).

Temperature has also been suggested to have an effect, as it was observed at the Bay of Biscay, the nutritional quality of particles increased with temperature (Díaz et al. 2007). This is probably related to enhanced bacterial activity that creates higher energy compounds. Changes in temperature are usually linked to seasonal shifts in insulation and more details on the seasonality effect will be given in the next section.

4.3 Seasonality

Because primary production of phytoplankton and the vertical flux of particulate organic matter (POM) can be highly seasonal, seston abundance and quality changes over time and this will result in shifts through time for the benthic communities. Temporal changes in the pool of POM are especially important in the case of costal benthic ecosystems as they are fuelled by very heterogeneous sources such as *in situ* production, riverine input, or dust transport. The different components of the POM have different nutritional values and their relative contribution often shows seasonal fluctuations (Grémare et al. 1997). Fate of POM-seston is influenced by benthic fauna through nutrition (Cammen 1980) and bioturbation (Lukenback 1986), and in turn POM influences faunal biomass and abundance, making relationships between POM and benthic fauna bidirectional.

Photosynthetic production usually concentrates at times of high nutrient input, intermediate light, and mild temperatures, in temperate seas, that usually takes place in two separate peaks one in spring and another in autumn. At higher latitudes like the poles, where light is very limited most of the year the production peak is concentrated in one single pulse coinciding with the summer months with some species even forming cysts during unfavorable conditions. Bacterial and dinoflagelate production may be less seasonal but can still present a clear seasonal cycle in most environments. So clearly seasonality will have a differential impact depending on the latitude with virtually none existing changes and pervasive low production.

Moreover, the seston biochemical characteristics, nutritional value, and abundance will change seasonally and this is coupled to changes in growth of deposit feeders but also with diversification of the benthic community (e.g., Clough et al. 2005; Elias-Piera 2014; Gili et al. 2006; Grémare et al. 1997). Seasonal changes in the size spectrum and biochemical composition of the suspended seston were recorded for 2 years in Logy Bay, southeast Newfoundland, Canada. It was reported that seston load depended on terrigenous input and phytoplankton productivity while the quality was directly linked to freshness of the organic matter (Navarro and Thompson 1995). Therefore the seston was more abundant and of better quality during spring when phytoplankton was more productive.

Primary production is clearly the system driver in places with strong seasonal shifts such as Antarctica. The seasonality of light and ice cover is responsible for the increase of the primary production of phytoplankton in spring-summer and the vertical flux of particulate organic matter (POM), composed by living fresh phytoplankton, fecal pellets, and detritus. Benthic organisms have adapted their feeding strategies to these seasonal POM pulse and can even stand long starvation periods. In fact, Antarctic benthic gorgonian communities have been shown to base their diet on sunk and resuspended material during the unproductive winter months (Gili et al. 2001).

Quality and quantity of seston are not necessarily linked in time. For example, in the Mediterranean a seasonal trend was observed with higher organic content coupled to lower gross sedimentation rates during spring-summer season (Rossi et al. 2003). Therefore while there will be less seston available, the particles will be of a higher quality hence meeting the nutrition requirements of benthic organisms. Rossi and Gili (2005) suggested a seasonal influence of wave height and river run-off on seston abundance. Similarly in the northwest Mediterranean, microplankton dominates from December to March while nano- and picoplankton are more abundant in the remaining months (Ribes et al. 1991). Heterotrophic contributors to seston organic C in the area were found to be bacteria with an abundance of $5.16 \pm 0.08 \times 10^5$ cells ml^{-1}. However, heterotrophic bacteria biomass showed a sharp decrease (40%) during winter periods due to diminished cell sizes (Ribes et al. 1991). A seasonal pulse of detrital material to bathyal and abyssal depths was reported in temperate latitudes (Billet et al. 1983). That pulse occurs soon after the spring bloom and continues throughout the early summer providing a periodic food source for the deep pelagic and benthic communities which otherwise will have very little access to euphotic zone production (Billet et al. 1983).

Atmospheric storms can also be seasonal and thus may cause periodicity in deep-ocean currents and nepheloid layers (e.g., Billet et al. 1983). But in that case the seasonality is due to changes in the physical conditions rather than biological production as seen in Sects. 4.1 and 4.2.

5 How Do We Evaluate Seston Nutritional Quality?

5.1 Sample Collection

The most common approach is the use of passive sedimentary traps. Traps are moored at the study area at the depth of interest to study seston's biochemical characteristics and their link to benthic communities. Traps should be placed close to the bottom but always leaving a gap to avoid resuspended material.

Another approach is to actively obtain the sample from the water column. Samples are gathered, often with a Niskin bottle or CTD (an array of Niskin bottles that also incorporates conductivity, temperature, and depth sensors). The collected water sample is then filtered through 0.7 GFF (glass fiver filter) or even a low 0.2 μ pore size filters if we are interested in all material present in the water column.

5.2 Biochemical Parameters for Seston's Quality Evaluation

The relationships between water column production and benthic activity or response to production events are difficult to quantify. Nonetheless, the knowledge of the diet and temporal variability of prey capture rates (i.e., annual variations) in suspension feeders is essential to understand ecosystem energy fluxes.

To see the effect of seston on benthic communities, a classical approach is to correlate sedimentary organics to quantitative benthic fauna characteristics (e.g., Grémare et al. 2003; Ibarrola et al. 1996). However, this poses two main problems: (a) finding the most appropriate unit to assess organics in the sediment or seston and (b) the nutritional process is complex encompassing ingestion, absorption, and assimilation and thus cannot be assessed linearly. For example, selectivity is associated to ingestion, furthermore not everything ingested is digested and absorbed by the consumers, and incorporation is dependent on meeting specific nutritional requirements (e.g., Elias-Piera 2014; Ibarrola et al. 1996; Grémare et al. 2003; Tsounis et al. 2006).

Quality of seston can be measured through total organic matter, organic carbon, nitrogen content, total and available proteins (TPRT and APRT), carbohydrates, and total and enzymatically hydrolysable (available) amino acids (THAA and EHAA). Parameters such as digestibility and composition are key to understand seston nutritional value (Grémare et al. 2003). Often integrated lipid, carbohydrate, and protein studies are performed (e.g., Isla et al. 2006, Table 2).

Available amino acids and lipids have been shown to be the best descriptors of food nutritional value and they are associated to the most labile faction of particular organic matter (Grémare et al. 2003), on the other hand carbohydrates are more resilient to degradation.

5.2.1 Bulk Biochemical Parameters

Bulk Organic Matter

Organic matter (or organic material) is matter composed by organic compounds that have come from the remains of organisms such as phytoplankton or nekton. The organic contents or organic carbon refers to the amount of carbon or other elements such as nitrogen that are bound in organic compounds. Organisms may secrete or excrete organic matter into their environment, for example through messy feeding (when organisms lose part of the food through inefficient trapping of food in mouth parts) or fecal pellets. The breaking down of the organisms' body will also result in an input of organic matter to the water column. Natural organic matter can vary greatly, depending on its origin, level of degradation, and its bio-physico-chemical function. For example, structural materials such as carbohydrates will be more resilient to degradation. Larger molecules of organic matter can be formed from the polymerization of different parts of already broken down matter, and those too will be more difficult to break down.

The amount of bulk organic matter is usually measured by differential degradation of organic and inorganic compounds either through combustion or acid hydrolysis. Organic content can be typically measured by combustion weight loss, in which case the sample is combusted at 450 °C for 5 h and the final weight is subtracted from the initial one to obtain the amount of organic matter that has been combusted.

Carbon

Carbon is the fourth most common element found in the universe and it forms the basic skeletons of all life on earth. As such, it is directly linked to organic matter and thus organic carbon (OC) is widely used to estimate production. However, there are also inorganic forms of carbon and thus all measuring techniques will be aimed at disentangling the two.

For example, to quantify organic carbon we can use an Elemental Analyser, after acidification with 1 N HCl (To remove inorganic carbon). In this case we obtain an absolute quantity of OC rather than the bulk organic matter that is measured though weight loss.

Nitrogen

Nitrogen is a common element in the universe, estimated at about seventh in total abundance in our galaxy and the Solar System. Nitrogen occurs in all organisms, primarily in amino acids (and thus proteins) and also in the nucleic acids (DNA and RNA). As such nitrogen content has been used to assess nutritious quality of seston. However, also in this case we can have organic and inorganic components which make it necessary to disentangle the two, for example, by acidifying the sample (which will degrade only inorganic N) before measuring the organic nitrogen content with the elemental analyzer.

5.2.2 Specific Biochemical Parameters

As nutrition results from processes which do not affect the whole sedimentary particulate organic matter (POM) pool, there is little hope to link benthic secondary production and biomass to bulk descriptors. This makes it essential to identify and use more specific biochemical parameters. More specific biochemical descriptors such as enzymatically hydrolysable amino acids or lipids show a better correlation to abundance and biomass of benthic fauna.

Amino Acids

Amino acids are compounds composed of amine ($–NH_2$) and carboxylic acid ($–COOH$) functional groups, along with a side-chain specific to each amino acid (Fig. 5). For seston quality assessment, amino acids are subdivided into total (THAA) and available (EHAA).

A sound biochemical approach aimed at assessing the nutritional value of POM must account for its digestibility and its capacity to meet the nutritional requirements of benthic fauna. This can be achieved, for example, by quantifying the amount of EHAA in marine sediments (Mayer et al. 1995). With this approach, digestion is mimicked through incubation in the presence of a nonautohydrolyzable enzyme, whereas potential limitations by nitrogenous compounds are assessed through the quantification of individual essential amino acids using high performance liquid chromatography (HPLC).

Spectra of both total and available amino acids were found to be almost constant irrespective of season and /or environment at the Gulf of Lions (Grémare et al. 2003). None the less available amino acids are part of the most labile POM fraction and as such have been shown to be very well correlated to seston's nutritional value (Grémare et al. 2003). In a study at the Bay of Banyuls-sur-Mer (northwestern Mediterranean), THAA and EHAA spectra were both dominated by glycine, aspartic acid, glutamic acid, and alanine. However, there were consistent differences between the two kinds of spectra. EHAAs were enriched in threonine, glutamic acid, leucine, and aspartic acid; and depleted in arginine, lysine, glycine, and histidine. EHAA spectra showed fewer temporal changes than THAA spectra. In all cases but one, significant changes in THAA spectra were related to glycine, aspartic acid, glutamic acid, and threonine and were indicative of the presence of degraded material, probably due to resuspension (Medernach et al. 2001).

To analyze THAA, samples undergo a strong acid hydrolysis (HCl). Then orthophtaldial-dehile solution is added to the neutralized extract to create a fluorescent signal that can be measured using a high pressure liquid chromatographer (HPLC) (e.g., Grémare et al. 2003). For the available amino acid fraction (EHAA) can be extracted using the biomimetic approach (Mayer et al. 1995). The samples can then be measured by Gas Chromatography (GC).

Proteins

A universally accepted method for assessing the labile fraction of sedimentary OM does not yet exist; however, it is believed that the capacity to assess organic nitrogen may be the key. Proteins are large biological molecules, or macromolecules, consisting of one or more long chains of amino acid residues with a C–N bond (**e.g**. Fig. 5). Proteins perform a vast array of functions within living organisms, including catalyzing metabolic reactions, replicating DNA, and transporting molecules from one location to another. Proteins are relatively short lived and as such have been linked to fresh seston material. Their complex structure and vast range of molecular weights and structures mean that usually the forming units (amino acids) are preferentially used as seston quality indicators.

Proteins can also be subdivided between total (TPRT) and available (CPRT), this distinction is made on the same basis that the one for amino acids in the previous section.

Carbohydrates

A carbohydrate is a large biological molecule, or macromolecule, consisting of carbon (C), hydrogen (H), and oxygen (O) atoms, usually with a hydrogen:oxygen atom ratio of 2:1 (as in water); in other words, with the empirical formula $Cm(H_2O)n$ (where m could be different from n) (Fig. 6). Some carbohydrates such as sugars can form penta- (e.g., sucrose) or hexacycles (e.g., glucose).

Carbohydrates perform numerous roles in living organisms such as energy storage (polysaccharides e.g., starch) and as structural components (e.g., chitin in

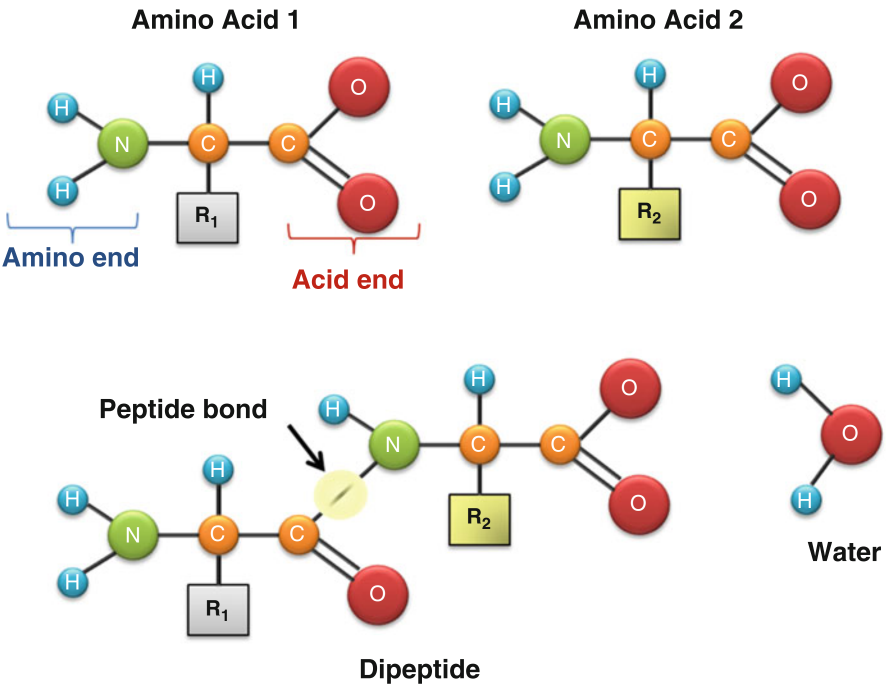


Fig. 5 Chemical structure of two amino acids and how they bond to form a peptide

arthropods). On the other hand, long chained carbohydrates like cellulose are more resilient to degradation, so they are not considered as a good tool to evaluate seston quality. They are usually measured with a spectrophotometer after sulfuric acid addition.

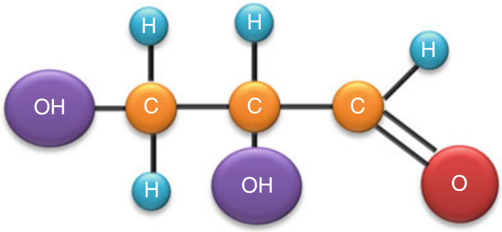
Lipids

It has been shown that lipid compounds in sinking particles in the ocean are of predominantly phytoplankton origin, being the microbial and terrestrial sources less important (Ittekkot et al. 1984).

Lipids are a group of naturally occurring molecules that include fats, waxes, sterols, fat-soluble vitamins (such as vitamins A, D, E, and K), monoglycerides, diglycerides, triglycerides, phospholipids, and others (Fig. 7). The main biological functions of lipids include storing energy, signaling, and acting as structural components of cell membranes.

Lipids also encompass molecules such as fatty acids and their derivatives (including tri-, di-, monoglycerides, and phospholipids), as well as other sterol-containing metabolites such as cholesterol. Lipids and especially available fatty acids are associated to the most labile seston fraction making them ideal to describe food's nutritional value (Grémare et al. 1997, 2003).

Fig. 6 Simple carbohydrate chemical structure



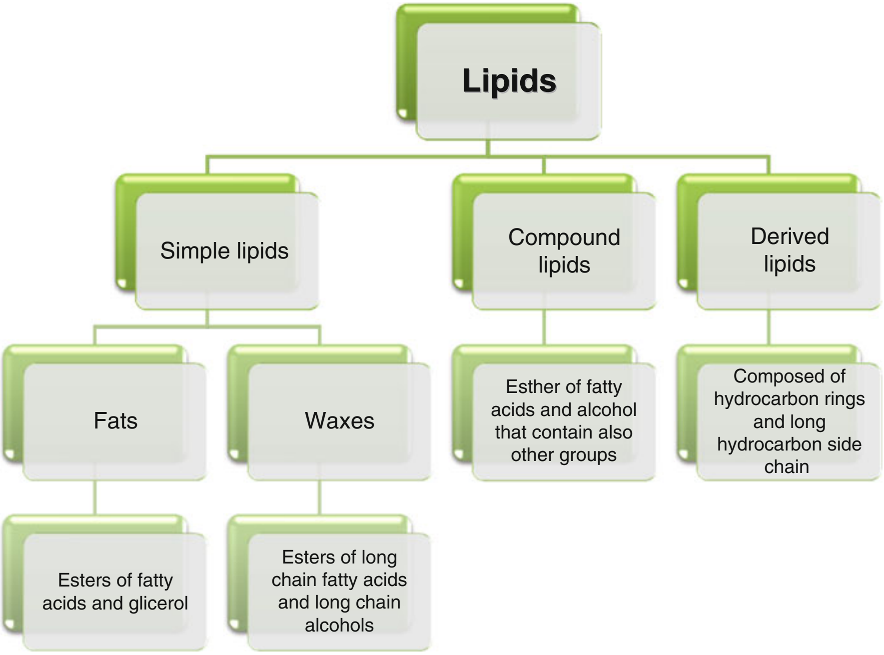


Fig. 7 Main lipid categories based on their chemical structure

Lipids and specially fatty acids are high energy compounds. Fatty acids are commonly used as they present simple structures. After extraction with strong alcohols such as dichloromethane (DCM) and methanol (Me), the fatty acids are methylated previous to analysis with a GC.

5.2.3 Indices to Measure Seston Quality

The results suggest that the gross analysis of the suspended particulate matter or the measurement of a single chemical variable cannot describe fully the nutritive value of the seston for a suspension-feeder. Therefore some indices have been put forward to try and evaluate the quality of seston.

The C/N Index

The **C**/N ratio (**C**:N) or carbon-to-nitrogen ratio is a ratio of the mass of carbon to the mass of nitrogen in a substance. It can, among other things, be used in analyzing sediments. Therefore, the C/N ratio serves as a tool for understanding the sources of sedimentary organic matter, which can lead to information about the ecology, climate, and ocean circulation at different times in Earth's history.

In the global oceans, freshly produced algae in the surface ocean typically have a C/N ratio of about 4–10 (Meyers 1994). The microbial communities utilizing the sinking organic carbon prefer to use nitrogen-rich compounds as N tends to be the limiting nutrient. These will result in an elevated C/N ratio in sinking organic carbon in comparison with fresh surface ocean organic matter that has not been degraded. An exponential increase in C/N ratios is observed with increasing water depth – with C/N ratios reaching 10 at intermediate water depths of about 1,000 m and up to 15 in the deep ocean (~ >2,500 m) (Meyers 1994). The C/N ratio can thus be used to estimate the freshness of the material and has been used to assess seston quality.

The Food Index

As the nutritional quality of seston cannot be expressed by gross biochemical measures, Navarro and Thompson (1995) proposed dimensionless food index based on the proportion of protein, carbohydrates, and lipid content. The nutritional quality of the seston was expressed by a food index, calculated as the ratio of food material (protein + carbohydrate + lipid) to total seston. This index followed the cycle of the phytoplankton bloom, with maximum values during spring and summer and much lower values during winter. The index was shown to have a strong correlation with bulk production descriptors such as organic matter, chlorophyll a, and particulate organic carbon and nitrogen (Navarro and Thompson 1995).

Thus food quantity is defined as the sum of the concentrations of protein, carbohydrate and lipid, and a food index was calculated as the percentage of food in the seston:

$$[(\text{Food}/\text{Total Seston})\ \text{X}\ 100] \tag{3}$$

Protein, carbohydrate, and lipid are converted into energy equivalents using the coefficients 24.0, 17.5, and 39.5 J mg^{-1}' respectively (e.g., Navarro and Thompson 1995).

The Food index, however, was found to not be able to fully describe the nutritive value of seston to a suspension feeder. Instead the authors suggest the use of the size spectrum and biochemical composition to better assess the nutritive value of seston (Navarro and Thompson 1995). Changes in the protein, carbohydrate, and lipid tissue concentration values are often used to explain the effect of seasonal fluctuations in seston quantity and quality on the benthic community (e.g., Rossi et al. 2006). However, some studies have shown that the food index is mainly correlated to the inorganic fraction and the particulate nitrogen which together account for 85% of the index change (Navarro et al. 1993).

The EHAA/THAA Index

As there is no sound information on either the kinetics or the possible causes of short-term temporal changes in amino acid concentrations and spectra a simple quantity measuremnt will not sufice. Usually EHAA measurements are expressed as a ratio to total hydrolyzable amino acid (THAA). The EHAA/THAA ratio is one of the biochemical indexes which have been proposed to infer the lability of POM (Mayer et al. 1995). According to these authors, EHAA/THAA ratios close to 14% are characteristic of areas where degradation processes are predominant, whereas ratios close to 50% are indicative of productive area.

6 What Changes in Seston Quality Affect Communities and How?

The seston represents a highly dilute food source to potential consumers. Consequently, three general properties may be expected of sessile filter feeders: (1) high retention efficiency; (2) possession of a low-energy pump system in active filter feeders; and (3) consumption of seston fractions in proportion to availability (i.e., opportunistic feeding).

Suspension feeders and other sessile and vagile organisms have adapted their feeding strategies to use both biotic and abiotic seston. These organisms compose a highly diverse benthic community, regardless their original food source is either similar or not. The rather constant environmental conditions and the high productivity in the spring and summer seasons allow different morphological, feeding, energy storage, and reproductive strategies expressed in a highly diverse macrobenthic assemblages. Main benthos filter feeders include, but are not limited to, corals, gorgonians, sponges, and bivalves.

In extensive shallow water ecosystems such as coral reefs, the planktonic community will be strongly dependent on the extension, distribution, and activity (predation, feeding) of the benthic community. Benthic sessile organisms will have to adapt their feeding and/or storage strategies while vagile organisms will mainly change their behavior. Clearly passive suspension feeders such as gorgonians will also be especially affected by changes in temporal or spatial distribution of prey as well as by currents (e.g., Tsounis et al. 2006). Other active suspension feeders, such as bivalves or sponges, even if they are sessile will be more able to cope with changes in seston quality and quantity.

Ingesta and assimilation may vary with seston concentration and quality, depending on the feeding strategy. As different species display different morphological, feeding, energy storage, and reproductive strategies they are able to adapt to a wide range of seston biogeochemical characteristics. The quality and quantity of seston has been correlated with benthic community parameters such as biomass, abundance, and reproductive success.

The seston and benthic community coupling is not unidirectional, as benthic organisms will also contribute and/or change the seston quality and quantity. This is clearly illustrated by a study by Asmus and Asmus (1991) that shows that parallel with the uptake of phytoplankton by mussel bed, a high nutrient release by the mussel bed takes place. Thus, potential primary production induced by the nutrient release of the mussel bed is higher than the uptake of phytoplankton by the mussel bed (Asmus and Asmus 1991). Such a strong coupling between benthic communities and carbon and nutrient regeneration was also reported from the Arctic (Renaud et al. 2007). The benthic community can also change the quality of the water mass. In a study done in the laboratory by Ribes et al. (2005), it was found that the particle removal from the water column was mainly controlled by "biomass" (area and numbers) of filter-feeding sponges and ascidians and the particulate flux of nitrogen and phosphate generated could major sources of nutrients for the reef.

6.1 Changes in Activity

Trophic constraints in sessile organisms have been studied in terms of the relationship between prey availability and prey capture, unfortunately this kind of information cannot really demonstrate feeding success. Many organisms commonly use energy storage to cope with seasonal food shortages, as such it has been suggested that protein, carbohydrate, and lipid levels may reflect food shortages in benthic aquatic organisms (e.g., Rossi et al. 2006).

Changes in the quantity of seston available will impact the benthic community. For example, research done on mussel beds at the Wadden Sea showed that higher phytoplankton concentrations triggered higher uptakes by the mussel beds (Asmus and Asmus 1991), showing a direct correlation between availability and consumption by some benthic organisms. For example, high activity levels of five passive suspension feeders were observed to be significantly correlated with low visibility (horizontal Secchi disk, high seston concentration) in Mediterranean waters during late spring (Rossi and Gili 2007).

Warm temperate seas have strong seasonal primary production, which in turn affects the quality and quantity of POM, resulting in changes on the benthic organisms' activity. In late winter and spring, following the maximum production peaks in the water column, there is an increase in the activity of the organisms (Rossi and Gili 2007), also showing higher energy storage (Rossi et al. 2006). For example, in the Mediterranean, the annual variation in seston abundance and hydrodynamic conditions are important. Summer conditions are characterized by clear, stratified water; after the plankton-rich winter–spring bloom this has been termed the summer "trophic crisis" (e.g., Coma et al. 2000). As a result, in summer most Mediterranean benthic communities will display little or no activity.

Biomass and activity of benthic communities is closely coupled to changes on seston biochemical parameters. Changes in activity linked to seston quality have also been observed. A study by Bayne et al. (1993) suggests that these responses to changes in the food environment comprise physiological adjustments which result in higher net rates of absorption than would be predicted from considerations only of the organic/inorganic ratio of the suspended particles and assumptions of a noncompensating feeding behavior. When fed a high concentration of seston of low organic content, mussels increased their filtration rate, rejected a higher proportion of filtered material as pseudofeces, and increased the efficiency with which filtered matter of higher organic content was selected for ingestion (Bayne et al. 1993). In a laboratory study it was observed that as food availability rises, the cockle *Cerastoderma edule* net absorption rates are maximized by means of two mechanisms: (i) feeding rates are adjusted, with resulting regulation of the total amount of food entering the digestive tube and (ii) rates of digestive investment contributing to digestion are varied according to food quality (Ibarrola et al. 1996). A study done in the Baltic Sea shows that in response to the phytoplankton bloom settlement, the benthic community responds differently depending on size-group (Graf et al. 1982). After input of phytoplankton matter, the benthic microbial activity was immediately stimulated, while the meiofauna response was delayed for a couple of months but then showed increased reproductive activity (Graf et al. 1982). No general pattern was observed for macrofauna, while sediment surface feeder *Macoma balthica* started to build up lipid and glycogen reserves right away, a delayed response was shown by *Nephtys ciliate* which feeds on sediments and small macrofauna (Graf et al. 1982). These findings seem to indicate that the considered lower organisms in the food chain will be the first to react to an increase in seston input and the response will get delayed in the higher organism. Trophic dynamics, including differential feeding, predation, and survival pattern among recruits, may provide a mechanism for the observed lag time between pulses of food and recruitment (Ambrose and Renaud 1997). In general, a strong link can be observed between reproductive activity and food availability. For example, studies in oogenesis and reproductive pattern in three deep-sea demosponge species from the foot of the Barents Sea continental slope suggests that sexual reproduction is triggered by the vertical flux of particulate organic carbon at least in one species (Witte 1996). This is not an isolated case, deep-sea species from many phyla exhibit distinct seasonality in reproductive effort and most of the seasonality is coupled to pulses in the sedimentation of phytodetritus.

The mechanisms associated with particle feeding and selection are complex, with species-specific processes based upon both physical and chemical characteristics of the particles. Depending on the size and shape of the seston particles filtration rate has been observed to vary. An experimental study on the hard shell mollusc *Meretrix lusoria* revealed that while particle size of the diet played an important role in determining the filtration rate the shape was also important. When fed regularly shaped particle *Meretrix lusoria* yield lower filtration rates and higher pseudofeces production than when given irregular shape particles (Chien and Hsu 2006).

Some organisms may have enough phenotypic plasticity to change their strategy depending on the available seston. A field study demonstrated that ribbed mussels from two locations in the northeast Atlantic coast of the USA used different feeding strategies to achieve the same absorption efficiency at the two sites locations with widely differing seston characteristics (Galimany et al. 2015). When mussels were moved from high plankton-organic rich area to a poor plankton zone with high inorganic content-particles, they were able to adapt within 6 days of being transplanted (Galimany et al. 2015).

6.2 Changes in Organisms Composition or Storage

Variation in the biochemical composition of the tissue of an organism may be read as a "record" of water column productivity fluctuations in the benthic community. For example, the reproductive effort will depend on which part of energy storage is expended on reproduction and which is deployed in preparing for periods of low food availability, and this in turn will be controlled by the overall food availability. The relationship between biochemical composition and reproductive output was examined on in a passive suspension feeder, the gorgonian *Paramuricea clavata* (Rossi et al. 2006). Clear seasonal trends in the lipid and carbohydrate levels were observed in *P. clavata*, with maximum values in winter–spring coinciding with maximum food concentration/quality and minimum values in summer–autumn coinciding with low food concentration/quality (Rossi et al. 2006). Although there was an evident overlap of the lipid accumulation and the gonadal development, the relationship between reproductive output and tissue concentrations of lipids, carbohydrates, and proteins was not straightforward.

7 Conclusions and Future Perspective

As we have seen in the chapter, seston can be biotic or abiotic (or a mixture of both), and the rate of these two components will affect the nutritious quality of seston particles. While the seston quantity will be mainly controlled by surface water production either primary or secondary, lateral transport may in some areas be crucial.

The quality of seston is affected by three main factors: (a) initial composition (autotrophic and heterotrophic origin), (b) time of transit, being it vertical or lateral, and (c) environment (some environments such as anoxic or suboxic waters will prevent or slow degradation of the organic matter in the particles).

Clearly the nutritious quality of seston cannot be linearly assessed with bulk parameters as the nutritional process is complex encompassing ingestion, absorption and assimilation. While so far amino acids and lipids have been shown to be the best descriptors of food nutritional value, the search for better, more accurate markers for seston quality warrants further research.

Many examples demonstrate that benthic communities will adapt to the changes in the quantity and quality of seston. Nonetheless, vagile feeders such as molluscs will be able to cope more easily with those changes due to their mobility, while the sessile active and passive suspension feeders will be more affected by seston quality and quantity variations.

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Activity Rhythm Measurement in Suspension Feeders

27

Jean-Claude Duchêne

Abstract

Measurement of activities of benthic species is a recurrent problem. Variability in the size, aspects, type of movements, structures created to filter or collect the particles suspended in the water column, and falling on the sediment surface implicates the development of versatile measuring devices. Suspension feeding is a time-consuming process for the benthic species. The time spent filtering can be observed and recorded with sensors running in the background, capturing the ongoing activity. Depending on their position on or inside the substrate, species will adapt their way of capturing the particles and develop strategies and timings for the feeding events. Passive or active suspension feeding will be related to different energies expended to collect food. Recording the behavioral patterns is an important step in the knowledge of the animal energy budget. Some species are able to switch between passive and active mode, depending on the varying environmental conditions, such as the flow rate or the detection of increased particle densities. Simultaneous measure of individual activity and environmental variables, using associated sensors, can increase this knowledge.

Indices describing this activity can be produced by image analysis, coupled with specialized libraries developed sometimes on a species basis. Other techniques like valvometry may be used for measuring long-term, high-speed activities related to the shell opening in bivalves. Indirect variables including temperature, fluorometry, or other techniques can be used to study the pumping rate or the bioturbation effect of animal activities.

In this chapter some examples will be provided on the way of measuring the benthic suspension-feeding activities, among passive and active suspension feeders.

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Contents

1 Introduction

1.1 Suspension-Feeding Dynamics

Suspension feeding mostly involves capture by pumping water through structures like siphons or grabbing particles passing by and trapped on mucus. Observation and quantification of the suspension-feeding behavior are closely related to the mechanical aspects of this process. Descriptions of such processes show the variety of the adaptations depending on the way of living of species (Jorgensen 1966). Planktonic species or species living on drifting supports or species inhabiting the benthic domain developed different techniques to grab and capture food. Passive and active modes cohabit.

Suspension feeders play an important role in the stability of ecosystems (Herman and Scholten 1990). As pointed out by Riisgård (2001), laboratory experiments are often difficult to interpret and compare. Most of the measures concerning rhythms are made in laboratory experiments. Even if measures are more accurate and complex in controlled conditions, an overestimation of filtration rate is often reported (Doering and Oviatt 1986; Cranford and Hill 1999). This is related to the choice of tested parameters in a vast majority of case studies, such as food concentration, current speed, or light.

In this chapter we will focus on measurements of activities related to food capture. In situ measures capture a mixing of observed responses. Laboratory experiments are more adapted to model trends in animal behavior facing precise levels of some parameters frequently experienced by animals in their usual environment. Extending individual response in controlled conditions to a population of individuals submitted to equivalent conditions but in a multispecific environment may be not too "realistic." Variability of the natural environment is much higher and less predictable. In these conditions indirect estimates are used such as collection of fecal pellets to estimate the grazing rates through defecation (Kotta et al. 2003).

Vagile suspension feeders relying their feeding strategies on the particles found in the water column (Bushek and Allen 2005) are even more difficult to analyze.

A challenge in measuring the animal activity is to limit interactions between measuring devices and the observed animals. Video provides methods for measuring with limited inferences. One restriction has been related, for a long period, with the necessary light conditions that will be enough for the sensors. The higher sensitivity of the new sensors coupled with the ability to record in the infrared or the UV portion of the light spectrum allows recording in a less intrusive manner the behavior of the studied animals. Infrared light suppresses most or all of the color information of the images, but allows the night condition recording or the animal activity in reduced light conditions. One example is the observation of night activity of the tentacular feeder *Eupolymnia nebulosa* (Maire et al. 2007a). In this case the use of step motorized tables allows observation of areas larger than the video frame, covered by the tentacles by moving the sensor across the area and creating a virtual larger image. The use of UV can also provide information on the sediment movements in the sediment surrounding the animal. The use of luminophores and UV light associated with video recording on flat aquaria allows visualizing sediment movement induced by the feeding animals (Bernard et al. 2012; Maire et al. 2008). It is then possible to make spatial analysis of particle mixing using, i.e., the continuous time random walk (CTRW) model.

In this chapter examples of activity measurements will be presented, based on (1) typical image analysis devices, (2) electronic sensors providing valvometric behavioral information, and (3) mixture of sensors associated to give access to more complex biological processes.

2 Measuring Descriptors of Individual or Colony Activity

Many works are based on video recordings, followed by visual analysis of the images (e.g., Cronin and Forward 1982, 1986; Forward et al. 1997; Champalbert and Le Direach-Boursier 1998; Sullivan et al. 1997; Buskey 2000; Job and Bellwood 2000; Shepherd et al. 2000; Bianchi and Reali-Costa 2002; Costa et al. 2011; Sarda and Aguzzi 2012; Aguzzi et al. 2015; Pinto et al. 2015). This method is very time consuming with subsequent evaluation of the video images by the researchers. The development of new devices and programs allows automated treatment of the images captured by video sensors (Duchêne 2010; Maire et al. 2007b, c, 2008). This has been extended to three-dimensional treatment of information (e.g., Rosenberg et al. 2008).

Examples concerning different types of measures made with species having different feeding behaviors are presented in the first part. It shows clearly that the measuring devices must be adapted to provide comparable responses. A set of examples of measures made with video sensors and image analysis shows how diverse the approaches can be. In a second part, a high-speed valvometric measurement is then presented for comparison. The third part shows some examples of analysis of more complex environments, using a mixture of video techniques and 3D laser techniques. This introduces future approaches mixing different sensors, electronic devices, and related sets of programs.

2.1 Automated Analysis Systems Using Image Analysis

Image analysis has been used to study larval motion and to assess feeding activity in suspension feeders and deposit feeders (Duchêne et al. 2000; Duchêne and Queiroga 2001; Duchêne and Rosenberg 2001; Hollertz and Duchêne 2001).

Most marine benthic macrofaunal species are buried in the sediment, feeding on the sediment surface. The activity concerns feeding on the sediment surface itself, for the deposit feeders, or collecting particles from the water column, often close to the boundary layer, for the suspension-feeder strategists. Some species are able to switch from one mode to the other depending on the particle concentration. Such activity may be recorded with image analysis systems. Video numeric tracking associated with electronic intelligent sensors may record and isolate benthic activities (Duchêne and Rosenberg 2001).

Image analysis techniques use extraction of differences in successive images (Fig. 1) associated with labeling and connected component analysis to track individual activities. Algorithms may be applied to extract information from the images. Images can be segmented with aggregation of surfaces to contour of detected objects (Forssén 2007). Hierarchical segmentation is a semiautomated way to obtain a delineation of such objects (Arbelaez et al. 2011). The presence of objects can be detected using object detection algorithms. Features and areas of interest may be computed with different methods including "key feature" detection. Feature detectors use algorithms like speeded-up robust features (SURFs) (Bay et al. 2008), or

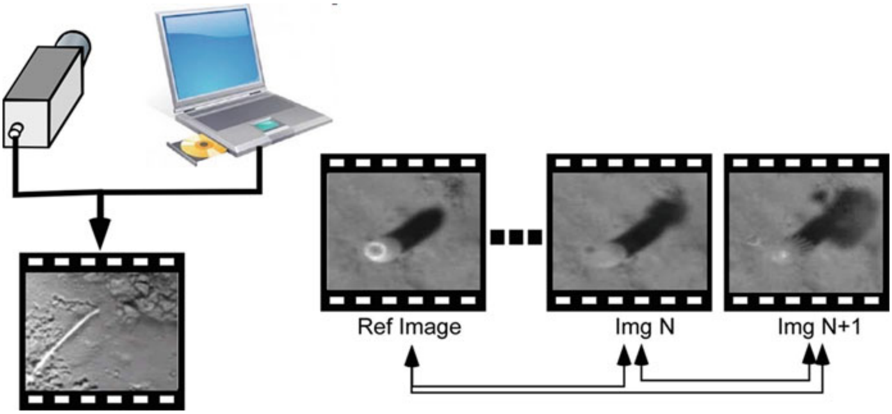

Fig. 1 Image analysis uses various devices for frame grabbing. Differences between images, collected from video input or from recorded films (*left* part of the figure), may be computed using successive images (from image N to image N + 1) or comparing each frame with a reference image, chosen among the available frames

features from accelerated segment test (FAST) (Rosten et al. 2010), or background elimination (MOG and Gaussian mixture model, GrabCut algorithm, K-means clustering, etc.). Within images and objects, the use of different colorimetric models and spaces (RGB, HSL, HSV, LAB, CMY, CIE, etc.), the computation of invariant moments (Hu 1962), or the use of co-occurrence matrix (Haddon and Boyce 1993) may help differentiating individuals. Difficulties arise to treat automatically the high variability of the source images and the fact that buried organisms often present a small portion of their body out of the substrate. Usually surface deposit-feeding activities give a much higher response in the number of modified pixels (i.e., the change in color or intensity of a pixel due to the activity of the organism) than suspension-feeding activities, where feeding structures may remain still while capturing particles.

The software AviExplore (by J.C. Duchêne) allows counting and measuring shape and color parameters for every detected blob (a blob is a patch of contiguous modified pixels inside an image), stores it inside a database, is used later to filter the blobs, and connects the blobs to labeled individuals in the images. Individual activity may be computed by adding blobs belonging to each labeled individual at every time and every frame in the image sequence.

Differences in images may imply a difference with a reference image, which is hardly obtained in an in situ recording, or difference between consecutive images. This needs the presence of a memory and a script running inside the embarked in situ device, able to store the preceding image, with a computing unit or a digital signal processing (DSP) to extract, compact, and store the results for the image differences and analysis. Background removal algorithms generally use a set of these images to compute the background. Usually results of the computations are compressed in a binary format for further extraction from the embarked device.

Image analysis is based on a grabber able to collect images from a real-time device or from a recorded series of images. In the first case, processing time is critical and computing algorithms must be optimized. In recorded series computation time is not any more a constraint and complex computations may be realized. Recording is an easier process when made as a laboratory experiment and much harder to realize in in situ operations. In the laboratory some shortcuts may increase the computation speed, when some fluctuation sources are known. Real-time images are sometimes difficult to handle as long as pixel collection and treatment must be processed within the fixed interval. If individual dynamics is fast, processors with high clock rates are needed. Time interval is essential in rhythmic activity measurements as long as specific individual dynamics is concerned. For example, benthic individuals do not respond to food events with the same speed (Duchêne and Rosenberg 2001; Fig. 2). Some organisms detect the changes and adapt their behavior very rapidly depending on the environmental and biological conditions. For these benthic species, time interval in data collection must be higher. In a mixture of *Amphiura filiformis* and *Melinna palmata* in the Gullmar fjord, *Amphiura* detect and react to the food incomes much faster than *Melinna* (Duchêne and Rosenberg 2001).

The measurements may concern global multispecific population, patches of selected individuals, or isolated individuals. When many species are concerned, a

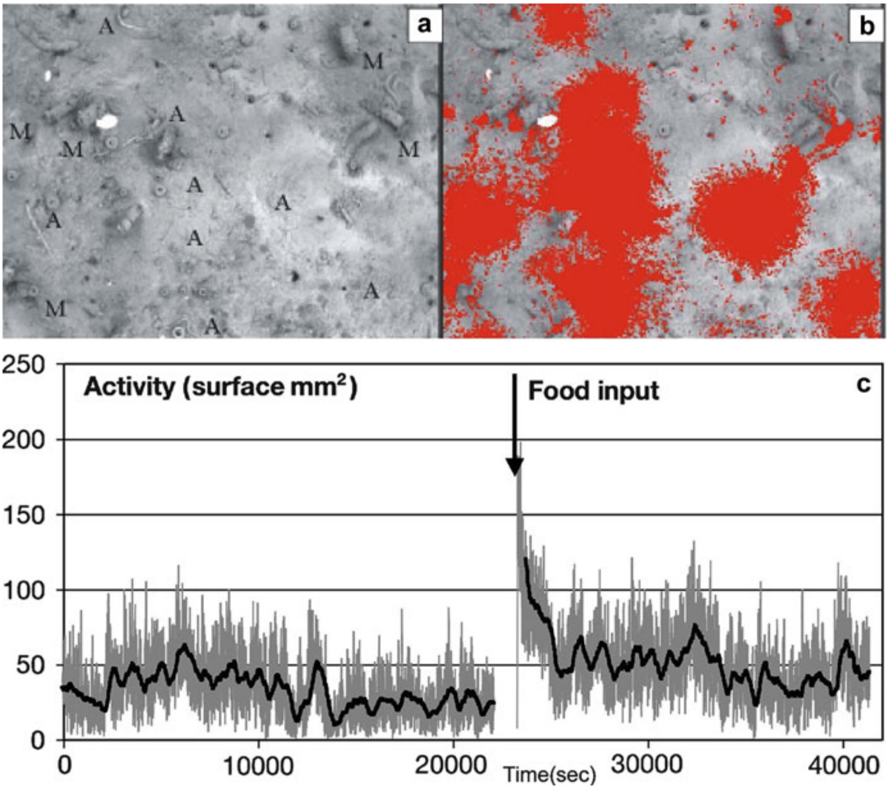

Fig. 2 Measurements of total activity at sediment-water interface. The activity (in mm^2/image) was recorded during 7 h on a sediment surface with identified species. (**a**) Two species present more than 95% of the recorded activity (A, *Amphiura* spp.; M, *Melinna cristata*). (**b**) Modified areas found on every frame were added on the same picture (*red* patterns). (**c**) The lower diagram shows recorded activity (*gray* patterns) with time, in seconds. The *left* part of the diagram is before food addition. *Arrow* indicates food addition over the sediment surface. The *black line* is a moving average on 144 images (Modified from Duchêne and Rosenberg 2001 MEPS)

treatment is necessary to compare species activity. This treatment generally uses image segmentation with hierarchic sorting (Arbelaez et al. 2011). It may use connected component labeling generally including human-based species identification. Measuring modifications of the interface related to the activity of each species gives an indication of the dynamics of response to environmental stimuli such as food concentration or quality (Duchêne and Rosenberg 2001).

2.1.1 Measuring Patches of Individuals: The Case of the Red Coral, *Corallium rubrum*

Measures on the extension of the polyps of *Corallium rubrum* can be recorded with image analysis device (Figs. 3 and 4). In this case *Corallium* branches are placed on pods inside a flume. Images are recorded from behind the colonies with a mirror to

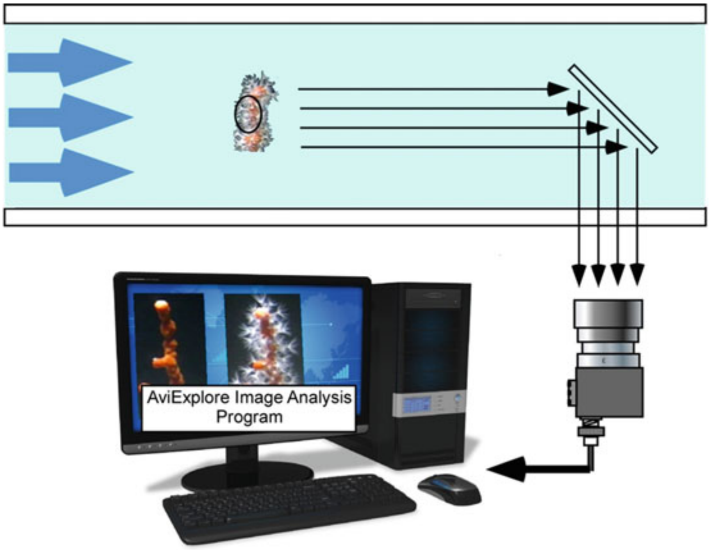

Fig. 3 Recording *Corallium* activities in a flume. Images are captured on a mirror located far behind the *Corallium* branch. High-resolution sensor sends images to a frame by frame analysis tool (AviExplore program, by J.C. Duchêne) computing activity indices on the frames

avoid any interaction with the current. The reference or background image is the "closed condition," when all polyps are retracted. Analysis of the visible polyp surface in every colony gives an estimate of filtration activity. When polyps start opening, the differences in images are recorded and analyzed. Influence of current speed, temperature, and the presence of food in the flume water can be quantified. Image recording can be done in complete darkness, using infrared illuminators. The flume is located in a cold-regulated laboratory.

2.1.2 The Case of Connected Individuals with *Parazoanthus axinellae*

Recordings on *Parazoanthus axinellae* colonies collected from coralligenous areas in Banyuls (Mediterranean Sea) are measured in a flume. The example shown in Fig. 5 presents three patches of *Parazoanthus*. Each patch contains polyps connected in the same mass. In each patch, polyps react synchronously. The global image is then separated into regions of interest (ROIs). Subsequent recordings concern each individualized patch. The screen capture of the AviExplore program (J.C. Duchêne) shows one frame of the analysis. The global aperture of one individual colony presents succession of opening/closing periods, with varying intensities of the openings.

2.1.3 Accessing Individual Filtration Events: The Case of a Serpulid Worm *Ditrupa arietina*

Ditrupa arietina is a serpulid polychaete that bases the food capture in the suspension-feeder strategy (Jorgensen 1966). Information on the filtration and

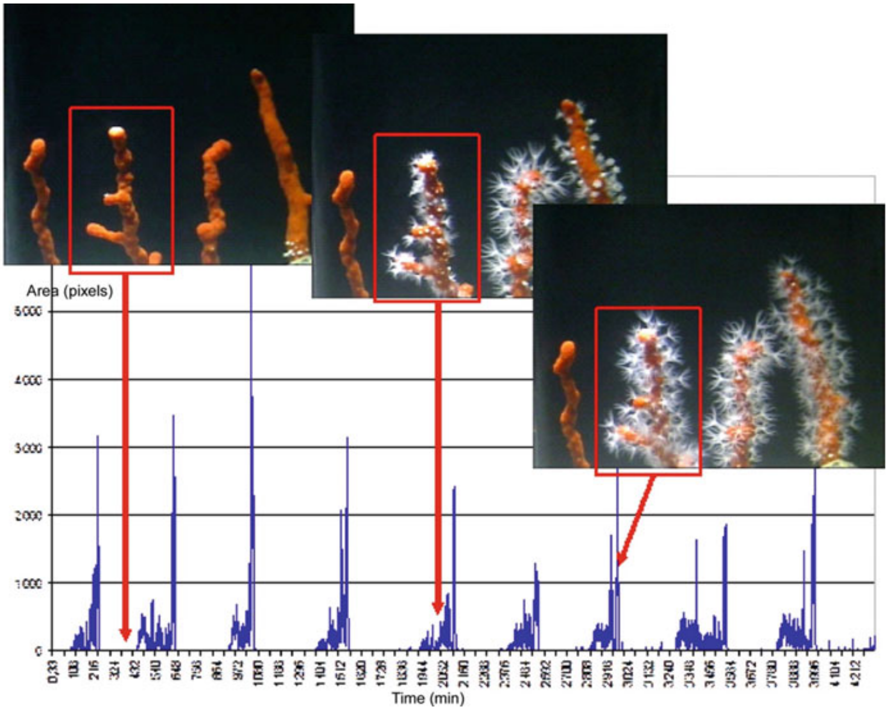

Fig. 4 Measurement in a flume of the opening of polyps of *Corallium rubrum* with temperature, current speed, and food addition variations (in collaboration with Sergio Rossi, Barcelona University). A rhythmic activity is visible. The *blue* signal corresponds to the apparent surface of a whole coral branch in pixels against time. Patterns reflect the polyp opening with closed condition (*left* photo), opening condition (*center* photo), and wide opening condition (*right* photo)

clearance rates in suspension-feeding polychaetes remains rather scarce (Aguzzi et al. 2000). The intensity of feeding basically depends on filtering capacity and filtering activity (i.e., time spent pumping; Foster-Smith 1976). Filtration can be affected by environmental constraints inducing coordinated responses and rhythm of activity (Dales 1957; Leonard 1989; Sanford et al. 1994; Vedel et al. 1994; Achituv and Yamaguchi 1997; Thorin et al. 1998; Jordana et al. 2000). Laboratory experiments with a controlled current situation (flume) show that the animal can rotate the gills to face the currents (Figs. 6 and 7). It presents succession of rapid movements, with a rhythm dependent on the current speed, of closure/opening possibly associated with current sensing. This behavior is observed with a high frequency and is independent of the global filtering time.

In long recorded experiments, the overall filtering activity of *D. arietina* was neither a continuous process nor even a process having a particular rhythm. Within the same batch of worms, total filtration durations could represent between 12.5% and 87.5% of the total experimental time. Figure 7 shows an example of change in the frequency of retraction events (higher curve) when current is high or low

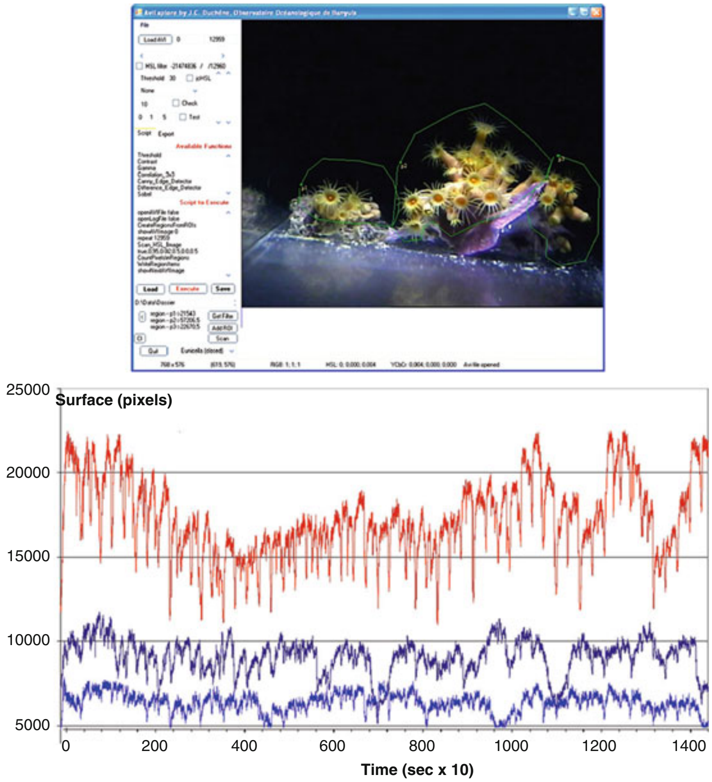

Fig. 5 *Parazoanthus axinellae* activity recording (the same recording conditions as in Fig 4). Top view: capture of an AviExplore window providing activities within three regions of interest (ROIs). Bottom view: time records of activities within the three patches (ROIs) of *Parazoanthus* polyps. Apparent surface in pixels of the three patches of polyps is presented versus time in seconds ×10

(as visible in the lower curve). Despite a strong interindividual variability, results showed the existence of pronounced seasonal variations in the activity of the gill crown (Jordana et al. 2000).

2.1.4 Switching of the Feeding Mode: The Case of Individual Activity of the Bivalve *Abra*

Abra is a small tellinid mollusk living buried in the sediment and using siphon to collect food from the interface that may also filter the water above the sediment surface (Fig. 8a, b, c). Different nutrition types were recorded in the species *Abra* switching from filtration to a surface deposit-feeding strategy (Wikander 1980a, b; Charles 1993). Recording of feeding activity made with image analysis systems allows splitting diverse feeding modes in this species (Rosenberg 1993; Grémare et al. 2004). In *Abra ovata* the siphon can be pointing vertically toward the water mass, in respiration and filtration events (Fig. 8b), or moving on the sediment surface

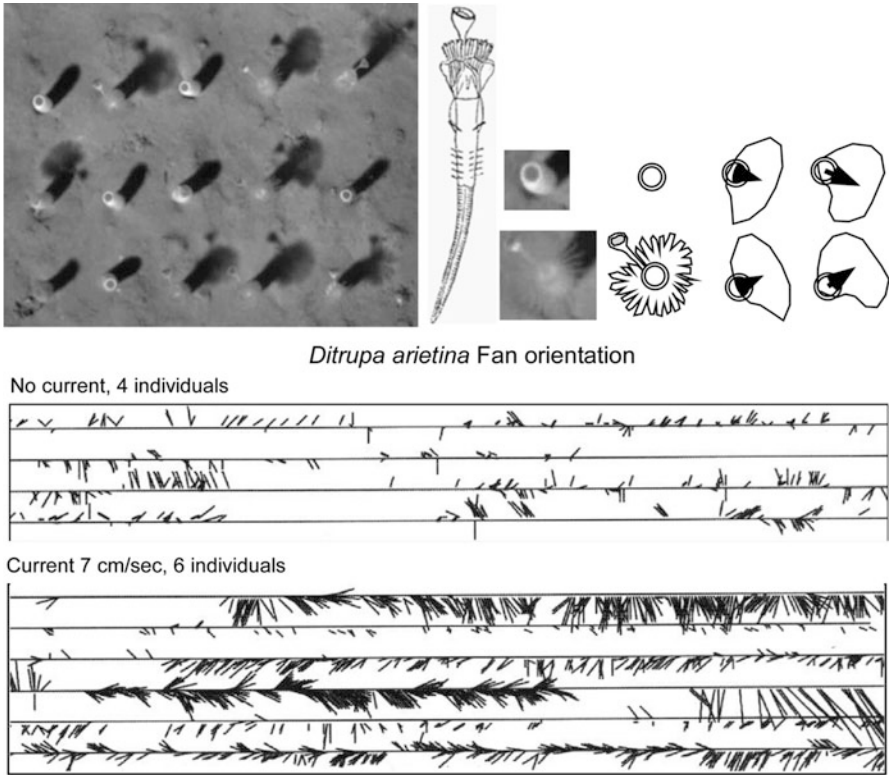

Fig. 6 *Ditrupa arietina* filtering activity. *Top left* image shows one image of a record from the *top* on a series of individuals. Individuals are filmed with a 45° orientated light providing shadows that can be used in the image analysis to quantify the amount of aperture. Image analysis is performed on isolated individuals. *Ditrupa arietina* gill orientation is measured (program AviExplore by J.C. Duchêne): the barycenter of the gill crown is located and compared to the position of tube aperture, giving a vector (*top right* diagrams), and confronted with current speed (lower diagrams). Without current orientation is erratic, with episodic body rotations, opening or closing. When current is applied in the flume, individuals orientate their gill crown. At higher current speed, progressive retraction occurs followed by a complete closing

collecting patches of sediment (Fig 8a). *Abra nitida* presents even more flexibility in its feeding modes (Grémare et al. 2004).

Image differentiation may be followed by a blob analysis, separating and labeling objects. A blob is a patch of contiguous pixels changing from image to image. A connected component analysis is then used to connect objects found in image N to objects found in image N + 1. This is used in Fig. 8 to distinguish activity for different individuals of *Abra ovata*. The software creates files that may display every single activity area, counts each labeled blob inside every single image, and creates filters to eliminate activities across the image borders. These files contain an index of activity based on the number or the surface of pixels changed within one time unit,

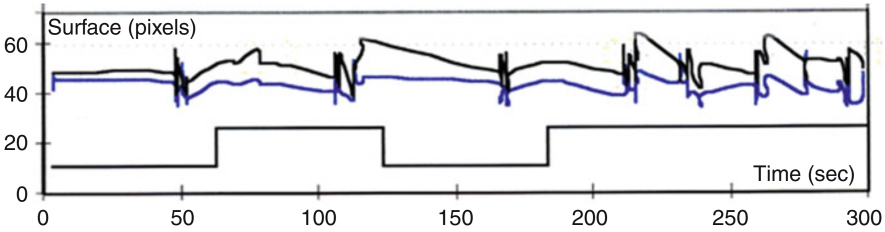

Fig. 7 *Ditrupa arietina*: recording of apparent surface, in pixels, with or without a 7 cm/s current (lower pattern). Individual shows episodic sequence of gill retraction with a higher frequency when current becomes stable (program AviExplore, by J.C. Duchêne)

for every individualized animal. Figure 8d shows cumulated areas of activity for three detected *Abra* for 1000 images captured every 20 s. Figure 8e shows a small portion of the recorded activity for the *Abra* #2 (green pattern on Fig. 8d). 3D analysis of the sediment surface shows that the sediment is grabbed in a circular movement around the buried shell (Maire et al. 2007c).

Filters allow detecting differences in the movement, associated with different feeding modes. When a siphon is filtering, the overlaying water is visible, pointing toward the surface and not moving. In this case image comparison is made with an initial reference image indicating an active siphonal activity. The siphon is active but pixels are not changing from image to image. Important features to collect are the start and the end of these sequences. When a siphon is feeding on the sediment surface, it moves around the bivalve position from inside the sediment inducing many changes in the surface pixel detection. The measured response is very different, with spatial repartition of detections related to the feeding being much wider.

2.1.5 Measuring Filtration Rates of Individuals or Patches of *Mytilus* with Image Analysis

A camera is placed in front of an aquarium with *Mytilus edulis* attached on a frame. Successive images are treated to extract information on each *Mytilus*, in regions of interest. The filtration activity as recorded by global image analysis of a patch of 18 individuals of *Mytilus edulis* shows clearly the variability in patches of individuals in a population. The average activity is shown in Fig. 9a. Every individual in the patch does not respond with the same intensity. The curve shown in Fig. 9a corresponds to the addition of pixel modification in apparent surface of 18 shells. Algal concentration is measured after the initial addition in the aquarium and allows computing of the clearance rate. The global analysis shows that a food addition induces, after the initial detection of food presence, an increase of overall animal activity, followed by a reduction of its activity when the food concentration is below an optimum value. This activity diminishment is not linear, being gradual up to the complete closure of the valves and the consequent stop of the bivalve filtration. Variability between individual responses is high. Results for individual measures cannot be easily extended to an entire population.

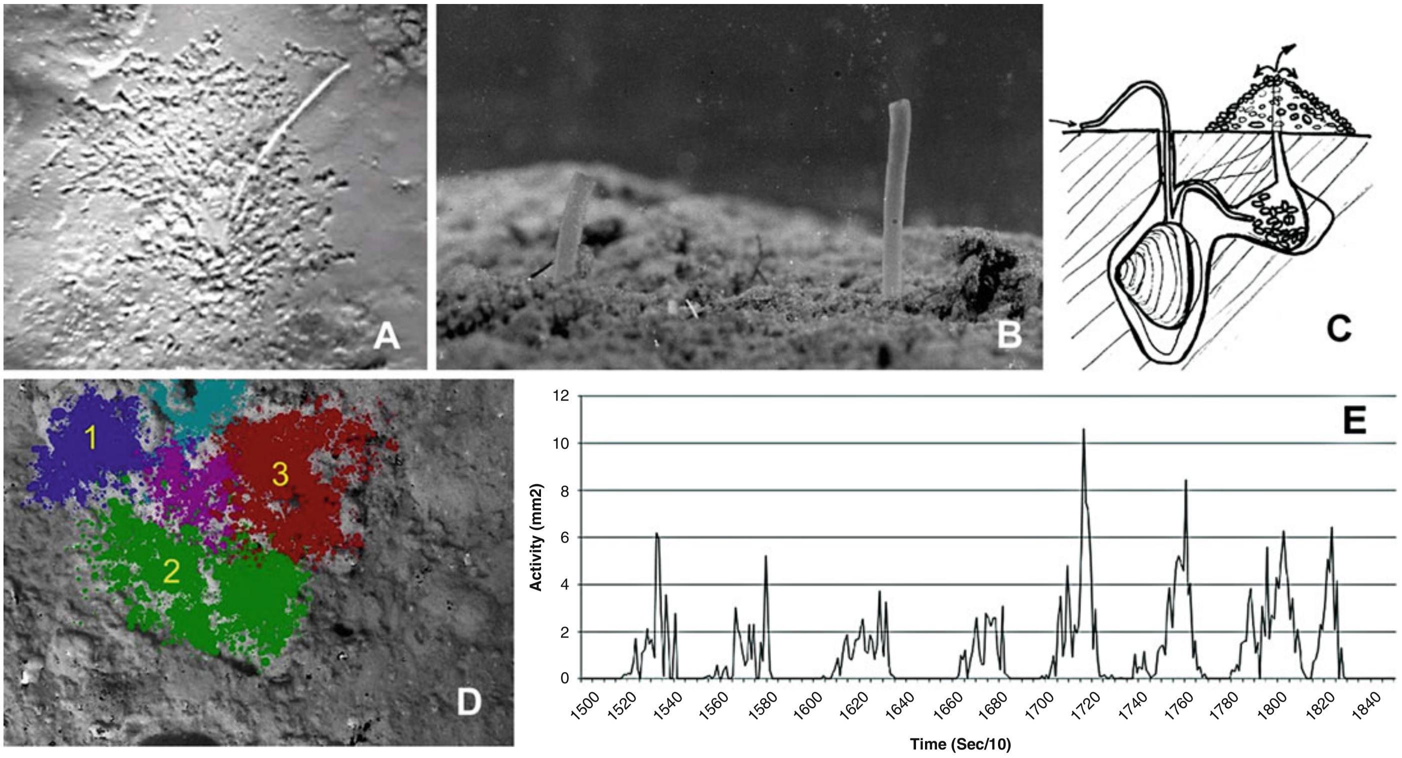

Fig. 8 *Abra ovata* individual activity. (**a**) Siphon explores the sediment surface and grabs portions of sediment, visible on the picture. (**b**) Suspension-feeding event. (**c**) Position of the bivalve in the sediment. (**d**) Cumulated activities of three labeled *Abra ovata* individuals (program AviExplore, by JC Duchêne). It is a superposition of every single pixel changed by an animal in every image, showing the extension of the animal activity during the experiment. (**e**) Raw record of activity index with rhythmic patterns (all the pixel surfaces changed by one individual counted in every image)

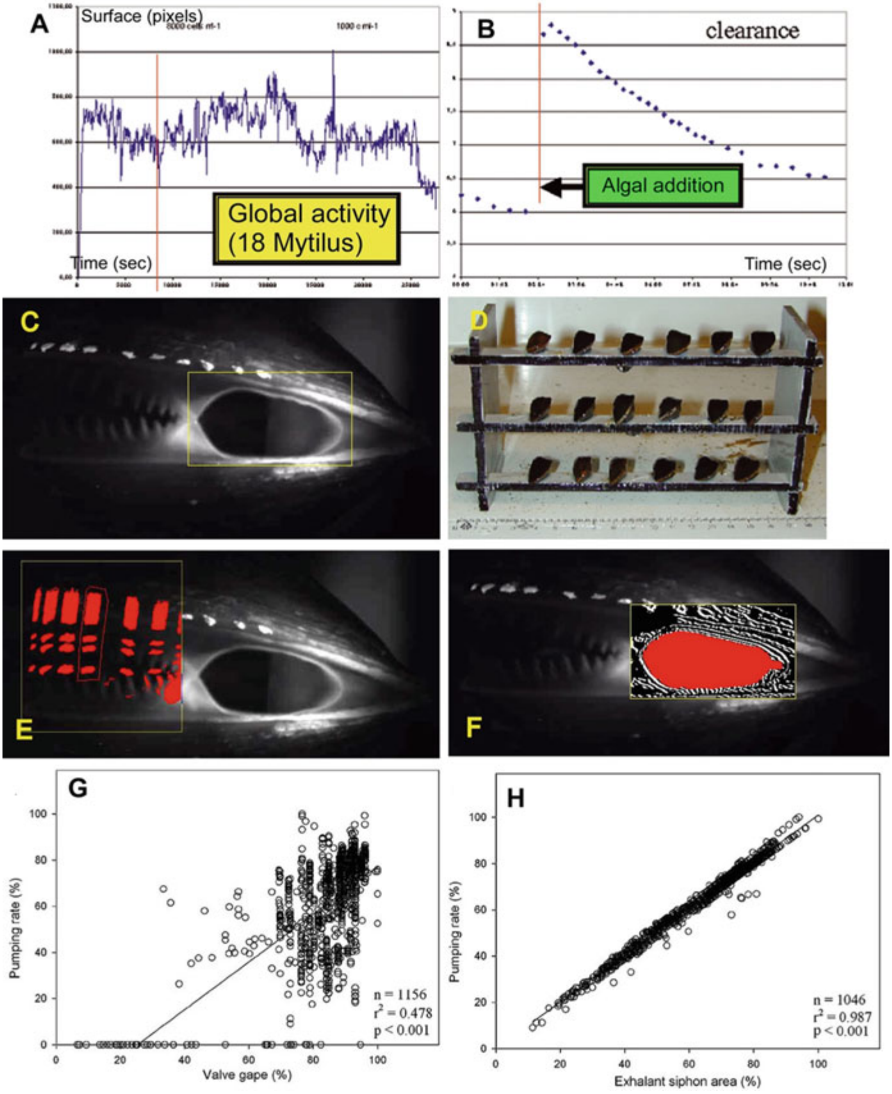

Fig. 9 Filtration activity in *Mytilus edulis* and *M. galloprovincialis*. (**a**) Global activity of a batch of 18 *Mytilus edulis* attached to a frame. Records use image analysis of the opening valves facing the sensor. Time interval is 10 s. (**b**) After food addition a clearance rate is measured by collecting water in the tank to measure the algal suspension concentration. Individual variability is high. After an initial increase in global activity, the filtration activity is reduced below a concentration of algae in the water, but maintained for a while before a higher general closure of the valves. (**c**, **d**, **e**, **f**) Image analysis of *M. galloprovincialis* activity using regions of interest. Measurements of valve gape (**e**) and exhalant siphon area (**f**). Successive positions of the *white* point used to assess valve gape are cumulated on the same image in *red* (**e**). Comparison of valve gape measures (**g**) and siphon surface (**h**) versus current speed in front of the exhalant siphon measured with a hot-film probe (Modified from Maire et al. 2007a)

2.1.6 The Case of Individual Filtration in *Mytilus galloprovincialis*

An automated image acquisition and analysis system allows frequent and simultaneous measurements of valve gape and exhalant siphon area (Fig. 9c). *M. galloprovincialis* are attached on a frame and white dots are painted on the side of the upper valve. The image analysis is made in two regions of interest (ROIs), one to track the dot movements indicating relative position of the valve and the other to measure the apparent area of the exhalant siphon.

Pumping rates are measured using hot-film probes. Image analysis gives two sets of parameters: (1) the valve gap, measured by identifying the small dots on the side of a valve, moving vertically with shell movement, and providing valve aperture (Fig. 9c, e), and (2) a measure of the exhalant siphon area, measured inside a region of interest (ROI) with an example visible in Fig. 9f.

Temporal changes in the exhalant siphon area are continuous as opposed to those of valve gape (Fig. 9g, h). Therefore, despite the significant correlation between these two parameters, valves and siphon are sometimes dissociated due to a reduction of the area or even a closure of the exhalant siphon while the valves remained open. The velocity of exhaled water tends to be constant irrespective of exhalant siphon area, and thus pumping rates are a linear function of exhalant siphon area.

2.2 Measures with High-Speed Valvometric Sensors: Long-Term Activity Estimates Using High-Frequency Noninvasive (HFNI) Valvometry

Valvometry allows measuring the valve gape in mollusks (Bouget and Mazurie 1997; Shaffer et al. 1999; Riisgård et al. 2003, 2006, Frank et al. 2007; Robson et al. 2010). Valve gape in mollusks can be estimated with electrodes attached on the valves, using Hall effect (Fig. 10). Associated electronics convert the signal that can be recorded and transmitted to a remote computer (Jou et al. 2013). High-frequency real-time measures in the natural environment give interesting information on the individual activities (Tran et al. 2011; Sow et al. 2011). Real-time data are made available on a website (http://molluscan-eye.epoc.u-bordeaux1.fr) with continuous online recording.

2.3 Measures with Mixture of Sensors

2.3.1 Analysis Using Combined Sensors and Different Species: Case Study of the Impact of Hydroid Activity on Serpulid Recruitment

This methodology allows measuring individual growth and activity as well as early larvae settling space competition. In this example, the analysis concerns panels immersed at about 25 m depth, collected by divers on a weekly base and analyzed for a few hours in the laboratory before being placed back at sea. Panels remain all the time in the water. Precise positioning (at the pixel scale) is realized with video sensors mounted on the motorized tables. The results showed competition related to

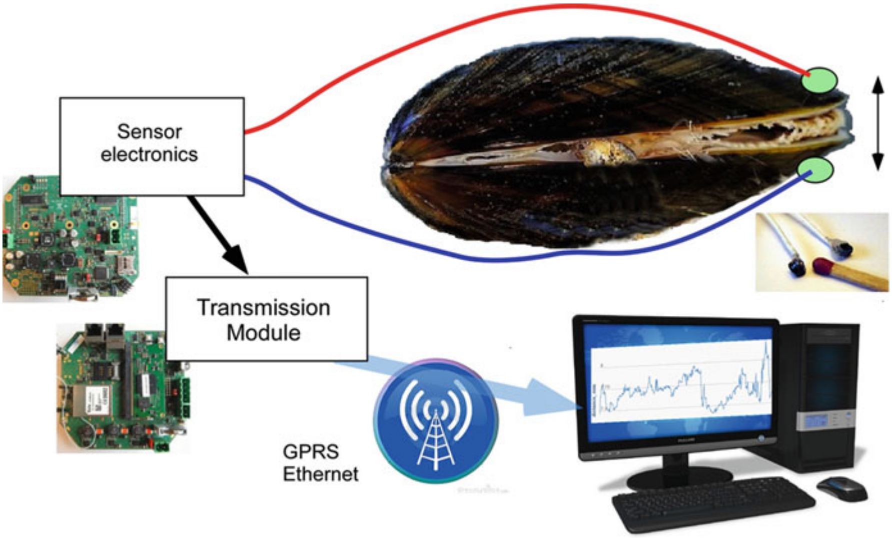

Fig. 10 High-frequency noninvasive (HFNI) recording of gape distances on mollusks (Modified from Tran et al. 2011; Sow et al. 2011). Electrodes are attached on the valves. Signals are treated, converted, and sent through GPRS or Ethernet to a remote station. Sample data in *blue* are records of *Mytilus* in Dalnie Zelentsy, a bay in the northeast of Murmansk in Russia

the species densities during settlement. Hydroid activity and its presence constrain a serpulid settlement (Duchêne 2012). Growth of hydroid colonies with the presence of many opened polyps grabbing particles from the water limits the settling of other species like the serpulid *Pomatoceros triqueter*. Growth of these colonies can be high (Gili et al. 1998). Without the hydroid presence, dense patches of *Pomatoceros* have been observed. Activities of the *Pomatoceros* have been recorded using the image analysis protocols as for the serpulid *Ditrupa arietina*. Hydroid densities and size have been recorded by scanning with a laser the surface of the recruitment panels installed on a buoy and periodically extracted from the buoy (Fig. 11a) for measurement. This laser scan is realized by a module of the AviExplore program that provides a 3D map of the surface. 3D maps from every sample may be compared to compute individual polyp growth and location across time (Fig. 11 screen captures c and d). The program allows slicing the peaks obtained, labels the isolated objects (Fig. 11g), and geolocalizes them with corresponding heights. Significant reduction of *Pomatoceros* settlement is observed when the larval cloud arrives on a surface previously colonized by hydroids (Fig. 11f).

2.3.2 Measuring with Combined Sensors: Shell Movements in *Cerastoderma edule*

Another example shows the mixture of image analysis with multiparametric variable assessment. The purpose in this case is measuring the resuspension effects during activity of the bivalve *Cerastoderma edule*. A simple image survey of the mollusk

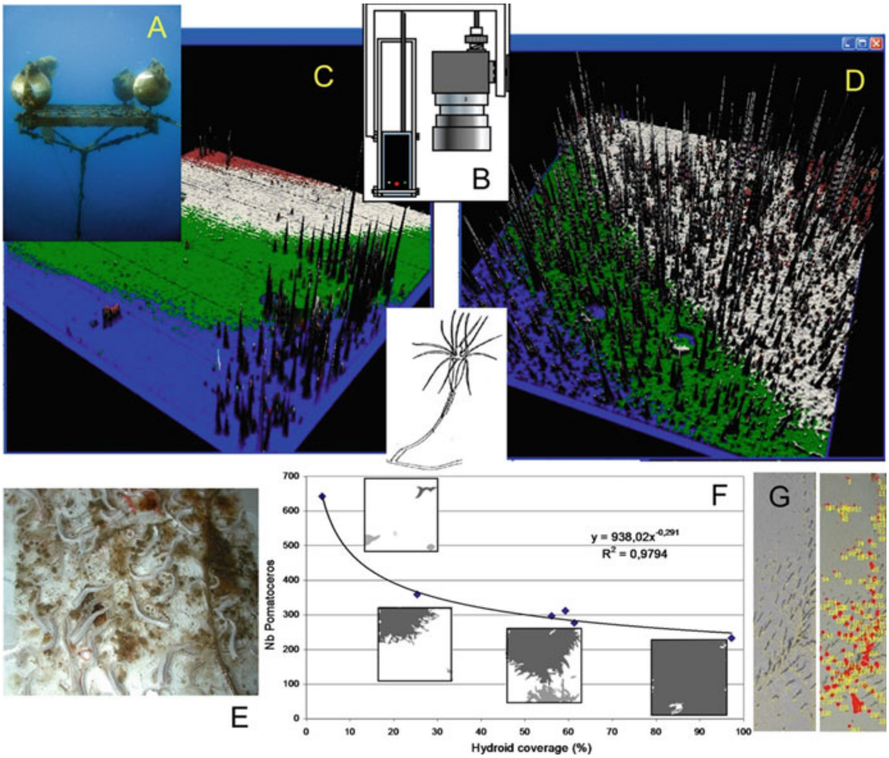

Fig. 11 Activity of colonies of the hydroid *Clytia*. Growth and activity of the colonies impact the recruitment patterns of other species (i.e., the serpulid polychaete *Pomatoceros*). Recruitment plates 140 × 140 mm are placed on underwater frames, 25 m depth (**a**). Every frame is periodically scanned with video and 3D laser survey (**b**). Every peak obtained with microtopography (**c**, **d** vertical resolution of 10 μm) is a polyp as shown in the center image. Recruitment of *Pomatoceros* (**e**) is limited by the coverage of hydroid colonies (**f**). In the study (Modified from Duchêne 2010) every polyp is identified and labeled (**g**)

from the top allows computing indices of shell movement and siphon opening by counting the modified pixels.

Cerastoderma is known for its strong impact on sediment cohesion during its suspension-feeding activity (Ciutat et al. 2007). Flume experiments have been made (Fig. 12e) using combined sensors (Ubertini et al. 2012a, b, 2013, 2015; Guizien et al. 2012): a video survey of the animal activity (Fig. 12c, i) is coupled with (1) the repeated 3D measure (Fig. 12b, g, h) of the sediment interface with a 10 μm precision; (2) the estimation of the physiological state of the biofilm (Fig. 12a, f) on the sediment, in relation to resuspension events (using an imaging PAM, a pulse-amplitude-modulation fluorometer, providing a map of the fluorescence of the sediment that can be superimposed on the video activity images and on the sediment 3D map); and finally (3) water analysis with a multiparametric

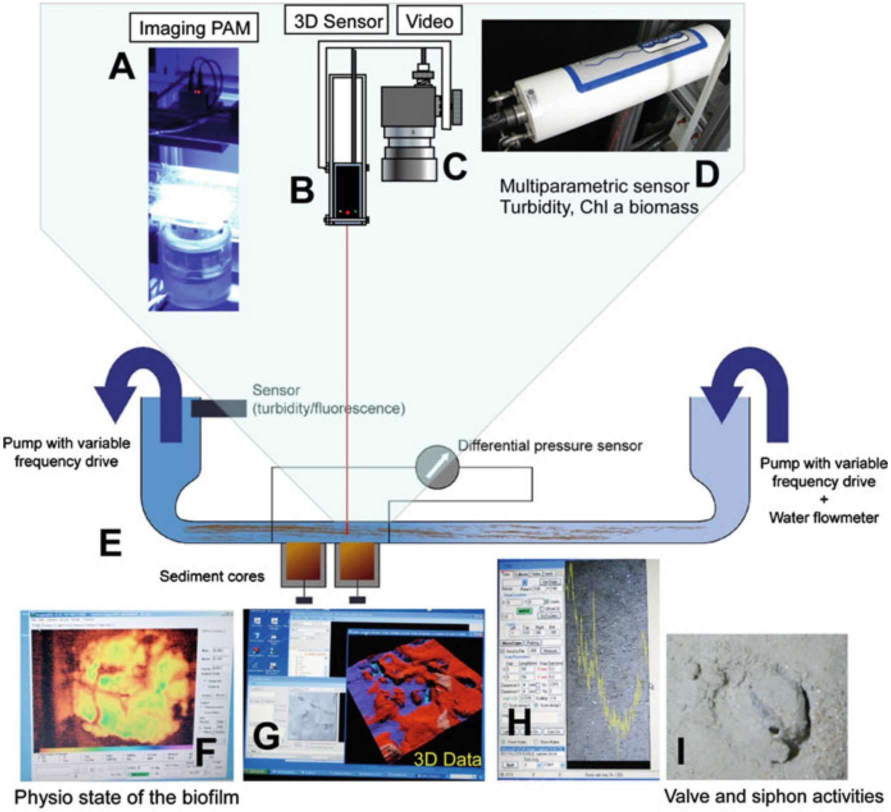

Fig. 12 Multiparametric measures of *Cerastoderma* activity. Flume experiment controls current speed and various parameters such as chlorophyll and suspended matter, activity recorded with video probes, 3D sediment motion assessed with laser telemetry, and physiological state of the biofilm obtained through imaging PAM and multiparametric sensor. Lower thumbnails show from *left* to *right* an imaging PAM output, a 3D output (AviExplore program, by J.C. Duchêne), an altitude transect on an image, and a video survey of *Cerastoderma* feeding

probe (turbidity, fluorescence, etc.) and periodic water samples for chemical analysis (extracellular polymeric substances (EPSs), ammonium concentration, etc.) (Ubertini et al. 2015).

Shell movement is measured with video sensor, measuring an index based on pixel changes of sediment surface moved by the valve activity (Figs. 13a, b and 14), and can be compared with the cartographies of 3D movements (3D elevation matrix). The 3D maps can be rotated and zoomed by the AviExplore program (Fig. 13c, start of an experiment; Fig. 13d, end of the same experiment) and superposed on images extracted at the same time from the video database of the program (Fig. 13a, b). The voxels (3D pixels) provided by the 3D analysis are 100 × 100 × 10 µm. The 100 × 100 µm surface of the voxel is selected to reduce the size of the images. The vertical 10 µm resolution of the voxel gives a good image of

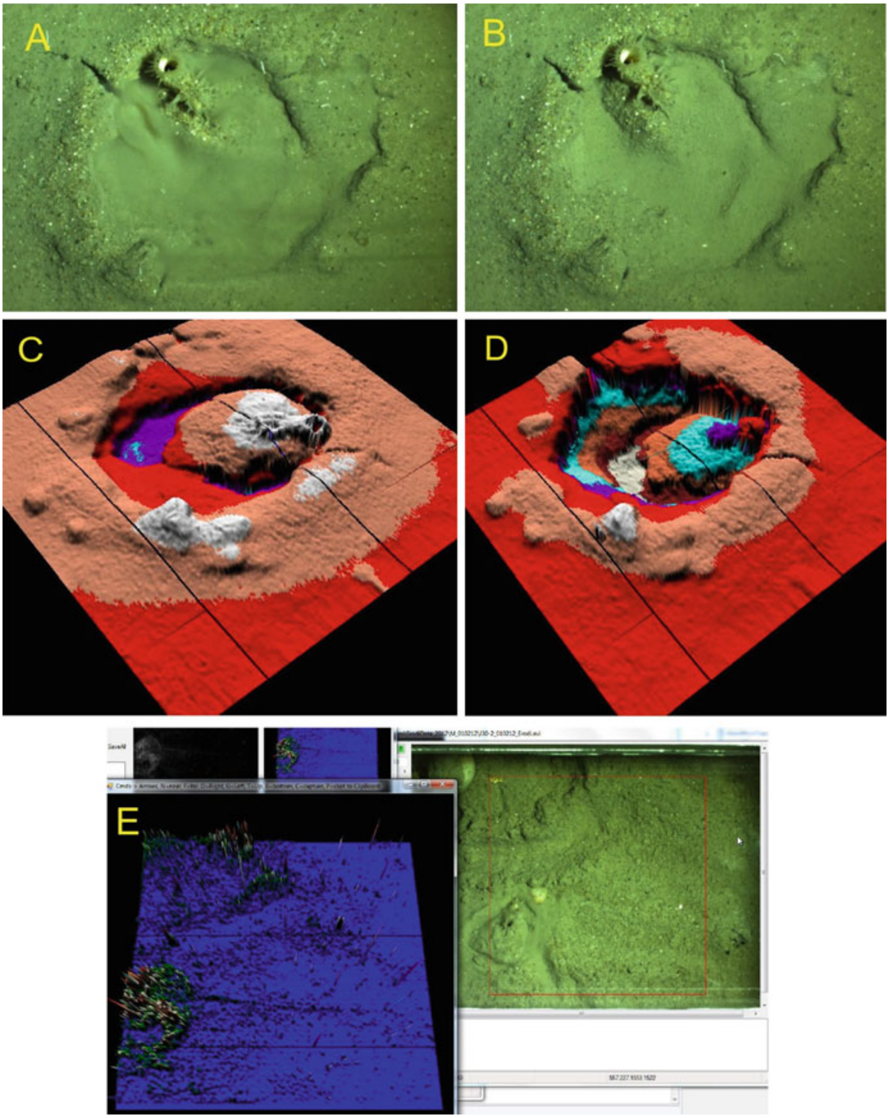

Fig. 13 Shell moves in *Cerastoderma*. Video records the valve opening/closing related to fine-sediment resuspension (**a**, **b** start of the experiment with resuspension of smaller particles during a shell movement in **a**, with current moving from *left* to *right*). 3D analysis allows quantifying volume changes in upper sediment structure (**c**, **d**). Video analysis shows areas where changes occur. (**e**) Shows cumulated activity on the sediment surface with activity related to the valves and to the siphons (all images from AviExplore program)

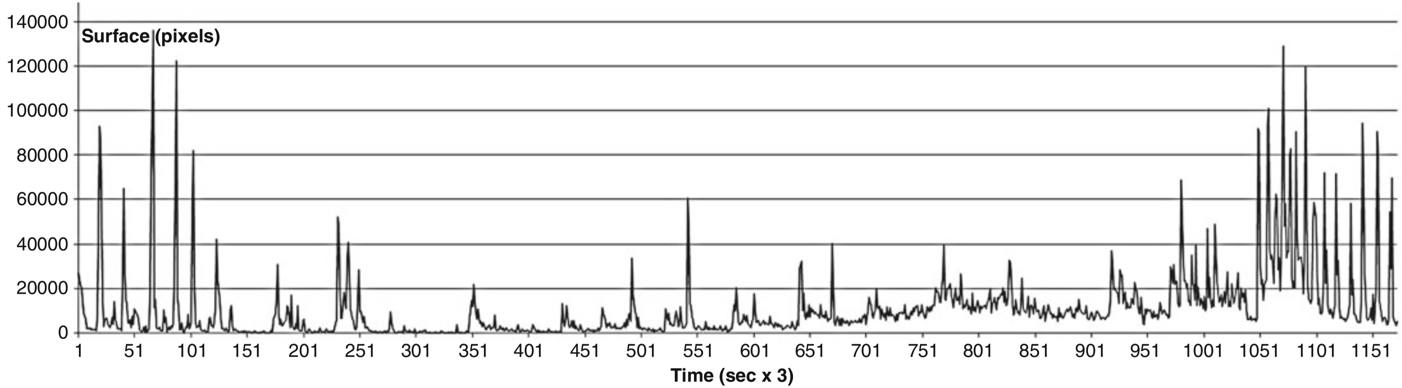

Fig. 14 Screen copy of the program used to track sediment surface activity (J.C. Duchêne). During a 4 h experiment, with increasing current speed, variation of every pixel of the image was tracked in a region of interest with *Cerastoderma edule*. Large peaks in the beginning and the end of the measure correspond to valve movements followed by shell vertical movement. At higher speed the mollusk is going deeper in the sediment. Between these two portions, basal activity is increasing with current speed with filtrating siphon repositions marked by intermediate peaks. At higher speeds, surface of the inhaling siphon reduces, ending with a complete closure. Last peaks before the final shell movements correspond to the siphon closure

modifications in the sediment surface. Two video cameras record target individual (smaller scale) and the whole sediment core (larger scale). Region of interest (ROI) can be selected later in the core view to position and measure the target individual. Statistics on the modified pixels across time show the regions where activity takes place when several individuals reside in the same core (Fig. 13e).

This set of measures allows searching the impact of this ecosystem engineer. Flume experiments are useful to quantify resuspension rates at small scale only (Ubertini et al. 2012a, b; Saint-Béat et al. 2014).

3 Future Directions

Suspension feeders develop large and complex communities adapted to the capture of the seston (alive or dead particulate organic matter). Some benthic species are able to switch from detritus feeding to suspension feeding in a passive or active mode. Understanding the feeding behavior of species adapted to such different environmental conditions is a challenge.

Observation is possible, but the precise measure of the time devoted to every event and the intensities of these events need an adaptation of automated video measuring devices. Examples of complex behavior are numerous. In situ recording concerns patches of mixed species, and the treatment of irregular regions of interest must consider possible extensions or reduction of the measured areas with time. Particles carried by the currents crossing at random the video field must be treated for elimination while still collecting the target activity.

Studying these species, with very different size and behavior, points out the lack of in situ versatile devices able to realize feeding behavior observation at the individual scale. Numerous devices are developed to study the water sediment interface. Benthic chambers, integrated measures of the exchange rates of oxygen flux in a noninvasive manner with Eddy correlation systems, and the use of planar optodes to access the heterogeneity of oxygen can bring very useful information on the environmental status of a community. But a large part of these devices are restricted to soft bottom communities and are not adapted to the individual level. Coastal rocky communities are more difficult to study, with higher tridimensional effect on water movements, food transport, and animal adaptations to this complex environment.

The use of ROV videos allows to collect information on transects. The AviExplore program has a complete module devoted to this kind of analysis with geolocalization of every single image. The main problem is detecting biological objects and then trying to identify them. Object detection is a rather easy problem, while identification is a very complex one. Real-time detection allows very rough separation to detect objects and split the results in different classes. It is difficult to embark a complete database on mobile devices until much higher integration is achieved. This operation is possible on recorded videos, but developments of knowledge databases require long computation times on powerful machines. The problem now is the training and learning phases of the systems and the accuracy of recognition. This information concerns animals large enough to be identified on a high-definition video device. At smaller scales motorized tables can be used to move the video sensor to precise locations stored dynamically in the interface, to measure several small objects in cyclic motion. Films are then reconstructed from every location. AviExplore program has such a module (Maire et al. 2007c). Limitations are related to the precision and speed of the motorized tables.

Many processes concerning suspension feeding are the fact of small individual or colonies spread across complex substrates, on the one hand. Techniques are developed to measure small-scale events, like the near real-time, in situ detection of larval species (Jones et al. 2008). The WormCam system developed at the Virginia Institute of Marine Sciences is a kind of a Sediment Profile Imagery (SPI) system taking pictures and films of the interface in soft sediment. A module of AviExplore was developed as a stand-alone program to treat SPI images showing cross sections of the sediment (Romero-Ramirez et al. 2013). As for the SPI system, localization of the vertical section is at random on a very small scale. This makes it difficult to select species to work with. There is a need for small-sized versatile observation systems with antifouling system to avoid development of fouling species on the lens, being able to record activities on precise locations. This system should be small enough to be installed inside rocks and crevices as well as on open surfaces.

On the other hand, in situ direct measurements of diet composition, filtration, and excretion rate are lacking. Techniques exist to measure filtration rate on small active suspension feeders: laser in situ scattering provides particle measurement and discrete water sample (InEx) (Yahel et al. 2005), based on simultaneous, pair-wise collection of the water inhaled and exhaled by the animal, and provides a way to analyze rate and efficiency of particle collection during the feeding events. Remote systems with camera exist, like the remote multi-camera system developed in the Ian Potter Foundation and the Australian Research Council (Mills et al. 2005).

Observation on activity patterns of individuals or group of individuals remains a predilection domain for video analysis. This type of studies can be coupled with new environmental sensors able to complement the set of information necessary for a better understanding of the processes. Common interfaces can manage drivers and pre- and post-process the signals collected by these drivers. 3D real-time cameras provide image with higher resolution and larger working matrices. Their present size and connections are limiting factors for small in situ observation devices. They can be used in laboratory experiments. A large field of research is open by the development of new algorithm and graphic tools. Code libraries and programs have to be improved to process in a more efficient way the nonintrusive information constituted by the collections of images recorded on videos. These measures and observations lead to realistic questions, new theories, and models that need new experimental setup and devices.

4 Cross-References

- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Filter-Feeding Zoobenthos and Hydrodynamics
- ▶ Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests

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Filter-Feeding Zoobenthos and Hydrodynamics

28

Hans Ulrik Riisgård and Poul S. Larsen

Abstract

This chapter summarizes recent years' studies on zoobenthic filter feeding in the sea. General principles are extracted based on experiments and mathematical modeling, mainly from own studies in shallow temperate Danish waters, in order to present primary characteristics of the sophisticated interplay between benthic filter feeders and hydrodynamics. Starting from the general concept of grazing potential and typical data on benthic population densities its realization is considered, first at the level of the individual organism through the processes of pumping and trapping of food particles for ingestion which relies on hydrodynamics. Studies have shown the importance of biomixing giving increased vertical seston flux due to mixing induced by exhalant jets of filter feeders, particularly in stagnant water but likely also in benthic boundary layers over mussel beds at moderate flow velocities. Mathematical models for such flows are discussed. At the scale of benthic boundary layers, mussels experience flows that are usually turbulent, but at the smaller scale of sublayers, colonies of bryozoans experience viscous-dominated flow that needs modeling. Finally, a case study from a particular shallow water area illustrates the effects of tide, current, and wind on vertical mixing, growth rates, and ecological implications. The main biophysical processes that may allow or prevent dense populations of filter feeders to control the phytoplankton biomass in shallow waters are presented along with remaining challenges for development of improved models for the

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benthic boundary layers, including effects of wall roughness, biomixing, and oscillating flows caused by waves.

Keywords
Grazing potential • Suspension feeding • Biomixing • Benthic boundary layer • Viscous sublayer • Modeling • Benthic-pelagic coupling • Grazing impact

Contents

1 Introduction

Filter-feeding (or suspension-feeding) benthic animals (= zoobenthos) strain food particles either passively or they actively create a feeding current directed toward a filter. Many invertebrates (bivalves, polychaetes, crustaceans) have adapted to a filter-feeding mode of life (Jørgensen 1966; Wildish and Kristmanson 1997; Riisgård and Larsen 1995, 2000, 2010; Riisgård 2015). Active filter feeders operate low-energy pumps that continuously process the surrounding water through filters appropriately dimensioned for coping with the phytoplankton concentrations of the biotope. Filter feeders among the benthic epifauna obtain their food from water masses that are often only little contaminated with resuspended bottom materials. The food conditions for such forms are therefore comparable to those of pelagic suspension feeders. However, many zoobenthic filter feeders live more or less buried in the sediment (infauna) and take their food from the water immediately above the bottom. They may still be suspension feeders although the suspended matter often originates from stirred up materials, and therefore the food conditions of these forms are not comparable with those of pelagic or typical epifaunal feeders. Deposit (or detritus) feeders utilize mainly the living components of the ingested sediment, i.e., bacteria, fungi, microalgae, and microfauna, whereas the predominant amount of dead organic matter (detritus) is not digested but primarily utilized by microbial decomposers. Surface deposit feeders take their food from the sediment surface, and subsurface deposit feeders ("burrowers") seek nourishment below the sediment surface (e.g., Riisgård and Banta 1998). Classification of feeding types into filter feeders and deposit feeders is frequently used, although it has become clear that some organisms are capable of switching between using either one of these feeding methods (Riisgård and Kamermans 2001; Riisgård and Schotge 2007).

Table 1 The present survey and discussion are confined to a small number of representative specimens of zoobenthos covering some obligate filter-feeding (or suspension feeding) and some facultative filter-feeding animals that are able to switch (*) between filter feeding and surface deposit feeding

Bryozoans
Membranipora membranacea
Celleporella hyalina
Electra pilosa
Alcyonidium hirsutum
Membranipora membranacea
Flustrellidra hispida
Amphipods
Corophium volutator * – mud shrimp
Polychaetes
Nereis diversicolor * (= *Hediste diversicolor*) – ragworm
Bivalves
Mytilus edulis – blue mussel
Cardium edule (= *Cerastoderma edule*) – cockle
Cerastoderma glaucum – cockle
Ascidians
Ciona intestinalis – sea squirt

Aside from these observations, the present chapter is devoted to the active filter feeders summarized in Table 1 that are representative for Danish waters. After an overall view of the concept and ecological importance of grazing potential and actual grazing impact, the starting point of hydrodynamic considerations is the water above the sediment (see Fig. 1) with the phenomenon of biomixing (studied for *Nereis diversicolor* and *Ciona intestinalis*), followed by benthic boundary layer flow (over a mussel bed), to then consider the small scale bryozoans in the viscous sublayer (on plant leaves or other surfaces). The final case study from a shallow Danish fjord provides an overview of an ecosystem.

Active filter-feeding benthic invertebrates are important elements in coastal ecosystems where they sustain life by removing suspended food particles from the water (Wildish and Kristmanson 1997). Biological and physical processes are particularly closely coupled in coastal waters (Jumars 1993; Mann and Lazier 1996). For example, water depth, which affects the importance of wind and tidal mixing, strongly influences the grazing impact of benthic filter-feeder populations, which may be considerable in shallow waters. Quantification of rates of energy transfer between the trophic components in a marine ecosystem is difficult and complex, and the role of zoobenthic filter feeding in the exchange processes is only just coming to light. However, it is clear that energy transfer through filter-feeding invertebrates is often an important route from the pelagic to the benthic components of coastal ecosystems. Recent work has produced evidence of the role of dense benthic filter-feeding populations in regulating plankton production in shallow marine waters. In this chapter, we extract some general principles, mainly from own studies in shallow temperate Danish waters, in order to present primary characteristics of the sophisticated interplay between benthic filter feeders and hydrodynamics for a limited number of suspension feeders (Table 1).

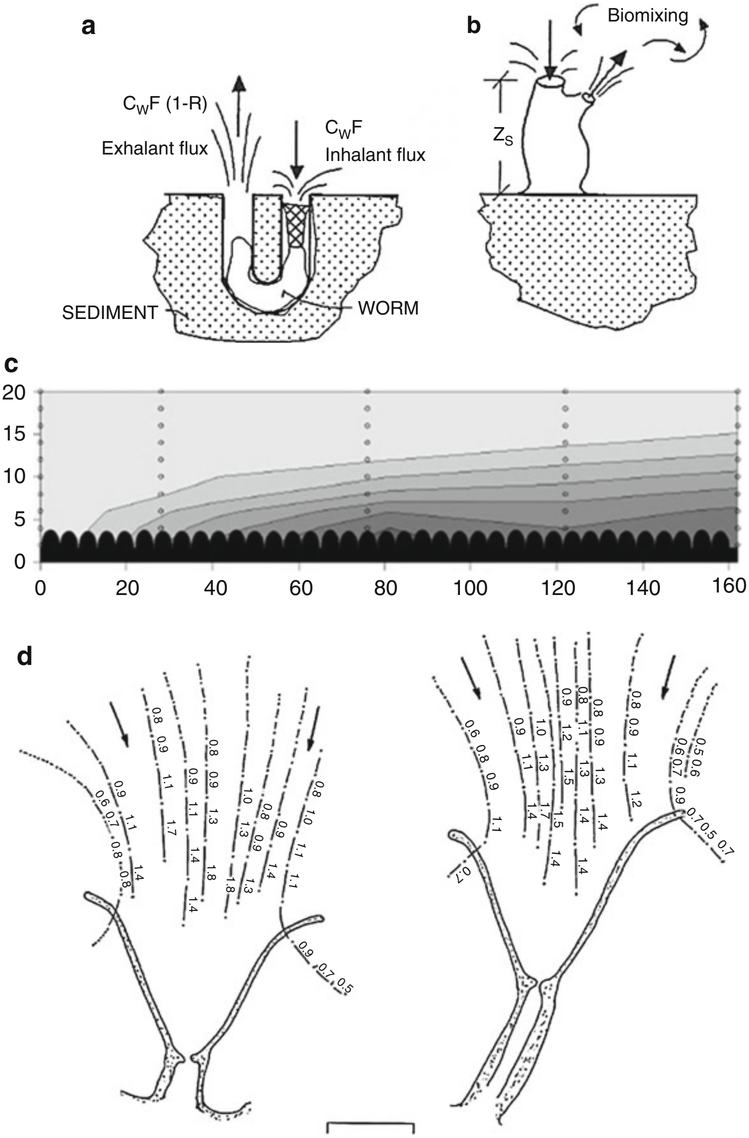

Fig. 1 Examples of zoobenthos filter feeding. (**a**) *Nereis diversicolor* and (**b**) *Ciona intestinalis* above sediment in stagnant water in aquarium revealing induced biomixing (from Larsen and Riisgård 1997, "with kind permission from Elsevier"). Benthic boundary layer flow at 4 cm s^{-1} above mussel bed, (**c**) *Mytilus edulis*, showing contours of decreasing concentration toward the bed (length scales: cm) due to biomixing in addition to turbulent mixing (From Lassen et al. 2006, "with kind permission from Inter-Research."). Velocity distributions by particle tracking at the entrance to the lophophore of zooids (**d**) *Membranipora membranacea* found in viscous sublayers. Flow lines and velocities are from tracked particles (mm s^{-1}, based on time interval of 0.02 s between subsequent video frames). Scale bar = 250 μm (From Larsen and Riisgård 2001, "with kind permission from Taylor and Francis.")

The objective of a fluid mechanical modeling of filter-feeding zoobenthos is to determine the distribution of particulate matter (seston) concentration above a given population density of benthic filter feeders, their individual filtration rate, the supply of seston from above, and the velocity and turbulence distribution of water flow. As a result one obtains the near-bottom depletion of seston (mainly phytoplankton), the rate of feeding and hence growth of the filter feeders, the carrying capacity of the site, and certain ecological implications. In terms of increasing complexity, we consider the simple one-dimensional, transient diffusion-sedimentation process in a stagnant water column above a given population to quantify biomixing and later the convection-diffusion process in a turbulent benthic boundary layer past a population of zoobenthos and finally particle trajectories affected by feeding currents of bryozoans located below the viscous (laminar) sublayer over smooth surfaces of a benthic boundary layer.

2 Grazing Potential of Filter-Feeding Zoobenthos and Actual Impact

Benthic filter-feeding macroinvertebrates have a pronounced grazing impact on the phytoplankton biomass in many shallow marine areas. The grazing potential of a given area is determined by counting each species of the benthic population in representative 1 m^2 areas and multiplying by the individual filtration rate known from laboratory experiments or the literature. The sum for all species gives the volume of water filtered per unit area and time. Population filtration rates are typically 1–10 m^3 water per m^2 area per day, or more, corresponding to a volume that may be several times that of the overlying water column. Thus, a dense population of the ascidian *Ciona intestinalis* (Fig. 2) may filter a water volume corresponding to the whole water mass of a 2–3 m deep shallow cove once per day (Petersen and Riisgård 1992; Riisgård et al. 1995, 1996a; Riisgård 1998).

Similar filtering potentials apply for the facultative filter-feeding polychaete *Nereis diversicolor* (Riisgård 1991, 1994; Vedel et al. 1994) and for the blue mussel *Mytilus edulis* which in dense beds may filter more than 100 m^3 m^{-2} per day^{-1} (Jørgensen 1990; Riisgård et al. 2006). Obviously the grazing impact is highly influenced by hydrodynamic processes and available nutrients. Without externally generated currents and mixing, the benthic population will quickly deplete the near-bottom layer whose thickness then depends on the degree of mixing induced by the filter feeders themselves, by the so-called "biomixing" (see next section).

As an illustration, near-bottom vertical profiles of phytoplankton caused by a dense population of facultative filter-feeding *Nereis diversicolor* have been observed in the field by Riisgård et al. (1996c). Water samples were simultaneously collected at different heights above the bottom where *N. diversicolor* were present, and it appeared that a phytoplankton-reduced near-bottom water layer of 0.05–0.1 m in thickness developed on calm days (Fig. 3). That such depletion of phytoplankton in near-bottom waters plays a significant role for this worm was demonstrated in field-growth experiments performed with worms transferred to

Fig. 2 Population of filter-feeding ascidians *Ciona intestinalis* in the shallow cove Kertinge Nor, Denmark

glass tubes placed at different height above the bottom (Riisgård et al. 1996c). An approximate ten times reduction in growth rate of bottom dwelling *N. diversicolor* compared with that of worms elevated just 0.1 m above the sediment surface indicated that extremely meager food conditions were prevalent near the seafloor.

The realization of the filter feeders' full grazing potential is highly dependent on currents and mixing of the overlying water. Grazing impact is enhanced by the turbulent mixing of the water mass due to wind, wave, and current action, coupling the benthic filter feeders to the pelagic biomasses. However, the grazing may be restricted by stratification of the water body (e.g., caused by salinity differences as frequently seen in the inner Danish waters). The stratification reduces or even prevents the supply of algae across the interface, decoupling the filter feeders from the pelagic biomass. Thus, a key to the understanding of spatial and time-dependent variations in pelagic biomasses is knowledge of the circumstances under which coupling/decoupling of benthic filter feeders take place.

The importance of hydrodynamic conditions for benthic-pelagic coupling have been studied in detail by Riisgård et al. (1996a, 1998) in a shallow Danish cove, Kertinge Nor. The main focus of these studies was on the importance of density-driven currents in determining the grazing impact of the ascidian *Ciona intestinalis*. The grazing behavior of *C. intestinalis* may at times be restricted to a boundary layer flow created by the density-driven currents which are in turn controlled by the varying hydrographic situation in the surrounding open sea (Great Belt). It was shown that the grazing impact caused by the ascidians on the horizontally flowing water could be described by means of a numerical model. A satisfactory agreement between observations and modeled predictions emphasized the importance of filter-feeding benthos (Fig. 4). For the idealized case, the model is expressed by

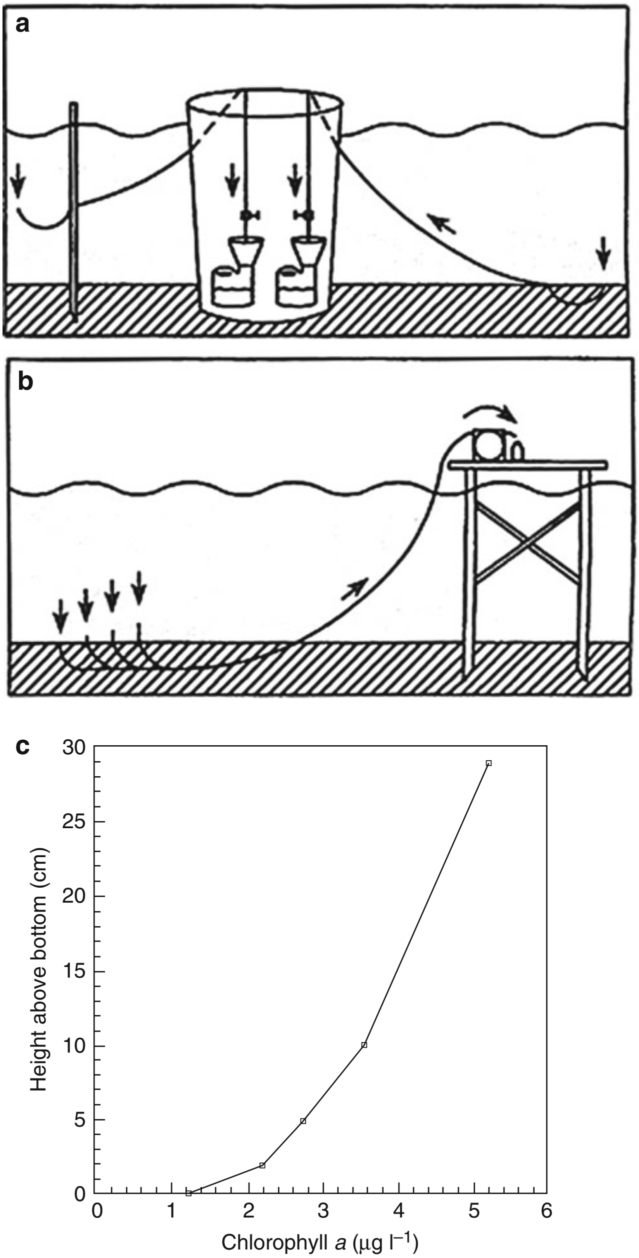

Fig. 3 Device used to sample water at different height (**a**, **b**) for measured concentration of chlorophyll *a* versus height (**c**) in Kertinge Nor, Denmark (From Riisgård et al. 1996c, "with kind permission from Inter-Research.")

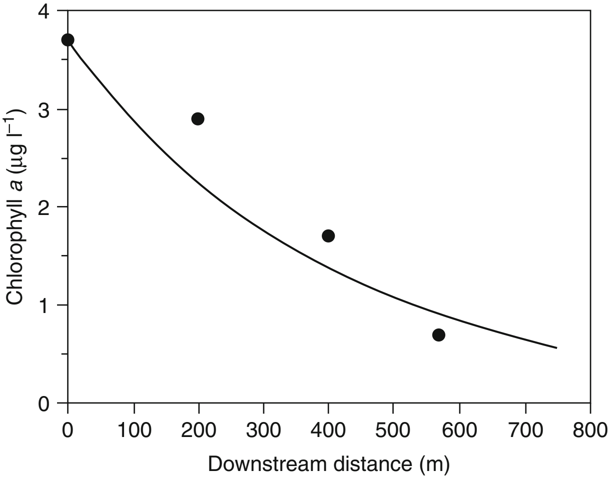

Fig. 4 Measured and predicted ($C_x = C_0 e^{-(fx/Y)}$, see text) reduction of chlorophyll *a* in the near-bottom water passing over the *Ciona intestinalis* bed in Kertinge Nor, Denmark (From Riisgård et al. 1998, "with kind permission from Taylor and Francis.")

the equation $C_x = C_0 e^{-(fx/Y)}$, where C_x = algal concentration at a distance downstream x, C_0 = initial concentration, and $f = F/v_c$; F = area-specific population filtration rate of filter-feeding benthos and v_c = current velocity; and Y = depth of mixed bottom layer. The above equation illustrates how the algal concentration decreases as a function of dimensionless scales for velocity and length.

3 Biomixing in Stagnant Water

It has often been supposed that the exhalant food-depleted jets of water expelled through siphonal openings of ascidians, bivalves, and other benthic filter feeders should prevent the once filtered water from reentering the animal (Vogel 1994). But another or complementary function of such jets may be to mix the near-bottom water. The extent of such "biological mixing" – hereafter designated "biomixing" – has so far only been examined for a few cases such as that of no external flow and of weak benthic boundary layer flows.

The simplest case of no flow and external mixing due to currents or waves was studied experimentally by Riisgård et al. (1996a, b) in an aquarium with the endobenthic *Nereis diversicolor* buried in the bottom sediment or the epibenthic *Ciona intestinalis* placed on the bottom, respectively (Fig. 1a, b). Starting from a uniform concentration of algae in the quiescent water, the development of vertical concentration distribution was measured at time intervals. Typical results for *N. diversicolor* in Fig. 5 show how the inhalant concentration drops to very low values but that biomixing continues to provide a downward seston flux as indicated by the gradients. Such data may conveniently be presented as the transient increase

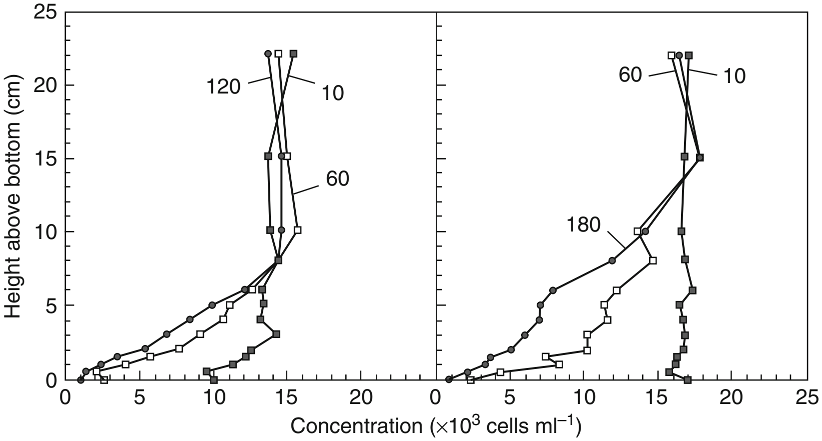

Fig. 5 Development of vertical concentration profiles of flagellate algal cells (*Rhodomonas salina*) in the aquarium of two laboratory experiments with *Nereis diversicolor*. Numbers indicate time (min) after start from a uniform profile. One thousand *R. salina* cells ml^{-1} corresponds to about 1.25 μg l^{-1} of chlorophyll *a*. Penetration of biomixing appears to be 10–15 cm (From Riisgård et al. 1996c, "with kind permission from Inter-Research")

of the concentration displacement thickness, denoted "ingestion layer", defined by the integral $\int_0^L [1 - c(z)/c_0]dz$, where c_0 and $c(z)$, respectively, are the initial and instantaneous concentrations, z the distance above the sediment, and L a sufficient distance that $c(L) = c_0$. The experiments show how the ingestion layer increases with increasing filtration rate and effective diffusivity.

The mathematical description of the foregoing experimental study was given by Larsen and Riisgård (1997) who modeled it as a one-dimensional, transient diffusion problem for the concentration distribution $c(z, t)$ in a stagnant water column above a sediment populated by filter feeders having a known area-specific population filtration rate F. This quantity was determined prior to each experiment by the clearance method by observing the reduction with time of mean concentration in the well-stirred aquarium. Assuming an initial uniform concentration c_0, no bulk convection, but including the possibility of gravitational settling with downward velocity V and localized source S, the conservation of mass of phytoplankton becomes

$$\partial c/\partial t - V\partial c/\partial z = \partial(D\partial c/\partial z)/\partial z + S, \tag{1}$$

subject to the boundary conditions

$$c(z,0) = c_0; Vc(L,t) + D(L)\,\partial c(L,t)/\partial z = 0, \tag{2a}$$

$$Vc(0,t) + D(0)\partial c(0,t)/\partial z = RFc(0,t). \tag{2b}$$

Equation 1 is the unsteady, one-dimensional Fick law of diffusion modified by possible gravitational settling of particles and a source term. Here, t denotes time, z vertical distance above the bottom, D the effective diffusivity, and S a volume source. The initial condition and two boundary conditions in Eq. 2a and 2b express, respectively, the initial uniform concentration, c_0; the fact that there is no supply of phytoplankton at the free surface, $z = L$; and that the net flux toward the bottom at $z = 0$ equals the flux of phytoplankton retained by the filter feeders, R being the efficiency of retention and F the area-specific population filtration rate (a characteristic velocity in terms of volume per unit area and time), or simply the filtration rate (Fig. 1a, b). The parabolic problem (1)–(2), after discretization, is readily solved numerically by standard methods. For *Nereis diversicolor*, having the inhalant tube-opening flush with the bottom (Fig.1a), the source term S equals zero. But for *Ciona intestinalis*, having the inhalant siphon opening located some distance z_S above the bottom (Fig.1b), the appropriate sink term should be accounted for at this location. In this case we put $S = -RFc(z_S, t)/\Delta z_S$, where Δz_S is the vertical extent of the negative source, and the right hand side of Eq. 2b is set to zero.

The difficulty with this model is the diffusivity $D(z)$ which is an empirical distribution that for the case of *Ciona intestinalis* was derived by Larsen and Riisgård (1997) by comparing calculations to experimental results (Fig. 6). A low non-zero value in the upper part of the water column is ascribed to the motility of the flagellate algal cells (*Rhodomonas salina*), while a high value just above the sediment is due to the biomixing generated by exhalant jets and inhalant flows of the filter feeders. The inhalant and exhalant openings situated about 0.05–0.1 m above the bottom and a high and inclined exhalant jet velocity of about 0.1–0.2 m s^{-1}, the concentration distributions lead to a nearly uniform depletion over a layer reaching a thickness of 0.2–0.3 m above the bottom due to high mixing in this. For *Nereis diversicolor*, having inhalant and exhalant burrow openings flush with the sediment surface and only a moderate exhalant jet velocity of about 0.01 m s^{-1}, the thickness of a well-mixed layer is limited by the low values of diffusivity prevailing at heights greater than about 0.05 m above the bottom. Numerical predictions of concentration distributions reproduced essential features of experiments and suggest near-bottom values of effective diffusivity of 0.3×10^{-6} and 150×10^{-6} m^2 s^{-1}, respectively, for *N. diversicolor* and *C. intestinalis*. It is suggested that the latter value is so large that the induced mixing should be included in modeling benthic boundary layers under moderate flow conditions.

For biomixing in stagnant water, a true mathematical model without empirical input should be based on direct numerical simulation (DNS), solving the unsteady Navier-Stokes equations and conservation equations of mass of water and of seston, resolving the detailed geometry and dynamics of a large number of inhalant/exhalant flows. Time-averaged fields would provide fluxes of seston and, when compared to mean fields of concentration, also the distribution of effective diffusivity. A possible experimental approach would be to use optical methods to record the vertical distribution of actual particle flux as well as concentration from which the effective diffusivity could then be extracted.

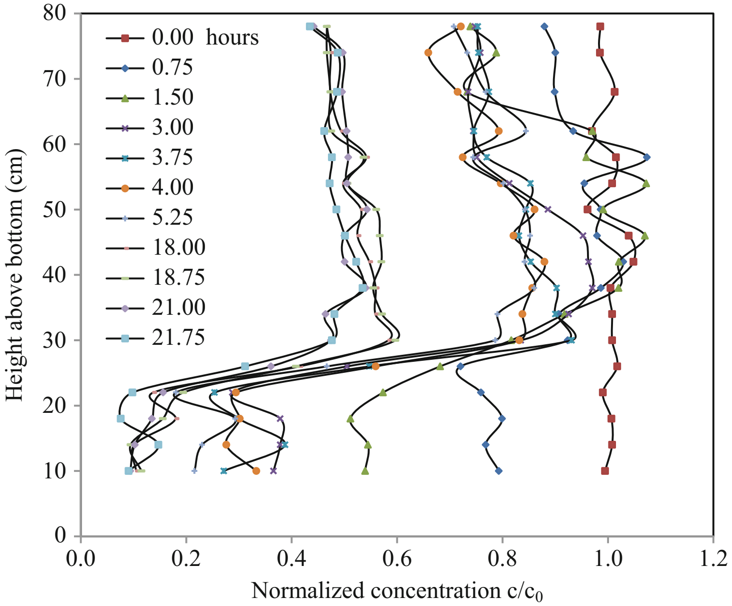

Fig. 6 Development of vertical concentration profiles of algal cells in the aquarium of a laboratory experiments with *Ciona intestinalis* lasting 21 h after start from a uniform profile. Penetration of biomixing appears to be 10–15 cm above the inhalant siphon situated about 10 cm above the sediment "(replotted from Larsen and Riisgård 1997, with kind permission from Elsevier)"

4 Filter Feeding and Biomixing in the Benthic Boundary Layer

Phytoplankton distributions have been recorded in flume experiments above pairs of inhalant and exhalant silicone tubes representing populations of filter-feeding clams (O'Riordan et al. 1993, 1995) and above live mussels (Butman et al. 1994; van Duren et al. 2006; Lassen et al. 2006). The purpose of using "model animals" was to use laser-induced fluorescence to study the formation of a concentration boundary layer at a constant and known benthic filtration rate (O'Riordan et al. 1993, 1995), thereby circumventing the problems that Butman et al. (1994) encountered with a reduced filtration activity of mussels during experiments due to insufficient algal supply. But, having kept the mussel bed in the flume for several months prior to the experiment, van Duren et al. (2006) did not encounter such problems in their flume study of the boundary layer structure over a bed of filter-feeding mussels, and they found that filtration activity may have an important effect on exchange processes in the near-bottom region. Evidence now exists that filter-feeding bivalves maintain a constantly high filtration rate in the presence of natural (low) concentrations of phytoplankton (e.g., Riisgård and Seerup 2003; Riisgård et al. 2006, 2011b). For the blue mussel, *Mytilus edulis*, a phytoplankton range between the lower starvation level of about 0.5 μg chl *a* l^{-1} and the upper saturation level of about 7 μg chl *a* l^{-1} secures a maximal filtration rate (Clausen and Riisgård 1996; Riisgård et al. 2013), whereas both starvation and saturation lead to reduced valve gape and thus to a reduction in the filtration rate.

The extent of biomixing caused by a dense population of *Mytilus edulis* was studied experimentally by Lassen et al. (2006) at two flow speeds (4 and 8 cm s^{-1}) in a laboratory flume channel at natural (low) algal concentrations in order to determine its relative importance compared to current-generated turbulence. The increasing reduction of algal concentration downstream in the developing boundary layer at low speed is shown in Fig. 1c. Distributions of algal cells a distance of 162 cm from the start of the bed showed a near-bottom depletion of about 58% and 45%, respectively, for the two flow speeds, which indicate the degree of re-filtration. In addition, flow structures were quantified in terms of distributions of velocity, turbulent shear stress, and turbulent kinetic energy in the benthic boundary layer at three levels of mussel filtration activity (maximal, reduced, and zero). Further, the filtration activity of *M. edulis* with and without added suspensions of algal cells which influence its valve opening degree and filtration rate was studied by Lassen et al. (2006) who concluded that biomixing enhances the flow-induced down-mixing of phytoplankton and can be identified as peaks in profiles of turbulent kinetic energy and turbulent shear stress. The associated increase in friction velocity over length of the mussel bed at maximal filtration activity amounted to 56% and 49% for the two flow speeds studied which shows the functionality of biomixing.

Filter-feeding bivalves process large amounts of ambient water to acquire the food needed for sustaining life, and an extensive literature deals with the amounts of water pumped through the gills of a blue mussel and the efficiency by which suspended particles are retained (Jørgensen 1990; Riisgård and Larsen 2010). Nevertheless there is a considerable variation between published values of the exhalant jet velocity of mussels (Jørgensen et al. 1988; Riisgård et al. 2011a), and little is known about the detailed fluid mechanics of flow near a mussel generated by the flow through the exhalant siphon appearing as a well-structured jet.

The exhalant jet flow in conjunction with a possible imposed external flow from currents or other mussels will influence the grazing impact and thus the concentration distribution of food particles reaching the inhalant aperture, hence affecting the feeding conditions of the mussel. Of particular interest is the undesirable phenomenon of re-filtration where part of the once filtered and exhaled water reaches the inhalant aperture of either the same or other mussels, which has been studied to some extent for mussel beds where a number of attempts have been made to model phytoplankton concentration gradients caused by dense beds of filter-feeding bivalves in relatively strong currents with a high degree of turbulence (Wildish and Kristmanson 1984, 1997; Fréchette et al. 1989; O'Riordan et al. 1993, 1995; Butman et al. 1994; Mann and Lazier 1996; Jonsson et al. 2005; Lassen et al. 2006). More recently, Riisgård et al. (2011a) made a detailed study of fully open mussels (*Mytilus edulis*) in terms of filtration rate, exhalant siphon aperture area, and jet velocity. The exhalant jet velocity was determined by three methods: (1) measured filtration rate divided by exhalant aperture area, (2) manual particle tracking velocimetry (PTV) using video-microscope recordings, and (3) particle image velocimetry (PIV). The latter provided detailed two-component velocity distributions near the exhalant siphon in five planes parallel to the axis of the jet and the major axis of the oval aperture, hence estimates of momentum and kinetic energy flows in addition to mean velocity. Data on particles inside the exhalant jet of filtered water was ensured by the use of TiO_2 seeding particles which were de-agglomerated by ultrasound to size range 0.7–2 μm prior to addition to avoid retention by the gill filter of the mussels. Notably it was found that the exhalant jet velocity is essentially constant, about 8 cm s^{-1}, and independent of shell length.

The transport of phytoplankton from the upper part of a water column to benthic filter feeders is facilitated by wave- and current-generated turbulence (and to some extent by settling) over most of the column height and supplemented by biomixing close to the bottom. In recent field experiments in Limfjorden (Denmark), Petersen et al. (2013) have measured profiles of chlorophyll *a* (chl *a*) concentration from 0.5 to 200 cm above a mussel bed site and a bare sandy site at about 6 m water depth for different conditions of wind and waves. While the chl *a* concentration was more or less uniform above the sandy site, the depletion of chl *a* near the mussel bed due to filtration by mussels gave rise to the steepest gradient in chl *a* well above the bed for the higher waves. One may interpret the chl *a* profiles to imply that biomixing is effective to a height of about 10 cm (region of nearly constant, low chl *a*) and that the gradient in chl *a* above this layer is a measure of the turbulent down-flux of chl *a*, hence related to mussel filtration rate through the magnitude of the effective eddy diffusivity.

In a similar but more comprehensive field study in the Menai Strait, (North Wales, UK), Saurel et al. (2013) measured profiles of both chl *a* concentration and velocity fields in the water column above mussel beds that included patchy regions. From the velocity gradient $\partial U/\partial z$ and Reynolds shear stress τ_{zx} obtained with the acoustic Doppler, values of eddy diffusivity $K_{z} = \tau_{zx}/(\partial U/\partial z)$ were found to be of the order of 2–3 × 10^{-4} m^2 s^{-1} at 50 cm above the bed in good agreement with values obtained from chl *a* profiles and clearance rate by in situ defecation methodology (Kotta and Møhlenberg 2002; Saurel 2008). Mussel filtration is responsible for food depletion in the benthic boundary layer above the mussel bed (<1 μg chl *a* l^{-1} at height <6 cm), and self-organization was found to be directly related to the interaction between feeding rates and the hydrodynamic processes that spatially affect food supply in relation to mussel bed patchiness, as observed using continuous video recording of mussel feeding behavior. Mussel size varied according to measured food gradients such that larger mussels were found at the edge of patches with smaller ones at the middle. The observed high filtration rates (mean 2.9 l $ind.^{-1}$ h^{-1} or 7.40 l g^{-1} dry body weight h^{-1}), which were comparable to those measured in the laboratory under optimal conditions (Riisgård 2001; Riisgård et al. 2011a, 2014) despite food depletion near the mussel bed, are believed to be due to the interaction of three hydrodynamic processes: vertical turbulent mixing, advection, and resuspension. Thus the presence of bare patches within the mussel bed facilitated the replenishment of seston and could thereby increase mussel-carrying capacity.

In regard to the mathematical and numerical modeling of benthic boundary layer flows, to date a number of attempts have been made to determine phytoplankton concentration gradients caused by filter-feeding bivalves in relatively strong currents with a high degree of turbulence. Moderate currents may generate enough turbulence in the benthic boundary layer to increase the supply of food to the filter feeders by turbulent mixing. For some details of various approaches, see Box 1. However, the additional biomixing induced by the filter feeders themselves has not yet been included in any model even though the degree of which exhalant jets affect the vertical mixing and thus the transport of phytoplankton down to the bottom could play a crucial role in determining the actual grazing impact of benthic filter feeders.

Box 1: Modeling of Benthic Boundary Layer Flows

An early empirically based algebraic model by Muschenheim (1987) was developed to interpret his experimental results of how the near-bed seston flux depended on the velocity field. The model was based on a developed, equilibrium, turbulent bed flow described by the log-law velocity distribution:

$$u(z) = (u* /\kappa)\ \ln(z/z_0), \tag{3}$$

where u^* denotes the friction velocity, κ the von Karman constant, and z_0 the roughness length, which is about 1/30 of the geometric bed roughness elements. The model ignores vertical diffusion and considers instead the sedimentation of entrained inorganic and organic seston to lead to the empirical vertical concentration profile:

$$c(z) = c(a)(a/z)^p; p = w_s/\kappa u* , \tag{4}$$

where $c(a)$ is the concentration at the reference height $z = a$ and w_s denotes the fall velocity of sediment. Although diffusion per se is ignored, it actually enters into the physical process of resuspension and settling of seston, leading to Eq. 4. The seston flux at any height, $c(z)\ u(z)$, has a maximal value at a height that depends on fall velocity hence particle size. For the organic seston particles, such a height suggests the optimal height above the bed a filter feeder would profit most. This model may be appropriate for benthic boundary layers with densely resuspended sediments, say for cases of shelf, slope, and abyssal environments, but not for shallow coastal situations.

Measured phytoplankton concentration distributions above an intertidal mussel bed by Fréchette et al. (1989) were compared to their model of a

(continued)

two-dimensional benthic concentration boundary layer developing in a turbulent flow past a 100 m long bank of mussels and a water depth of 2.25 m. Assuming a depth-limited parallel current flow with the typical log-law profile of Eq. 3 and initially uniform phytoplankton concentration c_0, the conservation of phytoplankton mass becomes

$$u\partial c/\partial x - V\partial c/\partial z = \partial(D\partial c/\partial z)/\partial z, \tag{5}$$

subject to

$$c(0,z) = c_o;\ \ Vc(x,H) + D(H)\partial c(x,H)/\partial z = 0, \tag{6a}$$

$$V\,c(x,0) + D(0)\partial c(x,0)/\partial z = RF\,c(x,0). \tag{6b}$$

As for Eq. 1, the Fick law of diffusion appears in Eq. 5, now in its steady form including spatial development in a boundary layer form, ignoring axial diffusion since it is small compared to axial convection. Here, x denotes downstream distance along the mussel bed, z vertical distance above the bottom, H water depth, V downward settling velocity of phytoplankton, and $D(z)$ effective diffusivity assumed to equal the eddy viscosity distribution, $D = \kappa u_* z\ (1\text{–}z/H)$, derived from the log-law velocity profile of Eq. 3. The initial condition and two boundary conditions in Eq. 6a and 6b express, respectively, the initial uniform concentration, c_o; the fact that there is no supply of phytoplankton at the free surface, $z = H$; and that the net flux toward the bottom at $z = 0$ equals the flux of phytoplankton retained by the filter feeders, R being the efficiency of retention and F the area-specific population filtration rate. In solving the problem numerically, Fréchette et al. (1989) ignored the settling of phytoplankton ($V = 0$ in Eqs. 5 and 6), thus reducing the problem to a balance between horizontal convection and vertical diffusion, which is a parabolic problem because axial diffusion $(\partial(D\partial c/\partial x)/\partial x)$ has been justly ignored compared to axial convection ($u\ \partial c/\partial x$). The constants u^* and z_0 were determined by matching a measured velocity profile to the log-law, and bottom roughness upstream of and along the mussel bed was assumed unchanged. Because of the slow change between flood and ebb of current velocity, each instant may be treated as separate quasi-steady problem, however, each requiring a new velocity distribution as input for a solution. If there is a change in effective bed roughness at the start of the mussel bank, an internal boundary layer develops which changes the velocity profile of Eq. 3, as found in the experimental flume study by van Duren et al. (2006). They also found that at moderate velocity, inactive mussels lead to a smaller bed shear stress, while actively filtering mussels raised the bed stress and turbulence level near the bed which indicates biomixing to be at play.

(continued)

It appears that more contemporary and elaborate turbulence models, such as the Reynolds-averaged Navier-Stokes (RANS) equations with an eddy diffusivity model based on mixing length or k-epsilon transport equations, or the second-order full Reynolds stress model, have not been widely used. Yet, an example of the former was the basis of the two-dimensional hydrodynamic and water-quality model used by Boegman et al. (2008) to study the reduction of algae stocks in the near-shore environment of western Lake Erie due to the invasive zebra mussels.

5 Filter Feeding in the Viscous Sublayer

For a long time, it has been recognized that a variety of processes of biological interest are strongly influenced by water motions at the boundary with the sea floor and that the processes in the bottom boundary layer may be modeled in flumes with widely different size, shape, and flow characteristics for manifold purposes (Wildish and Kristmanson 1997). But the use of flumes in studies of benthic filter feeding has mainly dealt with studies of boundary layer flows in supplying phytoplankton to mussels and other macro-benthic filter feeders. Thus, most studies deal with the "logarithmic" layer where the velocity varies as the logarithm of the distance above the bottom. The logarithmic layer is turbulent, but below this layer, due to viscous damping, there exists a thin layer of essentially laminar flow near hydrodynamically smooth surfaces. This layer is designated the viscous sublayer or the "linear sublayer" because the velocity varies linearly with the distance above the substratum (Mann and Lazier 1996; Wildish and Kristmanson 1997). The viscous sublayer is typically in the order of millimeters thick at low flow rates but decreases in thickness with increasing flow rate. Encrusting filter-feeding bryozoan colonies (Fig. 7) may often, or perhaps as a rule, reside within this viscosity-dominated layer and may serve as an example of filter feeding in the viscous sublayer (e.g., Hermansen et al. 2001). Due to their small size, bryozoans must be able to cope with thin boundary layers and steep velocity gradients above surfaces of marine macroalgae, rocky outcrops, etc., on which they live.

Bryozoans are active filter feeders working on energy-consuming lophophore filter pump (Riisgård and Manríquez 1997; Riisgård and Larsen 2000, 2010). Water from near the surface of a bryozoan colony is pumped downward by the lateral cilia on the crown tentacles of the individuals. The flow velocity at the entrance of the lophophores is typically 2–3 mm s^{-1}. The uppermost parts of the lophophores of encrusting bryozoans are typically raised only about 0.5–1.5 mm above the substratum. In encrusting colonial bryozoans, which form a continuous and often fairly smooth layer, the filtered water moves laterally along the substratum between the

Fig. 7 Side view of strip cut from encrusting bryozoan colony *Membranipora membranacea* and its substratum, about two rows of zooids wide, and 3–3.5 mm long, reaching from one "chimney" to another. Scale bar = 0.5 mm (From Larsen and Riisgård 2001, "with kind permission from Taylor and Francis")

individual lophophores, and finally in, e.g., *Membranipora membranacea* (Fig. 7), the water emerges from "chimneys" as a jet of substantial speed, about 12 mm s^{-1} (Larsen and Riisgård 2001) which may contribute to biomixing above the colony.

Turning to the mathematically and numerical modeling of feeding in a laminar current passed in an encrusted colony, Larsen et al. (1998) determined experimentally particle paths and velocities from video recordings above single-line colonies of bryozoans (*Celleporella hyalina*, *Electra pilosa*, *Alcyonidium hirsutum*, *Membranipora membranacea*, *Flustrellidra hispida*) placed at the bottom of a laminar flow flume in zones of constant velocity gradient (1–4 s^{-1}). Incurrents to lines of three to ten zooids typically distort trajectories of particles approaching the colony at heights 1–2 mm above the level of lophophore inlets, and they capture particles from paths 0.7 to 1.2 mm above this level. The computational modeling of this process used a standard commercial code (STAR-CD) to solve the three-dimensional Navier-Stokes equations subject to sink-source pairs representing individual lophophores in a line to obtain the full velocity field, into which particles were tracked to reveal trajectories in good agreement with experimental observations. Results also showed how the fraction of captured particles per zooid decreased downstream.

Another problem concerned the forming of "chimneys." Closely spaced zooids forming an encrusting colony experience hydrodynamic interference that results in a significant reduction of feeding current per zooid as the number of zooids increases because pressure builds up in the substratum under the canopy to force excurrents to escape at the rim of the colony (Fig. 8). As a result zooids at the interior of the colony bend or die to open the canopy to let excurrent water escape as an upward directed jet of substantial speed. For large colonies the spacing of chimneys appears to be more or less constant. Larsen and Riisgård (2001) presented a simple hydrodynamic model for the variation of pressure below the lophophore canopy, which determines the corresponding feeding rate of zooids, and found that a reduction of feeding rate to 30% of that of an isolated zooid would lead to the likely spacing between chimneys.

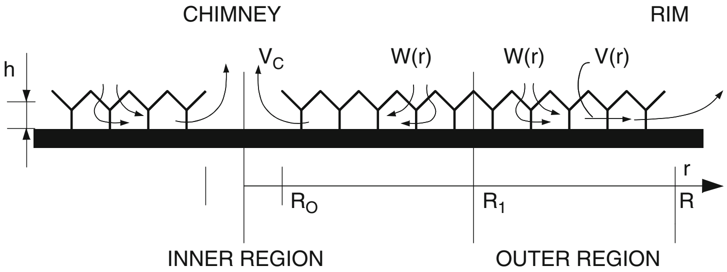

Fig. 8 Section of model colony showing inner circular region of radius R_1 with radial inflow under canopy of lophophores toward chimney of radius R_0, due to high pressure at R_1, and outer region with radial outflow to rim at radius R. When for a colony of increasing values of R_1 the feeding rate of zooids at R_1 has decreased to about 30% of that of an isolated zooid, the likely chimney spacing is suggested to be of the order $2R_1$ (From Larsen and Riisgård 1997, "with kind permission from Elsevier")

6 Case Study: Grazing Impact in Odense Fjord (Denmark)

The potential ability of a filter-feeding population of benthic macroinvertebrates to clear the water of particles may be expressed in several ways. One possibility is to relate the total filtration rate of the population (F_{tot}, $\text{m}^3\ \text{d}^{-1}$) to the total water volume (V_{tot}, m^3) in the area considered: $Q = V_{tot}/F_{tot}(\text{unit} = \text{d})$, which is denoted as the grazing impact. The individual filtration rate (F) of a zoobenthic filter-feeding organism in an aquarium with well-mixed seawater and 100% efficiently retaining algal cells may be measured by means of the clearance formula (Riisgård 2001): $F = (V/t) \times \ln(C_0/C_t)$, where C_0 and $C_t =$ algal concentration at time 0 and time t and $V =$ volume of water. From this it is seen that the time to half the concentration (halftime) for the algal cells is $t_{1/2} = (V/F) \times \ln 2$. Thus, it appears that the potential grazing impact of a population of filter feeders with a certain density (D, ind. m^{-2}) may also be expressed as the halftime: $t_{1/2} = U/\left(F_{pop}\right) \times \ln 2(\text{d})$ for the phytoplankton in the water column (U, $\text{m}^3\ \text{m}^{-2}$) above the filter-feeding population having a known area-specific population filtration rate $\left(F \times D = F_{pop}, \text{m}^3\text{m}^{-2}\text{d}^{-1}\right)$ assuming efficient vertical mixing. Clearly, when referred to the same population and the same volume of water, $t_{1/2} = Q \times \ln 2$, being also the mean residence time of phytoplankton under well-mixed conditions.

The total area of Odense Fjord (Denmark) is 60 km^2, the outer fjord is 49 km^2 with a mean depth of 2.7 m, and the inner fjord is 11 km^2 with a mean depth of 0.8 m. Odense Fjord is characterized by a large biomass of filter-feeding polychaetes (*Nereis diversicolor*), clams (*Mya arenaria*), and cockles (*Cerastoderma glaucum*), which together make up about 70% of the total animal biomass. A work conducted by Riisgård et al. (2004) has thrown light on the grazing impact of the filter-feeding zoobenthos in Odense Fjord. The mean value in the inner part was found to be $F_{pop} = 2.74 \pm 1.80 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$. Further, it was found that $Q = 0.29$ d and $t_{½} = 0.2$ d. In other words, *N. diversicolor* was found to be able to filter a volume of water equivalent to the whole water mass in the inner part of the fjord about three times per day, and – under the condition of efficient vertical mixing – the worm would be able to reduce the phytoplankton biomass 50% within less than 5 h, assuming 100% retention. The values for *M. arenaria* in the inner fjord were $F_{\text{pop}} = 1.76 \pm 1.87 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$, $Q = 0.46$ d, and $t_{½} = 0.32$ d, i.e., this clam was found to be able to filter a volume of water equivalent to the whole water mass in the inner part of the fjord about two times per day and potentially reduce the phytoplankton biomass 50% within less than 8 h. When also *C. glaucum* was included, it was found that the combined total potential grazing impact of the three filter-feeding species, using $F_{tot} = \Sigma F_{pop}$, was $Q = 0.17$ d, and $t_{½} = 0.12$ d, or only about 3 h.

In addition to these benthic filter feeders, a dense population of the facultative filter-feeding amphipod *Corophium volutator* may further help to exert a pronounced grazing impact in the inner Odense Fjord (Møller and Riisgård 2006). *C. volutator* lives in a U-shaped semicircular tube in the sediment on shallow water. Like *Nereis diversicolor*, *C. volutator* has two feeding modes: (1) surface deposit feeding and (2) filter feeding (Riisgård and Kamermans 2001; Riisgård and Schotge 2007); during the latter, particles larger than about 7 µm are retained. The ability of *C. volutator* to filter suspended particles from the ambient water was studied by Møller and Riisgård (2006) who assessed the area-specific population filtration rate (F_{pop}) of a dense population (up to about 18,000 ind. m^{-2} in August) of this burrowing amphipod in the inner part of Odense Fjord. The potential grazing impact varied between $F_{pop} = 1$ and $20.6 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ in January and July, respectively, and the estimated grazing impact varied between $\text{Q} = 20$ and 1 h, whereas the potential halftime varied between 14.5 and 0.7 h. This indicates that *C. volutator* is able to filter a volume of water equivalent to the whole column about 25 times per day, and – under the condition of efficient vertical mixing – the amphipod may reduce the phytoplankton biomass 50% within less than 0.7 h in June and July. However, it must be emphasized that the estimated grazing impacts are potentials that may only be realized if a decisive prerequisite is fulfilled, namely, that the filter-feeding animals on the bottom are exposed to the whole water column by effective vertical mixing of the water. In the shallow inner part of Odense Fjord with a mean depth of only 0.8 m, the water is often being well mixed by wind action. The short, down to 3 h, residence time for phytoplankton (with a generation time of about 1 day for larger species and down to 6 h for very small species) shows that the filter-feeding zoobenthos on especially windy days may control the phytoplankton biomass in the inner part of Odense Fjord, and therefore, depending on the actual wind speed, the biomass of phytoplankton strongly fluctuates. The ability of *N. diversicolor* and *C. volutator* to switch between deposit feeding and filter feeding is thus an appropriate adaptation for living in a fluctuating environment with frequent depletion of suspended food particles.

More extensive field studies in Odense Fjord involving time series of simultaneous measurements of vertical profiles of chlorophyll *a*, wind mixing of the water

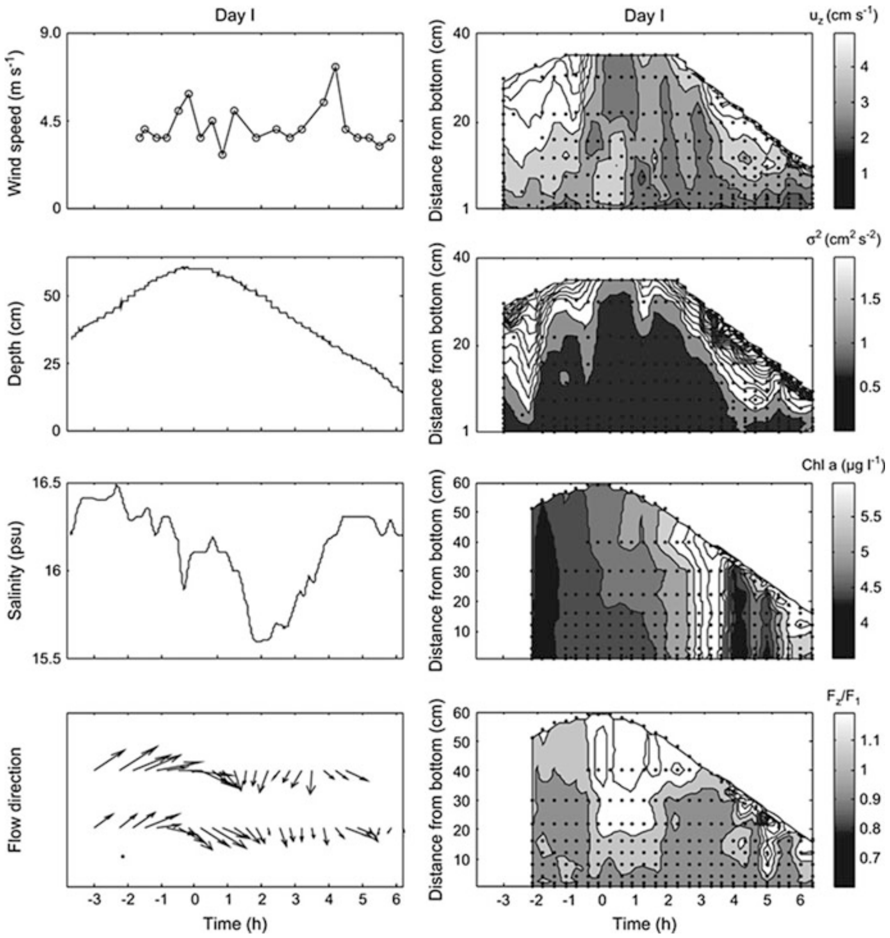

Fig. 9 Field measurements of chlorophyll *a*, wind mixing, and water current in Odense Fjord. *Left*, *top* to *bottom*, wind speed, water depth, salinity, and direction of flow measured 2 cm (*lower*) and 16 cm (*upper*) above the *bottom*. *Right*, *top* to *bottom*: contours of mean velocity, variance of velocity, concentration of chlorophyll *a*, and standardized fluorescence, where F_1 and F_z are the fluorescence at 1 cm and z cm above the *bottom*, respectively. The estimated area-specific population filtration rate of *Nereis diversicolor* and *Corophium volutator* was $F_{\mathrm{pop}} = 5.8$ and 4.1 $\mathrm{m^3\ m^{-2}\ d^{-1}}$, respectively (From Riisgård et al. 2007, "with kind permission from Elsevier")

column above the benthic filter feeders, and water current speed and direction (Fig. 9) were subsequently carried out by Riisgård et al. (2007) in order to further investigate the suggested causal connections. The field studies, supplemented with underwater video observations of the filter-feeding zoobenthos, showed that when the filter feeders are uncoupled, an algal depleted near-bottom layer is created soon after, and this change results in switching from a filter-feeding way of nourishment to surface deposit feeding in *Nereis diversicolor* and *Corophium volutator*, whereas filter-feeding bivalves withdraw their siphons and close their valves.

In controlled laboratory experiments, Riisgård et al. (2003) studied the regulation of opening state and filtration rate in three species of filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, and *Mya arenaria*) in response to low algal concentration. It was found that when the bivalves experience very low algal concentrations, this eventually leads to reduced siphon opening and valve gape, or complete closure, along with cessation of the filtration activity which lasts until the algal concentration is elevated above a lower threshold level. When initially unfed bivalves were offered algal cells, the animals soon opened their siphons/valves simultaneously with a pronounced increase of the filtration rate. On the other hand, when open and actively filtering bivalves experienced decreasing algal concentrations below a certain level, this led to a reduced opening state and cessation of filtration activity. The demonstrated regulation of the opening state and filtration activity in response to presence and absence of algal cells seems to represent a physiological adaptation to apparently frequent situations with transiently meager phytoplankton suspensions in the near-bottom water (Riisgård and Larsen 2015).

Our knowledge on zoobenthic filter-feeding activity, actual population grazing impact, and the importance of switching between different feeding modes in some animals is still limited and especially more field observations of feeding activity combined with measurements of flow rates and phytoplankton concentration distributions are needed to better understand the interactions between the sessile organisms and the hydrodynamics of the surrounding water, and such knowledge is a prerequisite for the development of new and more advanced models.

7 Conclusions

Laboratory and field experiments along with modeling of hydrodynamic processes have increased our understanding of the concentration distribution near benthic filter feeders and how it may be influenced by biomixing produced by the feeder itself or by turbulent mixing generated by external means. For the active filter feeder, the inhalant flow is like flow to a drain, i.e., coming from all directions of the immediate proximity to which food particles must be brought by other means such as sedimentation or turbulent diffusion. The exhalant flow is like flow in a jet with a considerable reach which suppresses re-filtration and promotes local turbulence denoted biomixing. Experiments for *Nereis diversicolor* and *Ciona intestinalis*, respectively, have shown velocities of exhalant jets of 0.01 m s^{-1} and 0.1–0.2 m s^{-1}, biomixing to reach 0.05–0.1 and 0.2–0.3 m above the bottom, and that mixing is equivalent to an eddy diffusivity of about 0.3×10^{-6} and 150×10^{-6}.

As mentioned, Saurel et al. (2013) found values of eddy diffusivity of the order of $2\text{–}300 \times 10^{-6}$ m^2 s^{-1} in the velocity fields above mussel beds, so it may be expected that biomixing from actively filtering mussels may be important for down-mixing of seston in benthic boundary layers at moderate velocities. Several flume studies have provided detailed data on distributions of velocity and turbulence in benthic boundary layer flows over mussel beds. But it appears that it remains to model such flow in detail using computational modeling, including the effect of mussel-induced biomixing. On the smaller scale, the viscous-dominated flow in the sublayer over bryozoan colonies is a simpler problem to model, and there exists many studies of particle trajectories and flow fields near the individual zooids.

Down-mixing of primary production from near the free surface toward the benthic region depends on bulk turbulence generated by wind and waves as revealed by field experiments that compare chlorophyll *a* concentrations above mussel beds and above bare sand. Mussels in patchy beds appear to benefit from the patchiness as compared to mussels in large uniform beds. Recent years' studies have improved our understanding of the role of benthic filter feeders in coastal ecosystems in terms of grazing impact, regulation of plankton concentrations, and energy transfer. Such aspects are quantified in a detailed case study from Odense Fjord (Denmark).

In general terms, the objective of a fluid mechanical modeling of filter-feeding zoobenthos is to determine the distribution of particulate matter (seston) concentration above a given population density of benthic filter feeders, their individual filtration rate, the supply of seston from above, and the velocity and turbulence distribution of water flow. As a result one obtains the near-bottom depletion of seston (mainly phytoplankton), the rate of feeding, and hence growth of the filter feeders, the carrying capacity of the site, and certain ecological implications. It is hoped that more efforts be devoted to these areas in the future, for example, to lead to improved models for the benthic boundary layers, including effects of wall roughness, biomixing, and oscillating flows caused by waves. This may be achieved by using advanced numerical methods such as direct numerical simulation (DNS), large eddy simulation (LES), etc. Flume and field experiments provide increasingly detailed data on flow, turbulence, concentration, and other properties by advanced optical and acoustic Doppler instruments of velocimetry which will contribute to verify and improve computational methods.

8 Cross-References

- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Conservation and Management of Vulnerable Marine Benthic Ecosystems
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Growth Patterns in Long-Lived Coral Species

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Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders

29

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Abstract

Marine benthic communities are dominated by suspension feeders, including those actively pumping water, passively encountering particles, or some combination of the two. The mechanisms by which particles are encountered and retained are now well known for a range of water flow conditions and organism morphologies. Recent research has attempted to quantify the energetic components of suspension feeding, including intake of particles, pumping rates, and metabolic costs of these activities. Energetic models depend strongly on environmental conditions, including temperature, flow speed, and food availability, for example. The effects of these variables have been combined for realistic scenarios using dynamic energy budget (DEB) models, and related models to examine components of fitness (growth, reproduction, population increase), for both existing conditions and for conditions expected for future environments. Detailed examples are provided from recent research on bivalve mollusks, cnidarians including sea anemones and corals, and barnacles. These examples cover several major phyla that are often important components of intertidal and subtidal benthic communities. All common phyla of benthic suspension feeders are discussed, though less extensively, especially given the paucity of energetics studies for some of these phyla.

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Contents

1 Introduction

Assemblages of benthic marine invertebrates are usually dominated by a diverse set of creatures that can be termed suspension feeders, despite quite a wide variety of morphologies, prey types, and modes of capture. Coral reefs, temperate zone rocky reef communities, polar benthic communities, and many types of soft-substrate communities are made up primarily of attached organisms that capture particles from the overlying water column. Some of the best examples of such communities are the dense barnacle zones in intertidal habitats, extensive mussel beds in both intertidal and subtidal habitats, coral reefs dominated by scleractinian corals and sponges, large ascidian aggregations, and subtidal rocky reefs dominated by sponges, octocorals, sea anemones, and others. In such habitats, suspension feeders are often the dominant biomass, as well as ecosystem engineers that build structures used by a diversity of other members of the community, both sessile and motile.

Suspension feeders compete intensely for space on primary substratum, which gives them access to resources in the water moving above the substratum. Ecologists term this “benthic-pelagic coupling” because it is an important mode of transfer for primary production in the water column, to secondary production on the bottom (see also ▶ Chap. 30, “Benthic-Pelagic Coupling: New Perspectives in the Animal Forests,” this volume). Such coupling is an example of a "spatial subsidy" where important resources are delivered to one community or habitat from another, which thus enhances energy and material flow through the former (i.e., local production is subsidized). Production by phytoplankton in large bodies of water can be delivered to the benthos either directly or once it has passed through upper trophic levels such as zooplankton. Primary production in shallow subtidal zones, by kelp for example, can be delivered to deeper communities with minimal primary production by water currents, in the form of kelp fragments or detrital particles. These suspension feeders, in turn, process the subsidies and transfer them in a form that can sometimes be used by other members of the benthic community, including egesta, mucus, fecal material, and sexual products. Pseudofeces and feces, for example, are rich in organic compounds that are acted on by bacteria and made more nutritious for benthic deposit feeders (Galloway et al. 2013).

Passive suspension feeders rely on water currents or wave induced flow to move particles past their capture surfaces. However, active suspension feeders produce their own internal currents that pull water through internal filters; this is particularly important when water flow is minimal but may also be energetically positive even when flow is substantial (Wildish and Kristmanson 2005, review). Some even manage to have it both ways, relying on water flow to induce currents through their body or colony, where particles can be removed from the water internally, then ingested (Vogel 1996). Obviously, water flow is an important component of suspension feeder biology and energetics and will be discussed in some detail in this chapter and in ▶ Chaps. 30, "Benthic-Pelagic Coupling: New Perspectives in the Animal Forests," and ▶ 28, "Filter-Feeding Zoobenthos and Hydrodynamics" in this volume.

2 The Diversity of Suspension Feeders

Most phyla of invertebrates, and even some vertebrates, have given rise to groups that can be considered suspension feeders. Among the single-celled organisms, there are many which remain attached to a surface and capture particles or other organisms that come into contact with them. The choanoflagellates, for example, use a flagellum to pump water through a mesh-like collar, which then retains particles that are later phagocytized into the cell. These protists, which are thought to resemble the ancestors of sponges, form colonies that presage future multicellular colonies working at a much larger scale. Sponges themselves are active suspension feeders, pumping large volumes of water through their internal channels, sometimes with very obvious jets of high velocity from the osculum. Sponges, however, are also the group in which induced flow was first noticed (chimney effect, Vogel 1996); they save energy by using the water flowing over openings in their highest points to produce a lower pressure that pulls in water through the pores covering their surfaces (ostia). Sponges form thin encrusting sheets, massive globular and vase-like structures, lacework masses, and tubes of glass fibers. They are among the most abundant and important members of benthic communities on hard substrata around the world and can be the largest fraction of biomass on some coral reefs.

Cnidarians represent another phylum that has generated many different types of suspension feeders. Hydroids, producing tall and flexible branching colonies, are often among the early colonists on new or recently cleared subtidal surfaces; they comprise numerous small polyps whose tentacles capture a variety of zooplankton. Scleractinian corals employ a similar morphology but have added a large massive or branching calcareous skeleton and polyps with a larger size range, and thus have a larger range of zooplankton and benthic prey they can handle. Sea anemones are basically corals that have lost their skeleton to become solitary motile polyps, some over a meter in diameter, and some with tentacles large enough to capture fish and large swimming invertebrates. The octocorals (soft corals, sea fans, and their relatives) generally have small to medium polyp size, and some are specialized for phytoplankton rather than zooplankton capture (Fabricius et al. 1998 and references therein). Other cnidarian suspension feeding groups include zoanthids, corallimorpharians, benthic scyphozoans, and stalked jellyfish. Hydroids, corals, and soft corals can form dense aggregations of tall colonies that cover large areas of the bottom – the epitome of animal forests.

Bryozoans (Phylum Ectoprocta) are usually not as large as some of the other suspension feeder colonies but can also cover large areas of substratum and produce “forests” on a smaller scale. They have invariably small individual units (zooids) each of which captures prey (bacteria, phytoplankton) via a tentaculate lophophore; ciliary tracts on the lophophores generate currents on a very local scale that bring particles into contact with the tentacles. Bryozoans are also early colonists in many benthic communities and can cover large patches of rock for months to years. Other lophophorate groups such as phoronids, brachiopods, and entoprocts are also common suspension feeders and can be locally abundant.

Polychaete worms (Phylum Annelida) provide a number of examples of benthic suspension feeders, and some even form dense beds or hard structures of cemented tubes. While many polychaetes occupy soft substratum, and suspension feed from burrows or tubes, others build attached structures on hard substrata, including coral reefs; these include the calcareous tubeworms (Family Serpulidae) which can form masses of conjoined tubes, and the feather-duster worms (Family Sabellidae) and Chaetopterids (Family Chaetopteridae) which form large parchment-like tubes or entangled networks of such tubes.

Bivalve mollusks (Phylum Mollusca) are abundant and sometimes large and spatially dominant suspension feeders in benthic communities, pumping large volumes of water and removing phytoplankton and other prey from the water, sometimes effectively enough to deplete the water column near the benthos (Wildish and Kristmanson 2005). Mussel beds dominate intertidal and subtidal habitats worldwide, and oyster reefs can be expansive and can even convert soft-substrate habitats to hard reefs. In the Chesapeake Bay, USA, it has been argued that oysters structure the planktonic community, and in fact could remove most of the suspended particulates from the whole bay in a matter of days. Clams form dense aggregations in soft-substrate habitats and some in hard-substratum communities, and scallops can also be important contributors in both habitat types.

Also among the mollusks, some gastropods such as the vermetids are the dominant taxa of bio-constructed intertidal rocky reefs in the Red Sea and Mediterranean (▶ Chap. 12, "Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean" of this volume). In particular, the Mediterranean vermetid *Dendropoma (Novastoa) petraeum* associated with the encrusting red algae *Neogoniolithon brassica-florida* are suspension feeders relying for their diet on less than 1 mm particles captured by mucus nets which are spread by wave action over the substratum. Hauling the net occurs many times per hour throughout the day. The spatial distribution, feeding, and reproduction of the vermetid gastropod *Dendropoma maximum* have been described; although *D. maximum* is not a specialized filter feeder, the highly developed ciliary mechanisms suggest that filtering may be an auxiliary feeding method (Hughes and Lewis 2009).

Considering the high intertidal zone, it is clear that barnacles (phylum Arthropoda, subphylum Crustacea) are the most successful suspension feeders in the physiologically stressful zones covered by water only a few hours a day and baked by the sun or frozen solid for days. Farther down the intertidal, they are still among the most abundant fauna in all zones, sometimes settling in almost continuous mats when disturbances have created cleared space on rocky shores. In subtidal communities, barnacles can still be among the most common suspension feeders and dominate space in some habitats. They also achieve very large individual sizes subtidally, some individuals larger than a human fist. On coral reefs, barnacles are important in intertidal zones and in cryptic reef habitats though they are usually a small part of reef biomass. Among the motile crustaceans, there are other suspension feeding groups, including certain crabs and amphipods.

Echinoderms include several groups of important suspension feeders, such as basket stars and brittle stars (ophiuroids), feather stars (crinoids), sea cucumbers (holothurians), and some sea stars (asteroids). Sea urchins also suspension feed, capturing large particles such as fragments of macroalgae as well as smaller detrital material. Although most echinoderms are motile suspension feeders, they often form aggregations that are stationary for long periods of time. Ophiuroids in particular can form dense beds on both soft and hard substrate surfaces, with fields of waving arms. Holothurians form dense subtidal aggregations as well, sometimes with their tentacles crowns filling the available space and forming another distinct "animal forest."

Ascidians (Phylum Chordata, Subphylum Urochordata) often comprise another spatial and biomass dominant group on subtidal reefs and certain intertidal habitats. Ascidians form colonies of small zooids, groups of zooids connected by stolons, or large solitary zooids. One large intertidal species (*Pyura stolonifera*), in northern Chile (Castilla et al. 2000), can form dense and thick intertidal beds of solitary zooids connected together by adhesion of their tunics. Individuals can be almost 30 cm tall, and the bed itself tough enough to withstand humans walking on it. These monospecific communities occupy the mid-intertidal zone usually claimed by mussels. Large solitary ascidians are also common on coral reefs, as are the various colonial forms. Subtidal rock in the temperate zones of the world is frequently covered by both colonial and solitary ascidians, many of which are fast growing, and some are problematic invasive species around the world.

2.1 Capture Mechanisms and Structures

Ocean water contains entire communities of organisms as well as nonliving particulates and dissolved substances that can be utilized by benthic suspension feeders (Wildish and Kristmanson 2005). Capturing particles from moving water presents a number of difficulties, however, since the suspended particles can be present at rather low numbers and mass per unit volume. Furthermore, the smaller the particles and capture devices involved, the more difficult it becomes to separate particles from the water. Suspension feeders have developed several different mechanisms for accomplishing this separation, which operate on particles ranging from tiny bacteria to creatures many centimeters in diameter (Fig. 1). It was recognized in the 1970s that suspension feeders are mostly not acting like sieves, i.e., they do not pass water through a filter that retains all particles above a certain pore size (Rubenstein and Koehl 1977). Although such mechanisms exist, most suspension feeders (or filter feeders) capture particles from the water by causing those particles to contact filter

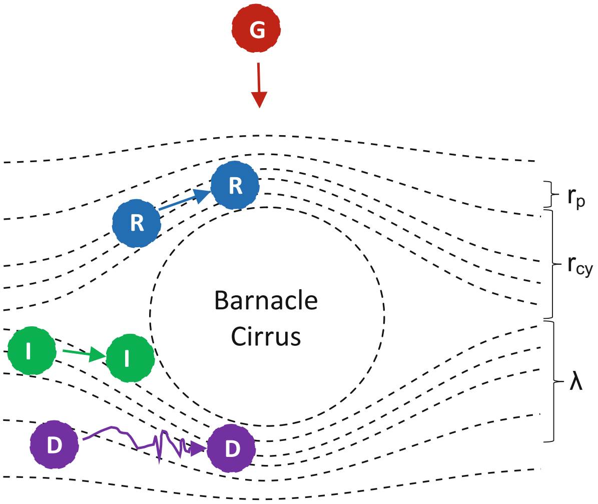


Fig. 1 Mechanisms of aerosol particle capture (After Shimeta and Jumars 1991). *Direct interception (R)* of a particle from flowing seawater as it moves along a streamline around the filter element. *Inertial impaction (I) occurs when* the momentum of a cyst causes it to deviate from the path of a streamline and contacts the cirrus. *Gravitational deposition (G)* can occur when sedimenting particles contact the element. *Diffusional deposition (D)* applies when particles exhibiting random paths collide with water molecules and are collected when they contact the element. λ is the effectively swept region (m), r_c is the radius of the cylinder (m), and r_p is the particle radius (m)

elements, even though the spaces between such filter elements can be much larger than the particles. These mechanisms were first described for mechanical air filters (aerosol filtration) but most work equally well in water and have been demonstrated in a variety of marine suspension feeders (Rubenstein and Koehl 1977; Shimeta and Jumars 1991; Jumars 1993).

Mechanisms of filtration have been reviewed extensively (Shimeta and Jumars 1991; Denny 1988), and there are many details and modifications that are important; we cannot cover them all here, so we will strive to give a useful overview that should encourage those interested to delve further. First, and simplest, particles suspended in water can simply impact a filter element (e.g., tentacle) because the diameter of the particle extends far enough from the streamline carrying the particle, such that it touches the tentacle (direct interception). Second, particles travelling fast enough carry inertia that causes them to keep moving straight ahead though the fluid around them deviates around an object (the bug on the windshield effect). Third, particles can be denser than the fluid they are in and gravity will cause them to settle out onto feeding surfaces. Fourth, there can be electrostatic attraction between the particle and the feeding structure (LaBarbera 1984), although this is minimal in seawater and may affect retention rather than attraction. Fifth, sieving can occur when particle diameters are larger than holes in a membrane or other structure. Sixth, diffusional deposition occurs when a particle moves out of its streamline by its own activity (swimming, for example) or by random motion, and thus encounters a capture surface. These mechanisms will be discussed in greater detail in the following sections, as they apply to specific suspension feeders.

2.2 The Prey Resource for Suspension Feeders

Suspension feeders have a variety of prey available from the overlying water column, but mechanisms that work well for one prey type may not work at all for prey of other sizes or swimming abilities. Organic particulates come in all sizes from hydrated gels to fragments of larger organisms (<1 um), and such particles often contain enough nutrition to be worth capturing. Bacteria range in size from <1 um to > 3 m (Jumars 1993) and are also among the smallest particles used by suspension feeders. Sponges, corals, and several other groups have been shown to capture bacteria and derive significant energy and nutrients from that size range of prey. Since particles only a few microns in diameter are much smaller than the spaces between most filter elements, it is clear that they must be captured by means other than sieving. They are also not likely to be substantially more dense than water, although some may be motile enough to affect capture rates. Such particles are usually captured by direct interception and retention on mucus strands or delivery in ciliary flow fields followed by adhesion to cilia alone (Romero et al. 2010). Sponges, however, have sieve-like collars on the choanocytes with pores small enough to retain prey of this size.

Phytoplankton often comprise the majority of planktonic particles and sometimes of biomass as well. They come in a great range of sizes, from a few microns to forms visible to the naked eye. A large fraction of suspension feeders specialize on phytoplankton, while still being able to capture smaller particles such as bacteria, detrital material, and small zooplankton and larvae. Bivalve mollusks, bryozoans and other lophophorates, ascidians, most echinoderms, barnacles, and some octocorals are among the groups that focus on phytoplankton. Phytoplankton are also quite diverse in shape, nutrition, skeletal material, and toxicity. Therefore, suspension feeders show distinct preferences and avoidance of certain types. Every suspension feeder studied shows such selectivity and has evolved mechanisms to detect and accept or reject individual prey items. This is also true for motile suspension feeders, such as copepods, which detect, contact, and assess each particle passing their antennae before deciding to capture and ingest it or let it go by.

Other groups of suspension feeders clearly focus on zooplankton as their primary food resource, though they may have the ability to capture other particle types. Corals, for example, are mostly specialists on medium to large zooplankton (Sebens et al. 1996b, 1997, 1998; Palardy et al. 2006; Houlbreque et al. 2009 review) but can also capture detrital particles (Mills and Sebens 2005; Anthony and Fabricius 2000) and bacteria (Sebens 1987a; Houlbrèque and Ferrier-Pagès 2009 reviews). Most corals do not capture phytoplankton, but certain octocorals have switched to that resource predominantly (Fabricius et al. 1998). Other cnidarians such as hydroids, sessile scyphozoans, zoanthids, corallimorpharians, sea anemones, and cerianthids also appear to be zooplankton specialists. Zooplankton captured by suspension feeders have a huge size range, from 20 μm to many centimeters; microzooplankton (20–200 μm size fraction) captured include groups such as rotifers, ciliates, flagellates, and small larval stages.

Even larger prey are also captured by suspension feeders, including nekton and mobile benthos. Certain coral species with very large polyps, many sea anemone species, and a few other cnidarians routinely capture such prey. This might be considered direct predation rather than suspension feeding, except that even these large particles are affected by water movement and are often carried to the tentacles by water flow, although their own swimming behavior also influences capture. Various large swimming crustaceans (shrimp, mysids, fish) are captured by corals and anemones (Sebens et al. 1996b, 1997) and benthic crustaceans and fish often enter the water column temporarily and are then captured by cnidarians. Some of the larger sea anemones depend on wave action or the activity of predators to dislodge benthic prey, which are then carried to them by water flow and gravity (e.g., mussels, Sebens 1982, 1987a, b, reviews). Some of these “particles” are well over 10 cm long, about the same as the diameter of their predators. Few other phyla have developed specializations for such large prey, although predatory sponges are one example. Sea urchins that capture drift algae, which can also be many centimeters long, are another example, and in this case the prey can be much larger than the predator.

2.3 The Role of Water Movement

Suspension feeders capture particles from moving water by using the water's intrinsic motion (passive suspension feeders), by causing water motion via some form of pumping (active suspension feeders), or by using a combination of both methods. Organisms that use induced flow may be passive at one level, but active at a smaller scale where particles are actually removed from the water. For passive suspension feeders, the ambient flow regime is critically important and may determine whether they can live there at all or whether their capture mechanisms will function effectively. Clearly, sea anemones that capture zooplankton from unidirectional currents, for example, would do very poorly in large intertidal waves. Flow regimes can be characterized by flow speed and direction as well as by the Reynolds number, a dimensionless index that depends on velocity, size of structures, and viscosity of the fluid. High Reynolds numbers occur with high velocity, larger structures, and lower viscosity. Low Reynolds number flow examples would be small capture structures in low flow, capturing small particles; the fluid viscosity becomes more important in this type of flow, and it is harder to move water between filter elements. Motile suspension feeders such as copepods are always dealing with this type of flow at the scale of their capture structures (Koehl and Strickler 1981), as are many of the sessile species we are considering here.

Most passive suspension feeders utilize unidirectional currents, since that is the normal condition for most of the world's subtidal benthic habitats. These creatures present a capture surface to the flow and remove particles as they encounter the filter elements on that surface. There are many mechanisms that function well in such flow, depending on the size of particle to be removed. Other passive suspension feeders rely on wave induced flow to carry prey to their feeding structures. Such flow is oscillatory and is often combined with unidirectional flow, especially in deeper habitats where the wave component is attenuated. For a passive suspension feeder, equal flow in two directions, for several seconds each direction, is at least equivalent to unidirectional flow for the same total time. Many studies of water flow in benthic habitats concentrate on the unidirectional element and filter out the bidirectional wave induced flow (vector-averaged flow). This is acceptable to calculate how far particles or larvae are carried in a given time unit, but it is not appropriate for calculating the arrival rate of particles impinging on suspension feeders. To calculate the flow past a suspension feeder or filter element, the magnitude of flow independent of direction should be calculated each fraction of a second (nonvector averaged), and those flows summed for the time period in question. Oscillatory flow can give a suspension feeder multiple chances to capture the same particle and can interfere with prey swimming and escape behavior, such that suspension feeders capture more prey in oscillatory than in unidirectional flow of the same total volume of water moved (Sebens 1987a, 1997, review).

The magnitude of flow is also a very important aspect of the flow regime. Subtidal benthos can be subjected to unidirectional currents well over a meter per second, and intertidal or shallow subtidal habitats experience wave-induced flows at least ten times that speed, up to 30 m s^{-1}. Such high flows represent a limitation for both survival and effective feeding, and most animals that live in such habitats have mechanisms to contract the body and thus reduce drag as well as very strong attachment to the surface (high Reynolds number flow). Despite the high forces involved, high flow habitats can be excellent locations for suspension feeders. Coral growth is highest in the shallow reef zones experiencing high light and high wave-induced flow; Charles Darwin recognized early on that high flow conditions produced the most rapid reef growth. There are numerous mechanisms to allow particle capture in high flow. Having a stout body and tentacles, which can function in high flow while limiting drag forces, works for large sea anemones in crashing surf (Sebens 1987a, b, reviews). They not only survive but benefit from the wave action dislodging and transporting prey. Coral colonies with dense thickets of short branches reduce flow within the colony such that some polyps are able to capture prey even when leading edge polyps are not (Sebens et al. 1996a). Certain bryozoans benefit from neighboring colonies by experiencing reduced flow also (Okamura and Partridge 1999).

On the other end of the spectrum, some suspension feeders must deal with very slow flows, small particles, and a comparatively viscous fluid at that scale (low Reynolds number flow). In fact, all of the suspension feeders capturing bacteria, phytoplankton, and small detrital particles generally function in a low Reynolds number environment. For such creatures, moving water between filter elements, and removing particles from water, becomes increasingly difficult; appendages act more like paddles than like rakes (Koehl and Strickler 1981). The classical example of this phenomenon is trying to remove a fly from a jar of honey with a fork; the honey does not move much between the tines of the fork, and the fly is pushed ahead of the fork. Two forks working against each other are much more successful, and that is how some crustaceans deal with the problem by squeezing the water through the filter and retaining the prey (Koehl and Strickler 1981).

3 Energy Intake and Feeding Surface Area

For passive suspension feeders, capturing particles from moving water involves presenting a capture surface perpendicular to that flow. Such structures can take the form of a paddle or fan (sea fans, some hydroids), cylindrical branches (octocorals, scleractinian corals), or elongate filaments (whip corals). At a smaller scale, each tentacle, pinnule, or other filter element is also oriented perpendicular to flow, which increases the probability of particle interception. The larger the cross-sectional surface area of these feeding surfaces, the more drag will be experienced, sometimes enough to damage or dislodge the entire colony (e.g., sea fans in storms). The trade-off between increased prey capture and decreased survival is probably one of the most important processes determining the shape and size of suspension feeders and their parts. Certain suspension feeders, such as cnidarian medusa, trail long tentacles parallel to the direction of motion and may rely on prey swimming to effect encounters.

For active suspension feeders, water is pumped into the body and through a capture structure, which may include mucus strands or nets, then is ejected. In ascidians, particles move through the stomata in the pharynx, with ciliary tracts on either side providing a feeding current, and particles are retained on a mucus net produced by the endostyle, then rolled into a cylindrical mass that is ingested. In bivalves, water is pumped across a complex gill surface, and particles are sorted by ciliary tracts, with some retained on mucus and ingested. Here too, a feeding surface is presented to flow but it is generally parallel to flow, although the individual mucus strands may be perpendicular to flow. The entire gill surface, for example, will determine the potential for particle ingestion. Pumping rate also influences the number of particles coming into contact with these structures, and thus helps determine energy intake. Here too, there should be some optimal flow speed across the capture surface that increases encounter rate, without causing too many particles to be missed or lost after capture.

Energetics models often consider intake to be a function of capture surface area (Sebens 1979; Kooijman 2010); for sheet-like colonies, surface area may increase linearly with biomass because growth involves producing more units of similar size and shape. For creatures that grow as cylinders, spheres, or other solids, surface area is expected to increase less rapidly than mass or volume (e.g., 0.67 power of mass). This is true only if growth is isometric. For allometric growth, surface area could be proportional to mass or volume for at least some size ranges. The trade-off between intake and drag forces could produce allometries that actually decrease the feeding surface to mass ratio as organisms get larger.

3.1 Energetic Costs for Suspension Feeders

Passive suspension feeders do not spend energy to move water past their surfaces; however, there is some cost involved in maintaining an expanded condition in flowing water and to producing the mucus, nematocysts, and other expendable materials used in feeding. Invertebrate suspension feeders are also mostly metabolic conformers, meaning that they respire at a greater rate when there is more oxygen in the ambient water adjacent to their tissues. An expanded cnidarian, for example, has a higher metabolic rate than a contracted one in part because expansion brings more surface area into contact with oxygen-rich water. The water inside a contracted body is usually quite depleted of oxygen. Anything that causes the animal to be more active (pumping), produce more feeding materials, or come into contact with more oxygen molecules (water flow, photosynthesis) increases the metabolic rate. Active digestion of prey also increases metabolic rate; this is termed “specific dynamic action.” When water is moving slowly, the diffusional boundary layer above tissue surfaces can be very low in oxygen even when the concentration in the bulk flow is quite high.

Pumping is an important energetic cost for active suspension feeders, though sometimes they can avoid it by using induced flow when conditions warrant this. Ascidians can use orientation of their incurrent and excurrent siphons to generate induced flow, and the tall columnar shape of many sponges also produces a strong induced flow (Vogel 1996, review). Barnacles, which pump water through their filters by extending and retracting their legs, sometimes stop that activity when water flow is high and unidirectional (Trager et al. 1990), becoming temporary passive suspension feeders. Even in slow moving water, sponges process huge volumes of water, with flows generated by flagella of the choanocytes; the result can be a vertical plume of exhalant water that is easy to see by introducing dye. Mussels and other bivalve mollusks also pump a lot of water through their siphons, with the pumping rate being accompanied by increased metabolic cost (Sebens 1987b, review).

3.2 Competition and Energetics

Most of the suspension feeders considered here are attached to hard surfaces, and thus must compete with other organisms for this primary space, a very limited resource. In some cases, an entire encrusting colony occupies a large fraction of the primary space, and in other cases attachment is by a small structure that allows the rest of the animal to protrude well above the substratum and above many of its competitors. Competing for space is also competition for access to the food resource in the water column and sometimes access to light. Because of this, there is a very obvious trade-off between energetic considerations and competitive ability. For example, it might be possible to determine the best size, shape, and branch spacing for capturing a certain class of particles at a range of realistic flow speeds. However, any particular suspension feeder of interest may not conform to that prediction because of interactions with competitors (including intra-specific neighbors).

One such example is the coral *Agaricia tenuifolia*, which differs greatly in branch size, shape, and spacing. This species often grows in dense stands with other colonies of the same species and a few others. Once a colony has filled available space, and is limited by its neighbors, it may be better to pack in more branches in the space attained, even if a wider branch spacing would be better for light or plankton capture (Helmuth et al. 1997; Sebens et al. 2003). Given a limited amount of space, more tissue can be produced, and ultimately more larvae released, in the former case. Another consideration for corals is polyp size; a colony with very small polyps has a high surface area to biomass ratio, which can maximize small particle or light capture. However, large polyps are more successful competitors for space using either sweeper tentacles or mesenteric filament extrusion (extracoelenteric digestion) (Lang and Chornesky 1990; Wellington 1982). There may thus be a stable coexistence between branching corals with small polyps but rapid growth rate and those with large polyps that can defend space from overgrowth (Sebens 1997).

Forming a canopy of branches well above the rest of the benthos is an excellent way to avoid some of this competition as well as to access prey in faster moving water higher within the benthic boundary layer. However, once such erect structures become abundant, they can compete among themselves for canopy space and they may also have an effect on the ambient flow regime. This effect can be negative at lower flow speeds, where downstream colonies experience much reduced flow, but positive at high flow speeds, where isolated colonies or branches experience flows too high for efficient particle capture (Sebens et al. 1996a; Okamura and Partridge 1999). In many benthic communities, substratum space is fully occupied by encrusting forms, and there can be one or more canopy levels above that. Hydroids and bryozoans, for example, often comprise a canopy level a few centimeters above rock surfaces, whereas tall sea anemones, gorgonians, and other erect forms reach tens of centimeters to over a meter into the water column.

4 Energetics and Growth Models for Suspension Feeders

Energetic models were first applied to active suspension feeders such as bivalve mollusks (e.g., Bayne and Widdows 1978) where energy intake was measured from clearance rates in laboratory aquaria, and metabolic rate was determined for a range of pumping rates. For bivalves, energy intake was found to scale with body mass as a surface area relationship or at an even lower power of mass ($< = 0.67$) while energetic cost had a higher power relationship ($> = 0.8$), suggesting that bivalves are more productive at converting energy to mass or reproductive output at sizes well below their maximum possible size (Sebens 1987b, review). These models also defined a “scope for growth” (Warren and Davis 1967) which is the difference between intake and cost, although reproduction was considered a cost in these models, thus the term “scope for growth.” If reproduction is taken out of that equation and only maintenance costs used, this becomes a “scope for growth and reproduction” [or “energy surplus”] which could, for example, all be used for reproduction. The difference between intake and cost is a useful measure of environmental suitability, especially if compared over a range of sizes.

For passive suspension feeders, energetic models also indicate that intake is related to surface area of the feeding apparatus, whereas metabolic costs generally scale as a higher power of body mass (Sebens 1979, 1982). For such creatures, this also suggests that there is some maximum size where all energy intake would be used to meet metabolic demands, and none would be left for growth or reproduction. Furthermore, these simple models could be used to predict an energetically “optimum” size which provides the greatest difference between intake and cost (Fig. 2). On purely energetic grounds, growth beyond that size would be maladaptive and growth should stop there to maximize reproductive output (Sebens 1979). Of course there are nonenergetic reasons why any particular organism might benefit from stopping growth at a smaller size (e.g., high predation on larger sizes) or grow beyond this energetic optimum (e.g., competitive advantage). To determine the actual optimum based on average individual fitness, the energetics model must be combined with a life history model that calculates the potential intrinsic population growth rate for hypothetical organisms with each life history strategy (Sebens 2002;

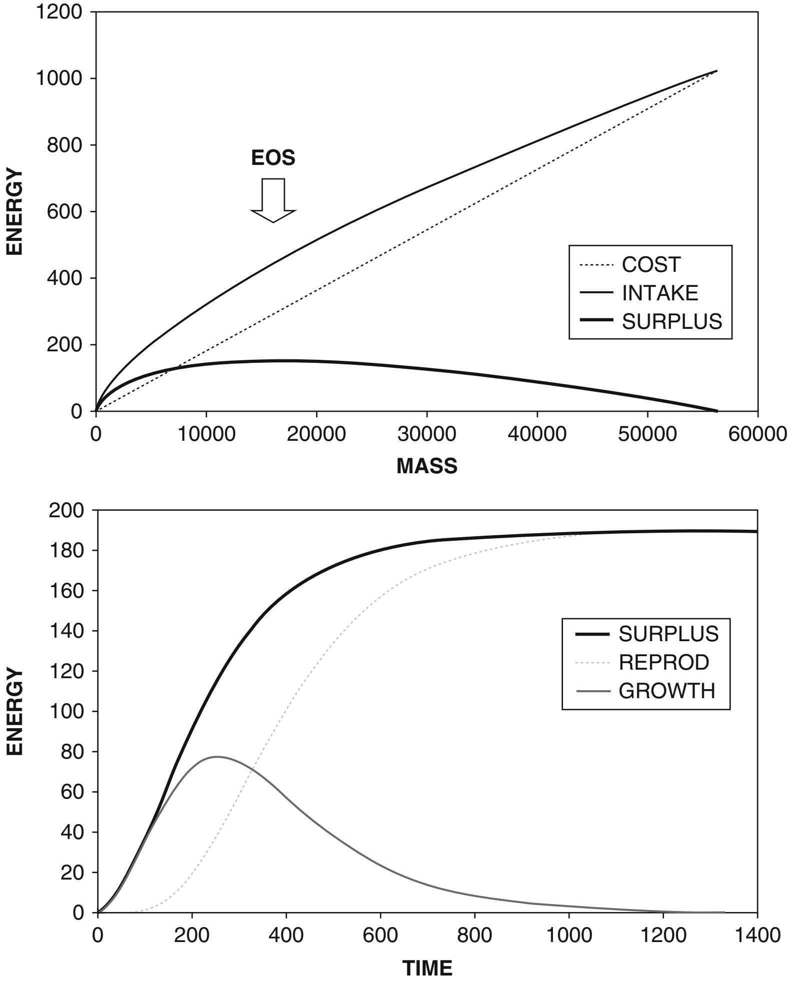


Fig. 2 Energy intake and cost functions for a suspension feeder, where intake scales as a function of surface area and cost scales as a function of mass. Energy and mass are in arbitrary units. EOS is the energetic optimum size (mass) where the energy surplus, the difference between intake and cost, is the greatest. The lower panel shows allocation of the energy surplus to reproduction and growth during an individual's lifetime (Replotted from model in Sebens 2002)

Sarà et al. 2013a, b; Carrington et al. 2015). This per capita growth rate (expressed as r or λ) can be considered an estimate of individual fitness or could be used for population projection; is the population expected to increase or decrease and at what rate under any set of conditions?

The relevant energetics and growth models were first developed by Putter and von Bertalanffy in the 1920s and 1930s (Sebens 1987b; Kooijman 2010, reviews). The basic formulation is:

$$E_s = k_1 M^{c_1} - k_2 M^{c_2} \tag{1}$$

where E_s is energy per unit time (surplus); c_1 and c_2 are exponents of mass (M) for assimilated intake and energetic cost, respectively; and k_1 and k_2 are fit constants for intake and cost, which change with environmental conditions (e.g., temperature, food availability, or salinity; Sebens 1987b review). Energetic cost comprises respiration, excretory losses, and production of lost material such as mucus, exudates, and expendable parts (e.g., nematocysts). The exponents c_1 and c_2 are scaling factors, part of the growth program of a given species, although environmental effects can influence these also (e.g., as morphology changes). E_s is energy surplus, intake minus cost, but not including reproductive costs (in the cost term). This value can be converted to units of mass (growth) and/or to units of reproductive output (mass, gametes) and can thus become the basis for a growth equation. Reproductive costs include construction of gonad, metabolic rate of gonad tissue, construction of gametes, and metabolic rate of gametes. Depending on how total metabolic rate is measured (i.e., with or without gonads present), some of those costs could be hard to separate out. However, we can more easily measure gamete output as a separate cost or as a separate category of mass increase. The maximum size possible occurs when intake equals metabolic cost, but this size allows no energy for reproduction.

If all reproductive costs are included in the cost term of the equation for energetic surplus, or scope for growth, there is no way to predict an optimum size. With both somatic growth and reproductive output dependent on E_s, the predicted optimum size occurs when E_s is at a maximum (i.e., where the derivative of (Eq. 1) is zero, $dE_s/dM = 0$):

$$M_{opt} = (c_2 k_2 / c_1 k_1)^{(1/(c_1 - c_2))} \tag{2}$$

This represents the maximum amount of energy (per unit time) that can be used to construct somatic tissues, reproductive tissues, and gametes (Sebens 1979, 1982). If growth stops at this point, maximum reproductive output occurs, and further growth would not be advantageous unless other fitness parameters are affected.

Neither the maximum nor optimum size predictions apply to whole colony energetics, where feeding surfaces and tissue mass are added as nearly identical units; in such cases, both intake and cost theoretically scale directly with colony mass ($c_1 = c_2 = 1.0$), although colony growth form could lead to allometric relationships. Colonies growing as a flat sheet are most likely to have intake and cost values that scale directly with whole colony mass, whereas complex branching colonies probably would not. Polyps on the lower or interior side of such colonies may experience lower food availability (Sebens et al. 1996a) as well as lower light and possibly oxygen concentration at night. Both intake and cost would thus be location dependent and neither would likely scale directly with whole colony mass. Sebens (1979) explored the energetic consequences of dividing up a given colony mass into units of different size, using the same equations presented above. This model predicted that the smallest possible unit size will provide the greatest energy surplus for the whole colony, and thus units should be just large enough to capture their prey and produce offspring. But, what happens when there is a range of prey sizes available? If we assume that larger units capture larger prey, and prey size is normally distributed, it turns out that having polyps just above the mean prey size is optimal. Above that size the colony is sacrificing feeding surface area, and below that size polyps are potentially losing the most abundant prey.

Note that the above equation for optimal size depends on fixed values of c_1, c_2, k_1, and k_2 which is certainly not the case in the real world, though average values might suffice. In reality, k_1 and k_2 derive from multiple functions incorporating food availability, and environmental temperature, and could include many more factors affecting both intake and cost. c_1 and c_2 are determined by the morphological and physiological scaling of a particular species. However, we know that both shape and physiological functions show phenotypic plasticity and can thus be determined by environmental conditions. While these simple energetic models are useful, much more complex models that incorporate temporal variation in physical conditions and food availability are needed to produce accurate models of growth.

5 Dynamic Energy Budget Models

Among the more recent methods of dealing with organism energetics, the most reliable and accepted approach is based on the dynamic energy budget theory (DEB; Kooijman 2010), which mechanistically depicts temperature-dependent metabolic processes with precision and enables us to make accurate predictions of an organisms' growth performance and other life history traits. Such an approach can be useful in an era when the pace of climate change (and the related observed and projected range shifts, Pacifici et al. 2015) is expected to be even greater in aquatic ecosystems compared to those on land. While intertidal habitats are extremely chemo-physically variable, due to tides which connect them with highly variable terrestrial environmental conditions, most subtidal habitats are comparatively stable over time from a chemical and physical point of view. As a main consequence, subtidal marine organisms are more narrowly adapted to such small changes of conditions in the surrounding environment. The DEB model, incorporating direct relationships between both metabolism and temperature and available food is able to capture such small influences of habitat change on organismal traits.

DEB is the core of functional trait-based mechanistic bioenergetics models which are based on characteristics of a species' fundamental niche (Sarà et al. 2011, 2013, 2014a, b). Such models provide the information (i.e., quantitative predictions about life history traits of one species, e.g., fecundity, body size, growth rate) necessary for predictions of where a species can persist, or not, and how it reacts, within the species-specific physiological boundaries, to environmental variability. This predictive ability meets one of the most important needs in ecology, i.e., being able to predict species abundance along spatio-temporal environmental gradients.

Mechanistic-based models provide the best and the most reliable quantitative information (and predictions) to determine how biological processes and life history strategies of individual organisms are altered by changing external conditions, and how these scale up to determine population dynamics and, ultimately, the success and distribution of species.

The development of predictive mechanistic species distribution models based on bioenergetics, with the ability to explore the vulnerability of marine species to environmental changes, supports the realism of the predictions in a context of climate change. For instance, it can help us foresee and anticipate ecological and economic costs of biological invasions, providing useful guidance for planning, conservation management and control strategies (Richter et al. 2013; Hamaoui-Laguel et al. 2015; Chapman et al. 2016), increasing the predictive capability with respect to where and when commercial stocks will become more vulnerable to collapse. It can also serve as an early-warning system (sensu Munroe et al. 2012) addressing successful management of resource exploitation and for the maintenance and enhancement of resilience in the context of the ecosystem-based management approach (Pikitch et al. 2004; Berkes 2012).

5.1 Why DEB Is an Improvement

DEB comprises a complete theoretical asset, at the whole organismal level, to link habitat, functional traits, and life history of any living organism. It allows one to mechanistically investigate: (i) how any species manages the available energy from the habitat and (ii) how the utilization of this energy is prioritized, i.e., the important choices that one organism has to activate (often not consciously) to optimize fitness over its life span. These two aspects are based on strict physical, chemical, and thermodynamic laws (the so-called first principles) governing the functioning of the world. Indeed, we know that every organism on the planet follows similar rules to gain energy from its surroundings and to transform it into biomass (e.g., tissues, skeleton, etc.) and gametes (e.g., eggs), while avoiding mortality for as long as possible.

The mechanistic properties of this approach rely on energy and matter flows from the habitat through organisms. But, flows of energy and matter are subject to conservation laws (Kooijman 2010) and, consequently, they are traceable (and budgetable) processes that can be used to predict the functioning of each species (e.g., any suspension feeder) and thereby the magnitude and variability of life history traits (Carrington et al. 2015). By analogy, any organism can be conceptualized as a washbasin (M. Kearney; unpublished; Sarà et al. 2013a). Energy flowing from the habitat (here, the large water container at the back of the washbasin) is modulated by numerous functional traits (the tap; e.g., the Holling functional response accounting for mutually exclusive functions such as searching, handling, ingestion of the food available, and assimilation). It reaches the washbasin and accumulates into reserves (the water present in the washbasin; i.e., stored as metabolites such as proteins, lipids, carbohydrates). Two drain pipes of different diameter leave the washbasin and allow the water (energy reserve) to reach two main (virtually separate) containers: the first is that of structures (i.e., the body structures) accounting for most of the flow rate (the so-called kappa); the second pipe is narrower than the first and supplies energy to the reproduction container (i.e., 1-kappa).

These two flows are connected by a trade-off (the kappa rule; Kooijman 2010) and are directly linked to the amount of reserves, which depends on the internally available energy managed by the organisms which, in turn, depends on the ability of organisms to manage the amount of energy acquired from the habitat. If, for some reason, the washbasin empties, there is no more energy to refill the two containers, and structure and reproduction both decline, based on outflows that represent maintenance costs. This situation will have important repercussions on organismal ability to cope with environmental variability (e.g., obtaining food from the habitat, interacting with other organisms, sustaining an immune-defence system, and producing gametes). While not every organism possesses vascular supply networks, all organisms mobilise internal energy and store material before metabolites are transported to fuel metabolism. The manner and the efficiency with which energy flows through an organism vary according to its metabolism; thus, energy flow is greatly affected by body size. In DEB theory, the structural volume V (i.e., the cube of volumetric length) represents body size and the conversion between physical length L and V is performed by including the shape coefficient, a dimensionless quantity (Kooijman 2010).

In a DEB context, volume and surface area play crucial roles in energetic exchanges and fluxes. For instance, acquisition rates are considered proportional to surface area (displayed in curved brackets), while maintenance rates requiring energetic costs are usually related to volume or mass (square brackets). The standard DEB model can be roughly partitioned into two separate large compartments: one (upper compartment in Fig. 3) dealing with feeding process that describes how energy coming from food is stored as metabolites (e.g., stored proteins, lipids, carbohydrates) and another (lower compartment in Fig. 3), in which the energy is allocated to maintenance and transformed into structures (i.e., growth) and offspring (i.e., reproduction). The link between the two parts is represented by a third compartment, the reserves, in which all the energy coming from the upper part is first stored, then made available for direct use (and is then available for the lower part). Organismal mass is usually a linear function of volume, and vice versa.

5.2 DEB Model: The Upper Part

Given a constant supply of food, the amount a suspension feeder can acquire is determined by the availability of food (delivery rate) and the rate at which the food itself can be removed from the environment (Fig. 3). In bivalves, for example, the flow of particles retained through filtration is equivalent to the product of clearance rate (CR) by the total amount of food (X_n). Once they arrive on the gills (of bivalves),

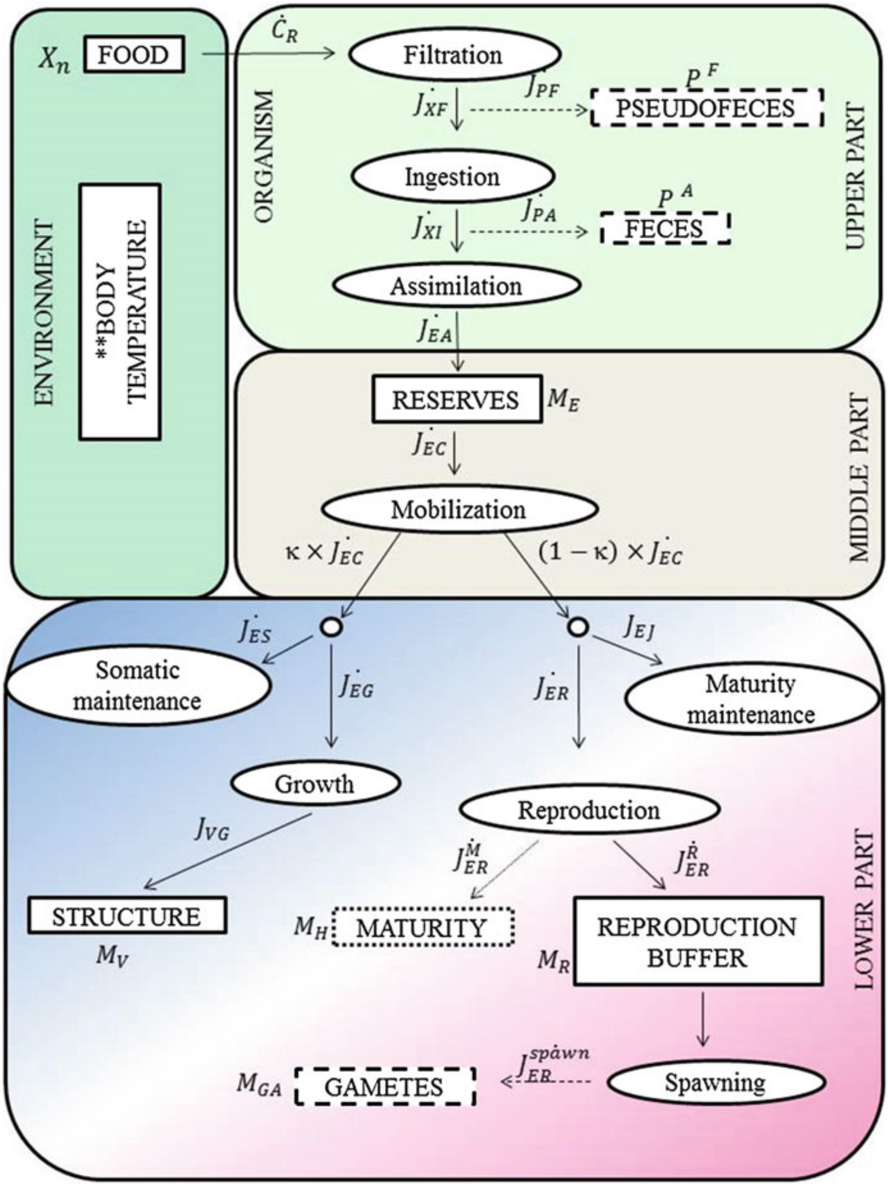


Fig. 3 Schematic representation of the standard dynamic energy budget model (Kooijman 2010) and the flux of energy through an organism, coming from the environment. Apart from food, another important constraint in the metabolic process is individual body temperature. Many suspension feeders, being ectotherms, can have their body temperature approximated as that of the environment, although this is not the case for intertidal invertebrates. This DEB model diagram uses suspension feeders (bivalves) as an example

particles are selected: a fraction (J_{PF}) will be rejected as pseudofeces, the rest are transported to the mouth to be ingested (J_{XF}) ˙. The ingestion rate (J_X).is defined as the passage of food to the gut and depends on food availability, body size, and temperature; according to DEB theory, its formulation follows the Holling type II functional response. The saturation coefficient (X_k) depends on food quality (e.g., the ratio between carbon and nitrogen in the organic matter composing food; sensu Pusceddu et al. 2003) and, for example, in suspension feeders it can be expressed by the concentration of chlorophyll-a (μg CHL-a l^{-1}; Sarà et al. 2012) or amount of carbohydrates, proteins, and lipids (Pusceddu et al. 2003), at which the value of ingestion rate is equal to the half of the maximum. In suspension feeders, the maximum ingestion rate X_k can be derived from ingestion rate measurements (*IR*, μg l^{-1} h^{-1}) based on typical clearance rate experiments (Sarà et al. 2013a). It should also be noted that the concentration of chlorophyll a can be used to predict food availability on average, though there will be times when chlorophyll a is high but the potential food species are of low quality or contain toxins (i.e., food availability is actually low). Ideally we would have a separate correlation for each time period or combination of potential prey species.

Since both filtration and ingestion in bivalves occur simultaneously, the ingestion rate is equal to the filtration rate. Not all energy coming from the ingestion process ($\dot{J}_{XI}$) is digested; differences in the chemical composition between bivalve reserve tissue and ingested food determine energy loss ($\dot{J}_{PA}$) as feces. Assimilation rate ($\dot{p}_A$) is the final step of food processing and is defined as the process where food is converted into the organism's reserves (Kooijman 2010). The rate of assimilated energy is assumed to be independent of the feeding rate per se but is explicitly related to food density through a functional response curve ($\dot{p}_{Am}$) is the maximum assimilation rate *per* unit surface area and describes the efficiency with which energy is converted into the organism's reserve.

5.3 DEB Model: The Middle Part

Reserves represent the core of DEB theory and one of the most important advances compared to classical energy budget models; reserves collect all the energy coming from the environment minus that lost during the feeding process (Fig. 3). An important assumption of the DEB model is that neither the feeding process nor reserves accrue maintenance costs. In the model, the rate at which this energy is used from the reserve follows the k-rule which asserts that a fixed fraction κ of assimilated energy is allocated to maintenance and somatic growth, and that the remaining fraction 1-k is available for maturity maintenance and reproduction.

5.4 DEB Model: The Lower Part

The lower portion of the DEB comprises all processes that require energy expenditure, i.e., maintenance of the biomass (metabolism), development, growth, and reproduction (Fig. 3). DEB theory stipulates that somatic maintenance has priority over growth and that an organism is able to use the reproduction buffer (and in extreme cases the structures) to cope with maintenance costs during starvation periods. Somatic maintenance involves all processes needed by an organism to simply survive (i.e., ignoring growth and reproduction); in ectotherms, generally, maintenance cost scales with volume (of structure, body mass). The parameter $[\dot{p}_A]$ is a good approximation of the organism's basal metabolism and is indirectly related to the measurements of oxygen consumption (e.g., Sarà et al. 2013a). Growth is considered as the increase in organismal body mass; the model is based on the growth of an organism under constant conditions and the growth rate in the DEB context reduces to the Von Bertalanffy equation with three parameters (time at length zero, growth rate constant, and maximum size). Growth ceases when all reserves, not used for reproduction, are required for somatic maintenance.

Apart from structural biomass and reserves, two other important variables characterizing the organism are maturity level, M_H, and the reproduction buffer, both of which also need energy to be maintained. Before an organism is able to produce gametes, a maturation level must be reached. The standard DEB model assumes that energy is allocated to the maturity buffer during the individual's juvenile stage. Once the maturity level (M_H) is reached, the organism become an adult, and a fixed fraction is continually transferred from the reserve to the reproduction buffer (after accounting for maturity maintenance) and then to gametes production and spawning. The resulting flux of energy moving into the reproduction buffer is defined as the difference between the energy mobilized from reserves and the costs related to the reaching and maintaining of maturity. The real amount of energy stored in reserves $[E_m]$ and that available for reproduction and growth $[E_G]$ cannot be estimated directly, but it is possible to derive them from somatic maintenance ($\dot{J}_{ES}$) and, specifically, the related parameter ($\dot{p}_M$). If seasonal patterns are known, these parameters can be estimated from energy content before and after the growing season.

5.5 How to Account the Role of Temperature?

The flux of energy inside an organism varies according to its own metabolism and thus depends on physiological rates. Since all physiological rates are strictly dependent on body temperature, it represents an important constraint in the DEB theory. To include the effect of temperature within a species-specific range, the relationship originally proposed by S. Arrhenius usually fits quite well (in Kooijman 2010):

$$\dot{k}_{(T)} = \dot{k} \times \exp\{T_A/T_1 - T_A/T\} \tag{3}$$

where $k_{(T)}$ is a physiological rate at the ambient temperature T, with T the absolute temperature (in Kelvin), and $.k_1$ the physiological rate at the reference temperature T_1. T_A is the Arrhenius temperature. The estimates of Arrhenius temperature (T_A) and of the lower and upper boundaries of the tolerance range can be extrapolated from literature data or estimated by a direct calculation of physiological rate at different temperatures. Activities such as locomotion, pumping, ciliary transport, polyp expansion, gut passage, and ingestion are also affected by temperature (e.g., Sanford 2002) which thus affects the intake parameters of the model as well as the energetic cost of each activity.

5.6 The Main Model Outputs

The mechanistic nature of the standard DEB model allows the bioenergetics features of an organism to be related to environmental conditions, so that ultimately fitness can be predicted. This is only feasible if the organismal body temperature and concentration of food in the habitat are known, and that all DEB parameters of the species are accurately estimated based on available information. The present versions of the DEB model allows us to quantify the (i) **Maximal habitat individual size (MHIS);** (ii) the **Maturation time (MT)** as the time in days to reach the minimal size that allows gamete development and maturation. MT is strictly habitat-specific (i.e., thermal conditions and available food density matter); (iii) the **Number of reproductive events per life span (RE)** strictly related to the environmental conditions, as the energy that replenishes the reproduction buffer depends on food availability. Furthermore, the standard DEB model assumes that the organism does not spawn until the temperature is above a threshold; this also means that temperature represents a constraint for the occurrence of RE; (iv) the **Total reproductive output (TRO)** is the total number of eggs *per* life span. When the energy of a reproductive buffer reaches a threshold, it is packaged into gametes, which are produced in a discrete number of spawning events. Since DEB assumes that the energy needed to build one gamete is usually constant (approximately 0.0019 J for one egg for bivalves) and that the amount is species-specific, TRO will depend on the amount of energy available for reproduction coming from reserves and stored into a reproduction buffer.

6 Detailed Examples of Energetics for Suspension Feeders

So far, we have provided an overview of particle capture, energetics, and energy allocation in benthic suspension feeders. In this chapter, it is impossible to go into great detail for all such groups, and thus we have chosen to discuss three groups that have been the focus of recent research efforts, including those of the authors.

6.1 Cnidaria

6.1.1 Energy Intake

Cnidaria comprise one of the largest and most important groups of suspension feeders in hard substratum marine habitats. Most cnidarians capture zooplankton by passive means, although a few are known to specialize on phytoplankton and bacteria or to capture suspended and sedimenting detrital particles (Houlbrèque and Ferrier-Pagès 2009, review). The feeding structures are tentacles, ranging from less than a millimeter in length to over 10 cm for benthic forms and much longer for planktonic ones. Ciliary tracts and mucus capture are also utilized by many cnidarians, especially for smaller particles, though mucus strands also function well to capture certain types of zooplankton. Once zooplankton contact tentacles, they are retained by nematocysts and are transferred to the pharynx area where ingestion occurs. Digestion happens in the coelenteron cavity, and particle ingestion can occur anywhere on the interior surface. Anthozoans have specialized structures (mesenteric filaments) that wrap around prey and form a temporary digestive space where enzymes can be concentrated and phagocytosis of partially digested prey occurs. The entire tentacle and oral disk surface areas can be involved in particle interception and capture, and in some colonial forms, the tissue between polyps can be involved as well.

For most sessile cnidarians, tentacles are oriented to intercept flow maximally and thus to maximize particle contact. This is also true for whole colonies, such as gorgonians, which orient the broad axis to flow even though this orientation greatly increases drag and can result in colony mortality during storms (Sebens 1997). Clearly, the benefits of high particle and light capture outweigh the high risk incurred for those infrequent storm events that are severe enough to dislodge entire colonies. Sea anemones display a wide range of tentacle morphologies from elongate thick tentacles capable of capturing large zooplankton and benthic mobile creatures to complex crowns of very small tentacles that can capture only the smaller zooplankton but which maximize surface area for particle interception. In all cases, particle interception depends on the cross-sectional surface area presented to flow, and the efficiency of capture for each range of particle size and type will be affected by tentacle and colony morphology. Corals have the same broad range of tentacle types and also greatly increase surface area by having branching or upright plating growth forms. Octocorals have less variability in tentacle form; their eight tentacles per polyp are generally small and have even smaller side branches (pinnules) that increase surface area and probably aid in capture of particles in the size range of phytoplankton to very small zooplankton (Sebens and Koehl 1984; Fabricius et al. 1998; Coma et al. 1994, 1998). Hydroids also utilize very small tentacles, but without the side branches, and seem best adapted to capture individual small to medium size zooplankton (Sebens 1987a, review).

Benthic cnidarians present a capture surface to moving water; this can be a whole colony surface (gorgonians, hydroids) or a tentacular area (anemones, corals, zoanthids) and thus we expect prey capture to be related to some aspect of surface area (e.g., a power function with 0.67 exponent). When colonies grow as thin sheets, or branches with similar repeated units, metabolism can scale linearly with mass. Energy intake, from prey particles, can also scale linearly with mass in this case since production of more polyps of the same size and shape results in more feeding surface. However, even among colonial forms, polyp size ranges over several orders of magnitude. Energy intake thus depends on tentacle size, shape, and surface area as well as on the size range of particles available and efficiency of capture for any cnidarian species. Capture rates are also modified by flow speed, which varies widely on all scales of habitat and over time. For these reasons, it is quite difficult to measure food availability in the environment and to use that information to model ingestion.

Corals capture a wide range of particle sizes and types; although zooplankton are the most important prey for many corals, others utilize organic material in suspended or depositing sediments as a source of nutrients and energy (Mills and Sebens 2005; Anthony and Fabricius 2000; Houlbrèque and Ferrier-Pagès 2009, review). Plating corals in deep reef habitats may be able to intercept a rain of sedimenting particles coming from the shallow reef habitats, including fish fecal material produced in copious amounts on reefs. Corals that can utilize suspended detrital material may be able to live in habitats that would be impossible for zooplankton specialists. In fact, sedimenting material was first studied as a stressor for corals, and it can be energetically expensive to remove for species that cannot make use of it. Anthony and Fabricius (2000) demonstrated marked differences in energy balance for corals living in Australian reef areas with high turbidity, with some corals much better able to utilize suspended organic material. Some tropical octocorals with symbiotic algae also feed on a range of small zooplankton, microzooplankton, diatoms and dinoflagellates (Ribes et al. 1998).

6.1.2 Energetic Costs

Benthic cnidarians are passive suspension feeders and do not have to effect much movement to capture their prey. They do move to expand and contract and probably have to have some water flow into their coelenteron to maintain their expanded condition via their hydrostatic skeleton. Medusoid forms, of course, swim continuously and use the swimming process to generate feeding currents. Cnidarians are metabolic conformers, so their oxygen consumption declines when the surrounding oxygen concentration is low. Metabolic cost scales as a higher power of mass than does energy intake, often between 0.75 and 1.0 depending on the exposure of tissues to water with high dissolved oxygen concentrations. If there are parts of an individual or colony that are far from the ambient water, and thus exposed to less oxygen, the metabolic rate is likely to scale as a power of mass less than 1. Some species can also produce low tissue oxygen conditions internally by contracting polyps and reducing the surface area in contact with the overlying water (Sebens 1987a, review). This can be a mechanism of conserving energy when conditions for prey capture are poor, as occurs in sea anemones, or during intertidal exposure when they probably cannot feed.

Coral growth is most prolific in shallow wave-impacted reef zones, and coral growth rate generally increases with flow at least for the lower range of flows measured on reefs (Sebens et al. 2003). The optimal flow conditions for any coral species thus depend on this balance of increased cost and increased intake with flow. It is also quite clear that water movement across tissue surfaces increases metabolic rate (Sebens et al. 2003) and that oxygen concentrations near coral tissues can be reduced to near zero at night in low flow conditions. Water flow changes the boundary layer profile, such that diffusion of oxygen to tissues becomes much more rapid under high and turbulent flow conditions (Denny 1988). Very slow flow produces a thick boundary layer that hinders diffusion of oxygen from overlying water, resulting in depletion near tissues. On the other hand, endosymbiont photosynthesis creates extremely high oxygen concentrations in tissues that can be damaging to cells, resulting in production of compounds that protect the cells from free radicals of oxygen. Removal of excess oxygen from tissues is also enhanced by water movement, and particle capture increases with flow at least in the lower range of flows (Sebens et al. 1996a, b, 1998). A few sessile anthozoans display a rhythmic pumping action of their tentacle crown, which may serve to break up the diffusive boundary layer and thus enhance both gas and nutrient mass transfer (e.g., octocorals). Another possible mechanism to disrupt the diffusive boundary layer is by ciliary activity; many corals have ciliated tracts on their surfaces that move mucus and food particles and which could also modify the water layer closest to tissue surfaces.

Energy budgets will thus change markedly with flow regime; corals living in a low flow and low light environment, such as in deeper reef habitats, face the greatest limitations. Although metabolic costs may be reduced under such conditions, both photosynthesis and particle capture will also be low. More water movement also increases photosynthesis in some coral species (Patterson et al. 1991), so corals in low flow habitats may have less energy to offset costs. In addition to toxic effects, high tissue concentrations of oxygen result in high rates of respiration during the day, which can be measured experimentally by darkening corals momentarily after high light exposure. The elevated metabolic rates during daylight hours represent a high cost to corals, but that high cost may be easily met by photosynthate production. In addition, high metabolic rates may also reflect greater rates of ion pumping for calcification, nutrient active uptake, or other metabolically expensive activities.

Stressful environmental conditions have the potential to increase metabolic costs for corals; examples of such stressors include increased sedimentation, high or low temperatures, and more acidic seawater conditions. Corals which have lost all or most of their zooxanthellae after a bleaching event have a lower metabolic rate because there is less tissue per unit area, which may help them survive the following months and potentially recover. Availability of prey, lipid storage before bleaching, and severity of bleaching can all affect the energy balance of affected corals and are important factors determining their probability of mortality. Corals facing more acidic seawater conditions, on the other hand, may have metabolic rates continually elevated to maintain calcification; this may be less of a problem in tropical high light habitats but could be a substantial additional cost in temperate and tropical low light habitats where there is no excess of photosynthate production. Additional prey availability can offset the higher costs of calcifying in more acidic conditions, but acidification has been shown to reduce feeding rates for at least one species (Houlbrèque et al. 2015).

6.1.3 Symbiosis with Primary Producers

Cnidarians of many types rely at least partially on photosynthetic endosymbionts to meet their energy needs. Hydroids, scyphozoans, and many anthozoans harbor zooxanthellae (symbiotic dinoflagellates) in their gastrodermal cells and others harbor zoochlorellae (symbiotic chlorophytes). In high light habitats, such symbionts can provide more energy than needed to meet daily metabolic requirements, and there may even be a loss of excess photosynthate to the surrounding water (Sebens 1987a, review). Having algal symbionts also helps facilitate calcification in corals, which is especially important under conditions of low aragonite saturation state (low pH, high pCO2). Energy produced by symbionts can be used to pump hydrogen ions across cell membranes adjacent to the calcifying space, reducing their concentration at the site of calcification. Energy derived from heterotrophy can also assist calcification (Ferrier-Pagès et al. 2003) and may thus allow corals to grow and build skeleton in conditions that are less optimal for calcification.

Despite being so advantageous to the energy budget, symbiont photosynthesis alone cannot provide the nutrients necessary for tissue growth and production of reproductive organs and gametes. In most cnidarians, those nutrients are garnered by prey capture. Yet, there are some cnidarian groups that appear to have very reduced digestive apparatus and are not known to ingest prey; in such cases, uptake of inorganic nutrients directly from seawater could be the source of other limiting nutrients (Sebens 1987a, review). This also appears to be true for mollusks, such as the tropical giant clams, that rely on zooxanthellae for their energy. Energy from photosynthate can be used to fuel active uptake of dissolved inorganic nutrients from seawater, and thus can indirectly assist with tissue growth.

There is also evidence suggesting that tissue growth and skeletal growth in corals are somewhat decoupled and that tissue thickness can serve a storage function. When prey are plentiful, but conditions may not be ideal for calcification, tissue growth can be rapid and the amount of protein per unit skeletal area can increase many fold (Ferrier-Pagès et al. 2003). On the other hand, when corals are stressed, such as after bleaching events, tissue thins substantially and protein per unit surface area can be reduced to less than a tenth of the maximum. This pattern may be adaptive in several ways; first, when conditions are good for tissue growth, the additional tissue per unit area accumulates but is later spread out as new skeleton is produced, even if prey are less abundant then. In poor conditions, the coral maintains its surface area for prey capture and nutrient uptake even when the tissue becomes very thin. Thus, the feeding surface area to biomass ratio is much higher with very thin tissue, and recovery will be assisted.

It has long been recognized that many corals depend on both photosynthesis and prey capture for their energetic needs, yet the question of how much energy they get from each source has been problematic. It is easier to measure the response of photosynthesis to light (P/I curve) and to determine the production of energy-containing carbon compounds based on net oxygen production during experiments. The contribution of zooxanthellae to coral (animal) respiration (CZAR) (Sebens 1987a; Houlbrèque and Ferrier-Pagès 2009 reviews) was an early attempt to quantify how much energy corals were getting from their symbionts, usually in short-term studies. It quickly became evident that shallow water coral species often had photosynthetic production that greatly exceeded the respiratory needs of the coral, whereas those from deeper reef habitats were generally not meeting those needs from photosynthesis, though it could still represent a large fraction of energy intake.

If shallow water corals were producing more than the coral needed, what happens to that photosynthate? First, energy needs and carbon needs are not the same. Carbon is needed to build molecules (anabolism) and to replace those that are broken down for precursors or for energy (catabolism) or are lost to the environment. When new tissue is produced, including gametes and reproductive organs, or when damaged tissue is replaced, carbon and energy are both needed. There is also substantial loss of carbon and energy in mucus production, nematocyst production, and other losses to the environment. So, CZAR has to be well over 100% to meet the needs of a coral for respiration, growth, reproduction, and replacement of lost tissues and compounds. Basal metabolism is usually the largest energetic cost in any time period, but it is not the only one. The algal symbionts are also respiring, reproducing, and replacing structures and whole cells. A CZCR might be more informative, defined as the contribution of zooxanthellae to coral (animal and symbiont) respiration.

On the other side of the balance, we can compare CZAR to a similar contribution from heterotrophy, termed CHAR. Again, this has been done for the short term and for experimental situations (Houlbrèque and Ferrier-Pagès 2009, review). Certainly there are coral species that do not have zooxanthellae or other photosynthetic symbionts, and such species must be getting all of their energy needs from plankton and particle capture or dissolved compounds, so we might expect this heterotrophic contribution to be substantial even for species that have symbionts, which it is.

Photosynthesis by symbionts is less effective in temperate zone cnidarians than for those in tropical habitats, due to colder temperatures and less irradiance seasonally. Nonetheless, both zooxanthellae and zoochlorellae symbionts are present in some species, such as the very well-studied *Anthopleura elegantissima* on the west coast of North America (Bingham et al. 2014). This species can be found naturally without photosynthetic symbionts, in caves and other low-light situations, where populations are generally not as dense as in the nearby high-light situations. Low intertidal populations in well-lit areas generally have large clonal aggregations, with large polyps and high biomass. Polyps capture both benthic and planktonic prey and can obviously persist on this resource alone in some habitats; the symbionts, however, provide enough additional energy that clones of symbiotic anemones would likely outcompete clones of asymbiotic anemones in the well-lit habitats (Bingham et al. 2014).

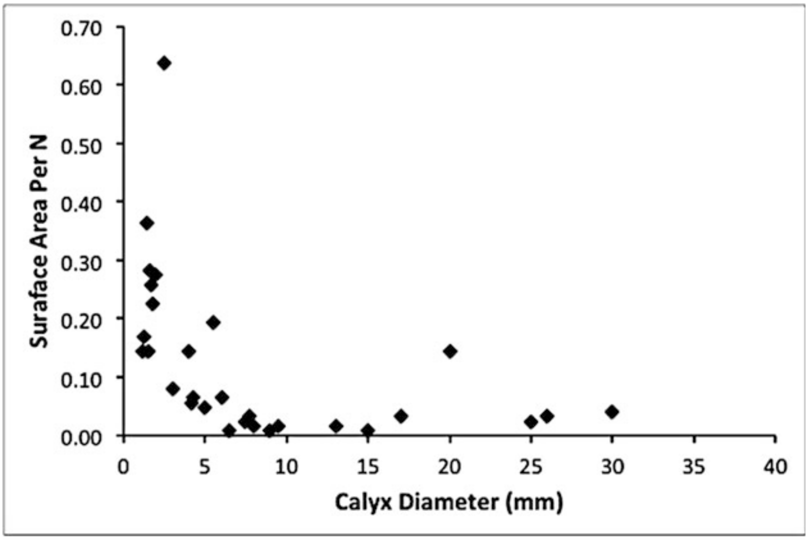
6.1.4 The Size of Feeding Units

Cnidarian polyps come in a wide range of sizes, from hydroids less than a millimeter to sea anemones nearly a meter in diameter (Sebens 1987a). Tentacle sizes also vary considerably, and tentacles of octocorals are furnished with side branches that make them very effective for capture of smaller particles (Sebens and Koehl 1984). The great advantage that accrues to small polyps in a cnidarian colony is the increased feeding surface area per unit mass and the fact that both feeding surface and metabolic cost scale linearly with mass (Sebens 1979), and thus colony mass can theoretically continue to increase without a loss of energy surplus per unit mass. However, there are also advantages to larger polyp size, which are primarily the ability to capture larger prey, and increased competitive ability (Sebens 1997; Lang and Chornesky 1990). Sebens (1997) examined the size of polyps for Caribbean scleractinian corals and found that most species had relatively small polyps and high surface to mass ratios (Fig. 4). Sebens et al. (1998) also found that corals with both small and medium sized polyps captured prey of about the same size range, though later work with some of the largest coral polyps showed that they do in fact capture larger prey (unpublished data), which is also true for sea anemones (Sebens 1987a).

An important trade-off is apparent when optimum polyp size within a colony or dispersed clone is considered. Clearly, if energy intake scales at a lower power of mass than energetic cost, smaller units are better. Although there is one predicted size optimum for a single individual, there is no such optimum for splitting up a given mass of tissue into a number of units, such as polyps. The same energetics model applied to this case predicts that polyps should be infinitely small (Sebens 1979). Dividing any mass into two units produces a situation where the ratio of feeding surface to mass increases and this just gets better the more units the mass is split into. Even among a defined group such as reef corals, most species in a reef or region have small polyps a few mm in diameter, while a few have larger polyps up to centimeters in diameter. For those corals that depend primarily on light capture (very small particles indeed), energetics models predict that polyps should be as small as possible and still be able to carry out all necessary functions, including reproduction (Sebens 1979). Hydroids form colonies of even smaller polyps from less than a mm to over a centimeter in polyp diameter. So, if the energetic considerations predict the tiniest polyps possible, why are all polyps not the same small size?

Sebens (1979) considered one possible explanation; given a normal distribution of prey biomass (in the energetics model) where polyps can consume prey whose length is about the same as polyp diameter (realistic, based on field data), polyps that are too small to capture much of the prey size spectrum are at a disadvantage. A new optimum size is predicted for polyps within a colony; polyps must be large enough to capture most of the prey sizes available, but small enough to take advantage of the high surface to mass effect. This optimum is just above the mean length of prey in this example. At this optimum, polyps sacrifice some prey capture (larger prey sizes) for the benefit of greater capture area. This result still predicts that all colonies would have small polyps, just not infinitely small. If most colonies have small polyps and specialize on the most abundant prey by biomass (small to medium sizes), that leaves an opportunity for other species to specialize on large prey. For these species, the availability spectrum is different because they have better ways to handle large prey but may then be less efficient at handling small prey.

Another possible reason for having large polyps is direct competition with other corals (Lang and Chornesky 1990). Sebens (1997) noted that corals with large polyps are positioned higher in the competitive hierarchy based on mesenteric filament egestion and use of sweeper tentacles. Corals with small polyps are generally fast growing species that can overtop or shade other corals, but corals with larger



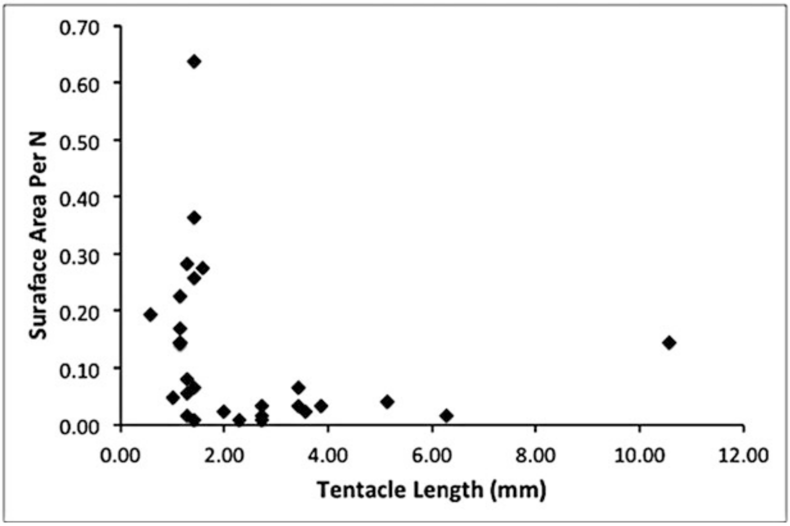


Fig. 4 Polyp sizes of Caribbean corals, surface to biomass ratios. *Top*: surface area per unit tissue nitrogen (biomass proxy) (mm^2/ug N) plotted versus coral calyx diameter (polyp size proxy). *Bottom*: surface area per unit tissue nitrogen (biomass proxy) (mm^2/ug N) plotted versus coral tentacle length. Species of each coral by calyx size are given in Sebens 1997 (Replotted from data in Sebens 1997)

polyps can prevent this overgrowth by digesting or damaging the faster growing (small polyp) species. Enhancing feeding surface area by forming upright branches, with high colony (skeletal) surface area to volume or mass, is another way to improve the energy intake situation.

Tall branching or plating corals, usually with small polyps, are also more susceptible to damage or removal in severe storms, whereas encrusting or massive mounding colonies, usually with larger polyps, survive these events. Thus, it may be equally advantageous, in fitness terms, to be an energy optimizer with small polyps or to be a survival maximizer with larger polyps. Coral species could thus coexist on the same reef by being part of a fugitive-dominant process, where some species are good colonizers and fast growers, and others are better long-term competitors and survivors. Disturbance, from severe storms or predator outbreaks (e.g., *Acanthaster*, crown-of-thorns seastar), provides open space that can be colonized and, within a given reef zone, certain coral will be competitive dominant and eventually outcompete the early colonists. Given that such disturbances probably occur on a multi-decadal scale, space could be opened up frequently enough to allow the fugitive species (also energy maximizers) to persist permanently on any reef.

6.2 Bivalve Mollusks

Bivalves belong to a large class of mollusks and penetrate habitats from subtidal (e.g., sediments hundreds of meters deep) to intertidal (e.g., tide pools). Bivalves are ecosystem engineers worldwide; by means of their shells they introduce complexity and heterogeneity into benthic environments and are important elements of habitat structure affecting population, community, and ecosystem-level processes.

6.2.1 Energy Intake

Bivalves are the masters of the strategy (from an evolutionary point of view) of "sit and wait" to obtain food. As mostly sessile suspension feeders when adults, they have evolved an efficient filtration apparatus allowing them to remove microscopic particles (from bacteria [~1 μm] to detritus and zooplankton [hundreds of μm]) of different nature that are selected first on the basis of size and later for quality. The size of particles maximizing ingestion rate is species-specific and is centered in a range of only few microns (e.g., *Mytilus* has maximum ingestion for the particle size range of 1 to 10 μm). Bivalves are essentially opportunistic organisms, relying on those organic particles falling in the optimal size range that are available in the water column and which enter their feeding apparatus by inhalant water flow. Indeed, to assure a sufficient amount of energy to support survival, somatic maintenance, growth, and reproduction, these animals need to pump and process very large amount of water through the filtration system.

Bivalves employ a hydromechanical and mucociliary mechanism of particle transport. The process of filtering in bivalves is based on the action of three types of cilia on the gill filaments. Lateral cilia move entering water by beating in metachronal waves allowing for constant water movement. Thus, water flows through gills, and particles are retained by laterofrontal cirri in a number of ways; particles may be sieved, intercepted, or may impact on gill filaments by inertia, motile particle motion, or deposition by gravity. While trapping by sieving is not strictly dependent on size of spaces between cirri, all other mechanisms depend on it. Also, particles are then transported at the level of frontal cilia by mucus trains or strings to labial palps and mouth. There are some deviations to this scheme of filtering, such as those occurring in scallops and oysters. However, when particles approach at the level of labial palps, a sorting action happens; particles here can be (i) transported to the mouth to be ingested or (ii) ejected through pseudofeces. Pseudofeces production represents a sort of compensatory process allowing bivalves to maintain food uptake at a high level, in spite of dilution of the food items with indigestible material, thereby increasing the total amount of organic material ingested per unit time.

There has been much controversy over the last decades as to whether there are well specified and evolved preingestive selection processes in bivalves as a function of particle quality or quantity. In general, most bivalves living under conditions of dense particulate mixtures (inorganic and organic) as in shallow waters wrap certain particles in mucus (secreted by the epithelia of the pallial organs) and then reject them through pseudofeces. Thus, those extra particles are expelled from the organisms without passing through their digestive tract. Being mucus compounds are highly labile, composed of mucopolysaccharides associated with particle processing, pseudofeces locally serve to couple benthic and pelagic habitats supplementing the flow of suspended particles falling from upper layers of the water column to benthic habitats.

6.2.2 Energetics Costs and Energy Budget

Bivalves are physio-energetically complicated animals despite their apparent simplicity! All have carbonate shells that, in the context of ocean acidification, will dissolve under certain conditions. Some are intertidal, and severe storms may stochastically influence their survival and thus their vertical position; they can counteract this by producing cement or byssus for stronger attachment. All bivalves need to produce endogenous mucus to assist food particle transport and wrapping of pseudofeces. All such factors affect energetic performances of individuals, with both direct and indirect effects at the population level (e.g., Carrington et al. 2015), and all are usually acting on different components of the energy budget. The influential assertion by Conover that a "bivalve's life is spent in a nutritionally dilute environment" is certainly valid for all bivalves. The amount of energy spent to gain food through filtration is based on low-energy pumps that continuously move the surrounding water through the gills. Feeding costs are proportional to feeding rate and are accounted for in DEB models by a reduction of energy gain per food unit (Kooijman 2010). In general, feeding costs per unit of food should increase with decreasing food density because of the increased effort of extracting food from the environment (they filter more when food is diluted in a matrix of inorganic particles such as silt).

Several studies have inferred high energy losses of several types, in a wide array of species. In *Mytilus edulis* and *M. californianus*, they were estimated at more than 20% of the ingested ration of algal cells. Mucus is an important element in suspension feeding (particle adhesion, movement, and pseudofeces wrapping), but there are not sufficient data on the energetic cost of its production. The cost is unlikely to be high since mucus produced in feeding is either reabsorbed or ingested, and the animal is generally in adequate energy balance to support the costs of mucus produced for rejection. In contrast, most intertidal bivalves could not feed if they do not remain fixed on substrata. To reduce the likelihood of dislodgment, they need to spend energy to produce byssus. This involves energetic costs and in current energetic theories (for example DEB) the energy to synthesize all somatic structures involved in survival (e.g., byssus and shells) are usually paid from the energy component used for somatic metabolic maintenance (Kooijman 2010). For byssus production, there are estimates of about 15–18% of the somatic maintenance component of the energy budget. Theoretical simulations have showed that decreasing byssus production can impair the ability of individuals to persist over time (Carrington et al. 2015), whereas increasing byssus production results in lower growth and reproduction. Fitness is maximized at some intermediate allocation of energy to byssus production.

Once food compounds are assimilated, according to current bioenergetic theory, they accumulate into reserves and from there energy is constantly allocated to different functions, first somatic and maturity maintenance and then the amount remaining (if any) is used for growth and reproduction. We can estimate the amount of energy spent for maintenance (i.e., the cost of processes needed by the organisms to survive, including all the biochemical processes necessary for basal metabolism – particularly costly protein synthesis/turn over; only indirectly through oxygen consumption experiments (Kooijman 2010; Sarà et al. 2013a, b)). However, oxygen consumption can also include the cost of feeding, digestion, and growth/synthesis. Maintenance costs can vary from 10 to 15 J cm^{-3} for some small mussels such as *Brachidontes pharaonis*, oysters such as *Crassosterea gigas*, and cockles such as *Cerastoderma edule* to over 30–60 J cm^{-3} for clams such as *Macoma baltica* and *Perna sp.* (Matzelle et al. 2014).

The large differences among cost estimates depend on whether byssus production is a part of metabolic cost, and whether cost is a function of habitat (intertidal, subtidal, etc.) or of maximum size, etc. (Kooijman 2010). Costs of structure (tissue needed to grow) in bivalves are high in energetic terms. The amount of reserve energy required to synthesize a unit volume of structure includes the energy stored in that tissue as well as the overhead costs for anabolism during its production. These values range from about 2,000–3,000 J cm^{-3} for clams, cockles, and oysters up to about 4,500–5,000 J cm^{-3} in mussels (*M. edulis*, Matzelle et al. 2014). Such large variation in components of the energy budget lead to the concept that (as for all animals) every extra energetic cost spent to cope with environmental variability (as expected in a context of climate change) has the potential to impair growth and reproduction and thereby lower the potential persistence of populations over time. Such a result is particularly important in bivalves which are ecosystem engineers, where changes in local density and abundance of these species can affect the whole associated assemblage causing a net biodiversity lost.

6.2.3 Putting It All Together: An Example Using the DEB Approach in Modeling Mussel Distribution

Using a fully mechanistic DEB-parameterized example for the Mediterranean blue mussel (*Mytilus galloprovincialis)* throughout that basin (Fig. 5; Sarà, unpublished), we show how having quantitative information implemented with the mussel's functional traits allows us to study the effect of increasing temperature (in 2020, with and without augmented hypoxia conditions) on the number of eggs produced over a lifetime. In this example, the species can produce eggs at high rates over most of the basin in 2020 with increased temperature, but both range and egg production are much reduced in the case of predicted hypoxic conditions. Outputs of such mechanistic models provide several applications for population management

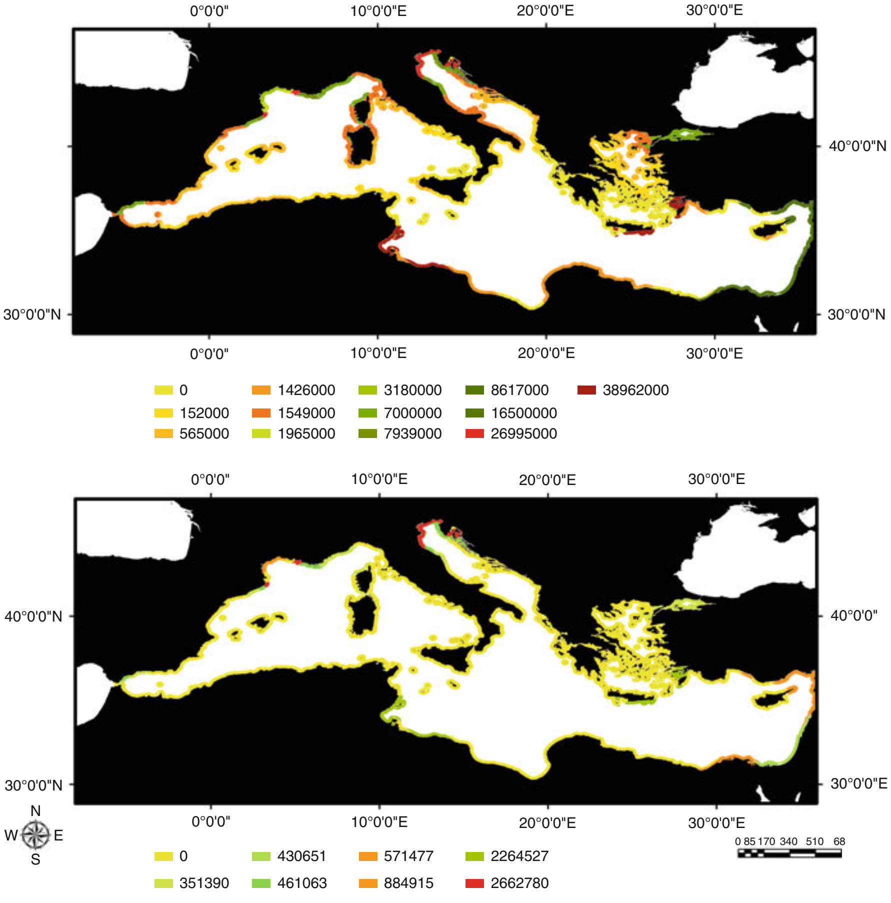


Fig. 5 Mechanistic DEB based prediction for number of eggs of *Mytilus galloprovincialis* (*top panel*) in 2020 (A1B scenario; IPCC, 2014) and the number of eggs per lifetime (*bottom panel*) in 2020 under hypoxia conditions. As shown, such a multiple-stressor condition will lead to a large recession of that species across the whole basin (G. Sarà, unpublished)

enabling managers to support adaptation and mitigation plans for species that are beyond reach of simpler statistical correlative approaches. This quantitative information (e.g., body size and fecundity) along European coasts at any point in time from now to 2050, and beyond whenever possible, will feed into population models for target species with time-steps matching the biology of each species. Most ecological processes are essentially density dependent. Thus, if we are able to quantitatively estimate fecundity, for instance, we have in our hands important information from which to derive the other main components of population dynamics.

6.3 Cirripede Crustaceans

Barnacles are found in all of the world's oceans and have persisted through periods of global warming (e.g., Palaeocene–Eocene Thermal Maximum) and cooling (e.g., Pleistocene glaciation). Given their ability to cope with a wide range of environmental conditions (Buckeridge 2012), understanding how barnacles respond to changes in temperature and water flow is an especially important topic in light of potential environmental variation due to climate change and/or species invasion into new habitats (Sanford and Menge 2001).

6.3.1 Energy Intake

Barnacles feed on a variety of planktonic food types that range in size from μm to mm. Ultimately, food intake depends on the velocity of the fluid medium carrying food particles, particle concentration, and the capture area presented by feeding appendages. Together, these factors contribute to the total flux of particles past barnacles, which possess an array of morphological and behavioral responses to enhance particle capture. Barnacles capture food with six pairs of biramous feeding appendages, called *cirri*. Each cirrus is segmented and each segment bears a set of small, hair-like protrusions called *setae*. The largest cirri form a cirral net, used to capture food particles, which are moved towards the mouth with the aid of the three sets of shorter cirri. Barnacles can actively move the cirral net via a combination of hydrostatic pressure and striated muscle fibers (Neufeld and Rankine 2012). Cirri may be extended for prolonged periods permitting passive capture of suspended particles or they may actively be extended and retracted into the water column (Geierman and Emlet 2009; Trager et al. 1990). Indeed, a range of behaviors have been defined that include: *testing*, where the aperture of the test opens, but only a single cirrus emerges; *pumping*, where cirri are extended, but the cirral net remains unfurled; *slow, normal*, *and fast beating*, where rhythmic expansion of the cirral net occurs and *prolonged extension*, where the cirral net is held open (Anderson and Southward 1987; Nishizaki and Carrington 2014a).

Cirral activity may be influenced by a number of environmental factors. For many barnacle species, cirral activity displays a thermal optimum (Anderson and Southward 1987, review). For some species, there is a behavioral switch from active beating at low flows to passive extension at higher flows (Trager et al. 1990). Active beating of the cirral net increases particle flux by both increasing the velocity with which fluid passes the cirral net and by creating a feeding vortex that draws food particles towards the cirral net. In oscillating flows, barnacles reorient the cirral net to face the direction of flow and presumably increase particle capture (Trager et al. 1990).

Under low water velocities, barnacles most commonly display beating behaviors that involve fully extended cirri (i.e., slow, normal, and fast beating), whereas at fast flows barnacles adopt abbreviated behaviors (i.e., pumping, testing) (Nishizaki and Carrington 2014a). This suggests that at high velocities barnacles withdraw cirri to prevent physical damage and extend cirri at slow flows to maximum food particle capture. However, barnacles also engage in pumping behavior under conditions of low O_2 (e.g., low flow, high temperature), presumably to increase ventilation (Nishizaki and Carrington 2014b). Moreover, cirral behavior likely serves to both maximize food capture and facilitate oxygen exchange (Nishizaki and Carrington 2014a, b).

Particle capture is presumably linked to morphology, specifically the size of the cirral net. Cirral morphology displays flow-induced phenotypic plasticity, with longer cirri for barnacles at low flow and shorter cirri at high flow (Arsenault et al. 2001; Gilman et al. 2013; Nishizaki and Carrington 2014a). This plastic response, however, is generally limited to water velocities < 0.6 m s^{-1} and is absent at faster velocities (e.g., 2.4–14.0 m s^{-1}; Li and Denny 2004). Barnacles in fast flow retract their cirri, allowing them to avoid damage and such behavior may explain why cirral morphology is invariant at high velocities. At low flows, longer cirri and larger cirral nets may represent a response to maintain high particle capture rates. Barnacles also develop longer cirri at higher temperatures, raising the possibility that cirral length is related to oxygen availability (Nishizaki and Carrington 2015).

The spatial distribution of barnacles (e.g., solitary versus aggregated individuals, density of individuals) may also affect particle capture rates. Barnacles can form elevated hummocks of tall, densely packed individuals, and individuals near the peaks of these hummocks have higher feeding rates compared to solitary individuals or barnacles in the troughs between hummocks (Bertness et al. 1998). This likely permits individuals at the peak to access faster flow speeds, higher particle concentrations, and ultimately flux of food particles. However, hummocks are also at risk of dislodgment by waves and thus risk of mortality may be higher there.

Patterns of particle capture can be predicted by models using the mechanisms of filtration as described above (see Sect. 2.1). Such models suggest that for *B. glandula*, particle capture by direct interception is between 10^1 and 10^8 times greater than capture by inertial impaction, gravitational deposition, or diffusional deposition (Nishizaki and Carrington 2014a). However, empirical patterns of particle capture across temperature and flow were accurately predicted by such models only when cirral beating behavior was incorporated. This suggests that the limits to feeding success, and thus energy intake, are not simply biophysical but also behavioral in nature. Although cirral activity is often used as a measure of feeding activity, the correlation between activity and gut content is weak. For instance, Nishizaki and Carrington (2014a) report that even with a high percentage of barnacles actively beating (68 ± 3%), a far lower percentage had actually ingested food particles

(22 ± 3%). This discrepancy suggests that cirral activity may also serve other functions and that cirral activity alone is a poor proxy for barnacle feeding rate (Nishizaki and Carrington 2014a).

6.3.2 Energetics Costs

As sessile ectotherms, barnacles have generally low metabolic rates and energetic costs. Although cirral activity does carry an energetic cost (Gilman et al. 2013), rates of oxygen consumption among different behaviors (e.g., pumping, normal, and fast beating) were found to be equivalent. In laboratory chambers, respiration rate increased with both water temperature and flow speed; flow had less influence on respiration at low temperatures and a greater effect at high temperatures (Nishizaki and Carrington 2014b). Although respiration rates in water are usually higher compared to those in air, long periods of emersion can make aerial respiration a significant energetic cost in their total energy budget during a period when they are not feeding. Molting is considered a minor constituent of the overall energy budget (~2%), but molting frequency increases with both turbulence and temperature and greater molting frequency is generally associated with more rapid growth.

Respiration rates are potentially limited by: the transport rates of dissolved oxygen from the water column to the surface of a barnacle (known as mass transfer limitation); reaction kinetics at the boundary that limit the ability of an organism to transport oxygen across the body wall (reaction kinetic limitation); or a combination of both (Patterson and Sebens 1989; Sebens et al. 2003). Knowing whether uptake rates are governed by mass transfer versus kinetic limitation is important for understanding whether physiological processes are regulated by factors internal versus external to the organism. In barnacles, respiration is mass transfer limited under low water velocity–high temperature conditions (Fig. 6). In contrast, limitation by uptake reaction kinetics, when the capacity of barnacles to uptake and process oxygen is slower than its physical delivery by mass transport, prevails under high flow–low temperature conditions. Moreover, there are intermediate flow–temperature conditions where both mass transfer and kinetic limitation are important (Nishizaki and Carrington 2014b). This suggests that, in slow-moving water, respiration may become mass transfer limited as temperatures rise, whereas faster flows could serve to ameliorate the effects of elevated temperatures.

6.3.3 Energy Budgets and Growth

An annual energy budget for the barnacle *Balanus glandula* has been constructed to predict the production of body tissue, gametes, shell, aquatic and aerial respiration, molting, and fecal production. This approach demonstrated that although individual barnacles show greater production compared to crowded barnacles, at the population level, crowding results in higher productivity on a per area basis (Wu 1980), and thus greater secondary production available to higher trophic levels.

A simple energy budget model based on feeding and respiration response curves predicts peak growth at moderate temperatures and velocities (Fig. 7; Nishizaki and Carrington 2015). These predictions were consistent with growth data collected under ecologically relevant thermal and flow experimental conditions. An advantage

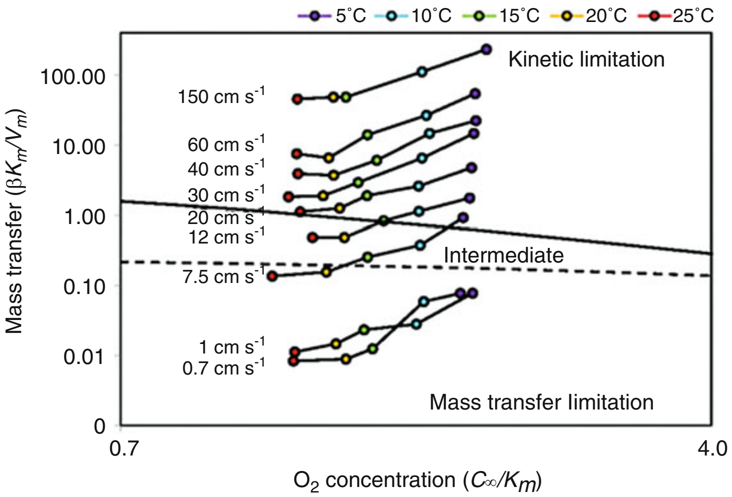


Fig. 6 Nondimensional mass transfer coefficient ($\beta K_m/V_m$) plotted against nondimensional oxygen saturation (C_∞/K_m). Each circle is calculated from means of three trials of the respiration experiment; colors indicate different temperature treatments and each line represents trials conducted under the same water velocity, as indicated on the graph. The *solid line* represents the upper limit for conditions of mass transfer limitation and the *dashed line* represents the lower limit for conditions of kinetic limitation. β is the mass transfer velocity (m s^{-1}), V_m is the maximum uptake rate (μmol O_2 m^{-2} h^{-1}), K_m is the oxygen concentration at which the uptake rate is one-half of its maximum (μmol O_2 m^{-3}), and C_∞ is oxygen concentration in the bulk flow (From Nishizaki and Carrington 2015)

of this type of approach is that it provides a mechanistic understanding of the behavioral and physiological processes underlying growth. For instance, low growth is expected at both low and high velocities due to lower encounter rates with suspended food particles and lower capture efficiencies, respectively. At high temperatures, growth is likely limited by high metabolic costs, whereas low growth at low temperatures may be a consequence of low oxygen availability (Verberk and Atkinson 2013) and/or slow cirral beating and low feeding rates.

Temperature may influence growth both through changes in physiology and changes in mechanics, via the viscosity of seawater. However, Verberk and Atkinson (2013) also suggest that the availability of oxygen may actually decrease at lower temperatures due to lower oxygen partial pressure, which may ultimately serve as a limit to body size. At high temperatures, elevated metabolic demand may be counterbalanced when high water velocity promotes the exchange of gases and nutrients that sustain metabolism. Moreover, these results advocate for approaches that consider the combined effects of multiple stressors and suggest that both increases and decreases in temperature or flow impact barnacle growth but through different physiological and behavioral mechanisms.

Gonad development shows a seasonal pattern that suggests temperature may be an important determining factor. Warm temperatures are generally associated with earlier reproductive maturation and a greater proportion of adults that are ultimately

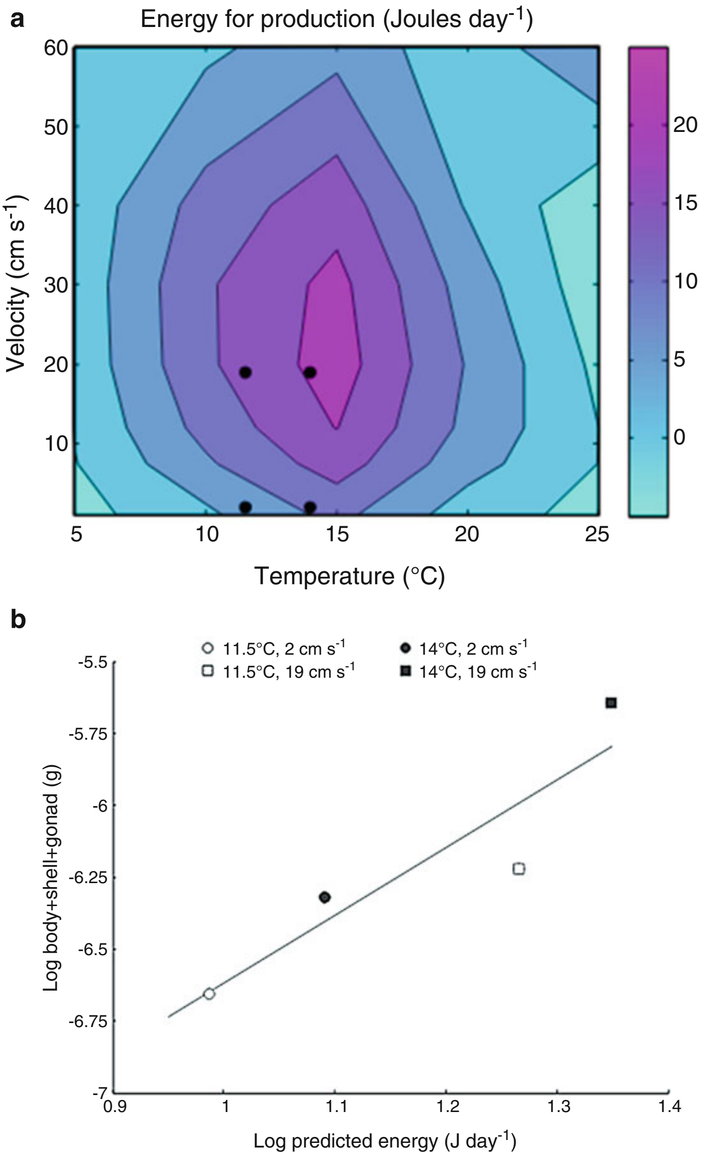


Fig. 7 Model predictions for barnacle growth. (**a**) Predicted energies available for production for *Balanus glandula* as a function of water temperature and velocity. *Contour lines* represent intervals of 5 J and *black circles* indicate environmental conditions used in the mesocosm experiment. (**b**) Comparison of predicted energy for production versus measured barnacle growth in mesocosm experiment. Growth was assessed at 11.5 °C (*open symbols*), 14 °C (*filled symbols*), 2 cm s^{-1} (*circles*), and 19 cm s^{-1} (*squares*) (From Nishizaki and Carrington 2015)

reproductively active. Experimental data for *B. glandula* in a mesocosm and field study confirm that barnacles show greater gonad production under higher temperatures and faster water velocities (Nishizaki and Carrington 2015). Gonad production is also influenced by crowding, as egg production from individual barnacles was 2.5 times higher compared to crowded individuals (Wu 1980).

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Benthic-Pelagic Coupling: New Perspectives in the Animal Forests

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Sergio Rossi, Martina Coppari, and Núria Viladrich

Abstract

Animal forests all over the world play an essential role in benthic-pelagic coupling processes. These processes can change according to the feeding strategies of benthic species, as well as their extension and biomass. From the oligotrophic coral reefs to the highly seasonal productive Antarctic ecosystems, suspension feeders (the main eco-engineers of the animal forest) have evolved feeding strategies depending on the environmental constraints, which shape their survivorship and partly explain their high biodiversity. In the process of benthic-pelagic coupling, these organisms also have the ability to retain part of the organic and inorganic matter in their long-lived structures. In this chapter, hypotheses related to benthic-pelagic coupling processes will be presented, along with the newest methodology used to quantify the capacity of animal forests to function as carbon sinks. Although the role of animal forests as carbon sinks is an essential ecosystem service, it has been largely neglected in the conservation models for the majority of marine environments. The importance of food availability (quantity and quality) in suspension feeding animals will be discussed with a new approach based on random pulses of energy input. This approach will help to better understand their nutritional condition and the health status of their populations. Finally, to allow making key evaluations of the influence of animal forests in benthic-pelagic coupling processes and as carbon sinks, this approach will be overlapped with the distribution, density, and population size

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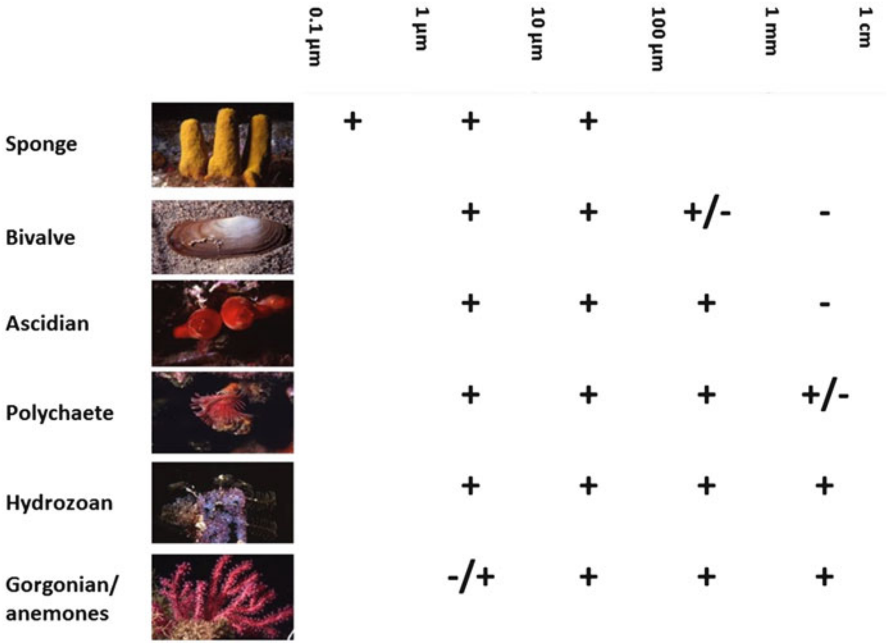
structure of benthic suspension feeders, obtained through the analysis of video or photo recorded via remotely operated vehicles (ROV). This new approach will be an essential tool for coastal, continental shelves and deep water coral area management and conservation, where animal forests are threatened synergistically by several direct and indirect impacts.

Keywords
Seston • Seasonality • Near-bottom water layer • Short time cycles • Food quality • Trophic crisis • Biomarkers • Lipids • Stable isotopes • Carbon sinks

Contents

1 Introduction

In shallow and deep oceanic waters all over the world, active and passive benthic suspension feeders play an important role in energy transfer from the water column to their sessile living structures (Graf 1989; Gili and Coma 1998). These organisms represent a big percentage of the biomass of benthic communities and an essential component of the “animal forest.” The animal forest is a living three-dimensional structure, similar to vegetation forests but composed primarily of animals (e.g., sponges, cnidarians, bryozoans, ascidians, and other sessile benthic animal organisms; Rossi 2013; Rossi et al., ▶ Chap. 1, “Animal Forests of the World: an overview” of this volume). The main three-dimensional structural builders are clonal organisms of animal origin, although there are non-clonal organisms that also may form these forests as bivalves or polychaetes. These clonal structures usually consist of replicates in branching, encrusting, or massive forms, where the “individual” is expressed by polyps (cnidarians) or zooids (bryozoa). In non-clonal organisms, individuals may form “clonal-like structure” (e.g., mussel beds or polychaete tubes) or simply settle on the benthos as isolated forms (e.g., solitary ascidians or individual polychaetes). In both cases, many of these organisms (colonial and/or solitary) form dense congregations (i.e., numerous individuals of the same species in the same area) that produce three-dimensional structures which may alter the current flow and increase the particle retention (Vogel 1994; Gili and Coma 1998; Riisgard



		0.1 µm	1 µm	10 µm	100 µm	1 mm	1 cm
Sponge		+	+	+			
Bivalve			+	+	+/-	-	
Ascidian			+	+	+	-	
Polychaete			+	+	+	+/-	
Hydrozoan			+	+	+	+	
Gorgonian/ anemones			-/+	+	+	+	

Fig. 1 Different examples of suspension feeders and their preference for different sizes of dead or alive preys depending on the morphology or the feeding structure. On the top, prey size ranges. The + symbol indicates preferred range of preys for most of this group, the – symbol means not preferred preys. The +/– symbol means that some organisms may capture these preys, but not all of them are adapted for this size range. Void means that the suspension feeder is not able to capture this prey size. The wide spectrum of trophic strategies is one of the keys to understand benthic suspension feeder diversity. For example, sponges are not capable to filter preys larger than 100 µm, due to their filtration system, while anemones may impact on dissolved organic matter and capture preys larger than 1 cm length (Transformed from Riedl 1984)

and Larsen THIS BOOK). Therefore, the formation of colonies, clones, and finally patches is energetically more favorable than the increase of the growth of an individual to its largest possible body size (Gili and Coma 1998).

These living structures generate and enhance nutrient exchange, capturing and retaining carbon, nitrogen, and other elements, which are incorporated into their living tissue and three-dimensional morphology. These nutrients are assimilated according to different trophic strategies, which change mainly according to different taxonomic groups (Fig. 1). However, all trophic strategies of benthic suspension feeders entitle a low energetic cost for their filter feeding. The trophic strategy of these animals could be completely heterotrophic (i.e., energy input coming only from dissolved or particulate organic matter, like nonsymbiotic gorgonians, bryozoans, or ascidians) or mixotrophic (i.e., energy input from the direct feeding and the presence of unicellular symbionts like many scleractinians, gorgonians, and sponges). Mixotrophic organisms' energy is derived from symbiotic cells that translocate their photosynthetic products to the host cells. In shallow waters animal forests, either symbiotic or nonsymbiotic species can dominate depending on factors as light penetration and food availability. In deep waters, organisms are not able to use the light, indeed photosymbiotic algae are constrained to the first 50–150 m depth (depending on the light attenuation). Since the vast majority of the ocean floor is found at depths greater than 150 m, heterotrophic benthic suspension feeders are the dominant organisms all over the world.

In addition to increase the capture and retention of nutrients, the self-organization in modular marine organisms enhances biomass and biodiversity of associated organisms, also increasing the ecosystem's complexity. The more complex the animal forests are, the longer is their history of growth and structure, being the mature colonies/individuals larger and more architecturally complex, being also the patch structure highly complex (Santangelo et al. 2007). The highly structured animal forests have a higher capacity to alter major current flow, increasing particle retention, concentrating more zooplankton, eggs, larvae, juveniles, and adult organisms within the canopies they form (Vogel 1994). In contrast, the less structured animal forests have smaller surface areas exposed to major currents, and therefore their capacity to retain particles is much lower (Rossi et al. 2012). For example, a harvested red coral (*Corallium rubrum*) patch may consist of 96% of the colonies having less than two branches and an overall height below 3 cm (Rossi et al. 2008). Colonies of this size class typically have about 100 polyps exposed to the water column, which is the only mode of particle capture in these organisms. In non-harvested red coral patches, a single 10 cm colony may have twenty-five primary branches, eight secondary branches, three third-order branches, and one fourth-order branch, yielding a mean number of 3,000 polyps exposed in the water column. In deeper red coral populations characterized by larger colony size, a single colony may have more than 6,000 polyps (Priori et al. 2013). Even if small colony density is higher than in well-structured, mature patches, the number of polyps will still be overwhelmingly higher in the mature patches respect the immature ones (Rossi et al. 2008). Larger colonies are vital to the success of the entire population; they account for the major gonads production, making the reproductive contribution of younger colonies almost negligible (Rossi et al. 2008; Priori et al. 2013). Mature animal forests are also carbon sinks, retaining part of the ocean productivity in their living structures for long periods, from decades to possibly even centuries (Rossi 2013; Priori et al. 2013; Coppari 2015) (Fig. 2).

The ability of the three-dimensional alive system to reach maturity (sessile suspension feeders) depends largely on the structure of their main builders, but it may also depend on anthropogenic direct or indirect impacts, such as harvesting, aquaculture, tourism, etc. (Rossi 2013). However, the food quantity and quality of near-bottom live or detrital particles (seston) are also a determinant for benthic fauna distribution, complexity, and diversity (Grémare et al. 1997, 2002). Some premises have to be considered and explained to adequately assess the impact of seston on the benthic organisms. First, it is essential to understand the best way to calculate the quantity and quality of near-bottom seston available for benthic suspension feeders. Second, the dynamics of the near-bottom water layers are far from constancy; therefore, a complementary temporal approach (seasonal and short time cycles) is

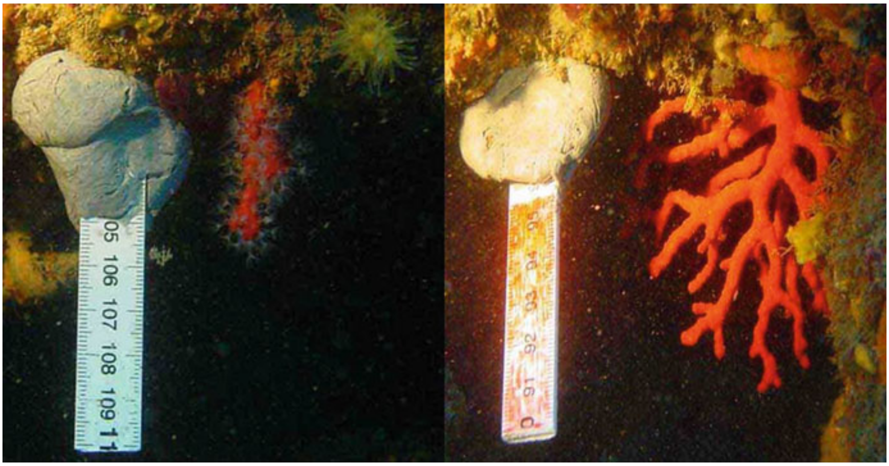


Fig. 2 Size matters. Colonies of *Corallium rubrum*, showing a clear difference in the ramification pattern and polyp number depending on size. On the left, a small, almost non-branched colony belonging to a harvested population. On the right, a non-harvested colony 5–6 cm long, with a clear branching pattern (being a small colony compared to those abundant in ancient times that could easily reach 20–30 cm height, Tsounis et al. 2010). It is crucial to understand that differences in the polyp number in the colonies result in different impact on the near-bottom water layer surrounding the animal forests organisms and, more in general, in a different impact in benthic-pelagic coupling processes

essential to understand the distribution of the energy input over time. Third, depending on their location and bottom topography, it is expected that communities with different composition and biomass processed the food arriving to the sea floor differently (Renaud et al. 2008). Therefore, it is essential to consider and quantify such variables in order to better understand the real impact of the overlying seston on the community. Finally, it is essential to choose appropriate tools, which will show how animal forests affect benthic-pelagic coupling processes, and how the available seston is influencing their global energy budget. Such tools may explain differences in activity, reproductive output, energy storage (in the form of macromolecules), growth, or any other variables that integrate seasonal or local changes in the components of the animal forest (Fig. 3).

2 Epibenthic Water Layer and the Quality of Available Food

The near-bottom water layer is a turbid layer, which extends above the bottom (Towsend et al. 1992). The induced turbulence that depends on topography, water current intensity, and the presence of living three-dimensional structures inhabiting the area (i.e., macroalgae, phanerogams, suspension feeders, etc.) represents a major factor determining the stratification of the seston in this near-bottom layer (Rossi and Gili 2009). In general, these water layers presented the most of seston concentration in the first 1–3 m above the sea floor (benthic boundary layer; Thomsen 1999;

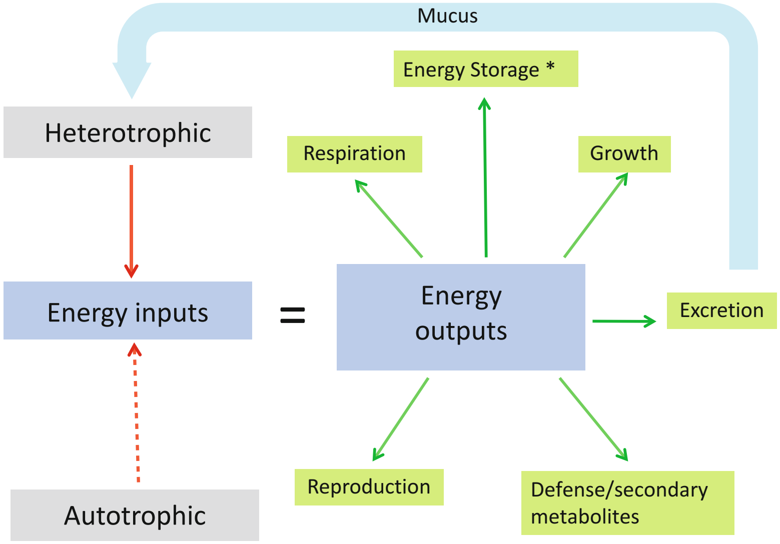


Fig. 3 Benthic suspension feeders' energy inputs and outputs. The inputs may be only heterotrophic (*solid line*) or both autotrophic (*dashed line*) and heterotrophic. All the suspension feeders have an heterotrophic input even if the autotrophic (symbiotic algae) carbon translocation contributed significantly to the energy needs (e.g., scleractinian species bearing *Symbiodinium* cells). In the outputs, mucus produced by coral species may be used as source of food by other suspension feeders (e.g., tropical gorgonians, sponges, Coffroth 1984).* The energy storage (mainly lipids or carbohydrates) will be invested in respiration, growth, reproduction, or defense/secondary metabolites)

Rossi et al. 2013). The particles forming the seston may simply fall down from upper layers, being passively transported by currents, or having their own autonomy depending on locomotive structures (e.g., cilia, flagella, legs, etc.). Besides the vertical input, lateral transport caused by currents is largely recognized as one of the main factors determining seston concentration in the benthic boundary layer (Thomsen 1999). Nevertheless, the turbulence generated in near-bottom layers not only affect the concentration but also the dynamics and growth of microbes through resuspension processes (Graf and Rosenberg 1997). To better understand the effect of current speed and direction on seston, the knowledge of the benthic topography is essential. In fact, current speed and therefore lateral transport and resuspension are normally higher in slope areas or zones with an abrupt bottom change, compared to areas with plain or slightly inclined shelves. Some studies have shown that moderate currents may generate enough turbulence in the near-bottom layer to increase the supply of food to suspension feeders (Riisgard and Larsen 2000). However, at low velocities, the particles available for feeding come from the sediment surface, which only is accessible for deposit-feeding animals when no currents are present. At higher velocities, resuspension also allows for suspension feeding but too high velocity makes particles retention difficult for the feeding structures (Riisgard and Larsen THIS BOOK). Recently deposited sediments can be resuspended by currents (lateral flux) of 7 cm s^{-1}. These particles may be up to four times more important than vertical particle flux when the sediments are rich in organic phytodetritus (Rossi and Gili 2009). However, the quality of organic matter is up to two orders of magnitude higher in fresh particles sinking from the water column than in resuspended sediment (Isla et al. 2006; Rossi et al. 2013). This seston is richer even though it has to be considered that the organic matter generated in surface or medium water layers pass through several trophic paths (zooplankton, microbial loop degradation, etc.) and transformations before reaching the sea floor (Rossi et al. 2013). In other words, planktonic organisms, such as salps, copepods, or mysids, remove a large part of this productivity before it reaches the ocean's floor; the amount that is left over may be subsequently consumed by benthic organisms such as holothurians, sponges, gorgonians, etc. Even so, during high productivity episodes like blooms, the surface phytoplankton might reach the bottom almost ungrazed when the cell growth is overwhelming (Rossi and Gili 2009), and thus all benthic organisms can also take advantage of this food source. This accumulation of fresh ungrazed material is one of the keys to understand the high biomass and diversity of benthic communities associated with highly productive zones, like Antarctica or deep sea water canyons (Isla et al. 2006).

In some cases, benthic filter feeding communities may act as a natural control of algal blooms and as regulators of eutrophication. For example, mussel populations in shallow waters can deplete phytoplankton over several meters of water layers in 1 day (Cloern 1982; Nielsen and Maar 2007). Conversely, when the animal forest formed by filter feeding communities is almost disappeared, primary productivity enters the microbial loop of the sediments and may provoke hypoxia or even anoxia (Jonas 1997). However, in what we can consider a normal set of conditions, animal forests are influenced by the abundance of available food and needs these fresh inputs of material for their survivorship. Grémare et al. (2002) showed that lipids, and to a lesser extent enzymatically hydrolyzable amino acids, are correlated with the continental shelf fauna abundance and biomass. In suspension feeders, the available seston quality and quantity, which vary during seasons, directly influence on the growth rates and reproductive output (Grémare 1997; Gori et al. 2013).

3 Seasonality in Benthic-Pelagic Coupling Processes

Seasonality influences almost all organisms on the Earth. Photoperiod, light intensity, food availability, oxygen concentration, salinity, and temperature vary throughout seasons, influencing metabolism and expenditure in marine planktonic and benthic organisms (Valiela 1995). For this reason, depending on the period of the year and environmental conditions, the size and abundance of phytoplankton, zooplankton, and seston may vary (Ribera d'Alcalá et al. 2004; Fig. 4). Thus, the seasonal patterns of the primary productivity become a key factor in understanding quantity and quality of seston available for benthic suspension feeders. In coral reefs, for example, the eukaryotic phytoplankton (<5 μm) could contribute up to 70% of

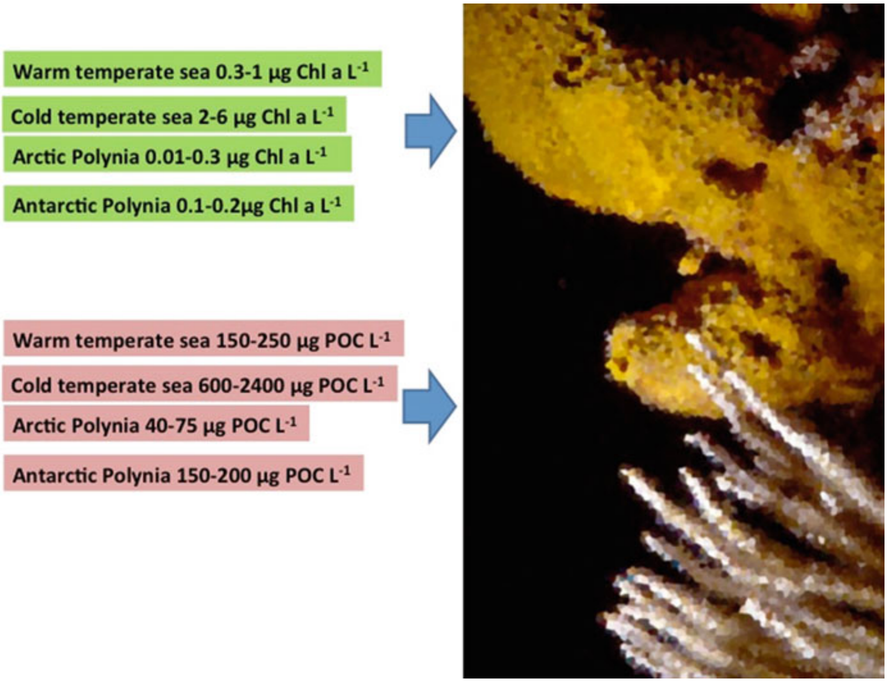


Fig. 4 The available organic matter in near-bottom water layers can be very different along the year in benthic ecosystems. Highlighted in *green*, data of chlorophyll *a* found in four different areas where the primary productivity is different. Highlighted in *pink*, particulate organic carbon (*POC*) quantified in the same water layers. The data presented are indicative and may change depending on the local conditions. The picture represents a passive (*Eunicella singularis*) and an active (*Aplysina aerophoba*) suspension feeders (Data from Rossi and Gili 2009. Photo (modified with Photoshop) by Sergio Rossi)

the total carbon depleted by suspension feeders in winter during the winter, while *Synechococcus* (<1 μm) is more relevant in the summer time (Yahel et al. 1998). In Antarctica, the spring-summer season is characterized by the primary productivity bloom, which is caused by the ice melting and high light absorption. This bloom of primary production is an important source of food for the benthic and the pelagic system for the rest of the year (Arrigo et al. 1998). In warm temperate seas, the diatoms are the more abundant component in late winter-early spring and the dinoflagellates in the calm late spring and summer waters (Rossi and Gili 2009). In this case, the sun irradiation is also the main driver of physical processes affecting primary productivity: the seasonal oscillation increases light harvesting in vegetal cells, raising also the temperature which favor the photobiology of the primary producers (Estrada 1996).

Despite the importance of seasonality in understanding the animal forest trophodynamics, this approach has not been fully considered in many environments. Life cycles of suspension feeders from temperate to polar waters show marked seasonal patterns of feeding, growth, reproduction, and abundance, but only recently

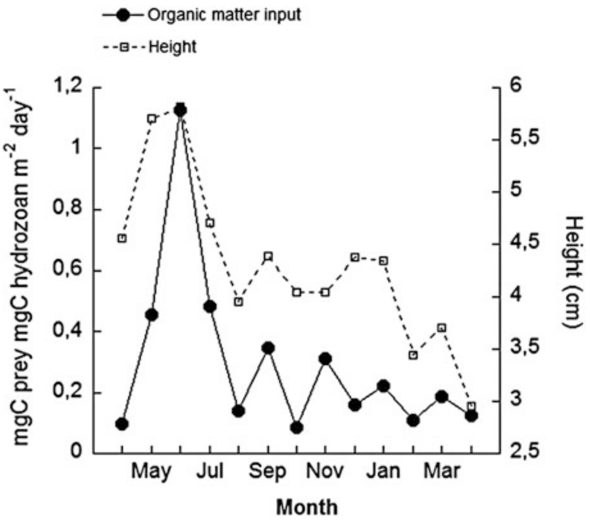


Fig. 5 The impact of the benthic suspension feeder *Eudendrium racemosum* (Hydrozoa) increases with its size and patch structure. *E. racemosum* changes its patch density and population structure over the year. In the reproductive season, hydrocauli are larger and less dense, bearing a higher quantity of polyps per unit surface. Considering the same surface, the mean impact may increase three times in the reproductive period (Redrawn from Rossi et al. (2012))

seasonality has been considered as a key factor in tropical animal forests. In fact, although temperature variations are minimal and the primary productivity does not change drastically at low latitudes, the rain-dry season alternation may have a direct effect on symbiont concentration in symbiotic corals and on the water column conditions (Fitt et al. 2000).

An example of how seasonality influences benthic-pelagic coupling processes and the organism response to higher or lower energy inputs throughout the year, is shown on the hydrozoan *Eudendrium racemosum* of Mediterranean shallow littoral. This heterotrophic organism is considered omnivorous, with a high energy input coming mainly from zooplankton (Rossi et al. 2012). Predation on seston by individual colonies is negligible, but considering the feeding surface (polyps covering a determinate area) as a whole, patch capture rates can be very high. Considering the change in hydrocaulus height and the number of polyps per linear centimeter, energetic inputs differ between the reproductive period (i.e., May to June) and the rest of the annual cycle (Fig. 5).

The 344 preys per hydrocaulus calculated for the reproductive period (38.3 μg C hydrocaulus^{-1}) are three times higher than in the nonreproductive period, with 117 preys hydrocaulus^{-1} (and almost four times less C entry, 10.9 μg C hydrocaulus^{-1}). The diurnal mass-specific ingestion rate (in%) also varies according to patch dynamics of *E. racemosum*; maximal values are achieved during reproductive periods (45–120%) compared with nonreproductive periods (10–40%; Rossi et al. 2012) and are among the highest for hydrozoans (Gili and Hughes 1995). This finding reinforces the hypothesis that there is a favorable period in which the structure of the hydrocauli changes, enhancing the feeding capability of this ephemeral organism. The higher presence of lipids in the hydrocauli also confirms this hypothesis: spring is the period in which energy can be stored for its life cycle processes and to face further potential feeding shortages (Rossi et al. 2012).

Spring phytoplankton and phytobenthic blooms produce high amounts of organic matter that will be assimilated and used by the animal forests directly (alive or dead algal cells) or indirectly (through detritus or secondary production, e.g., zooplankton) (Rossi and Gili 2009). In the NE Atlantic, for example, gamete production of the deep coral *Lophelia pertusa* follows phytodetritus food fall, and the species is likely to spawn after the springtime (Roberts et al. 2006). In shallow areas, spring diatom blooms have been correlated with increase of gonadal volume, and spawning periods depends on the planktotrophic or lecitotrophic strategy of the larvae (i.e., feeding and nonfeeding larvae, respectively). For instance, the spawning planktotrophic larva of blue mussels is triggered by the release of a chemically unidentified ectocrine produced by phytoplankton in the Gulf of St. Lawrence (Starr et al. 1990). On the other hand, the release of lecithotrophic larvae of octocorals is closely related with seasonal constraints, whereas the maximum food available is linked with highest sexual products development (Ribes et al. 2007). Although the main driving factor remains food seasonal fluctuation, sediment resuspension caused by increased hydrodynamics is also important in modulating the responses of the benthic fauna. Moreover, particular benthos features (topography, hydrodynamics, oxygen concentration, etc.) may be a source of variability for the animal forest. Close to the sea floor, the temporal and spatial heterogeneity of the substrate and currents could be very high due to the interaction between water column and sea floor communities (Fig. 6).

Another crucial factor affecting benthic suspension feeder survivorship is the low food availability in certain periods (trophic crisis), which has been largely neglected in the equation of the energy budget for benthic organisms. Let us give two contrasting examples. In warm temperate seas, such as the Western Mediterranean, the highly productive season (late winter-spring) is followed by periods of column stratification and high water temperature (summer), with low water motion and a decrease in primary production (Estrada 1996). However the quality of seston (low concentrations of particles in the water column, rich lipid content) is very high (Rossi et al. 2003). This water stratification and high water temperature create adverse conditions for benthic shallow suspension feeders, which may temporally disappear or become dormant (aestivation) (Coma et al. 2000). After the second productivity peak, in early autumn, another period of low food availability (refractory seston) is caused by river runoff and easterly storm events (Grémare et al. 1997; Rossi et al. 2003, 2006). Indeed, the Sverdrup model (Sverdrup 1953) shows that excess of turbulence and turbidity in the water column may lower the minimum compensation point for phytoplankton or phytobenthos, resulting in reduced algal productivity, even if high concentrations of nutrients are available (see also Smetacek and Passow 1990). For this reason, though nutrient concentrations may be high in coastal waters in autumn, abundance and productivity of phytoplankton, pico and nanoplankton, have been reported to be very low (Ribera d'Alcalá et al. 2004; Rossi et al. 2004; Rossi and Gili 2009).

The feeding activity of benthic suspension feeders are influenced by low plankton density and low detritus quality, and the high amount of refractory suspended seston may clog filtering structures (tentacles, siphons, oscula, etc.) (Rossi 2002). Besides,

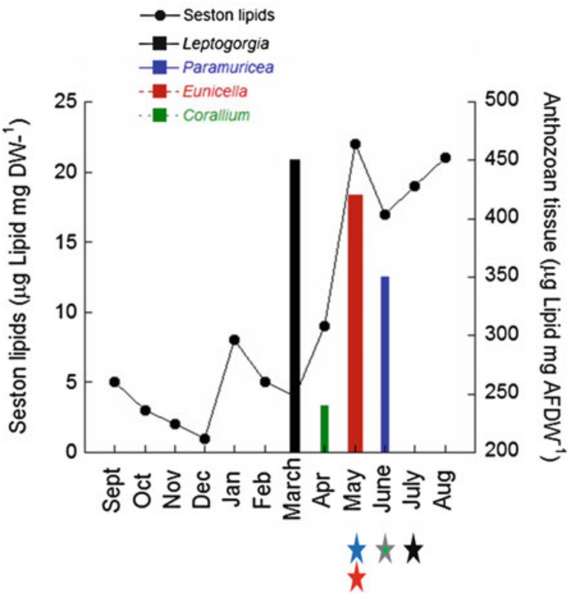


Fig. 6 Lipid storage may not always occur in strict coincidence with the maximum seston quality. In warm temperate seas, seston quality in near-bottom water layers increases in spring-summer, but the maximum accumulation of lipids, in different octocoral species of warm temperate seas, may occur before (*bars*). Stored lipids will be partly transferred to the offspring (*stars* indicate maximum gonadal development of the four octocoral species, *Leptogorgia sarmentosa*, *Paramuricea clavata*, *Eunicella singularis*, and *Corallium rubrum*), but are also invested during different moments of the year to face food constraints (Data from Rossi (2002); Rossi et al. (2006); Rossi and Tsounis (2007); Gori et al. (2012))

the low seston quality may decrease energetic input (Rossi et al. 2006, 2012; Rossi and Tsounis 2007). Because the energy input variation is strongly related with sesaonal environmental conditions, especially with water temperature and seston quantity and quality, the biochemical analysis, such as lipid and carbohydrate, can provide useful tools to identify these trophic constraint periods.

The second example of the influence of seasonality on the annual cycles of the animal forest comes from Antarctic waters. In this area, the seasonality is even stronger compared to the Mediterranean Sea (Arrigo et al. 1998). A short period of productivity (December to February, depending on the areas) is followed by a longer elapsed time in which phytoplankton do not have the optimal conditions for growing (and, from May to September, the light is not present to satisfy the photosynthetic compensation point, being dormant beneath the ice sheet). Benthic suspension feeders take advantage of the fresh organic matter coming from the phytoplankton blooms (Rossi et al. 2013) not only in the productivity period but also during autumn and early winter (Isla et al. 2011). The benthic suspension feeders accumulate energy during the productivity period, mainly coming from direct vertical inputs or (Elias-Piera et al. 2013). These phytodetritus, accumulated in green carpets after weeks of production (Gutt et al. 1998; Isla et al. 2006), are resuspended by tidal currents

(Isla et al. 2009) and partly captured by these benthic organisms during the autumn-winter period (Gili et al. 2009). There is also a trophic crisis, always dependent on the high seasonality of the system, lasting from late winter to early spring.

This crucial phenomenon of food shortages may be extrapolated to other communities that have clear seasonal patterns. The food shortage is a potential factor to be considered for the understanding of benthic-pelagic coupling processes in the animal forest, sometimes overlooked, poorly understood, and, in the case of warm temperate seas, masked by the apparent abundant but poor quality seston (in late autumn-early winter).

4 The Importance of the Short-Time Approach and the Activity of Benthic Organisms: Food Pulses

Benthic-pelagic coupling processes present high dynamism, even over very short temporal scales (Rossi and Gili 2009). Indeed, the available particulate organic matter may drastically change in few hours, which may increase by three to ten times the potential carbon input on suspension feeders (Sournia 1974; Rossi and Gili 2007; Rossi and Fiorillo 2010; Fig. 7). For this reason, one of the main problems on description and quantification of benthic-pelagic coupling processes is to find the ideal temporal scales, as the frequency of food pulses may be one of the keys to understand energy inputs and outputs of benthic fauna. It has been shown that the input of fresh organic matter of high nutritional value causes a burst of activity, and the fluctuations in suspension feeder abundance is related to parallel fluctuations of phytoplankton biomass, even over short periods of time (Valiela 1994).

As mentioned above, seasonal changes on several environmental factors (i.e., storms, sudden rain and runoff, tidal currents, etc.) may generate discontinuous physical and chemical features affecting coastal biological communities. Errors in computed seasonal production diminish as the frequency of sampling increases, and a daily sampling may not be enough to detect sudden changes that may explain benthic variations in seston capture and assimilation. For example, light and temperature stimulate algal blooms, but river input on coastal waters or wind stress may be a crucial contributor to algal bloom in short time periods (Grémare et al. 2003; Rossi and Gili 2007). In tidal cycles, concentration ranges of near-bottom seston, chlorophyll *a* or carbon of a single tidal cycle may be higher than annual range of daily mean values found in the same area (Fegley et al. 1992). There are more examples about the importance of short time periods respect the comprehension of benthic-pelagic coupling processes. The highly fluctuating near-bottom tidal current speed in Antarctic waters influences the sediment resuspension, which is transferred to the benthic community in form of food pulses rather than in a constant form (Rossi et al. 2013). In fjords and upwelling systems, sedimentation pulses of spring phytoplankton blooms may occur on few hours due to tidal currents (Rossi and Fiorillo 2010). Another important effect on the near-bottom seston productivity is the influence of heavy storms. Grémare et al. (2003) found that heavy storm increases significantly the total suspended matter through resuspension, with a

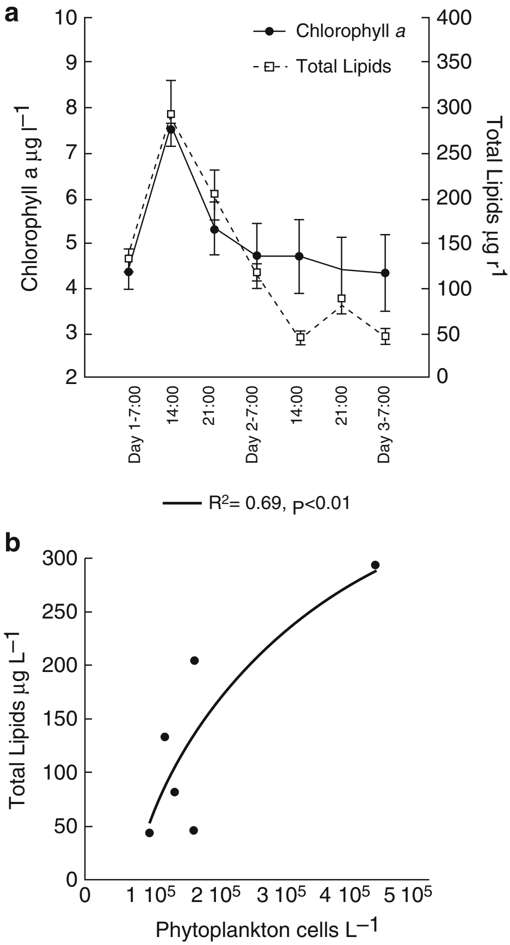


Fig. 7 Available seston in near-bottom water layers may drastically change in few hours. In this example of the Humboldt Current upwelling system, in only 7 h the chlorophyll a and phytoplankton associate lipids increase dramatically (**a**). The cell concentration may be directly related with the lipid concentration (**b**). When part of the food comes from resuspended refractory organic matter, the relationship may not be so straightforward (Redrawn from Rossi and Fiorillo (2010))

subsequent increase in the gross sedimentation rates and changes in bacterial activity and phytoplankton concentration (dilution and breakage of seston patchiness). Therefore, current speed and noncontinuous episodes may have a synergistic effect in the animal forest, increasing seston transport and resuspending particulate organic matter and, in consequence, prey capture rates of the benthic suspension feeders (Naylor 2005).

However, not only the physical variability but also the phytoplankton diversity and biology should be considered when quantifying biomass and production of food availability in near-bottom or sediment-water layers. Indeed, in gorgonians, alcyonarians, and zoanthids, the frequency of available food is a more crucial factor than physical factors in understanding polyp expansion and, thus prey capture rates (Rossi 2002; Rossi and Gili 2007; Duchene THIS BOOK) (Fig. 8). For example, variation indices of the environmental parameters were higher in the early spring

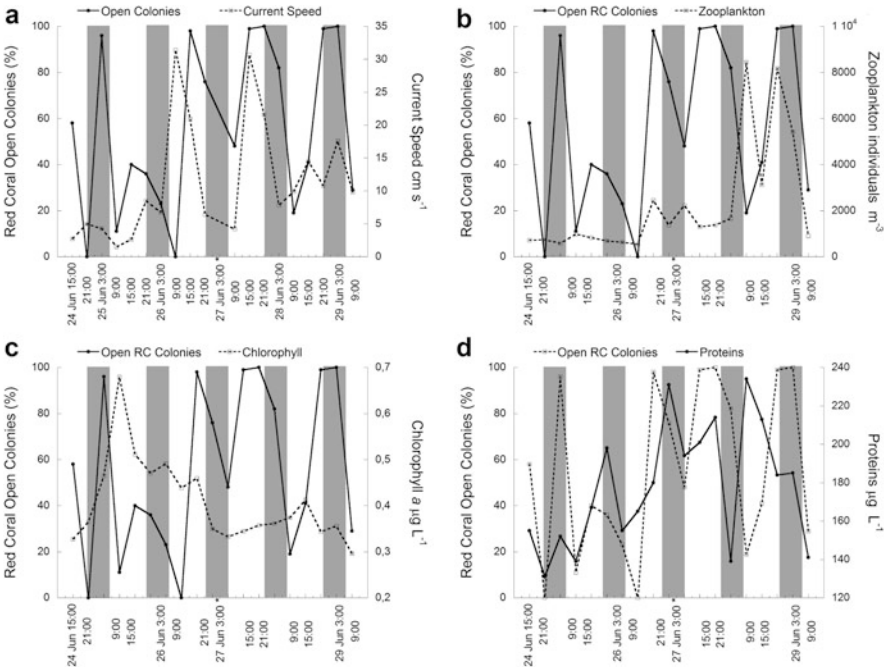


Fig. 8 Polyp activity of the red coral (*Corallium rubrum*, RC) associated with environmental and biological changes of the water column. Currents (**a**) may suddenly change, passing from 2–5 cm s^{-1} up to more than 30 cm s^{-1}. Zooplankton (**b**), Chlorophyll *a* (**c**) and seston proteins (**d**) may also suddenly change, being the main factors that start the activity of the octocoral species. In *gray*, nighttime is represented (Redrawn from Rossi (2002))

compared to late spring in near-bottom layers of warm temperate water (Rossi and Gili 2007), while the activity of benthic passive suspension feeders was only correlated with the high seston concentration in late spring. This means that a higher frequency of food pulses will affect the benthic community, with such variability essential to making adequate calculations of potential energy inputs on animal forest organisms.

Increasing the frequency of current strength and available epibenthic seston may be a driver of pulse-like temporal changes in particulate organic matter available in the water column for the energetic budgets of animal forest communities. The relationship between maximum prey capture rates and high concentrations of plankton is one of the key factors in understanding energetic balances in animal forest components (Sebens and De Reimer 1977; Sebens et al. THIS BOOK). In intertidal systems, there is a clear relationship between energy invested in feeding activity (or capture rates) of suspension feeders and tidal water mass fluxes (Naylor 2005). In the optimal foraging theory, Hughes (1980) showed the need, for a single colony, as well as for a population, of taking advantage of favorable feeding pulses. Understanding how the presence of food random pulses influences energy inputs of these organisms, as well as the synergistic effect of current speed and particle concentration, could change our vision of the energy budgets of benthic communities.

5 The Return to the System

Once ingested, nutrient and organic matter return to the system as fecal pellets and catabolites. In the animal forest, suspension feeders play a prominent role in seston recycling. Nutrient fluxes at the sediment-water interface can influence or regulate the nutrient composition of the water column with benthic animals behaving either as sinks or sources of inorganic nitrogen, phosphorous, and silicon (Nixon 1981). Indeed, higher concentrations of organic nutrients near benthic fauna compared to the rest of the water column are the evidence of the role of benthic communities in organic matter remineralization, which might be the result of interface-feeding macrofauna (e.g., nutrient input from excretion process). For example, the rapid degradation of the protein constituting the valve of the diatoms leaves the cell naked and ready to be digested (Gili et al. 2008), so that dissolved silica is subsequently eliminated by external excretion, returning to the system. The nitrification process, fuelled by some benthic suspension feeders, is important for the near-bottom phytoplankton productivity in shallow waters (Ward 2000). On one hand, in coral reefs it has been shown that the activity of scleractinians enhances pico and nanoplankton growth through their exudates. These exudates cells are considered an important part of the autotrophic community. On the other hand, corals also release a significant concentration of dissolved organic carbon and nitrogen, especially when fed and excretion is stimulated (Ferrier-Pagés et al. 1998), increasing the nutrients available for the surrounding organisms.

Although remineralization mechanisms are present in all animal forest taxa, it is generally accepted that active suspension feeders may have a more significant role in nutrient return to the system compared to passive ones. For example, and due to the current flux generated for feeding, mussel beds enhance nutrient release from the sediment that could be taken by phytoplankton and improve their growth (Kanaya et al. 2005). However, a specific contrast between a passive and active suspension feeder-dominated animal forests is not yet available. In sponges, bacterial activity has also been recognized as an important process of remineralization, either from ammonium excretion or nitrate excretion (Jiménez and Ribes 2007). The differences observed in remineralization capacity among sponge species may be due to the abundance of bacterial symbionts, despite it hardly has been quantified. Indeed, and due to high biomass of bacterial cells in the Porifera tissues, the nitrification by Mediterranean sponges can reach values from 2500 to 7,900 mmol N L^{-1} day^{-1} which represents several orders of magnitude higher than rates reported for Mediterranean plankton (Jiménez and Ribes 2007).

The most important return of organic matter from the animal forest to the system components is, undoubtedly, the reproductive output (Coma et al. 1998). Reproductive effort (i.e., fecundity and egg volume) consumes a high quantity of energy, previously stored during favorable periods. This reproductive effort has been used to estimate the reproductive investment in suspension feeders. However, this approach does not account for the energetic cost caused by gamete production or by tissue repair associated with spawning, and thus, the reproductive investment may be potentially understated (Calow 1979). The energy transferred from maternal colonies to larvae might depend on reproductive effort-strategy and/or feeding of maternal colonies. Reproduction and spawning in benthic suspension feeders depend on the quantity and quality of food availability, so these processes must be finely tuned with seasonal productivity periods. In fact, the maximum development of sexual products in benthic invertebrates is related to food availability directly influencing the timing of gametogenesis. Moreover, phytoplankton blooms triggering the spawn of sexual products in several benthic suspension feeders (Starr et al. 1990). In fact, these phytoplankton blooms would allow the transfer of high-quality organic matter to the next generation of suspension feeders, either directly (in the case of planktotrophic larvae) or after settlement (in the case of lecithotrophic larvae). Energy is stored mainly as lipid reserves in adults that it can be transferred to the offspring and contributes to their development (Viladrich 2015). Longevity and competence periods of released larvae are related, among others, to their energy storage capability. Therefore, knowing the initial amount of energy contained in the lecithotrophic larvae would allow for an estimation of the time in which the metamorphosis process can be delayed.

6 Long-Term Integration of the Animal Forest Trophic Ecology: Biomarkers

This chapter shows how important it is to comprehend the food availability and the prey capture rates of animal forests' species to fully understand benthic-pelagic coupling processes. Trophic ecology of the animal forests' organisms has been widely studied in terms of the relationship between prey availability and prey capture, using a punctual sampling (Gili and Coma 1998). However, this information cannot properly demonstrate feeding success, as well as not reflect the whole importance of the energy input available for the animal forest components. The biochemical balance could be one of the best approaches to demonstrate the effect of feeding input periods on organism's nutritional condition, summarizing a set of trophic processes occurring within a short-medium time term. Proteins are mainly used in structural, enzymatic, transport, and regulatory functions in the cell. Carbohydrates represent the principal source of basic energy, as they are quickly catabolized to obtain immediate energy. In contrast, lipids constitute the main energetic reserves in animals and can strongly affect the survival, reproduction, and growth. Thus, biochemical balance may reflect the nutritional condition of organisms (Fig. 9).

Total lipid content is the sum of several lipid compounds such as wax esters, phospholipids, triacylglycerols and free fatty acids (FFA; Imbs 2013). Phospholipids are the major constituents of cell membranes and are not involved in metabolism, whereas the wax esters and triacylglycerols are considered stable energy reserves that can be oxidized to provide energy in form of FFA. The FFA are characterized by

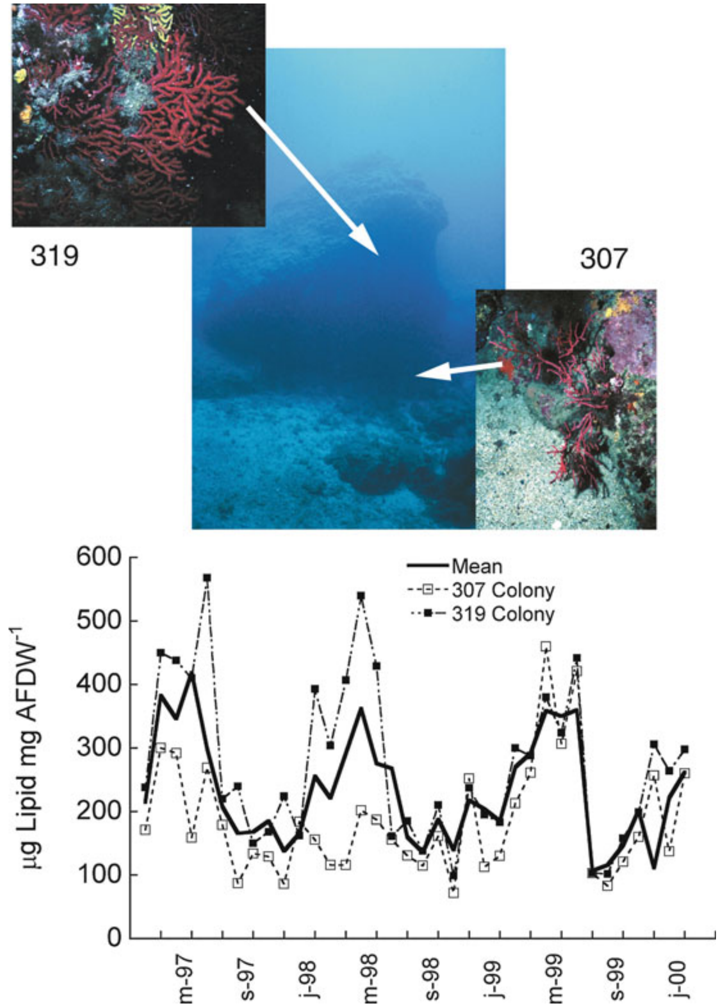


Fig. 9 Lipids may be a good tool to detect not only seasonal changes but also how the different position of suspension feeders within the patch influences their capability to store energy. In this figure, the mean female lipid concentration of an octocoral (*Paramuricea clavata*) population in a 3-year cycle is presented. The mean values of an *upper* located colony (319) always stand with a high concentration of lipids. The mean values of a lower located colony (307) always stand with a lower lipid concentration. The position of the colonies with respect to the main currents is essential for a proper understanding of the survivorship and nutritional condition of the colonies and, therefore, their role in the offspring production and the permanence of the populations (Partly redrawn from Rossi (2002) and Rossi et al. (2006))

high power efficiency (high ATP/FA molecule; Sargent et al. 1988) and, thus, their content can be used as a measure of metabolic demands. Indeed, FFA content can increase under stress situations, such as starvation and thermal stress, in order to compensate for the increment of metabolic needs (Sargent et al. 1999). Also, FFA composition may reflect the nature of metabolic demands (i.e., energetic requirements) (Imbs 2013), and the amount of different kinds of FFA [saturated free fatty acids (SFFA), monounsaturated free fatty acids (MUFFA), and polyunsaturated free fatty acids (PUFFA)] may reproduce the fitness of individuals. Indeed, PUFFA are mainly used to overcoming stress conditions, since they can be converted into many other FA, while MUFFA and especially SFFA are used for basic metabolic energy consumption (Sargent et al. 1999).

In the intraspecies level, the quantity of energy reserves (lipid content), as well as its consumption (FFA content), depend on environmental conditions. Indeed, it has been shown that corals and gorgonians experience a natural variation in lipid concentrations over the year, in response to many factors such as water temperature, food availability, reproduction and, in case of symbiotic species, light intensity and *Symbiodinium* photosynthetic productivity (Rossi et al. 2006; Rodrigues et al. 2008; Seeman et al. 2013). In long-term integration, lipid content also allows for an important key point: the spatiotemporal comparison. In addition, in interspecies level, the quantity of energy reserves and its consumption depend on the life strategy of sessile organisms, since the resistance and resilience of these organisms are closely related to their trophic feeding strategies (Viladrich et al. 2016a). For example, heterotrophic food may occasionally become a constraining factor for nonsymbiotic benthic suspension feeders, while in symbiotic species with mixotrophic feeding, symbiotic algae can provide energy to their hosts and, therefore, stabilize the discontinuous energetic input caused by food random pulses (Gori et al. 2012; Viladrich 2015).

For these reasons, lipids may be a biomarker useful to understand how benthic-pelagic coupling processes change over time, and how animal forest species respond to food availability. However, the question remains: How can we detect the source of food and delimit the trophic position of different animal forest components? Gut contents are difficult to quantify, because suspension feeders might quickly digest the preys. Also, in areas difficult to reach (deep sea, Antarctic waters, etc.), current methods of analysis (i.e., gut contents, controlled clearance rates experiments, etc.) are not the best way to have a complete picture of energetic fluxes. An attractive alternative for diet analysis is the use of trophic markers, such as stable isotopes and fatty acid (FA) composition.

The stable δ13C and δ15N isotopes may be a good proxy to establish the trophic position of animal forest components (Elias-Piera et al. 2013; Fig. 10). Using this method allows for the description of the food incorporation, of the organisms' trophic position in the food chain, and partially the way they use this energy (Valiela 1995). In contrast with the information provided by gut contents, stable isotopes show long-term nutrition (Valiela 1995), integrating information about the characteristics of assimilated food (Carlier et al. 2007). In fact, natural δ13C measurement is efficient in identifying the relative contributions of potential food sources, since δ13C of animals are only slightly enriched relative to their diet (i.e., typically by 1‰ according to DeNiro and Epstein (1978)). The δ15N values can be efficient in estimating trophic levels of organisms within food webs, since factor in δ15N between two consecutive trophic levels is high (i.e., close to 3–4‰; Post 2002).

Another complementary approach designed to identify the dietary components is FA composition (Kelly and Scheibling 2012). These biomarkers have been

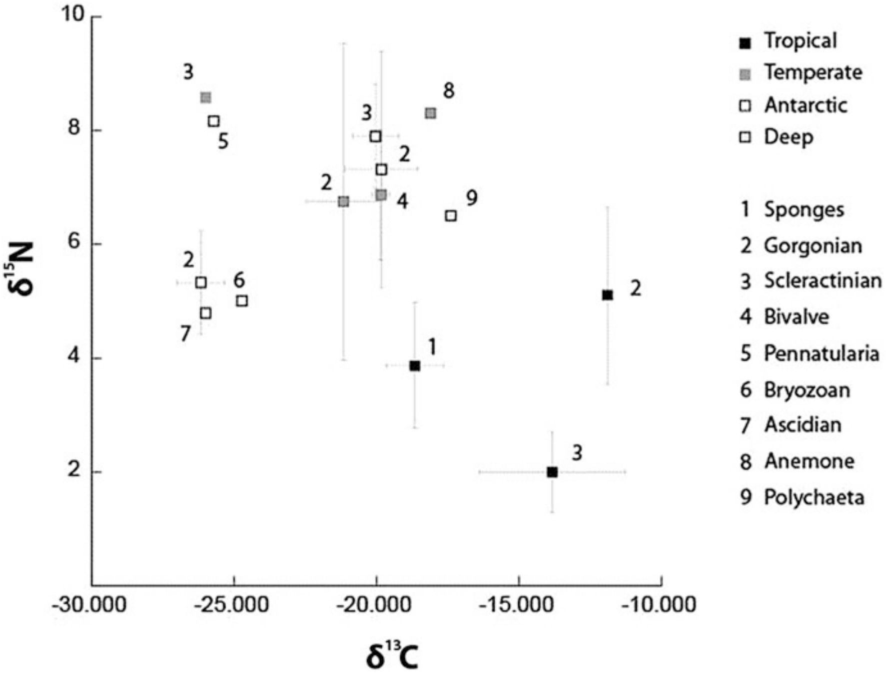


Fig. 10 Stable isotope ($\delta^{15}N$ and $\delta^{13}C$ proportion, in ‰) composition in main animal forest components in tropical (*black squares*), temperate (*gray squares*), Antarctic (*white squares*), and deep ecosystems (*black and gray squares*) (mean of different values ± SD). This tool could be very useful to understand the trophic position ($\delta^{15}N$) and the carbon source ($\delta^{13}C$) in different environments. Moreover, seasonal trends may reflect differences in the food sources (Data from, Sponges: van Duyl et al. 2011; Weisz et al. 2010; Gorgonians: Baker et al. 2010; Cocito et al. 2013; Gori et al. 2012; Elias-Piera et al. 2013; Jacob et al. 2005; Carlier et al. 2007; Scleractinian: Alamaru et al. 2009; Grottoli et al. 2004; Reynaud et al. 2002; Ferrier-Pagès et al. 2011; Carlier et al. 2009; Bivalve: Carlier et al. 2007; Pennatularia, Bryozoan, Ascidian: Jacob et al. 2005; Anemonae: Carlier et al. 2007; Polychaeta: Carlier et al. 2009)

used extensively in pelagic and benthic food webs, especially to identify the source of food (diatoms, flagellates, bacteria, etc.) and to characterize the diet of zooplankton (Kelly and Scheibling 2012). Diatoms and dinoflagellates differ in their FA composition, and zooplankton tends to retain dietary FAs in their tissues. Unlike pelagic systems, where phytoplankton is the major source of primary production, the benthic systems are supported by a diversity of primary producers, like macroalgae, phytoplankton, and bacteria. Therefore, certain FA can reflect dietary input and can be used as natural biomarkers to trace and quantify diet type. Knowledge on their quantity (FA content), quality (% SFA, MUFA, PUFA), and composition (FA components) may give information about the relative importance of autotrophy versus heterotrophy and the main source of heterotrophic organic matter inputs. Although FA may be transformed during digestion, the largest signal remains intact and can be detected in the tissues of

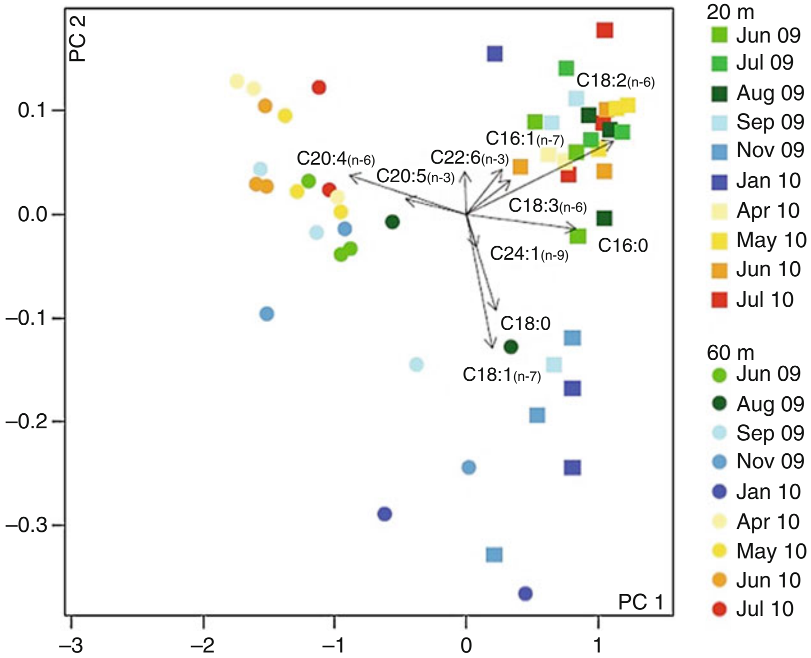


Fig. 11 Fatty acids may be a good biomarker to understand not only the nutritional condition and the stress of the animal forest components but also the seasonal preferences in a mixotrophic or heterotrophic species. In the figure, the gorgonian *Eunicella singularis'* free fatty acids are shown, depicting differences from shallow and deep populations. In shallow populations, this octocoral bears *Symbiodinium*, being part of the energy input of autotrophic origin, especially in spring-summer time (*square symbols*), while deep gorgonians (below 60 m depth in this case) only have a heterotrophic input (*round symbols*). This variation is reflected in the fatty acid markers throughout the year (Redrawn from Gori et al. (2012))

the consumers (Kelly and Scheibling 2012), providing information on the dietary intake. However, it has to be remarked that FA alone may give a limited and possibly difficult to interpret information about trophic connections and dietary preferences (Fig. 11).

FA and stable isotopes have been both proven to be a good synergistic set of biomarkers to interpret trophic positions or elucidate the major sources of organic matter contributing to the diet of benthic marine invertebrates. Studies conducted combining diet and stable isotopes or diet and FA have shown to be more complete than those of diet, stable isotopes, or FA analyzed separately (Gori et al. 2012). In addition, these two analyses can be complemented with biochemical balance (protein-carbohydrate-lipid), to understand how different organisms invest their energy depending on their trophic level, and especially on their reproductive strategies (Gori et al. 2012).

Long-term integration also allows for an important key point: the spatiotemporal comparison. Previous studies have shown the quantity and quality of available food may affect the health status of benthic suspension feeders depending on environmental and biological parameters of the area. For example, the quantity and quality of food may be essential to understanding the presence or absence of mussel beds, taking into account temporal changes (Gardner 2000). If environmental conditions change over time the quality of food changes insfluences the nutritional condition (i.e., the capability to store energy and use it not only to survive, but also for reproduction, Viladrich et al. 2016b) of the animal forest components (Rossi 2002). In fact, it has been shown that different lipid availability may be key for understanding potential nutrition of passive suspension feeders in different areas (only few kilometers apart from each other) (Rossi et al. 2003). The same suspension feeder species may have different growth strategies, partial mortality, reproductive output, and energy storage depending on the available source of food (Rossi 2002), being both the stable isotope and lipid concentration tools to interpret energy sources and capability to store macromolecules (Elias-Piera et al. 2013). Understanding the benthic-pelagic coupling processes is essential to interprete species distribution, having a key role the environmental conditions of the area to understand such distribution (e.g., currents, primary production, seston concentration and quality, etc.) (Gori et al. 2011).

7 New Approach for C Sinks Estimation: Combining Seascape Ecology and Experimental Design

Optimization of resources captured by suspension feeders constituting animal forests passes through an increase of complexity of the living structures. In octocorals and hexacorals, as well as in bryozoans, the bigger the colony, the higher the number of polyps or active lophophores; in ascidians and sponges, increasing the size of the specimens, the pumping rates the number of channels and coenocytes increase as well; in bivalves the larger the individuals the higher the volume of water that passes through their digestive system. In the above mentioned example of *Eudendrium racemosum*, it is not the prey per polyp that is favorable in the reproductive period (Rossi et al. 2012), but the change in morphology of the hydrocaulus that optimizes the feeding surface of the patch and allows the hydrocauli to accumulate essential energetic stores. This energy will be partly transferred to their offspring. More importantly, as the patch structure changes to larger colonies, the trophic impact increases. This point suggests that larger colonies have a prominent role in benthic-pelagic coupling processes, in biogeochemical cycles, as well as in the carbon sequestration than denser patch of smaller colonies. In this example, carbon retention passes from ephemeral, fast-growing plankton to more stable structures (the hydrocaulus of the hydrozoans). In long-lived species, seston passes from the water column to the structural parts of animals, which can retain carbon for decades or centuries.

There is an increasing interest in the impact of larger structures (land forests, kelp forests, sea grasses, animal forests) in carbon retention as they become older and more mature. In gorgonians, large colonies have a larger trophic impact and energy output (in terms of gonadal output, growth, and carbon retention in their structures) (Coma et al. 1998; Rossi et al. 2006). The organisms constituting the animal forests represent important carbon sinks but are completely neglected in the overall equation of C circulation in our changing world. It has to be considered that marine ecosystems, as well as terrestrial ones, generate goods and benefits useful for human welfare (the ecosystem services, ES). As stated throughout the chapter, species forming animal forests are responsible for the generation and the increase of nutrient exchange, for the capture and the retention of carbon (C), nitrogen (N) and other elements from the water column into their structures (Gili and Coma 1998; Rossi et al. 2012). Due to the long-life cycles of the species forming these animal-dominated ecosystems, they might accumulate elevated quantities of C as biomass. This C might last for decades, centuries, or millennia, stored in the body structures of these species. Although some attempts of measuring these two ecological functions (impact on benthic-pelagic coupling and role as C sinks) have already been undertaken at small scale or for vegetal ecosystems (i.e., the so-called blue carbon; Duarte et al. 2010), there are almost no broad-scale studies for animal-dominated ecosystems.

The main problem of calculating the C retention is, basically, the largely unknown extension of animal forests, especially at great depths. In the past few decades, the development of remotely operated vehicles (ROV) and their decreased operational cost have provided for an opportunity to perform broad-scale detailed sampling of benthic species, from shallow to deep waters, with no impact on benthic communities (Rossi et al. 2008). The analysis of ROV video transects provides both qualitative and quantitative data of species distribution and size class of species populations (Rossi et al. 2008; Gori et al. 2011; Coppari et al. 2014; Fig. 12a, b). These broad-scale data of size, spatial, and bathymetrical distribution of benthic species, coupled with experimental or observational results of feeding, reproduction, respiration, or growth, allow for large-scale calculation of the impact of benthic suspension feeders on benthic-pelagic coupling processes and consequently as C sinks. An asymmetry in the organisms' abundances at certain depths has been observed as well as a different seasonal C and N inputs (Coppari et al. 2014, 2016).

For example, higher densities and bigger specimens of the ascidian *Halocynthia papillosa* concentrated between 20 and 50 m depths, with this depth range also showing the highest quantity of C retained and ingested N, compared to shallower or deeper bottoms where very low impact is recorded. The low presence of species at depths shallower than 15–20 m may be due to increased hydrodynamics and temperature constraints, as well as to the presence of faster growing macroalgae competing for space (Fig. 13).

Another good example of carbon sinks and efficiency in benthic-pelagic coupling processes in these three-dimensional structures is represented by gorgonians. These anthozoans are long-lived, slow-growing organisms with a life span that can exceed 100 years, being particularly sensitive to environmental and human-induced disturbances. In a recent study, the amount of C retained by three gorgonian species with different distribution and trophic strategy was calculated in spring as a difference between ingested and respired C and was as high as 1.4×10^{-2} t C ha^{-1} (Coppari

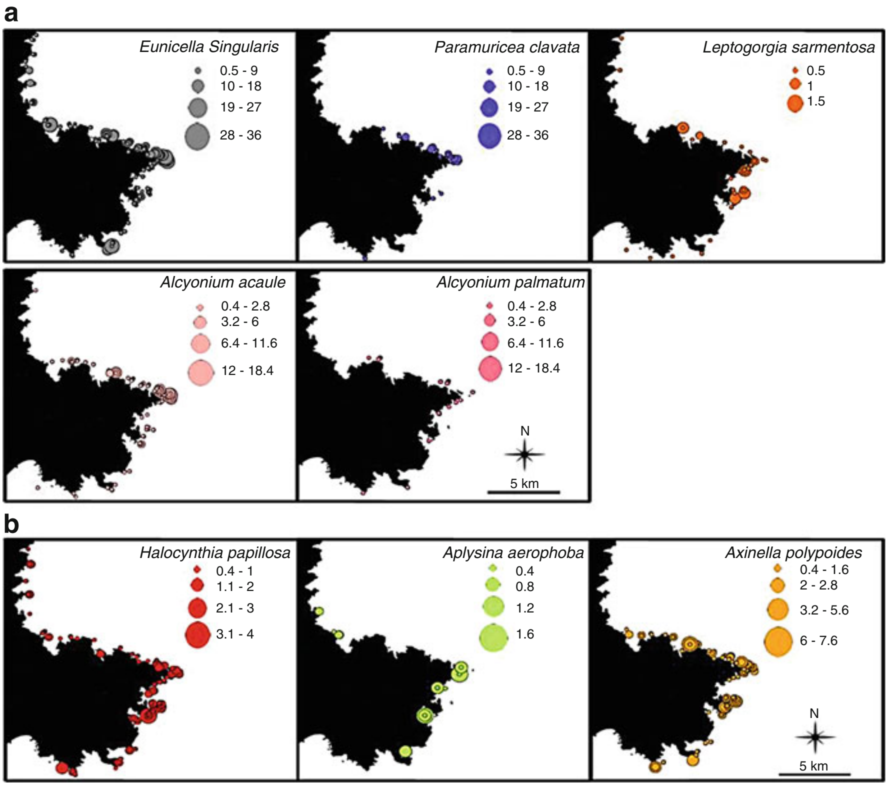


Fig. 12 (**a, b**) Distribution and density of passive and active benthic suspension feeders in Cap de Creus, NW Mediterranean Sea. Clear asymmetries can be observed, with the passive suspension feeders (**a**) (octocorals) concentrated in the northern part of the cape, where the environmental conditions (currents, wind stress, seston availability) are more favorable. Active suspension feeders (**b**) have a more regular distribution and density throughout the cape, probably due to their independence respect the main currents. Circles indicate densities (individuals or colonies m^{-2}). The observed species are *Eunicella singularis*, *Paramuricea clavata*, *Leptogorgia sarmentosa*, *Alcyonium acaule*, *Alcyonium palmatum* (octocorals, passive suspension feeders), and *Halocynthia papillosa* (ascidian), *Aplysina aerophoba*, and *Axinella polypoides* (Porifera) (active suspension feeders) (Redrawn from Gori et al. (2011), Ambroso et al. (2013), Coppari et al. (2014), and Coppari et al. (2016))

2015). Previous literature estimates the role as C sink of both land and marine ecosystems: Grace et al. (1995) pointed out that undisturbed Amazonian forests retain 1.02 t C ha^{-1} year, Duarte et al. (2010) calculate the amount of C accumulated by sea grass meadows being as high as 6.7 t C ha^{-1} year, and Eong (1993) found out that mangrove forests retain 1.5 t C ha^{-1} year. The C retained by the three gorgonian species is thus two orders of magnitude lower than the above-mentioned ecosystems. Data from Coppari (2015) are still a rough estimate, but highlight that Mediterranean gorgonians may be important as C sinks (Fig. 14). Even if the C per hectare is lower in comparison to other land and/or marine ecosystems, the importance of gorgonians

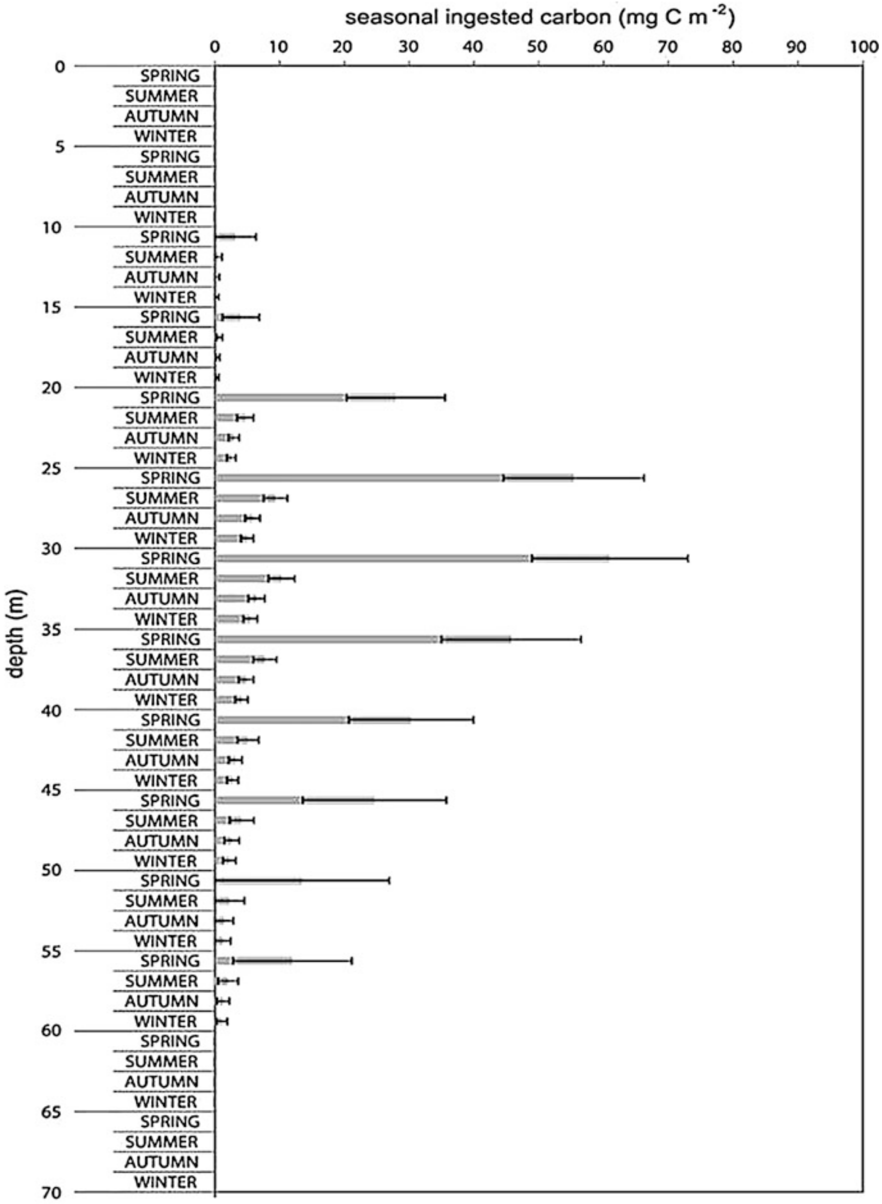


Fig. 13 Seasonal carbon ingestion of *Halocynthia papillosa* (a solitary ascidian). The season but also the distribution of the species along a depth gradient will be essential to understand where benthic-pelagic coupling processes are more concentrated. *Halocynthia papillosa* has the maximum impact on seston in spring between 20 and 55 m depth in the study area (Cap de Creus) (Redrawn from Coppari et al. (2014))

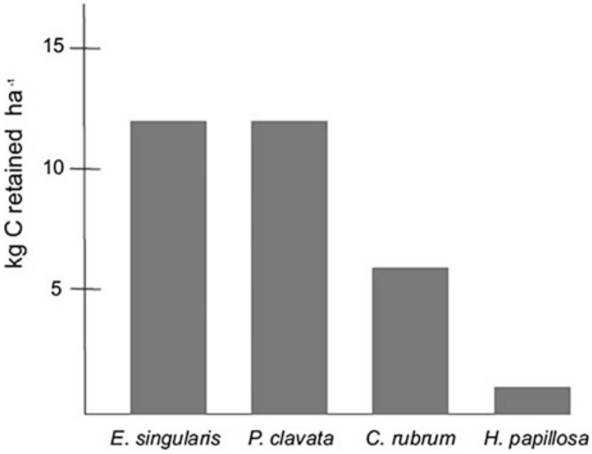


Fig. 14 The animal forest is a carbon sink, and the C sequestered (difference between ingested and respired C) depends on the demography (abundance, distribution and population size structure) of the species. Similar quantities of C retained are found in the symbiotic gorgonian *Eunicella singularis* and in the nonsymbiotic *Paramuricea clavata*. The octocoral *Corallium rubrum* seems to have a lower impact in the water column. In this case, the overharvesting of this species, drastically reducing the number and size of *C. rubrum* colonies, is the main driver of such poor impact in the C cycling, highlighting the importance of the population size structure to maintain higher C retentions. The ascidian *Halocynthia papillosa* is a solitary ascidian; its role as C sink is almost neglectable compared to the above-mentioned octocorals because of its low density in the same studied area (Redrawn from Coppari (2015))

as C sinks might be higher than previously thought, if we consider the extension of unexplored oceans. Coastal gorgonians have demonstrated their importance in benthic-pelagic coupling processes, and confirmed that crossing data from experimental feeding experiments with quantitative data about marine species abundance is a useful methodology to estimate benthic-pelagic coupling processes over large areas. Currently, the paramount role played by benthic suspension feeders in the biogeochemical cycles and especially in the transfer of energy and matter from the water column to the benthos is clearer, but there is still a long way to go to make a definitive picture of their role as carbon sinks of different animal forests of the world.

8 Conclusion

The animal forest distribution depends on the available seston and benthic-pelagic coupling processes. The study of suspension feeders distribution has to take into account not only substrate and environmental parameters (light, temperature, salinity, currents, etc.) but also primary productivity, seston resuspension, lateral transport, and seasonal fluctuations of phyto- and zooplankton abundance. The influence of these parameters on the animal forest distribution is essential, but at the same time, complex three dimensional structures have the ability to modify the characteristic of the near-bottom water layer. As an example, increasing patch size, morphologies, diversity and branching patterns of octocorals will influence significantly the particle retention and recycling, so it will be one of the keys to understand why mature animal forest all over the world should be preserved. In the near future, we need to better understand not only how the diet and capture rates influence the benthic-pelagic coupling processes but also how metabolism and physiology are involved in the species presence, abundance, and coexistence with other competitors. Short-time approaches, intended to "capture" the food pulses and make a better energetic balance, will be essential to understand benthic-pelagic coupling processes. Also, this more complex approach will let us understand how the entire system works and which are the more favorable periods in the different animal forests of the world.

Tools like biomarkers will continue to be good approaches for these interpretations. However, we are, in some way, in the infancy of a good approach using such markers. We deduce that, for example, free fatty acids are involved in stress response in critical moments as reproduction (Viladrich et al. 2016a), but we still don't know which are the real mechanisms and how to differentiate different periods (reproduction, starvation, etc.). Also, it is clear that depending on their trophic strategy (mixotrophic and autotrophic), the metabolism and the capability to store energy will be very different. Understanding these points will be a crucial part of the future work, beyond the descriptive work made up to now.

The seasonality is a strong constraint that forces metabolic changes in suspension feeders (Rossi et al. 2006), but we have few clues to understand how these high and low food availability periods are influencing sessile organisms. Understanding which is the role of the output efforts (e.g., reproduction, growth, respiration, etc.) will be a key to also understand the limits of distribution and tolerance of the different components of the animal forests of the world. These limits are changing fast due to the climate change, the species invasions, and the local impacts like contamination, river discharge, or coastal use. The use of old and new tools combined together will be a key factor to improve our knowledge not only on benthic-pelagic coupling processes but also of the role played by these organisms in biogeochemical cycles and as carbon sinks.

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9 Cross-References

- ▶ Activity Rhythm Measurement in Suspension Feeders
- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests of the World: an overview

- ▶ Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems
- ▶ Deep-Sea Suprabenthic Communities: The Forgotten Biodiversity
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Filter-Feeding Zoobenthos and Hydrodynamics
- ▶ Growth Patterns in Long-Lived Coral Species
- ▶ Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests
- ▶ Mesophotic Coral Ecosystems
- ▶ Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles

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Symbiotic Versus Nonsymbiotic Octocorals: Physiological and Ecological Implications

31

Nadine Schubert, Darren Brown, and Sergio Rossi

Abstract

Octocorals are a major component of the sessile benthic fauna worldwide, especially important in tropical regions, such as the Indo-Pacific and Caribbean, where together with hard corals they represent the most common group of macrobenthic animals of coral reefs. Despite their importance, little is known about their physiology, specifically the importance of their symbiotic relationship with the algal endosymbiont from the genus *Symbiodinium*, and the advantages/ disadvantages associated with this symbiosis. In symbiotic species, the energetic contribution from *Symbiodinium* to the host might increase their resistance and/or recovery from stressful conditions, but the presence of these algal endosymbionts also limits octocoral distribution to the photic zone, where light is available. During the past few decades, octocorals have gained dominance in some tropical areas where scleractinian corals have declined due to climate change and local perturbations, increasing the need for research related to this understudied group. This chapter summarizes the current knowledge available about the ecology and physiology of octocorals, focusing on differences that are the result of the

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presence or absence of endosymbionts, and discusses the implications of having endosymbionts in the context of how octocorals may respond to global climate change.

Keywords

Autotrophy versus heterotrophy • Calcification • Climate change • Depth distribution • Phase shift • Photosynthesis • Symbiont acquisition • Symbiosis

Contents

1 Introduction

In the marine environment, the symbiosis between the phylum Cnidaria (e.g., hard and soft corals, sea anemones, jellyfish, and hydrocorals) and dinoflagellates of the genus *Symbiodinium* (commonly referred to as zooxanthellae) is an important constituent of tropical coral reefs. The symbiosis between reef-building scleractinian corals and *Symbiodinium* is well studied, demonstrating that *Symbiodinium* contribute significantly to the scleractinian host energetic budget. In contrast to the well-studied scleractinian-*Symbiodinium* symbiosis, the symbiosis between octocorals, the second-most abundant macroinvertebrates on many Indo-Pacific and Caribbean coral reefs, and *Symbiodinium* has received far less attention. Similar to scleractinians, many octocoral species host *Symbiodinium*, but recent studies have shown that both groups diverged from an ancestral nonsymbiotic lineage (Kitahara et al. 2010; Stolarski et al. 2011). It has been hypothesized that throughout their evolutionary history, octocoral species have repeatedly acquired and lost their symbiosis with *Symbiodinium*, even within a single genus (e.g., *Briareum*, *Junceella*, *Euplexaura*, and *Muricea*; van Oppen et al. 2005), resulting in the presence and absence of symbionts within closely related genera.

Octocorals are currently divided into three orders (Alcyonacea, Pennatulacea, and Helioporacea), all of which include symbiotic species. The majority of symbiotic octocoral species are found in the Alcyonacea (soft corals and gorgonians), which contain 48 of the ~274 described genera. In the Helioporacea (blue corals), only one symbiotic species has been reported, *Heliopora coerulea* (Harii et al. 2002), and within the Pennatulacea (sea pens) at least two shallow-water species (in the genera

Cavernularia and *Virgularia*) harbor symbiotic algae (Williams 2011). These organisms are conspicuous components of benthic ecosystems (Kinzie 1973), with their architecturally complex three-dimensional structure allowing them to escape the constraints of the two-dimensional plane characteristic of most benthic communities. The three-dimensional branches of octocorals increase heterotrophy by extending into the water column where polyps are able to capture seston, as well as increasing autotrophy by increasing light absorption through increased surface area.

The presence of *Symbiodinium* is beneficial due to the energetic surplus from symbiont photosynthesis, but they can also impose certain restrictions (e.g., bathymetric distribution) and risks (e.g., higher increase in reactive oxygen species under stress conditions due to O_2 released through photosynthesis). The relative contribution of photosynthetically fixed carbon provided by *Symbiodinium* to their octocoral host seems to be species specific (Sorokin 1991), though it is generally accepted that the trophic contribution of the symbiotic dinoflagellates to the octocoral energy budget is low in comparison to scleractinian corals (Fabricius and Klumpp 1995; Ferrier-Pagès et al. 2015). Therefore, octocoral dependency on heterotrophy is higher compared to scleractinians (Fabricius and Klumpp 1995), with high variability in the contribution of heterotrophic versus autotrophic nutrition, depending on species, depth, season, and coral health. This high plasticity, with respect to nutrition (mixotrophy), has been related to a higher resistance to stress conditions that induce bleaching, as the loss of symbionts may not cause a determinant ecological change in the energetic input of the octocoral. The contrary is the case for scleractinian corals, which strongly rely on the phototrophic energetic input from *Symbiodinium* a feature that might drive community phase shifts toward octocoral-dominated reefs, when the environmental conditions are too harsh for hard corals.

2 Distribution of Symbiotic and Nonsymbiotic Octocorals

Octocorals are globally distributed, occurring from littoral waters down to the deep-sea abyss and from the Arctic to Antarctic oceans. Geographical and bathymetrical differences in distribution are strongly influenced by the presence or absence of endosymbionts.

Symbiotic and nonsymbiotic species are found worldwide; however, their relative proportions vary depending on region. In the Indo-Pacific and Mediterranean, nonsymbiotic species are dominant, while symbiotic species are found in half or more of the Eastern Pacific, Caribbean, Australian (Great Barrier Reef), and Red Sea octocoral taxa (Fig. 1). The high proportion of nonsymbiotic species reported here for the Caribbean diverge from the general assumption that most of the Caribbean octocorals harbor *Symbiodinium*, with only a few (6–9) nonsymbiotic species (e.g., Goldberg 1973; Kinzie 1973; Jordán Dahlgren 1989). The disproportionately low number of nonsymbiotic species is most likely due to previous surveys being conducted by SCUBA, which limits the sampling to a depth of 0–70 m. However, a recent deep-sea survey in the Colombian Caribbean, using trawl nets and dredges, was able to explore depths of up to 500 m, finding 48 nonsymbiotic species that were

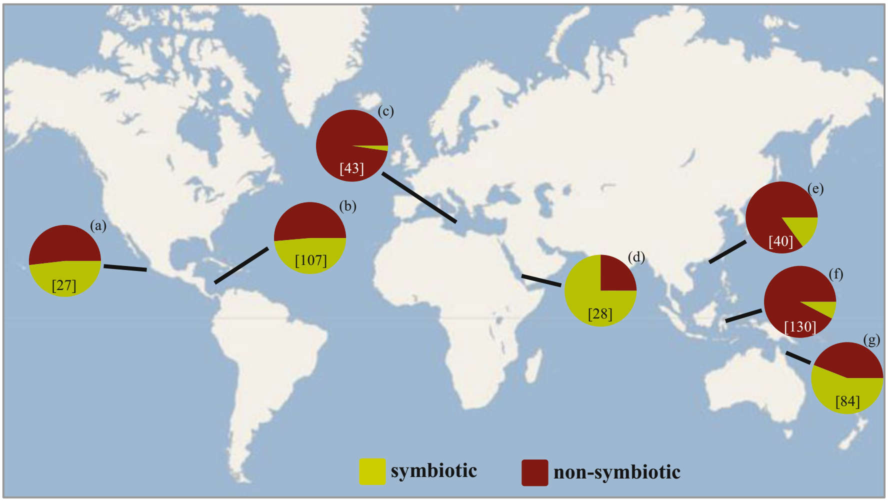


Fig. 1 Relative numbers of symbiotic and nonsymbiotic octocoral species in different regions. Numbers indicate the total number of reported species and letters indicate literature cited (*a* Eastern Pacific, van Oppen et al. 2005; *b* Caribbean, Kinzie 1973, Jordán Dahlgren 1989, Santodomingo et al. 2013; *c* Mediterranean, Vafidis et al. 1994; *d* Southern Red Sea, Benayahu et al. 2002; *e* Hong Kong, Fabricius and McCorry 2006; *f* Sulawesi, Indonesia, Rowley 2014; *g* Great Barrier Reef, van Oppen et al. 2005)

not previously reported for the Caribbean (Santodomingo et al. 2013). When combined with previous reports on shallow-water octocorals, this shows that about half of all described Caribbean species are nonsymbiotic (see Fig. 1).

In contrast to other regions, the Mediterranean has only nonsymbiotic species, except for the facultative symbiotic (or aposymbiotic) species *Eunicella singularis*. This species hosts symbionts when found in shallow-water photic zones (10–30 m), but at depths between 40 and 60 m, symbionts are absent (Gori et al. 2012a), a feature accompanied by the expression of different morphotypes (Fig. 2). Interestingly, this is the only known octocoral species which appears to be facultative in respect to acquiring *Symbiodinium*, showing a gradual loss of symbionts due to increasing attenuation of light in the water column, while all other octocoral species in the Mediterranean Sea are strictly heterotrophic, satisfying their energetic demands with the abundant seston.

The presence/absence of symbionts plays an important role in the bathymetric distribution of octocorals. Generally, this group is found in varying densities in most marine habitats, and their abundance depends mainly on physical environmental parameters such as light, sedimentation, current regime, and flow rates (e.g., Kinzie 1973; Sánchez 1999). The impact each of these parameters has on abundance depends partially on the presence/absence of symbionts. For example, light availability is considered one of the main factors controlling the vertical distribution of symbiotic species (Kinzie 1973), due to the dependence of *Symbiodinium* on available light energy for photosynthesis. Therefore, most symbiotic species are

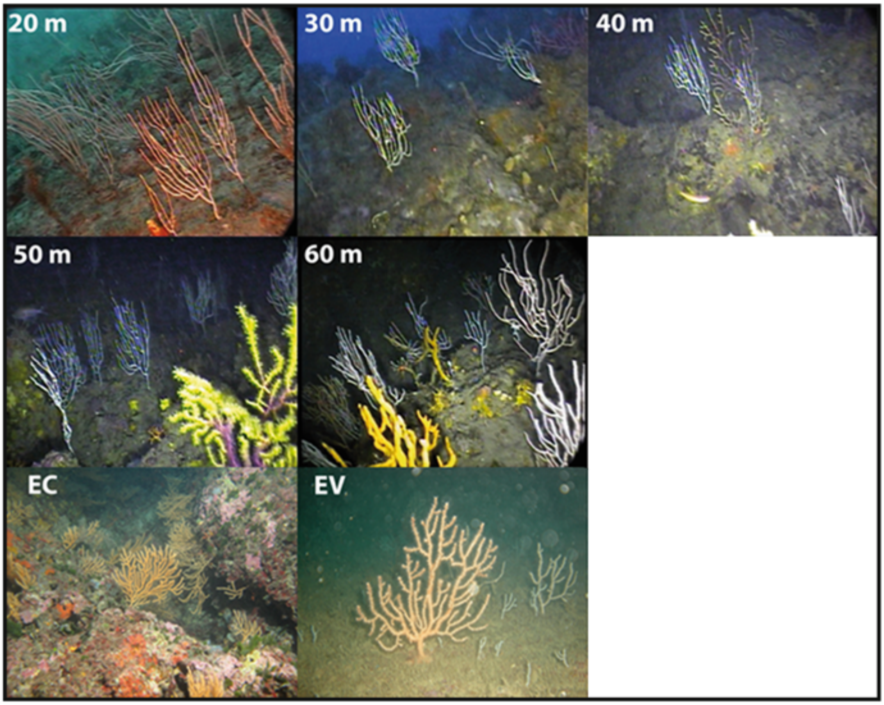


Fig. 2 Symbiotic and nonsymbiotic morphotypes of the aposymbiotic Mediterranean species *Eunicella singularis*, found along a depth gradient, from 20 to 60 m depth. Colonies are symbiotic between 20 and 40 m depth, and then they visibly decrease their symbiont cell density at lower depths (not present at 60 m depth). In comparison, two other nonsymbiotic Mediterranean species of the same genus: *Eunicella cavolini* (*EC*) and *Eunicella verrucosa* (*EV*) (Photos provided by Andrea Gori and Sergio Rossi)

usually restricted to shallower and/or less turbid areas (<50 m), even though some species are able to penetrate deeper (see Fig. 3). Nonsymbiotic species are predominantly found deeper, where light is limiting (Fig. 3), and their abundance is mainly affected by water movement, as their energetic demands depend on suspended particulate food from the surrounding water.

Over 3,400 octocoral species are distributed worldwide, with 75% occurring in depths greater than 50 m, and are mostly dominated by nonsymbiotic species (Fig. 3). The depth limit for symbiotic octocorals can vary for several reasons, such as benthic topography and water quality. For instance, symbiotic species can be found deeper when there is a gentle slope, while alternatively nonsymbiotic species can be found shallower when there are steep slopes (Fig. 4a, b, e.g., Kinzie 1973). In addition, reduced light availability, caused by poor water quality, can reduce diversity of symbiont-hosting taxa. These conditions have little to no effect on the diversity of nonsymbiotic octocorals, causing shifts from symbiotic to nonsymbiotic octocoral communities, even in very shallow areas, as has been reported for the reefs surrounding Hong Kong (Fig. 4c; Fabricius and McCorry 2006).

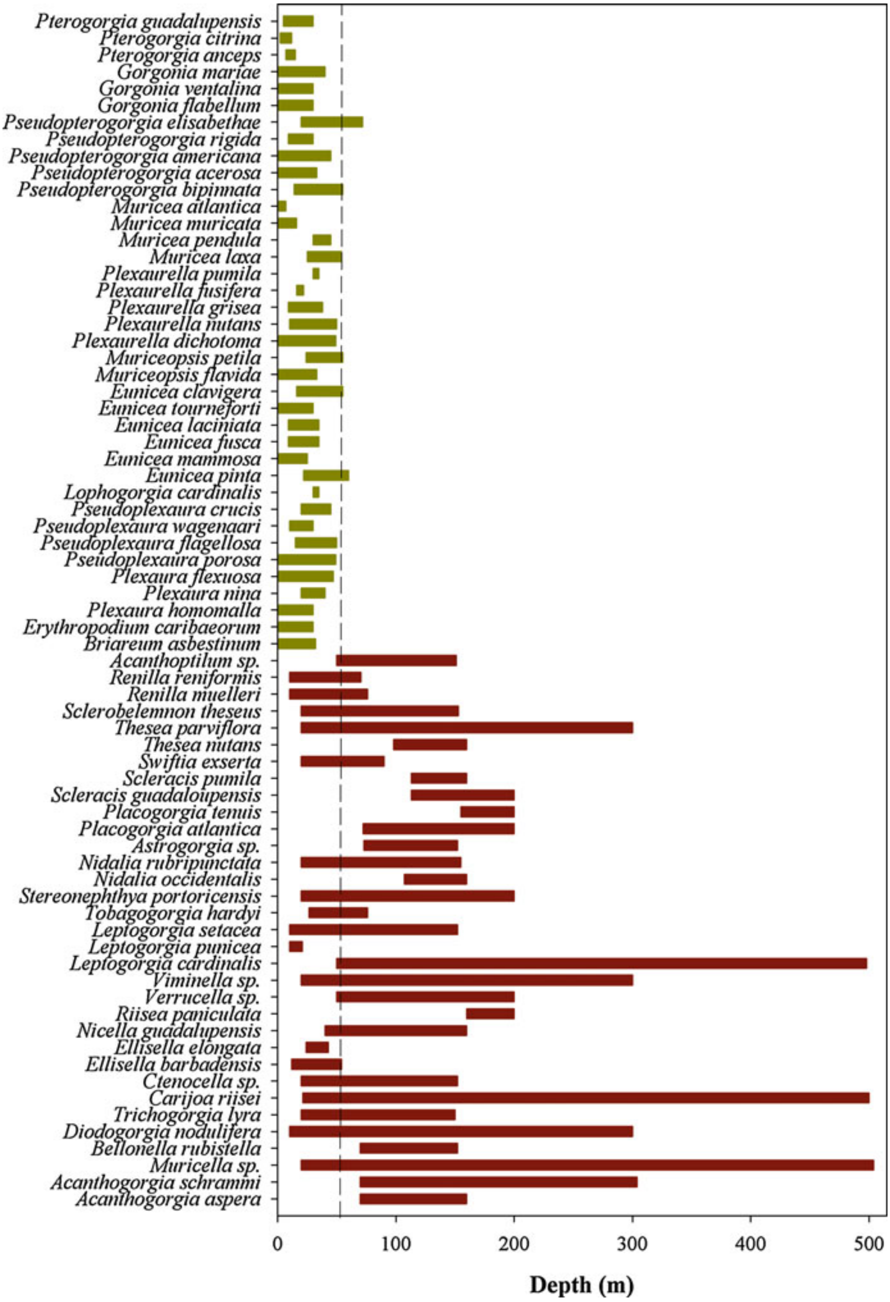


Fig. 3 Bathymetric ranges reported for symbiotic (*dark yellow bars*) and nonsymbiotic (*dark red bars*) Caribbean octocoral species (According to Goldberg 1973, Kinzie 1973, Santodomingo et al. 2013)

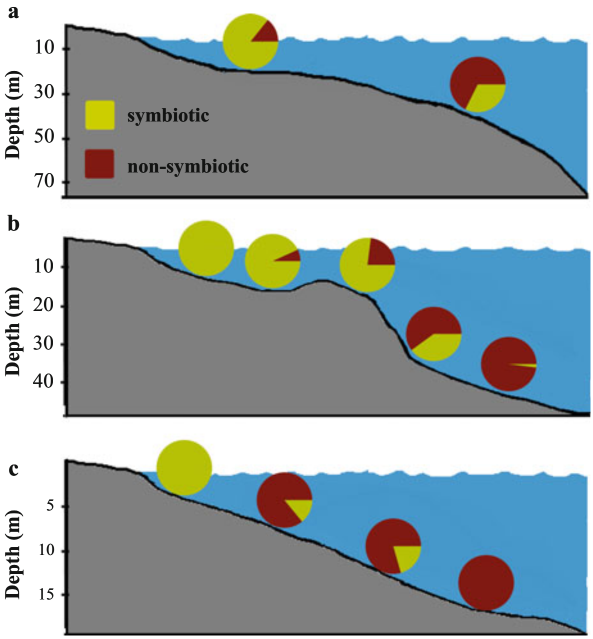


Fig. 4 Relative abundances of symbiotic and nonsymbiotic octocoral species along depth gradients in different locations: (**a**) Caribbean coast of Colombia (Sánchez 1999), (**b**) southeast coast of Florida (Goldberg 1973), and (**c**) reefs around Hong Kong affected by low water quality (Fabricius and McCorry 2006)

3 Symbiont Acquisition and Specificity

Octocorals, like other Cnidarians that host symbionts, can exhibit two possible modes of symbiont acquisition: vertical transmission (acquisition by maternal inheritance) and horizontal transmission (acquisition from the environment by either larval or adult stages). Octocorals that acquire symbionts through maternal (vertical) transmission, *Symbiodinium* cells, are present in the egg or brooded planulae larvae prior to their release from the parent. Alternatively, eggs, zygotes, or brooded larvae of the coral can be released without symbionts, acquiring new symbionts each generation from the surrounding environment.

In octocorals, the reproductive traits are far less studied compared to other groups (e.g., scleractinian corals, ~400 species; Baird et al. 2009). So far, the symbiont acquisition mode has been reported in only 27 species, and it seems that acquisition from the ambient environment is far more common than maternal inheritance in this taxonomic group (Fig. 5). All of the studied broadcast spawning species show horizontal symbiont transmission, as well as a proportion of the brooding species, producing nonsymbiotic planulae that acquire their symbionts at the primary polyp stage (Fig. 5). Within the brooding species, about 60% show vertical transmission, releasing larvae that already harbor symbiotic algae (Fig. 5). These differences are not well understood yet, but they might indicate possible differences in maternal energy investment efforts depending on the reproductive strategy.

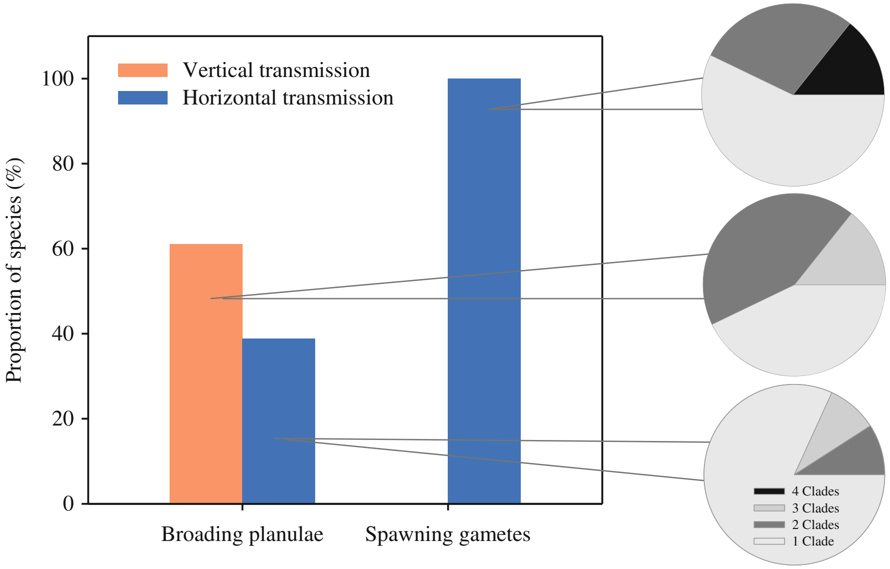


Fig. 5 Proportion of octocoral species ($n = 27$ species) expressing one or another mode of symbiont acquisition (vertical or horizontal) in different reproductive traits (see Table S1). *Pie charts* show the relative numbers of different *Symbiodinium* clades reported for these species

In octocoral species expressing the horizontal symbiont acquisition mode, it has been shown that newly settled polyps initially acquire a diverse range of symbionts whose identity appears to depend on the settlement habitat (e.g., Coffroth et al. 2001). However, during the following months, the initial distribution of symbionts progressively adjusts to the most common distribution found in adjacent adult colonies, suggesting that many algal types initially enter the host, but there is symbiont specificity, with less efficient and/or less competitive genotypes replaced by more efficient and/or more competitive genotypes (e.g., Douglas 1998).

Species with aposymbiotic polyps can survive the first steps of development without acquiring symbionts from the surrounding environment. However, the presence of symbionts significantly increases survivorship of juveniles, as shown in *Heteroxenia fuscescens* (Yacobovitch et al. 2003), suggesting that the presence of *Symbiodinium* represents a significant benefit to their host, even at this early stage. Similar to other symbiotic cnidarians, the benefits provided by the translocation of carbon produced through photosynthesis increase the survivorship of the larvae. A similar study on scleractinians also showed that symbiotic planulae larvae have a much lower caloric value compared to nonsymbiotic larvae, indicating lower maternal investment, which might suggest a significant contribution of the symbiotic algae to the energetic budget of the planulae (Ben-David-Zaslow and Benayahu 1998). A study on the energetics of the scleractinian coral *Pocillopora damicornis* planulae showed that symbionts can contribute up to 70% of their total photosynthetically derived fixed carbon to their larval host (Gaither and Rowan 2010).

Between the two symbiont acquisition modes, vertical transmission can be seen as a closed system, while horizontal transmission represents an open system. Generally, it is hypothesized that the diversity of symbionts in species expressing the vertical transmission mode may be lower compared to species acquiring symbionts from the surrounding environment (Fay and Weber 2012). In octocorals, multiple *Symbiodinium* genotypes are harbored by species exhibiting both horizontal and vertical transmission modes (Fig. 5). Some studies indicate that octocorals with vertical symbiont transmission might possess the ability for exogenous entry and residence of symbionts from the environment, indicating the possibility of both vertical and horizontal symbiont acquisition, which may be essential for potential survivorship when facing an environmental change (Forcioli et al. 2011). Thus, the mode of symbiont acquisition (i.e., maternal versus horizontal) might not affect symbiont diversity in octocorals, which is similar to findings in scleractinian corals. As previously stated, a possible relationship between the symbiont acquisition mode and the susceptibility to environmental stress has been suggested (Fay and Weber 2012), as hosts with horizontal transmission may have the opportunity to associate with different symbionts than those of their parents. Hence, they are able to obtain viable partnerships with multiple symbiont lineages simultaneously or in series, which allows them to exploit a wider range of environmental conditions, than hosts with vertically transmitted symbionts. Horizontal transmission has been shown in the adult Caribbean species *Briareum* spp. (Kinzie 1974), which exhibited symbiont “switching” due to exogenous algal uptake after bleaching, even though this symbiont relationship later reestablished to the original complement (Lewis and Coffroth 2004). The change in symbionts as a response to environmental stress might be related to nonselective *Symbiodinium* acquisition by juvenile hosts (Coffroth et al. 2001). In contrast, another species expressing horizontal symbiont acquisition, *Gorgonia ventalina* (Andras et al. 2011), demonstrated a stable symbiont relationship upon temperature-induced bleaching, acquiring the same algal strain after a stressful event (Kirk et al. 2005). The differing responses indicate that more explorations into the response of symbiont assemblages to environmental stress in these cnidarians are required to identify a possible relationship between symbiont acquisition mode and metabolic processes that may help octocorals respond to the current threats of climate change.

In symbiont-harboring octocorals, five of the nine clades (A to I) of *Symbiodinium* have been found (see Franklin et al., 2012), and biogeographical patterns in the symbiont diversity, as well as in the most common symbiont clades, have been identified (e.g., van Oppen et al. 2005; Goulet et al. 2008). At the genus level, symbiont clade diversity is higher in octocorals from the Great Barrier Reef (GBR), compared to other tropical regions, and includes all five clades (A–D, G) found in octocorals, with clade C being the most common (Fig. 6). Clade C is also dominant in the Red Sea, the Tanzania coast, and Thailand, even though these regions present lower clade diversity, with only two to three clades present (Fig. 6). In contrast, in the Caribbean, clade B is the most common of the three clades reported for this region (Fig. 6).

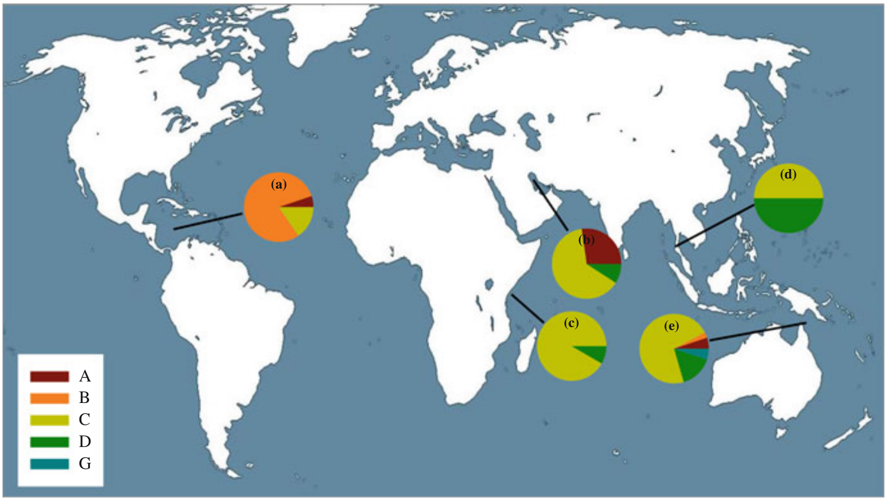


Fig. 6 Distribution of *Symbiodinium* clades in octocoral species of different tropical regions (Barneah et al. 2004; Franklin et al. 2012). Letters indicate the region: *a* Caribbean ($n = 31$); *b* Red Sea ($n = 12$); *c* Western Indian, Tanzania ($n = 12$); *d* Thailand ($n = 6$); *e* Great Barrier Reef, Australia ($n = 35$)

In general, octocorals exhibit low symbiont diversity in comparison to scleractinians, which has been hypothesized to be related to octocorals having a greater dependence on heterotrophy, resulting in a decreased reliance on symbiont flexibility (Baker and Romanski 2007). The majority of octocoral species examined so far harbor a single algal clade suggesting specificity at least at the clade level (see Franklin et al. 2012). Here, evidence from in vitro infection studies demonstrated that there is discrimination on the part of the host and/or symbiont, as not all algal strains can colonize a given host, with the native (paternal) symbiont performing best in the symbiosis (Kinzie 1974). Each *Symbiodinium* clade is characterized by a considerable level of diversity, which can result in several different *Symbiodinium* types in some octocoral species (see Franklin et al. 2012). Some *Symbiodinium* types in octocorals are distributed globally, while others exhibit a more limited distribution (see Goulet et al. 2008). For example, the most common *Symbiodinium* type at GBR, C1, can also be found in other regions, although in much less dominance. In comparison to the GBR, *Symbiodinium* type B1 is the most common in the Caribbean, while type C3, a type found in the GBR, is also present (see Franklin et al. 2012).

4 Octocoral Physiology

Mixotrophy and heterotrophy provide octocorals with a trophic flexibility/plasticity allowing for one taxon to successfully settle in different habitats in high abundances, as it maximizes nutrient acquisition and ecological success in environments where light and plankton concentration can be highly variable and often limiting (Grottoli et al. 2006). Food availability may be a constraining factor for nonsymbiotic corals, especially in tropical oligotrophic waters, while the trophic plasticity of mixotrophic species allows for increased energy acquisition through an energy surplus with respect to nonsymbiotic species (e.g., Gori et al. 2012b). Thus, morphological and physiological features of species may define their success in specific habitats.

4.1 Effect of Polyp Morphology and Behavior on Metabolic and Feeding Rates

As stated above, for octocoral species harboring algal endosymbionts, light is considered the main factor in determining their vertical distribution, as symbiont photosynthetic activity, and hence the autotrophic contribution to the octocorals energy budget depends on light availability. In this context, it has been predicted that certain morphological features, which aid in increasing the surface area to volume ratio (SA/V), maximize the light-capturing ability and carbon autotrophic input in corals (Porter 1976). Increased SA/V can be achieved at different scales: (1) at the macro- and mesoscale, by increasing branching patterns of the colony and by thinner branches, and (2) at the microscale, by decreasing polyp diameter and height. Using the aforementioned morphological properties, previous studies have suggested that symbiotic scleractinian corals exhibit smaller polyps, while non-symbiotic taxa benefit from larger polyps for zooplankton capture, trading off high surface area (for photosynthesis) to gain the ability to increase capture rates (Porter 1976; Dai and Lin 1993). However, when comparing polyp sizes and densities of different octocoral species, no apparent relationship of these parameters is seen with the presence/absence of algal symbionts (Fig. 7; Lewis 1982). This might be partly related to the fact that the true surface area of an octocoral polyp is not only characterized by the polyp diameter but rather by the diameter and the expanded tentacles, which varies significantly between species (e.g., Lewis 1982). Also, previous studies have shown that smaller polyps are able to capture the same range of prey as larger polyps, with much higher rates of prey capture per unit coral biomass (e.g., Lasker 1981).

Polyp size, tentacle morphology, and tissue surface area vary widely among octocoral species (Fig. 8), with all three factors contributing to the photosynthetic activity in symbiotic species, as well as prey encounter and capture rates. In symbiotic taxa, a certain plasticity with respect to polyp size and density in relation to depth (and hence light availability), has been reported. For example, polyp diameter and also polyp density in octocorals have been shown to decrease with depth, with the first related to an increase in SA/V, while lower polyp density has been suggested to reduce self-shading between polyps under lower light availability (Kim et al. 2004; Prada et al. 2008). In order to optimize light conditions, octocorals also might increase the internal light field through skeletal light scattering, similar to scleractinian corals (Enríquez et al. 2005), as sclerite morphology and size may affect internal light reflection, facilitating and maximizing light harvesting of algal

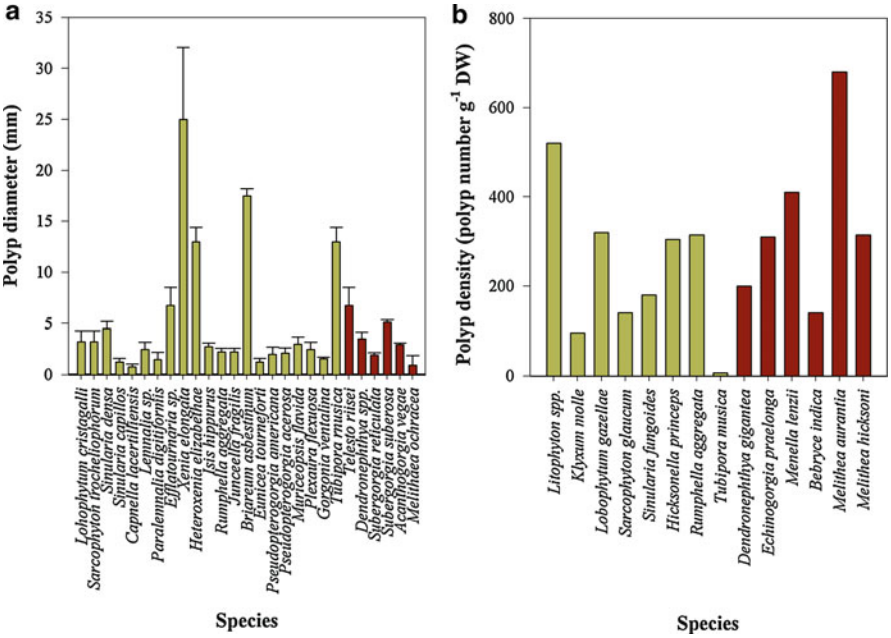


Fig. 7 Comparison of polyp size and density between symbiotic (*dark yellow*) and nonsymbiotic (*dark red*) octocoral species. Data for polyp size from Lewis (1982) and Dai and Lin (1993) and for polyp density from Sorokin (1995)

endosymbionts (Rowley 2014). This is supported by similar chlorophyll *a* specific absorption in Caribbean shallow-water octocorals compared to reported values for scleractinian corals (Ramsby et al. 2014). The number, size, color, distribution, and morphology of sclerites may be a key factor for understanding the potential light dispersion through the cnidarian tissue and, hence, its effect on symbiont light-harvesting efficiency. There are several studies that support this argument, such as the increase in sclerite size with depth, as found in *Eunicea flexuosa* (Kim et al. 2004; Prada et al. 2008). Also, the presence/absence and abundance of colored sclerites might influence the internal light scattering. An experiment with the deep-water species *Gorgonia mariae* showed that organisms transplanted from 30 m to 1 m depth showed a marked increase in colored spicules. In the area of new growth, the percentage of red spicules increased from 0.08% to 48% in 25 days (Kinzie 1973), which might lower light scattering within tissue, lowering the amount of light reaching symbiont cells at this shallow depth, where light may be excessive for photosynthetic functioning.

In addition to the regulation of SA/V by changes in polyp size and density, octocorals are also able to vary their SA/V temporarily, through polyp expansion and contraction, which can considerably increase the total area of photosynthetically active tissue (e.g., 300% increase in surface area of *Capnella gabonensis*; Farrant

Fig. 8 Polyp morphologies of symbiotic Caribbean octocoral species: *Plexaurella* spp. (*left*), *Eunicea tournefortii* (*middle*), and *Pseudoplexaura* spp. (*right*) (Photos provided by Eric Jordán Dahlgren)

et al. 1987). Since the greatest proportion of symbionts is located within polyps (some are also embedded into the upper tissue layers of the coenenchyme), polyp contraction causes shading, as well as limited gas exchange, therefore significantly reducing photosynthetic and respiration rates (Fabricius and Klumpp 1995). The magnitude of this effect seems to be related to polyp size, as it is greater in species with larger polyp diameter (Fig. 9). In addition, polyp behavior has a direct effect on prey capture, being that heterotrophic input is also limited when the polyp is not operating.

Besides the positive effect of polyp expansion on metabolic rates, by maximizing the diffusion and consumption of oxygen in the tissue, some octocoral species of the Xeniidae family also exhibit vigorous and perpetual pulsation of their polyps (Kremien et al. 2013). This unique feature has been shown to enhance symbiont photosynthesis by an order of magnitude, but decreases at high O_2 concentrations in surrounding seawater. This indicates that the beneficial effect is related to a greater efflux of oxygen from the coral tissue, which alleviates the reduced affinity of RuBisCo to CO_2 under conditions of high oxygen concentrations (Kremien et al. 2013).

The aforementioned evidence shows that polyp behavior in octocorals can greatly affect the organisms' metabolic rates, with polyp expansion (and pulsation) maximizing diffusion and consumption of oxygen in tissue, increasing symbiont photosynthesis, but also increasing feeding efficiency. On the other hand, polyp contraction stops feeding and reduces respiration, as well as autotrophic input through symbiont photosynthesis (Fig. 9; Fabricius et al. 1995). As symbiotic and nonsymbiotic species rely on different nutritional strategies to cover their energetic demands, it has been suggested that the polyp expansion behavior of symbiotic corals relates to the energetic equilibrium between autotrophy and heterotrophy (Levy et al. 2001). It could be hypothesized that differences in diurnal polyp activity patterns may be due to more diurnal rather than nocturnal activity of octocorals harboring symbionts, while nonsymbiotic corals might show predominantly nocturnal polyp activity. Studies on octocoral polyp activity show that most symbiotic

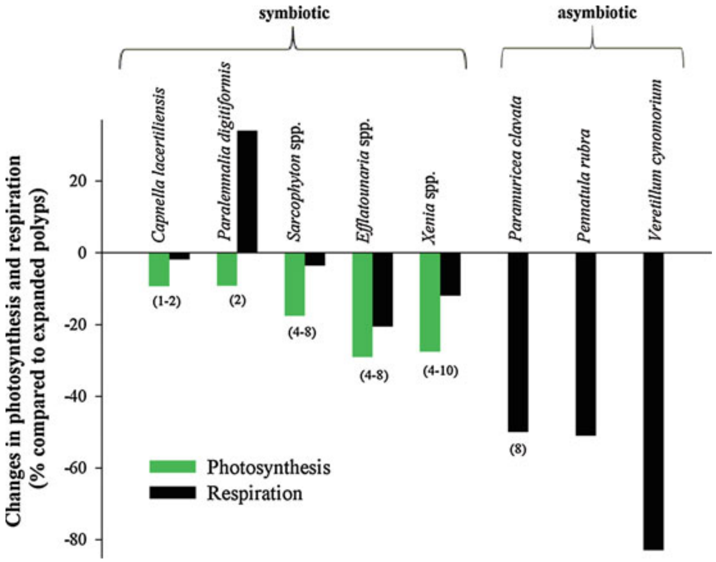
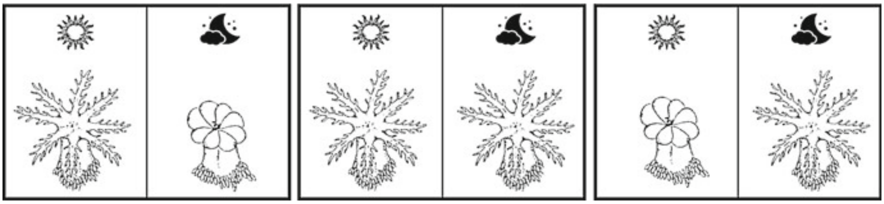


Fig. 9 Effect of polyp contraction on photosynthetic and respiration rates in shallow symbiotic octocoral species from the Great Barrier Reef (Fabricius and Klumpp 1995) and nonsymbiotic Mediterranean species (Brafield and Chapman 1965; Coma et al. 1998). Numbers in parentheses indicate polyp diameter in mm

species expand their polyps during the day and night (Fig. 10), which is similar to observations in scleractinian corals (e.g., Lasker 1979) and sea anemones (e.g., Sebens and DeRiemer 1977). In contrast, studies on nonsymbiotic species indicate that polyp contraction during the day is likely to facilitate energy conservation, since it reduces the oxygen concentration in tissue, reducing metabolic costs at times when prey capture is unlikely (Fig. 10; Sebens and DeRiemer 1977; Rossi 2002). So far, the number of studies conducted is small, and the observations are often contradictory. For example, for the Great Barrier Reef, the majority of symbiotic octocoral colonies that have been observed expand their polyps at night, with polyp expansion during the day being highly variable between taxa, while the same genera from the Red Sea were found to contract their polyps during night (Fabricius and Klumpp 1995). In Caribbean reef octocorals, it has been reported that most expand their polyps during the day and contract them at night, though differences in polyp behavior between species were observed (Wainwright 1967). Interestingly, in the Mediterranean symbiotic octocoral *Eunicella singularis*, the pattern of activity is not related with available light (Rossi 2002). For *E. singularis*, the opening-closing of polyps seems to be strictly related to the available seston, similar to nonsymbiotic species.

Along with irradiance, water flow and food availability are the most important triggering factors for polyp expansion/contraction (Rossi 2002). Polyp contraction



Gorgonia spp., *Pseudopterogorgia americana*, *Xenia* spp.

Alcyonium hibernicum, *A. digitatum*, *Sarcophyton* spp., *Sinularia* spp., *Paralemnalia* spp., *Capnella gaboensis*, *Briareum asbestinum*, *Pseudoplexaura porosa*, *Paramuricea clavata**

*Dendronephthya hemprichi**, *Cavernularia obesa**

Fig. 10 Polyp behavior reported for symbiotic and nonsymbiotic (*) octocorals (see Table S2)

has been shown to occur at very low and very high flows (e.g., Dai and Lin 1993; Fabricius et al. 1995); however, smaller polyps are expanded over a wider range of water flow velocities (Dai and Lin 1993). This might be related to higher distortion of larger polyps at high flow rates, explaining their reduced feeding success relative to smaller polyps. Although, when comparing feeding effectiveness, species with smaller polyps are usually less effective, compared to species with larger polyps, which represents a trade-off between polyp size, and therefore feeding effectiveness, and being able to feed over a greater flow range (Fig. 11).

Temperature is another environmental factor influencing octocoral polyp activity and photosynthetic and feeding rates. In Mediterranean octocorals, a decrease in polyp activity at high temperature has been observed in both symbiotic and nonsymbiotic species, which resulted in decreased oxygen consumption. The inverse relationship between polyp activity and temperature is also reflected in seasonal patterns of polyp expansion/contraction, with the majority of polyps contracted during summer (up to 80%), while the contrary is found during other seasons (Coma et al. 1998; Rossi 2002). As polyp behavior is tightly linked to oxygen production/consumption and feeding, these processes respond similarly to seasonal variations in temperature. Octocoral respiration is reduced during summer months (Coma et al. 1998, 2002), a feature that seems to contradict the widespread patterns of respiratory increases with temperature. However, this may not only be related to polyp behavior but also to low rates of synthesis of new tissue during summer (Coma et al. 2002). The reduced feeding rates in summer found in Mediterranean octocorals (Coma et al. 1998) coincide with lower water flow and food availability during summer in the Mediterranean (Ribera D'Alcalá et al. 2004), which are potential factors triggering polyp expansion/contraction (e.g., Dai and Lin 1993). In addition to exogenous factors, there are also endogenous factors (internal clock, see ▶ Chap. 27, "Activity Rhythm Measurement in Suspension Feeders" by Duchêne (this volume)) acting on polyp expansion and contraction. The lack of studies on polyp activity, as well as the overlap of external stimuli versus internal cycles, creates difficulties in the development of a general model to predict polyp behavior (Rossi 2002).

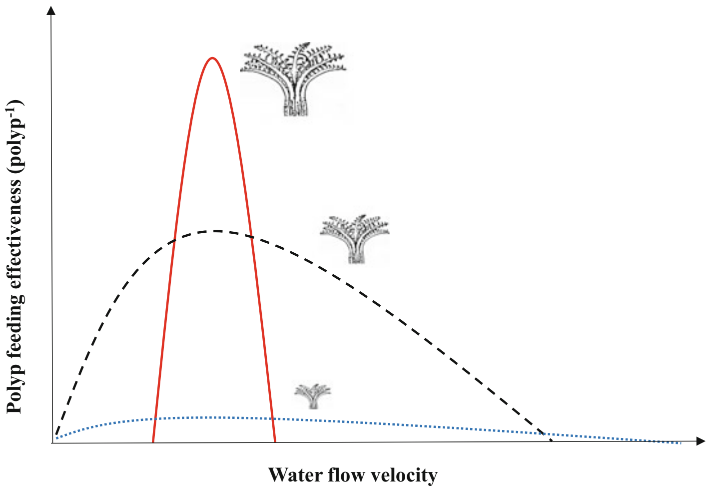


Fig. 11 Trade-off between polyp size and feeding effectiveness over a range of flow velocities (Adapted from Dai and Lin 1993)

4.2 Autotrophic and Heterotrophic Contributions to the Energetic Budget

In general, it is assumed that the presence of symbionts increases metabolic costs of octocorals due to higher respiration rates related to higher oxygen concentration within their tissue, as result of symbiont photosynthesis (Svoboda 1978; Coma et al. 2002). The few studies reporting octocoral respiratory rates show a trend toward lower respiration rates in nonsymbiotic species at the Great Barrier Reef and the Red Sea (Fig. 12), indicating that even though the presence of symbionts increases metabolic costs of the organism, the benefits of photosynthesis apparently exacerbate these costs, contributing to the octocorals energetic demands. In the Mediterranean, however, higher respiratory rates were found in nonsymbiotic species (Fig. 12), but this result may be biased as there is only one symbiotic species found in this region.

The ability of octocorals to utilize autotrophic and heterotrophic energy sources has been examined in a variety of species, mainly focused on tropical ecosystems, where low rates of primary productivity suggest a dependence on both autotrophy and heterotrophy to meet their metabolic needs (Sorokin 1991; Fabricius and Klumpp 1995; Ribes et al. 1998). Here, photosynthesis to respiration ratios (P/R) are used as indicators of autotrophic contribution to the coral metabolism ratio. In general, a P/R ratio >1 (when extrapolated over 24 h) indicates that the coral-algal association produces more organic material than it consumes. Comparing the scarce number of studies from different regions that report P/R for octocorals, it seems that tropical species rely on photosynthates translocated from symbionts to a greater degree in comparison to temperate species (Fig. 13).

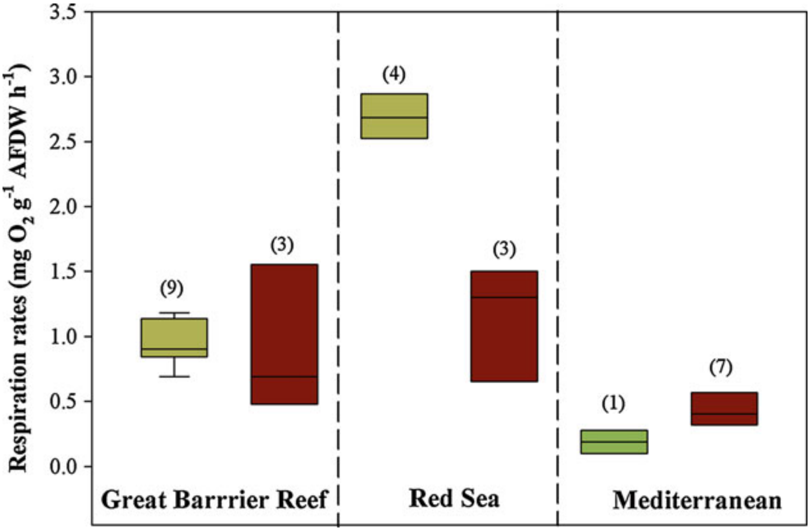


Fig. 12 Comparison of respiratory rates of symbiotic (*dark yellow*) and nonsymbiotic species (*dark red*) from the Great Barrier Reef (Fabricius and Klumpp 1995), the Red Sea (Svoboda 1978; Fabricius et al. 1995), and the Mediterranean (Brafield and Chapman 1965; Coma et al. 1998; Ribes et al. 2003; Previati et al. 2010; Ferrier-Pagès et al. 2015). Numbers of species included are given in parentheses

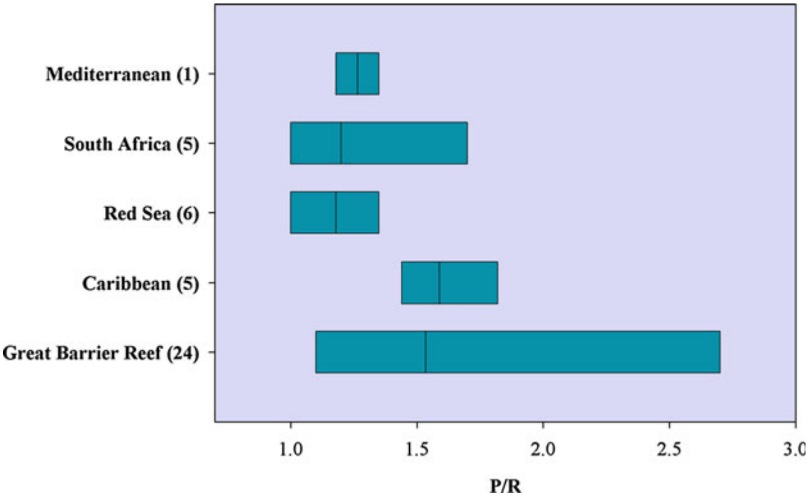


Fig. 13 Comparison of the variability of photosynthesis to respiration ratios (P/R) reported for octocoral species in different regions (see Table S3). For comparison between values reported in different studies, P/R was calculated using the photosynthetic maximum (P_{max}) and is integrated over the day, using the equation [(P_{max}*12 h)/(R*24 h)]. Numbers of species for each region included in the analysis are given in parentheses

This general pattern, however, has to be considered carefully due to the small number of reports. The comparison of values between studies is also difficult due to failures in experimental design (e.g., no stirring during incubation), differences due to polyp expansion and contraction (Fabricius and Klumpp 1995), or variations related to differences in depth (Fabricius and Klumpp 1995) or seasons (Farrant et al. 1987, Bednarz et al. 2015). For example, the reported variation in P/R of octocorals along a depth gradient (5–20 m) did not show a common pattern, as in some species P/R increased with depth, while others showed the opposite pattern (Fig. 14; Fabricius and Klumpp 1995). In addition, seasonal variations in P/R have been reported, which seem to differ depending on region. In the subtropical species *Sarcophyton* spp., the P/R was lowest in summer (Bednarz et al. 2015), while in the temperate species *Capnella gabonensis*, the highest P/R values were found during spring and summer (Farrant et al. 1987). Lastly, P/R estimations are based on dark respiration, which is usually lower than the respiration during the day when photosynthesis is active, resulting in an overestimation of the ratio.

In addition, there is high variation regarding the dependence on the autotrophic contribution to the organisms' energetic demands between species. For example, *Heteroxenia fuscescens* has been reported to fulfill nearly all its carbon requirements through photosynthates from their symbionts (Schlichter et al. 1983), similar to *Eunicea flexuosa*, in which feeding on zooplankton and other plankton accounted for $<$ 1% of its respiratory requirements (Ribes et al. 1998). In the warm temperate species *Eunicella singularis*, the autotrophic/heterotrophic contribution to this species energetic demands varied depending on season (Gori et al. 2012b). Except in early spring, feeding on zooplankton and seston in general has a low contribution to the respiratory demands of this species (Previati et al. 2010). Therefore, to meet basal metabolic requirements, this species depends on autotrophic input through symbiont photosynthesis, which has been shown to fulfill *E. singularis* respiratory demands during summer (Ezzat et al. 2013; Ferrier-Pagès et al. 2015). In contrast, the temperate *Capnella gabonensis* relies very little on carbon transfer from symbionts (translocation of approximately 10% of photosynthates; Farrant et al. 1987) and uses heterotrophic input to fulfill its energy demands. Variation in the importance of autotrophic and heterotrophic nutrition has also been shown with depth. Lasker et al. (1983) reported a decrease in photosynthesis with depth and vice versa when deeper organisms where transplanted to shallower depths in two *Plexaura* species. In this context, a decrease in symbiont cell numbers with depth has also been reported for several species (e.g., Forcioli et al. 2011; Rowley 2014), indicating a decrease in the reliance on autotrophic energy when light becomes limited. All this indicates that symbiotic octocorals are highly flexible with respect to autotrophic contribution to their energetic demands, which explains their ecological success, as they are able to populate shallow environments, but also deeper regions by increasing heterotrophy relative to autotrophy to fulfill their energetic requirements.

The combination of autotrophic input, through symbiont photosynthesis, and heterotrophic feeding in symbiotic octocorals may be a way of maximizing nutrient acquisition, and it could be hypothesized that they dispose over higher or more constant energy reserves, compared to nonsymbiotic species (Viladrich 2015). This

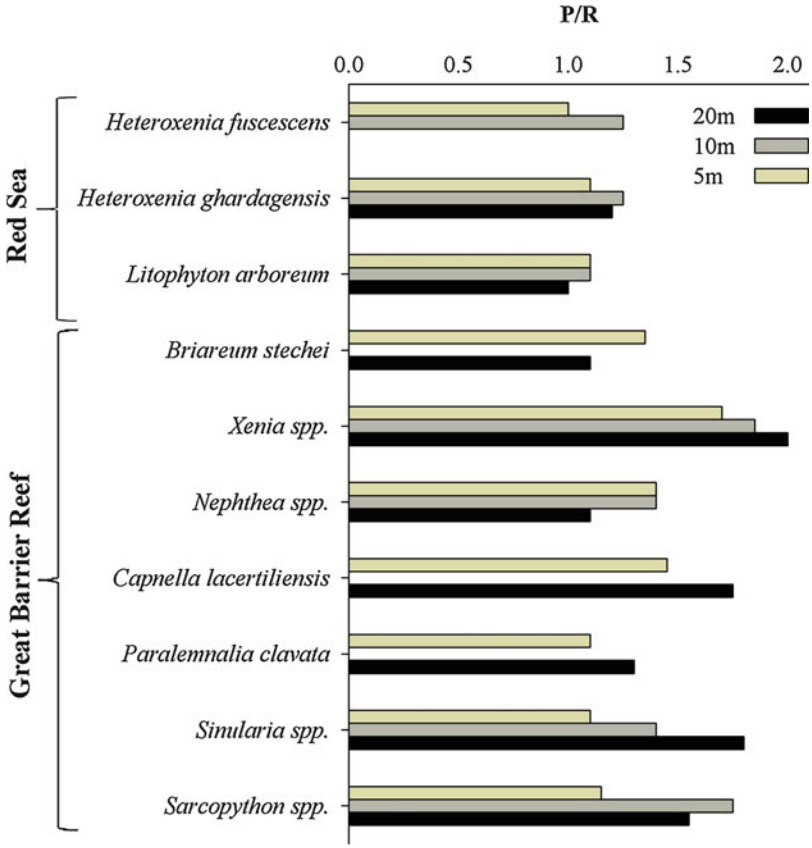


Fig. 14 Variability of photosynthesis to respiration ratios (P/R) with depth in octocoral species from the Red Sea (Svoboda 1978) and the Great Barrier Reef (Fabricius and Klumpp 1995). For comparison of values reported in different studies, P/R was calculated using the photosynthetic maximum (P_{max}),and is integrated over the day, using the equation [(P_{max}*12 h)/(R*24 h)]

might affect important life processes, such as reproduction, with a higher or more constant energetic investment due to high parental nutrition in symbiotic species, as reported for echinoderms (e.g., Thompson 1982). However, a recent study on Mediterranean octocoral species showed no direct relationship between energetic reserves and parental investment in reproduction, as energy allocation during larval release was similar between the symbiotic *Eunicella singularis*, with higher lipid content, and the nonsymbiotic *Corallium rubrum*, with lower lipid content (Viladrich 2015). Yet, comparing symbiotic (shallow, 20 m) with nonsymbiotic (deep, 60 m) *E. singularis* populations, the latter had a lower volume of sexual products and energy storage molecules (Gori et al. 2012b), supporting the importance of autotrophic energetic input in reproduction. In addition, the higher energy reserves in the symbiotic *E. singularis*, due to the energetic surplus obtained by algal symbionts, lowered the inter-annual variability in this species compared to the nonsymbiotic *C. rubrum* and might act as a buffer against the variability in environmental conditions. Therefore, in the context of understanding the distribution and abundance of octocoral species, it is still not known how much energy is actually required for reproductive success and maintenance of the colony during stressful events.

5 Octocorals Under Climate Change

Similar to scleractinians, octocorals are affected by global climate change-related threats, principally ocean warming (OW) (Lasker 2003, Marshall and Baird 2000) and acidification (OA) (Bramanti et al. 2012; Brown and Edmunds 2016), but the magnitude of these effects on octocorals differs in comparison to scleractinians. Increased seawater temperature is considered a serious threat to some shallow-water tropical octocorals (e.g., Celliers and Schleyer 2002), but many octocoral species show higher resistance (e.g., *Plexaura kuna*; Lasker 2003) and/or resilience (e.g., genus *Rhytisma*; Norström et al. 2009) to a bleaching event, which can be responsible for the observed phase shifts from scleractinian to octocoral dominance.

High octocoral resistance to OW, compared to scleractinian corals, has been attributed to octocorals ability to lower their dependency on autotrophic input and a greater contribution of the organisms' energetic demands through heterotrophy (Fabricius and Klumpp 1995; Baker and Romanski 2007). The relationship between the ability to increase heterotrophic nutrition during thermal stress and subsequent recovery and resilience to bleaching events has been shown in scleractinian corals (Grottoli et al. 2006). However, seemingly not all symbiotic species are capable of upregulating heterotrophy, as shown in scleractinian corals (Grottoli et al. 2006), and the example of the Mediterranean octocoral species *Eunicella singularis*, which showed a lack of increased heterotrophic feeding upon collapse of photosynthesis caused by high temperature (Ezzat et al. 2013). The nutritional plasticity of octocorals, which seems to allow for an increased resistance to stressful conditions, might make it unnecessary to rely on a high symbiont diversity related to symbiont shuffling, a protective mechanism to acclimate to changing environmental conditions reported in scleractinian corals. Studies on octocorals investigating the effect of thermal stress on *Symbiodinium* composition have not found a change in symbiont type in response to temperature increase (Table 1). In the context of resistance to thermal stress, the presence of symbionts in octocorals can be both beneficial and harmful. The energetic surplus from autotrophy has been suggested to cause a higher thermal resistance and a higher recovery rate, resulting in higher resilience of symbiotic species to thermal stress, compared to nonsymbiotic species (Previati et al. 2010). This is also supported by findings of lower inter-annual variability in energetic reserves in the symbiotic *E. singularis* compared to the nonsymbiotic *C. rubrum* (Viladrich 2015), suggesting mixotrophic species might be less affected by environmental variability due to energetic surplus obtained by trophic plasticity. In contrast, symbiont photosynthesis not only gives nutritional benefits but also poses a risk through environmental perturbations, especially as elevated temperature

Table 1 Summary of studies on octocoral responses to OA and thermal stress (* indicate nonsymbiotic species)

Species	Experiment settings		Duration	Response	Location	Ref
	OA	Temperature				
Clavulariidae *Phenganax parrini*		+5 °C (32 °C)	12–18 h	Symbiont migration into stolons	Culture	1
		+4.5 °C (31.5 °C)	24 h			2
		+5 °C (32 °C)	24 h	Symbiont migration into stolons No response in respiration and photosynthesis		3
Alcyoniidae *Sarcophyton* spp.	In situ, volcanic CO_2 seeps 550–650 ppm CO_2 (pH 7.9)			↓ Cover	Indonesia	4
Sarcophyton spp.	1917–3898 ppm CO_2 (pH 7.6 and 7.3)		5 months	No response in symbiont cell density and pigment concentration	Red Sea	5
S. elegans	In situ, volcanic CO_2 seeps 550–970 ppm CO_2 (pH 7.9)			↑ Photosynthesis, ↑ night decalcification, no response in light calcification	Japan	6
S. ehrenbergi		+2–6 °C (30–34 °C)	48 h	↓ Symbiont cell density	GBR	7
		+2–8 °C (30–36 °C)	48 h	Bleaching, necrosis		8
Sinularia spp.		+2–6 °C (30–34 °C)	48 h	↓ Symbiont cell density	GBR	7
S. lochmodes		+2–8 °C (30–36 °C)	48 h	Bleaching, necrosis	GBR	8
S. capitalis		+8 °C (33 °C)	48 h	↓ Symbiont cell density, ↓ lipid content	South China Sea	9

(*continued*)

Table 1 (continued)

Species	Experiment settings		Duration	Response	Location	Ref
Xeniidae *Xenia* spp.		+2–6 °C (30–34 °C)	48 h	↓ Symbiont cell density	GBR	7
X. macrospiculata	1917–3898 ppm CO_2 (pH 7.6 and 7.3)		42–90 days	No response in symbiont pulsation rate, cell density, pigment concentration, and sclerite weight per polyp	Red Sea	5
	1917–3898 ppm CO_2 (pH 7.6 and 7.3)		42 days	No response in sclerite microstructure	Red Sea	10
X. elongata		+2–8 °C (30–36 °C)	48 h	Bleaching, necrosis	GBR	8
Heteroxenia fuscescens	1917–3898 ppm CO_2 (pH 7.6 and 7.3)		32–90 days	No response in symbiont cell density and pigment concentration	Red Sea	5
Bayerxenia spp.		+6 °C (30.5 °C)	7 days	No changes in symbiont type and cell density, no necrosis	GBR	11
Sarcothelia spp.		+5 °C (32 °C)	12–16 h	Symbiont migration into stolons	Culture	1
		+4.5 °C (31.5 °C)	24 h			2
		+3 °C (30 °C)	24 h	Symbiont migration into stolons ↑ Respiration, ↓ photosynthesis		3
Sympodium spp.		+4.5 °C (31.5 °C)	12–24 h	Symbiont migration into stolons	Culture	2
Plexauridae *Eunicea fusca*	285–4568 ppm CO_2 (pH 8.1–7.1)		28 days	↓ Growth, ↓ calcification	Florida Keys	12
E. tournefortii		+5 °C (31.5 °C)	35 days	↓ Symbiont cell density	Caribbean	13

E. flexuosa	1081 ppm CO_2 (pH 7.85)		49 days	No response in growth and sclerite structure	Caribbean	14
Paramuricea clavata *		+9 °C (25 °C)	+2–3 °C every 10 days	↑ Respiration, ↓ polyp activity	Mediterranean	15
Gorgoniidae *Gorgonia ventalina*		+3.5 °C (30.5 °C)	12 days	No changes in symbiont type	Florida Keys	16
Pterogorgia anceps		+3 °C (32 °C)	10 days	↑ Peroxidase activity	Caribbean	17
Eunicella singularis		+6 °C (24 °C)	33 days	No response in calcification, Fv/Fm, and chlorophyll concentration	Mediterranean	18
		+8 °C (26 °C)		↓ Calcification, ↓ Fv/Fm, ↓ chlorophyll concentration		
		+8 °C (26 °C)	2 months	Bleaching, ↓ chlorophyll concentration, ↓ photosynthesis, ↓ respiration		19
		+7 °C (27 °C)	~50 days	↑ Necrosis		20
		+9 °C (25 °C)	+2–3 °C every 10 days	↑ Respiration, ↓ polyp activity		15
*E. cavolini**		+9 °C (25 °C)	+2–3 °C every 10 days	↑ Respiration, ↓ polyp activity	Mediterranean	15
Coralliidae *Corallium rubrum**	800 ppm CO_2 (pH 7.81)		314 days	↓ Calcification, ↑ total organic matter Aberrant sclerite morphology	Mediterranean	21
		+9 °C (25 °C)	+2–3 °C every 10 days	↑ Respiration, ↓ polyp activity		15
		+7 °C (25 °C)	25 days	↓ Polyp activity, ↓ calcification, necrosis		22

(*continued*)

Table 1 (continued)

Species	Experiment settings		Duration	Response	Location	Ref
Soft corals community	In situ, volcanic CO_2 seeps 850–950 ppm CO_2 (pH 7.7)			↓ Octocoral cover ↓ Octocoral species richness	Papua New Guinea	23

(1) Parrin et al. Biol Bull 2012; 223:245–256; (2) Parrin et al. J Exp Mar Biol Ecol 2016; 474:73–80; (3) Netherton et al. J Exp Biol 2014; 217:1469–1477; (4) Januar et al. AIMS Environ Sci 2016; 3:239–248; (5) Gabay et al. Ecol Evol 2013; 3:465–473; (6) Inoue et al. Nature Climate Change 2013; 3:683–687; (7) Strychar et al. J Exp Mar Biol Ecol 2005; 320:159–177; (8) Sammarco and Strychar. PLoS ONE 2013; 8:e54989; (9) Imbs and Yakovleva. Coral Reefs 2012; 31:41–53; (10) Gabay et al. PLoS ONE 2014; 9:e91553; (11) Ziegler et al. Coral Reefs 2014; 33:1085–1099; (12) Gómez et al. Coral Reefs 2015; 34:451–460; (13) Drohan et al. Bull Mar Sci 2005; 77:257–266; (14) Enochs et al. ICES J Mar Sci 2015; fsv159; (15) Previati et al. J Exp Mar Biol Ecol 2010; 390:39–48; (16) Kirk et al. Biol Bull 2005; 209:227–234; (17) Pearson HJ. PhD thesis. University of Mississippi 2014; (18) Ferrier-Pagès et al. J Exp Biol 2009; 212:3007–3015; (19) Ezzat et al. PLoS ONE 2013; 8:e64370; (20) Pey et al. CR Biologies 2013; 336:331–341; (21) Bramanti et al. Global Change Biol 2012; 19(6):1897–1908; (22) Torrents et al. J Exp Mar Biol Ecol 2008; 357:7–19; (23) Fabricius et al. Nature Climate Change 2011; 1:165–169

or irradiance can lead to the production of reactive oxygen species (ROS), which can damage membranes and proteins, and cause “bleaching” or even the breakdown of the symbiosis (Weis 2008). Therefore, symbiotic species have to invest in antioxidant defenses and/or they can express within-colony symbiont migration under light and temperature stress as a protective mechanism from the detrimental effects of increased ROS, as observed in different octocoral species (Table 1).

While scleractinians have been extensively studied, only a fraction of coral research, in particular the response to stress factors related to climate change, have been focused on octocorals, with even fewer species studied in the laboratory (Table 1). Thermal stress responses, studied in short-term (hours) and long-term (days to months) experiments, showed either no response or negative responses, inducing bleaching and necrosis and compromising symbiont photosynthesis (Table 1). In contrast to scleractinians, studies on temperature stress outweigh the few studies on the response of octocorals to OA, probably due to the reliance of scleractinians on calcification rates, which is greatly affected by OA, to a much larger degree than octocorals. In general, it would have been expected that OA conditions affect octocoral calcification, as even though most octocorals do not deposit a rigid calcium carbonate exoskeleton; they form discrete sclerites that are composed of high magnesium calcite with 5–13 dw% $MgCaCO_3$ (e.g., Velimirov and Böhm 1976), which is more soluble than aragonite precipitated by scleractinians. However, as the sclerites are loosely dispersed in the fleshy mesenchyme, without any direct contact to surrounding seawater, it has been suggested that the tissue exhibits a protective role against OA (Gabay et al. 2014). This is supported by the few OA studies on symbiotic octocorals, which showed no effects of increased pCO_2 on symbiont cell density and pigmentation, or growth and sclerite structure (Table 1). On the other hand, negative effects on growth and/or calcification have been reported in *Eunicea fusca*, when exposed to a wide range of pCO_2, and in the nonsymbiotic *Corallium rubrum* (Table 1). These results are in accordance with in situ studies on volcanic CO_2 seeps, which showed a decrease in octocoral cover and species diversity (Table 1). However, the scarce number of OA studies, as well as the complete lack of studies on the combined effect of temperature and high pCO_2 on octocorals, makes it difficult to derive general conclusions about octocoral responses to climate change, as well as the decreased or increased susceptibility of species related to the presence of symbionts.

The increased frequency in bleaching events due to climate change may lead to increased coral mortality in future decades, which may reach up to 60% in areas where corals are the fundamental part of benthic communities (e.g., Buddemeier et al. 2004). This, together with the general lower bleaching susceptibility and seemingly higher resistance to anthropogenic impacts of octocorals, compared to their scleractinian counterparts, may cause phase shifts toward soft coral dominance, as has already occurred in some regions (Fig. 15). Octocorals, like scleractinians, can function as ecosystem engineers, even though they are considered transitional builders as, with a few exceptions, they are not able to create as complex three-dimensional habitats similar to scleractinian corals. A few species (e.g., *Heliopora coerulea*, *Tubipora musica*, and *Corallium* spp.), however, contribute to reef

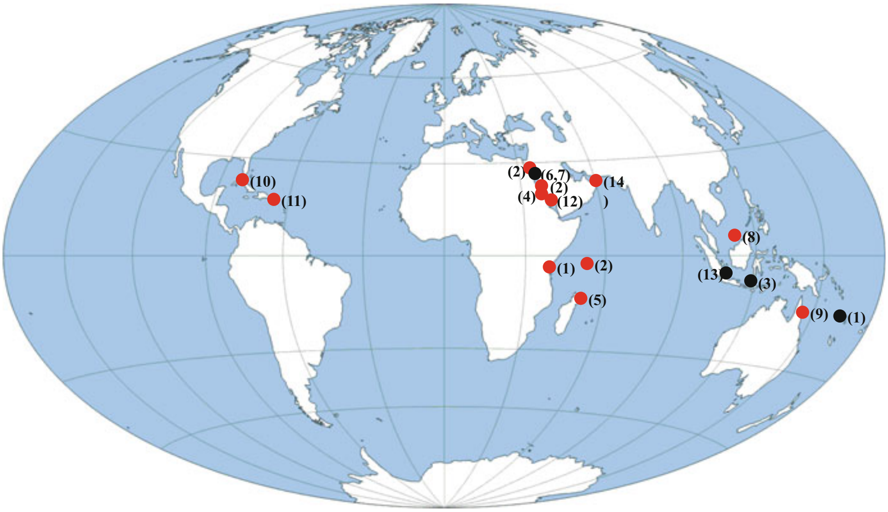


Fig. 15 Reported phase shifts from hard to soft corals caused by natural disturbance, such as bleaching, storms, cyclones, El Niño, or crown-of-thorns starfish (red dots), and anthropogenic impacts, such as blast fishing, pollution, and tourism (black dots). Numbers adjacent to the marks indicate the literature source: (*1*) Hoffmann (2002), (*2*) Wilkinson (2002), (*3*) Fox et al. (2003), (*4*) Reinicke et al. (2003), (*5*) Stobart et al. (2005), (*6*) Al-Zibdah et al. (2007), (*7*) Tilot et al. (2008), (*8*) Wood and Dipper (2008), (*9*) Wakeford et al. (2008), (*10*) Ruzicka et al. (2013), (*11*) Lenz et al. (2015), (*12*) Bruckner and Dempsey (2015), (*13*) Baum et al. (2015), (*14*) Coles et al. (2015)

framework and sedimentary deposits, as they produce a solid skeleton, similar to scleractinian corals (Spiro 1971; Zann and Bolton 1985; Grillo et al. 1993). The blue coral *H. coerulea* is especially peculiar as it is an octocoral with a massive aragonite calcium carbonate skeleton similar to scleractinians and is known as a prominent reef builder in Indo-Pacific coral reefs (Zann and Bolton 1985). Also, some species of Alcyonacea contribute to reef structure and sediment stabilization by depositing massive trunks of consolidated sclerites that can reach decimeters across and meters in height (Schumacher 1997). The discovery of these rocks composed of octocoral sclerites, termed spicules (Konishi 1981), reported in Southern Japan, Southern Taiwan, Australia, the Red Sea, and Somalia (Konishi 1981; Schumacher 1997; Jeng et al. 2011), supports the suggestion that octocorals contribute to reef construction and growth (Schumacher 1997; Jeng et al. 2011).

Besides their contribution as reef builders, the sclerites of octocorals can constitute a large proportion of their biomass (up to 84% of their dry weight; Velmirov and Böhm 1976), thus contributing to the formation of reef limestones through their release after death of the colony. However, with the few exceptions mentioned above, octocorals do not create wave-resistant platforms providing coastal protection and a durable habitat for other taxa. Moreover, flexible, branching octocorals are likely to be favored for shelter by a different suite of vertebrates and invertebrates compared to those normally associating with rigid scleractinians. These differences in biology of octocorals compared to scleractinians indicate that reefs dominated by each taxon will function in different ways, likely changing the ecological goods and services provided by coral reefs.

6 Future Directions

Next to scleractinian corals, octocorals represent one of the main components of tropical reef ecosystems. Their role in tropical reefs may become even more important in the near future, as the abundance of scleractinians decreases under global climate change, while octocorals seem to be more resistant. However, despite their importance, when comparing the research published for scleractinian corals, the octocoral group is greatly understudied, with large knowledge gaps related to their physiology and therefore their responses to a changing environment.

This chapter represents a synthesis of studies on octocoral physiology, with an intent of discovering patterns and responses in this group related to the presence/absence of symbionts. However, more studies are required to be able to deduce general patterns in this group. First, more basic physiological studies in symbiotic and nonsymbiotic octocoral species are needed, in order to infer the importance of autotrophic and heterotrophic nutrition. In this context, understanding the role of polyp expansion and contraction in short time cycles, as well as determinations of the amount of carbon translocated from the symbionts to the host and possible differences depending on symbiont types, will be helpful. Also, the determination of the seasonal variability between autotrophic and heterotrophic contribution to energy budgets will be essential to understand how different species will face stressful conditions and which will be more susceptible to global and local threats. In addition, comparative studies on energy allocation during reproduction ("mother care" sensu Viladrich 2015) are required, as they can be crucial for understanding the survivability of parental colonies and offspring and, hence, the resilience of the species. This knowledge will be essential for predicting the response of different species to threats posed by global and local stressors and, therefore, future trajectories of coral reefs and other ecosystems in which octocorals have a relevant role.

7 Cross-References

- ▶ Activity Rhythm Measurement in Suspension Feeders
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Filter-Feeding Zoobenthos and Hydrodynamics

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Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems

32

Pål Buhl-Mortensen, Lene Buhl-Mortensen, and Autun Purser

Abstract

Cold-water coral ecosystems differ from each other greatly in structure, faunal makeup, and ecological function. Attributes such as substrate type, 3-D complexity, biological community, and nutrient supply also change over small temporal and spatial scales. In this chapter, we present an overview of food gathering strategies employed by a range of cold-water corals. Furthermore, the importance of corals as habitat providers for associated fauna and thus biodiversity is discussed. The coral habitats support ecosystems at various spatial scales ranging from local exposed skeleton patches on gorgonian branches to the various zones on a reef. Comparison is made between many types of animal forests made up by cold-water corals, including several types of coral gardens and coastal and offshore reefs from a wide range of environmental settings. The trophic ecology of reef types is compared, and the variation in feeding behavior across particular reefs is also discussed.

Keywords

Animal forest • Cold-water coral reef • Coral garden • Trophic ecology • Associated fauna • Filter feeders

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Contents

1 Introduction

Cold-water corals (CWC) can form animal forests (see ▶ Chap. 1, "Animal Forests of the World: an overview") of great structural variety, in response to local environmental and food supply conditions, within a range of cold-water environments. CWC animal forests have previously been characterized as either "reefs" or "coral gardens" (OSPAR 2008a, b). More specific classification of these CWC forests has been predominantly determined by the composition of key taxa constituting the "forests." Scleractinian corals, in both shallow and deep waters, may develop reefs with multigenerational growth on hard or mixed substrates (colonial- or pseudocolonial scleractinians) or occur in relative high densities as cup-coral fields on soft substrates (solitary scleractinians). The difference between colonial and pseudocolonial can be illustrated with the common species *Lophelia pertusa* and *Paragorgia arborea*. Polyps in a colonial species like *P. arborea* share internal organs and are connected with living tissue, while *L. pertusa* lack such connections. The individual polyps of *L. pertusa* are only connected with an outer mucoid coenchym. Whether the cup-coral fields fall into a strict definition of coral garden (CG) or forest is unclear and illustrates the fact that the defining criteria are not well established. The diversity of habitats comprised by octocorals is much higher than for hexacorals, with representatives on both hard and soft substrates. Little is known about the CWC forests' trophic support of associated species and other ecological functions of corals in deep-water ecosystems or how these may be linked with the shallower shelf and pelagic ecosystems.

In this chapter, we will present an overview of what is known about trophic ecology and ecosystem functioning for CWC forests. We will focus on provisioning functions and services related to trophic support, habitat provision, and biodiversity support.

1.1 Types of CWC Animal Forests

The ecosystem functioning support is a common attribute for CWC forests that could be used to explain why some anthozoan communities are regarded as "special and valuable" habitats (e.g., reefs and CG) whereas others (e.g., sea anemones) are regarded as "common" species. The operational definitions of the special anthozoan habitats are largely based on expert evaluation, and the confusion of terminology is clearly illustrated for the sea pens.

The division of classes of CWC forests used in this chapter is the following:

1. Sea pen stands (sea pen and burrowing megafauna communities)
2. Coral gardens, including:
   - (a) Soft-bottom coral gardens
     - (i) Cup-coral fields
     - (ii) Scleractinian gardens
   - (b) Hard-bottom coral gardens
3. Cold-water coral reefs

Sea pens may occur in dense stands (identified as "seapen and burrowing megafauna communities" by OSPAR (Curd 2010)) or may be important members of CG (Christiansen 2010), (OSPAR designates all gorgonian communities of a certain density of colonies as CG). CG can consist of very different species and groups of corals inhabiting the seafloor in close spatial proximity. It is therefore entirely appropriate to split this loosely defined biotope into "soft-bottom CG" and "hard-bottom CG.". Most gorgonian corals live on hard bottom, but some species of Isididae and Chrysogorgiidae corals and Antipatharia (black corals) can form dense stands on sandy mud (e.g., *Radicipes gracilis* and *Isidella lofotensis* in Norwegian waters, and *Acanella arbuscula* in the western and central Atlantic). *Isidella* is mainly found at 300–400 m depth, in the larger fjords of Norway (Hardangerfjord, Trondheimsfjord, and Andfjord) (Buhl-Mortensen and Buhl-Mortensen 2013) (Fig. 1). *Radicipes* has a wide distribution along the slopes in cold, deep water in the western and central Atlantic. It had not been observed in Norway until the MAREANO mapping programme found relatively dense concentrations of this sea whip at 800 m depth in the area known as the Bjørnøya slide (Buhl-Mortensen et al. 2015b). Another group of corals that may be regarded as member of the soft-bottom CG are the unattached solitary scleractinians. These may constitute "cup-coral fields" commonly comprised of specimens of the solitary coral *Flabellum* spp.

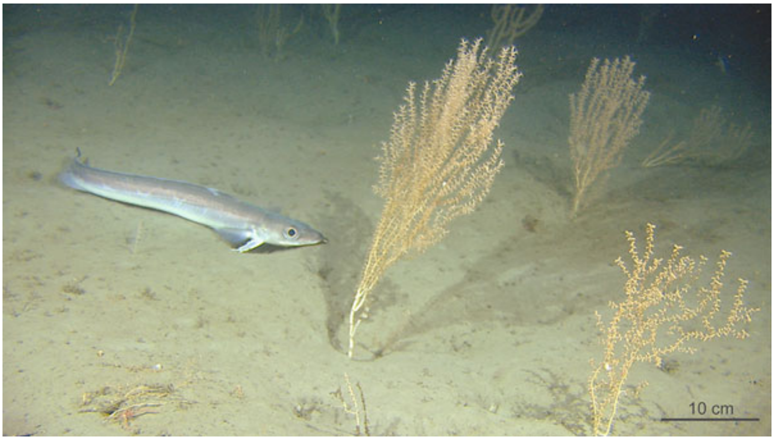

Fig. 1 Soft-bottom coral garden with *Isidella lofotensis* and *Molva dypterygia* in Hardangerfjorden, western Norway (Buhl-Mortensen and Buhl-Mortensen 2013)

(Caryophyllidae), at various depths from ~150 m and below, depending on the temperature of bottom waters. This soft-bottom CG is quite widespread and occurs, for example, on the shelf both off Nova Scotia (western Atlantic) and Norway (eastern Atlantic).

Hard-bottom CGs often occur in locations where currents are generally quite strong (with maximum current speeds exceeding 1 knt) and the sea bottom is hard. They may be characterized by gorgonian or antipatharian species occurring in stands. The most common CWC species in the Northeast Atlantic, making up hard-bottom CG, are *Paragorgia arborea*, *Primnoa resedaeformis*, *Paramuricea placomus*, and *Swiftia* spp. Antipatharians are also common key species within hard-bottom CG in the central part of the North Atlantic Ocean, south of the Wyville-Thompson ridge, along the mid-Atlantic Ridge and along the north West Atlantic margin (Mortensen et al. 2008; Bullimore et al. 2013). However, Antipatharians are not observed in the Norwegian Sea. Although there is less biodiversity associated with the various corals comprising this biotope than associated with CWC reefs, they often sustain a large number of individuals and host-specific species that are not found in other biotopes (see ▶ Chap. 23, "The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep").

There are few cold-water scleractinians that build reefs (see ▶ Chaps. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems", and ▶ 25, "Framework-Forming Scleractinian Cold-Water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective"), and based on current knowledge, one of these (*Lophelia pertusa*) is far more common than the rest. These mainly occur in the North Atlantic Ocean (e.g., along the Norwegian shelf, around the Faroes, the Logachev mounds, and the Porcupine Bank) and the Mexican Gulf. The number of verified *Lophelia* reefs off Norway (>1,200 verified and >6,000 indicated from detailed bathymetry) increases rapidly as the Norwegian habitat mapping program

MAREANO proceeds (www.mareano.no), and it is clear that the shelf off Norway represents a core area for this species, almost at the end of the "Gulf Stream."

Many colonial scleractinians do not form reefs, and reef-forming species such as *Lophelia pertusa* may occur in assemblages without presenting the characteristics of a reef. These may be termed "scleractinian gardens." Scleractinians may grow on vertical solid substrates, such as bedrock walls on seamounts, in canyons and in fjords, as well as on human made structures such as oil rigs. On a vertical substrate, coral debris cannot aggregate, and therefore reefs will not develop. *L. pertusa* gardens on steep substrate have been documented from the steep slopes around the Azores (Marina Carreiro-Silva IMAR/DOP, University of Azores, pers. comm.), the French, and Spanish Mediterranean canyons (Orejas et al. 2009) and the Whittard Canyon in the Northeast Atlantic (Huvenne et al. 2011). Off Galicia (Spain), "forests" of *Dendrophyllia ramea* are found on infralittoral and circalittoral bottoms and *Dendrophyllia cornigera* on circalittoral and bathyal rocky bottoms (OCEANA, pers. comm.). *D. cornigera* is found down to 600 m depth, whereas *D. ramea* occurs down to ca 150 m depth. Whereas *Lophelia* reefs are found near the west coast of Scotland (the Mingulay Reef Complex), Howell (2010) and Bullimore et al. (2013) have observed and described scleractinian CG west of Scotland, characterized by discrete colonies of *L. pertusa* and *M. oculata* and solitary scleractinians (*Caryophyllia* sp.) on hard substratum. In this chapter, we regard these as varieties of discrete scleractinian colonies on hard substratum.

2 Trophic Ecology

2.1 Framing Environment

The biological value of the trophic support and habitats provided by the cold-water host coral for the marine ecosystem depends on the surrounding habitat matrix, or what may be termed the "framing habitat" (Buhl-Mortensen et al. 2010). The framing habitat or surrounding environment is an important source of modifications of the communities of CWC forests. In locations where the framing environment is deep-sea soft sediments, the hard substrate offered by exposed coral skeleton represents a scarce habitat resource, offering a locally unique opportunity for sessile filter feeders to colonize. This habitat will often be colonized by species that are not common in the surrounding area and they are therefore often local hotspots of activity and diversity. *Lophelia pertusa* larvae are motile for extended periods of time (Larsson et al. 2014), and often larvae are to be found in suspension but unable to settle successfully due to less than optimum substrate conditions. On the deep-sea floor, commonly comprising of vast regions of soft sediment/low current environments, the occurrence of an area of firm substratum elevated into higher flow velocity waters will provide a habitat and stepping stone for sessile filter feeders. The presence of CWC forests and solitary suspension feeding megafauna may thus be a significant factor for the trophic ecology of a wider area than just within colonies.

2.2 Food Transport by Near-Bottom Currents

The near-bottom transport of food particles is vital for all benthic organisms, with delivery dependent on benthic boundary layer (BBL) conditions. The BBL is the zone of water which transports particulates immediately above the seafloor (see Riisgard and Larsen, ▶ Chap. 28, "Filter-Feeding Zoobenthos and Hydrodynamics" in this volume). Within the BBL a strong gradient of energy, dissolved and solid chemical components, suspended matter, and fauna may be found (Boudreau and Jørgensen 2001; Perlin et al. 2005) (Fig. 2). The BBL is not a physically distinct layer but is defined as the interface between the surface of the solid seafloor and an arbitrarily layer a selected distance away from the surface, where the shear effect on flow becomes "negligible" (Boudreau and Jørgensen 2001). The BBL is subdivided into a very thin "diffusive boundary layer and a viscous layer" a few millimeters thick, dominated by molecular viscosity and turbulence generated by the water body passing over the roughness of the seafloor and a "logarithmic layer." The logarithmic layer is comprised of waters in which the velocity profile is represented by a logarithmic increase in flow velocity with distance from the seafloor. In deep-sea environments with slow currents and fine sediment in suspension, the BBL is narrow, whereas in the high-current environments of shallow waters, the BBL may comprise a larger part of the water column (Souza and Friedrich 2005).

The general pattern of decreasing BBL thickness and corresponding decrease in food particles availability at increasing depth implies that a slight elevation of even just a few centimeters above the soft-bottom, deep-sea seafloor into the logarithmic region of the BBL may well result in a marked change in the quantity and composition of suspended food available. Higher living structures, such as gorgonian

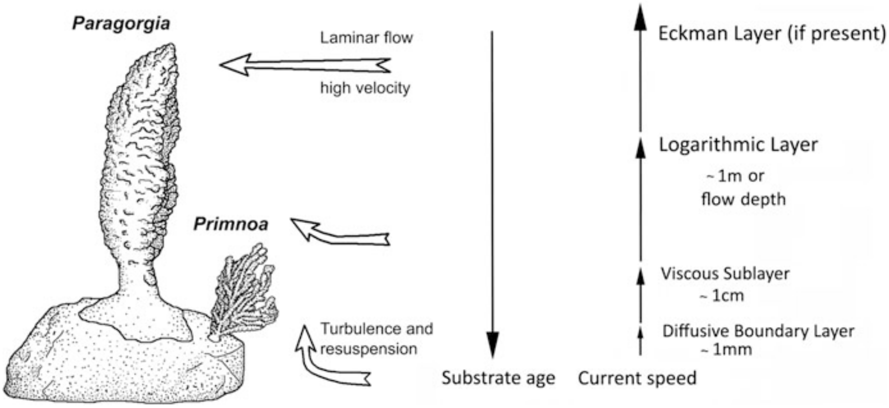

Fig. 2 Morphological adaptation to local current patterns illustrated with the gorgonian coral *Paragorgia arborea* and *Primnoa resedaeformis* (Modified from Mortensen and Buhl-Mortensen 2005). The benthic boundary layer (*BBL*) is subdivided into diffusive and viscous layers a few millimeters thick, dominated by molecular viscosity and roughness creating turbulence, and a logarithmic layer (Boudreau and Jørgensen 2001). The logarithmic layer involves flows in which the velocity profile is represented by a logarithmic increase away from the bottom substratum

corals, elevated into the laminar currents above the more turbulent near-bottom BBL may obtain other food sources (e.g., zooplankton) (Fig. 2) (Mortensen and Buhl-Mortensen 2005).

2.3 Feeding in Cold-Water Coral Forests

For coral forests to develop, sufficient substrate and food must be available at a location to allow for successful larval settlement and coral growth to occur. CWCs display a great variety of growth morphologies that aid their suspension/filter feeding. Growth morphology is quite flexible in some species and can vary in response to food availability and environmental conditions to maximize colony fitness in a particular location. Given a hard substrate and sufficient food, *Lophelia pertusa,* for example, can over successive generations form reefs tenss of meters in height, of densely packed coral polyps, such as these occurring in larger reefs in Norwegian waters. *L. pertusa* growth morphology may vary in response to suspended inorganic particulate concentrations. Given a less abundant food supply, though a similarly suitable seafloor habitat, *L. pertusa* can form low height thickets of individuals, subsisting but with colonies not thriving or resulting in vertical reef-like growth.

Hydrodynamics in the vicinity of the seafloor are greatly influenced by surface roughness and topography. The development of coral reefs and gardens increases 3D complexity, with the development of the habitat both responding to and in turn influencing the hydrodynamic conditions present. Large developed reefs, such as in the Sula reef complex off Norway, commonly consist of a cap of live corals, with living polyps on all sides around the reef mound supplied by suspended food particles coming from different directions during the tidal cycle. The “dead” zones of these reefs are commonly characterized by reduced flow velocities. The reduced flow velocity conditions at the lower part of the reefs does allow some transported material to settle from suspension, supporting other filter feeders colonizing the “dead” coral facings, such as brittle stars, anemones, and hydroids.

In locations with near uniform current flow direction and high velocity currents, extended “cigar reefs” may form. Over time, successive generations of corals move in an upstream direction, with downstream corals slowly being staved of material for growth. These reefs, such as found at Traena and off Vesterålen (Norway), consist of small front sections of *Lophelia pertusa* interspersed with other suspension feeders such as the bivalve *Acesta excavata*, a fringe of gorgonian corals and transient *L. pertusa* growth and a tail section of less abundant corals (Fig. 3).

Temperature may well be a major factor in determining the amount of food a coral has to capture in order to thrive and for a species to contribute to a CWC animal forest (see ▶ Chap. 1, “Animal Forests of the World: an overview”). Experimental work has to date only been carried out with a few species, though for the key reef-forming coral *Lophelia pertusa* it seems small changes in temperature correlate with large changes in coral respiration (Dodds et al. 2007; Hennige et al. 2015). This would indicate that for a particular temperature sensitive species to continue to

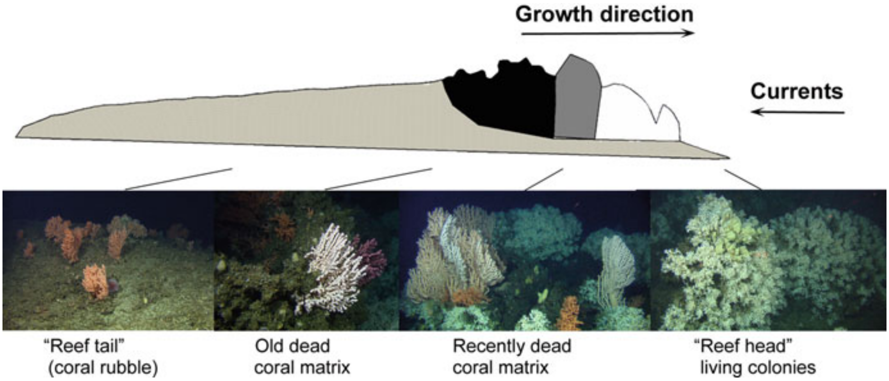

Fig. 3 Schematic illustration of an elongated reef, growing towards the main currents. Examples of the different reef habitats are from reefs in the Hola trough off Vesterålen (Images by MAREANO, Institute of Marine Research, Norway)

flourish in warmer waters, a higher abundance of suitable food would need to be supplied. From laboratory prey capture studies conducted with corals collected from the Norwegian fjord reefs and the warmer Mediterranean canyon, this would seem to be the case. Prey capture rates of *L. pertusa* polyps collected from the ~7 °C fjords in Norway capture roughly 10% of what polyps collected from the ~15 °C Mediterranean canyons capture, all other conditions being equal (Tsounis et al. 2010; Purser et al. 2010).

Feeding mechanisms of CWCs within animal forests vary, both by coral species and food type. It seems likely that mucus entrapment and digestion of prey outside the coral polyp occurs in some species (Wijgerde et al. 2011). In others, mucus may be used to capture material from suspension, perhaps after increasing local turbulent flow conditions as a result of polyp tentacle extension, then retracting this mucus and entrapped food into the polyp (Wijgerde et al. 2012). For prey of a suitable size, or motile prey items, *L. pertusa* use polyp tentacles directly to catch food. For small or motionless particles tentacles are not used (moved) but the food is transported by ciliary motion on the tentacles' surface (Mortensen 2001). There is also the indication that dissolved material within bottom waters may be utilized directly by corals (e.g., Mueller et al. 2014). Some species may employ these methods to varying degrees, as the environment and food availability dictates, though other factors, such as coral polyp spacing, polyp distance from seafloor, and prey capture surface area, also influence suitability of a particular niche for colony growth.

Recent experimental work and in situ observations with high temporal resolution instruments indicate that the long reported paradigm that CWC species best capture prey under environmentally high flow conditions may not be wholly, or in the case of all species, correct. For *Lophelia pertusa*, it has been observed that flow velocities in areas of high abundance may often be higher than in adjacent, sparsely inhabited regions of seafloor. However, these currents seldom exceed 25 cm s^{-1}. The currents commonly show tidal variations with periods of velocities below 10 cm s^{-1}. Higher flow provides an increased flux of food. However, it may also complicate prey capture by deforming feeding apparatus, rendering feeding mucus less effective, and detaching recently captured or partially digested food. Also, it may deliver elevated concentrations of undesirable, refractory material. Similar mechanisms have been described for shallow-water octocorals. In the laboratory, *L. pertusa* collected in the NW Mediterranean canyons have been shown to capture prey most effectively at velocities of 5 cm s^{-1} (Tsounis et al. 2010) and specimens from the Norwegian fjord at 2.5 cm s^{-1}. From fieldwork conducted at the Mingulay Reef (Scotland) and the Tisler Reef (Norway), such reduced current velocities may occur as tidal direction changes, with higher flow conditions prevalent for much of the tidal cycles (Davies et al. 2009). At the periods with strong currents, polyps may retract into the calyx (skeletal polyp houses) until the current slows down and the feeding conditions are favorable again. At Mingulay at least, this reduction in velocity is associated with increased food availability at a CWC reef site (Duineveld et al. 2012). There are indications that this might also be the case at the Tisler Reef (a sill reef in Norway, just north of the border to Sweden).

Corals are “messy” feeders. A percentage of food removed from suspension by whichever feeding mechanism is employed will not be ingested by the individual polyp. The mucus produced by cnidarians for cleaning and prey capture can be resuspended by currents or “drip” from the generating organism, taking with it any embedded food. This material may be transported downstream and out of the animal forest environment be redeposited or recaught by other corals, or be delivered to the complex microhabitat formed amongst coral branches, in the case of scleractinian reef-forming corals. Further, food trapped by CWC corals can be utilized by associated organisms. In the case of both gorgonian and scleractinian corals, shrimp can be commonly present in locally elevated abundances on living coral colonies, with their patterns of distribution perhaps determined by polyp spacing, as they grab entrapped food from their hosts. Amphipods are common and abundant on many gorgonians and likely also benefit from secondhand food delivery, either directly from entrapped material or from suspension in the locally lowered flow velocity conditions associated with the coral branching (Buhl-Mortensen and Mortensen 2004a).

3 Cold-Water Corals as Habitat Providers and Biodiversity Hot Spots

Individual CWC colonies, be they gorgonian, scleractinian, or antipatharian, have been shown to support numerous associated species, with species richness and individual numbers within and surrounding coral branches found to be in some cases orders of magnitude higher than in surrounding seabed (see “▶ Chap. 23, “The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep”). With sufficient corals present to allow the ecosystem to be characterized as an animal forest habitat, this boost to local species richness and biomass support is further increased by the physical provision of additional habitat

Table 1 Habitats and resources provided by major biotic habitat-forming taxa (From Buhl-Mortensen et al. (2010))

Biotic habitat	Available habitat			Resource for associates		Detritus trapped	Predator protection	Food
	On	Among	Within	Current	Substratum			
Lophelia								
Live		x		x			x	
Dead	x	x	x	x	x	x	x	
Rubble	x		x		x	x		
Gorgonians								
Live	x	x	x	x			x	x
Dead	x		x			x		
Seapens	x		x	x	x		x	x
Glass sponges	x		x	x				
Demospongia	–	x	x		–	x		x
Xenophyophoridea	x		x		x	x	x	x

niches. The understanding of the trophic support of CWC animal forests must rely on knowledge of the associations between other species and CWC.

At a local scale, colony morphology shapes the environment by modifying the hydrodynamics, providing shelter against strong currents, and facilitating local deposition of particulate matter (Table 1). Such local environmental conditions are extremely difficult to study in situ in the deep sea. Therefore, indices calculated from architectural attributes can be used to explain structural differences between biotic agents. Such descriptors include size (height and width), volume (total, between branches or in canals), surface area, and branching patterns (meander system, fractal description, etc.). The flexibility of the biotic substrate is another factor which affects epibionts, similar to the effect of sediment grain size on substrate stability.

CWC forest habitats are, as already mentioned, numerous in type. However, most studies of CWC associated fauna have focused on *L. pertusa* (Jensen and Frederiksen 1992; Mortensen 2001; Mortensen and Fosså 2006; Henry and Roberts 2007; Purser et al. 2013), whereas few have focused on other CWC species (Buhl-Mortensen and Mortensen 2004a, 2005; Mosher and Watling 2009; De Clippele et al. 2015). The term "associated fauna" here is used to describe any animal found on or in a coral colony. Corals have a complex architecture that offers a great variety of microhabitats for other organisms, and provides substrata of different ages, and different stages of colonization. CWCs provide physical niches in terms of suitable substrate for sessile epifauna, or the coral skeleton and tissues may be inhabited by cryptofauna (hidden inside the skeleton) or endoparasites (e.g., arthropods, nematodes, fungi, or sponges). Sheltered cavities within a colony can contain organically rich sediments, while outer parts provide high water flow with little sedimentation smothering risk. The tree-like morphology of most corals allows their polyps to be elevated from the relatively still boundary layer close to the substratum into the faster flowing waters above (Wainwright and Koehl 1976). In addition, the orientation of colonies perpendicular to prevailing currents, which is common for many species, maximizes the volume of water passing the polyps (Wainwright and Dillon 1969; Mortensen and Buhl-Mortensen 2005). This enables the polyps in the colony to have maximum food access, an advantage that is passed on to any filter-feeding epizoic animal associated with the colony.

Branches of living corals can be foci for use by many invertebrates, which may either collect food directly from coral polyps or use the structure as a means to attaining a greater elevation in the water column (e.g., basket stars, galatheids, isopods, shrimp). Dead coral framework from gorgonians/antipatharians may provide suitable refuges for mobile fauna, such as galatheid crabs, shrimp, and small fish.

The structure of the corals, and the close proximity of colonies within a CWC forest, provide a range of turbidity regimes and flow patterns which may support a range of associated species. In low flow regions, fauna subsisting on small particulate material or dissolved material may find suitable habitats, whereas closer to the leading edge of forests or the peaks of colonies, areas of high flow and/or nutrient entrapping turbidity loops may be present. These two contrasting habitat niches may be separated within a CWC animal forest by just a few tens of cm, one of the many examples of high habitat heterogeneity in CWC forests.

As forests develop over time, coral colonies can grow or die off, as a consequence of nutrient delivery, external damage, environmental change, senescence, etc. These changes have a knock on effect on the flow conditions of a habitat and therefore there are temporal variations in the suitability of niches to various organisms. Extreme environmental changes have happened in the past during and following glaciation events when change in sea levels, as well as the change in food delivery following ice retreat, has been proposed as a factor in the waxing/waning of CWC animal forests on seamounts on the Irish margin (Rüggeberg et al. 2007). Areas at one time highly suitable for CWC animal forest development may become less optimal over a scale of centuries.

Trophic support and habitat provision differ with coral species and age of the host. Small species with no exposed skeleton, e.g., sea pens and broccoli corals, offer few habitats (De Clippele et al. 2015) whereas larger species with more complex branching patterns allows for provision of a greater number and diversity of habitats (Buhl-Mortensen and Mortensen 2005). As the host grows larger and older additional habitats are provided, e.g., pockets of detritus and exposed skeleton in old parts of the colony, and provision of access to elevated location with stronger currents and a higher food flux to the upper and outer parts of the colony (Tables 2 and 3). Below we present the general characteristics of associated fauna for three main types of CWC forest (sea pen stands, hard-bottom coral gardens, and *Lophelia pertusa* reefs) separately.

3.1 Sea Pen Stands

It seems like the fauna on sea pens in general is less abundant and diverse than for gorgonians (De Clippele et al. 2015). Sea pen associates are dominated by shrimps and ophiuroids, which use the sea pens as shelter and/or as feeding

Table 2 Overview of microhabitats provided by major biotic habitat-forming taxa and water masses where they mainly occur. X: most common. X: less common (From Buhl-Mortensen et al. (2010))

	Protista		Porifera		Octocorallia			Scleractinia	
Habitat	Xeno	Hexact	Demo	Calc	Penna	Alcyo	Gorgon	Soli	Col
Live tissue									
Inside						x	x	x	x
Outside	x	x	X	x	x	x	X	x	x
Exposed skeleton									
Inside									
Outside	x	X							X
Sheltered space									
Cavities	x	x	x	x					x
Canals	x		X						
Water mass (depth)									
Shallow		x	x	X	x	x	x	x	x
Intermediate	x	x	X	x	X	X	X	X	X
Deep	x	X	x	x	x	X	x	X	x

Xeno xenophyophoroidea, *Hexact* hexactinellida, *Demo* demospongia, *Calc* calcarea, *Penna* pennatulacea, *Alcyo* alcyonaria, *Gorgon* gorgonacea, *Soli* solitary, *Col* colonial

Table 3 Overview of habitat aspects (size, substrate flexibility, and 3-D complexity) of major biotic habitat-forming taxa

	Size		
	Small (<25 cm)	Medium (25–300 cm)	Large (>3 m)
Substrate flexibility			
Rigid	Solitary scleractinians, Xenophyophoroidea (some)	Colonial Scleractinia	Reef-forming scleractinians
Flexible	Porifera, Gorgonacea, Antipatharia,	Porifera, Gorgonacea,	
	Pennatulacea, Xenophyophoroidea	Antipatharia, Pennatulacea	Reef-forming sponges
Soft	Porifera, Alcyonaria, Xenophyophoroidea	Porifera, Alcyonaria	
Complexity (surface⁄volume)			
Low	Sponges, Gorgonacea	Sponges, Gorgonacea	
Medium	Solitary scleractinians	Sponges, Pennatulacea, Gorgonacea	
High	Xenophyophoroidea	Colonial Scleractinia	Reef-forming scleractinians

platforms (De Clippele et al. 2015). A role as nursery habitat for redfish has also been suggested (Baillon et al. 2012). The ophiuroid *Asteronyx loveni* is most common on *Funiculina quadrangularis*, which is used as a platform to reach better feeding conditions. The squat lobster *Munida sarsi* is often observed close to the sea pen *Kophobelemnon stelliferum* which presumably offers shelter against predators.

Off the Norwegian coast, De Clippele et al. (2015) observed 12 taxa on four sea pen species (*F. quadrangularis, Pennatula phosphorea, Virgularia mirabilis*, and *K. stelliferum)* and report that only a small proportion (5%) of studied colonies having associated fauna. However, a greater proportion (15%) of the colonies had organisms such as the squat lobster, *Munida sarsi,* occurring in close proximity.

The association between the *A. loveni* and *F. quadrangularis* is probably an example of obligate commensalistic relationship, which is relatively common for brittle stars and octocorals (Buhl-Mortensen and Mortensen 2004a; Mosher and Watling 2009). De Clippele et al. (2015) found that *Funiculina quadrangularis* was the only sea pen that hosted this brittle star, which occurred as solitary individuals on 7.5% of 278 inspected colonies. Only one colony hosted two individuals. The brittle stars were found predominantly on the central or upper parts of the colony with only two specimens observed in the lower part of the colony. Most individuals extended one to four arms out from the colony.

3.2 Hard-Bottom Coral Gardens

The widespread cold-water gorgonians *Primnoa resedaeformis* and *Paragorgia arborea* host a rich fauna in the Atlantic. *P. resedaeformis* is a bush-forming coral that can occur in dense tickets on rocks and boulders. Maximum height is around 1 m, which a colony would need at least 70 years to reach. This coral deposits annual rings within its skeleton, just like a tree, which can be used to determine the age of the colony (Sherwood and Edinger 2009) (see also ▶ Chap. 22, “Growth Patterns in Long-Lived Coral Species”). A parasitic anemone (*Epizoanthus* sp.) can take over the skeleton of this coral when the skeleton is exposed due to tissue damage (Fig. 4). The anemone, which has been mistaken for a coral, can cover whole colonies. The anemone received an increase in three-dimensional space from the coral skeleton, together with better access to food particles.

P. arborea forms larger “trees,” white, pink, or red in color on boulders or bedrock. This gorgonian can reach a height of at least 2 m. A coral of that size is probably more than 100 years in age (Mortensen and Buhl-Mortensen 2005).

Many associated species thrive on the corals or in their vicinity. Basket stars (*Gorgonocephalus lamarckii, G. eucnemis*, and *G. caputmedusae*) can be found on the outer branches of *Paragorgia* (Fig. 5). This is a brittle star belonging to the group Gorgonocephalidae (“Gorgon-headed”), which is named after the snake-haired sisters of Greek mythology. The basket star snags plankton and other organic

Fig. 4 Cold-water coral reefs off Ghana display many similarities with Lophelia reefs from the Northeast Atlantic. The red fish in this image is a blackbelly rosefish (*Helicolenus dactylopterus*) (Image courtesy: Bjørn Serigstad, Institute of Marine Research, Norway)

Fig. 5 A parasitic anemone (*Epizoanthus* spp.) may take over the skeleton and gain increased three dimensionality and better access to food particles. In the Northeast Channel, off Nova Scotia, *Epizoanthus* cf. *americanus* has been observed as a parasite gradually overgrowing and killing *P. resedaeformis* (Buhl-Mortensen and Mortensen 2005)

particles in its canopy of branching arms and ushers them to its mouth on the underside of the center disk. Redfish (*Sebastes* spp.) are often hiding amongst the coral colonies. These fishes often have prolonged periods of resting on the bottom when they need to hide from predators and strong currents.

The cold-water gorgonians offer different microhabitats for both sessile and mobile invertebrates. Buhl-Mortensen and Mortensen (2005) identified two main types of microhabitats on the colonies: "Habitat 1," young parts of the colony covered with live tissue and "Habitat 2," old or dead parts of the colony with detritus deposits and exposed skeleton.

3.2.1 Paragorgia

Habitat 1

Young and live substrate. Organisms are found both on the surface of the colony and inside the polyps or skeleton. In general few species are associated with this habitat, and the most common organisms are parasitic copepods. On the surface, a parasitic lichomolgid copepod may occur in hundreds on a single colony. Inside polyps on the branches of outer parts of the colonies a lamippid copepod, *Gorgonophilus canadensis* lives endoparasitically (Buhl-Mortensen and Mortensen 2004b). The copepod induces malformation in the producing gall-like structures containing egg sacks, large females, and several smaller males. The echinoderm *Gorgonocephalus lamarckii* seems to be associated with high velocity current to which the branches of *P. arborea* are exposed. *G. lamarckii* specimens on *P. arborea* are predominantly large individuals with disc diameters of 1.5–6 cm. Buhl-Mortensen and Mortensen (2004b) observed 15 individuals on one large *P. arborea*. Various sea anemones may also be attached to the colony branches and polynoid polychaetes occasionally observed clinging firmly to the surface of the coral.

Habitat 2

Old and dead substrate. Here, particulate deposits are commonly observed between the basis of branches. In these parts of the colony, with thick branches, the pigmented outer living tissue can disappear and the spongy, pale skeleton is exposed. Organisms may be found both on the surface and within the skeleton of the coral. Polychaetes belonging to the families Sabellidae, Nereidae, and Polynoidae may be present in burrows within the skeleton. In detritus laden areas, the amphipod *Ischyrocerus megacheir* may use the organic particles to build nests. Hydroids are sometimes found close to the center of the fan-shaped colonies, attached to small areas of exposed skeleton. The hydroids in turn are hosts to a number of secondary associates such as cirripeds, foraminifers, amphipods, ostracods, isopods, and mites.

3.2.2 Primnoa Resedaeformis

Habitat 1: Young and Live Substrate

In this species as well, associated species can be found both on the surface of the colony as well as inside the polyps. In general, species richness of this habitat is quite low. The shrimp *Pandalus propinquus* may be found on the branches and mites can be observed on close examination on the surface. The parasitic lamippid copepod *Enalcyonium* cf. *olssoni* probably living inside the polyps is frequently encountered. Male and female decapods (*Dorhynchus thomsoni*) have also been reported in this habitat.

Habitat 2: Old and Dead Substrate

In *Primnoa*, this habitat is represented by its hard-exposed skeleton which is the substratum for many sessile epizoans. The skeleton is often colonized by hydroids, molluscs, bryozoans, foraminifers, and cirripeds. A parasitic anemone, *Epizoanthus* sp., sometimes covers large parts of the skeleton in the western Atlantic. Amphipods and isopods are often found amongst hydroids, together with the cirriped *Ornatoscalpellum stroemii*. A rich fauna of foraminifers occur in this habitat, some of which are attached to the hydroids. Several bivalves (especially Anomidae and Pectinidae species), cirripeds, and bryozoans also often occur attached to the coral skeleton. The exposed skeleton may also be colonized by octocorals such as smaller and more rare gorgonians.

4 Cold-Water Coral Reefs

Of all CWC fauna, the framework forming scleractinian species have been the most extensively studied, particularly *L. pertusa*, the most abundant framework forming coral in European waters (see also ▶ Chaps. 8, “Global Biodiversity in Cold-Water Coral Reef Ecosystems” Henry and Roberts and ▶ 25, “Framework-Forming Scleractinian Cold-Water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective” by Wienberg and Titschack in this volume). However, this species is common elsewhere in the Atlantic Ocean, and studies are being undertaken in regions where this coral was little known such as western Africa (Le Guilloux et al. 2009). Figure 6 illustrates that CWC reefs off Ghana display many similarities with *Lophelia* reefs from the Northeast Atlantic.

The framework forming species can produce sizable calcium carbonate structures over time, with overall morphology dependant on seafloor composition and substrate, regularity of flow direction, food abundance and food quality, as well as a host of other environmental conditions. In these highly complex ecosystems, a number of microhabitat categories can be identified, each providing useful niches for a range of organisms. Below we present the two main habitats within CWC reefs.

4.1 Habitat 1: Live Coral Zone

Commonly in scleractinian CWC reefs, a distinct region of the structure is thickly covered with live coral polyps. This is usually the area most regularly exposed to freshly transported nutrients in suspension, i.e., facing into the prevailing current (Fig. 7). Where current direction is near uniform, “cigar” shaped reefs may form (Buhl-Mortensen et al. 2010), whereas in locations with more varied current flow

Fig. 6 The Basket star (*Gorgonocephalus* sp.) uses the coral to get access to food particles (Photo courtesy: MAREANO/Institute of Marine Research)

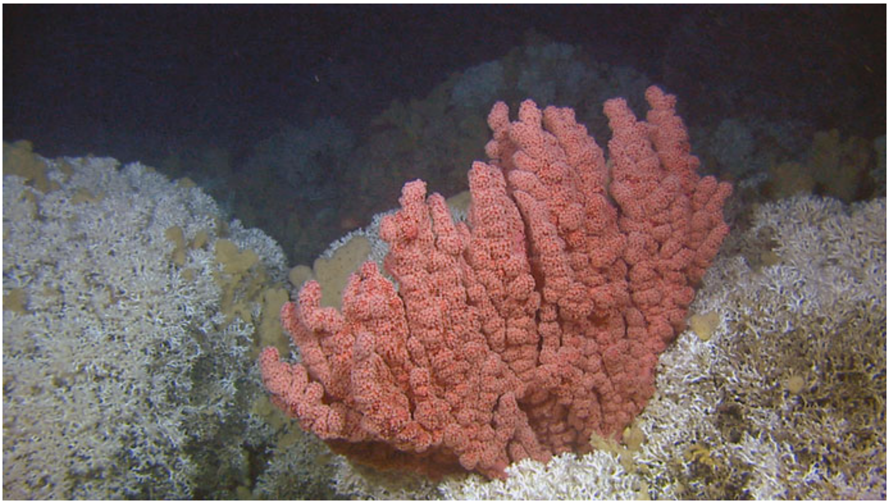

Fig. 7 Animal forests often occur as a mosaic of habitats, and on the *Lophelia* reefs off Norway, the gorgonian *Paragorgoia arborea* commonly occur in higher densities than in other habitats. The orientation of the colonies indicate the main prevailing current direction. Here this is especially evident in the red *Paragorgia* colony, growing in the middle of a live *Lophelia* colony (Photo courtesy: Institute of Marine Research, Norway)

conditions, this living reef habitat may form the flanks of seamounts or the crests of coral ridges. In contrast to shallow-water scleractinian reefs, CWC reefs are formed by one or few scleractinian species in a particular location. The live reef habitat is a useful area to colonize or utilize for filter feeders requiring exposure to elevated currents, and several species of fish, shrimp, and various other arthropods may occupy the coral surface to reach higher flow conditions. Protected by a thin layer of living tissue (coenosarc) sessile filter feeders find colonization of this habitat difficult, though damage to the reef can expose skeleton to colonization by the gorgonians *Paragorgia arborea* and *Primnoa resedaeformis (*as well as other filter feeders such as hydroids and bivalves, e.g., *Acesta excavata*) and the sponge *Mycale lingua* in European waters (Purser et al. 2013), with other species occupying such locations elsewhere in the world ocean.

4.2 Habitat 2: Dead Coral Zone

As a scleractinian reef develops the living fringe of coral is overgrown by subsequent generations better placed to extract material from the water column. Previous generations die, presumably due to reduced water flow and food supply, with retreating coenosarc coverage opening the skeleton to colonization. As mentioned for gorgonian corals, these exposed skeleton regions offer opportunity for internal colonization of structures by parasitic sponge, fungi, and anemones, with these organisms extending internally within the coral structure to attack still-living polyps. The skeleton also provides structural refuges for fish and other mobile fauna and provides substrate for colonization of sessile suspension feeders. This part of the reef is the most diverse, with microhabitats of coral skeletons at various ages, allowing for simultaneous presence of parallel successions of communities (Fig. 8).

Fig. 8 The diversity of species is highest in the dead coral matrix zone of CWC reefs. Here live *Lophelia* also occur but much less extensive than in the live zone. New surface from dying corals are constantly made available to new settlers, and new and old substrates are found side by side (Photo courtesy: Institute of Marine Research, Norway)

Commonly, the upper regions of dead coral, close to the live coral zone, are preferentially occupied by suspension feeders such as hydroids and anemones.

4.3 Habitat 3: Rubble Zone

Following death, the coral structure is slowly degraded by physical and biological action, and depending on local conditions, a potentially extensive region of seafloor surrounding habitats 1 and 2 can become covered in a mix of broken coral fragments and deposited sediments. This can provide a range of habitat niches for infauna and sessile filter feeders. In areas downstream of CWC reefs colonization by ophiuroids, soft corals, sponges, anemones, or other filter feeders can be extensive. The rough topography of this habitat provides turbulent bottom flow conditions, which allow for regular resuspension of entrapped materials.

5 Cold-Water Coral Forests as Feeding Place and Nurseries for Fish

The majority of studies of fish in coral forests suggest that the presence of CWCs supports high abundance and diversity of fish assemblages, whereas some studies report that the existence of such a relationship is ambiguous (Biber et al. 2014). Coral forests provide habitat for associated fish species and support high diversity and abundance of potential prey species for fish (Mortensen et al. 2005) Kutti et al. (2014) report a generally higher abundance of fish in and around Norwegian CWC reefs, but they also point out that these elevated populations are transient, and that the habitats do not seem to be essential for most commercial and observed fish species. A similar pattern is also reported from Mediterranean CWC reefs and adjacent habitats (D'Onghia et al. 2012) – utilization being opportunistic rather than essential within the lifecycle of the fish. There are not many studies on the diet of fish in coral forests, but Husebø et al. (2002) compared the stomach content of redfish (*Sebastes marinus*), tusk (*Brosme brosme*), and ling (*Molva molva*) caught on reefs with the same species caught in other habitats. They report that these fishes tend to be larger on the reefs. The diet of the three fish species included the same prey groups in all habitats, but prey differed at the species level.

Tusk is common on NE Atlantic CWC reefs, utilizing small caves in the coral framework, in which to rest, hide, or prepare ambush attacks on potential prey. Whereas tusk seem to be using reefs as their preferred feeding habit, redfish are more likely to use the reefs as a resting place to ride out periods of strong currents. There are indications that zooplankton and other particles are concentrated over CWC reefs (Mienis et al. 2014). For redfish, these potential prey organisms are not available during the periods of a tidal cycle when the current is at its strongest. During such times the fish can be observed resting between coral colonies. During slack tide,

Fig. 9 A colony of *Paragorgia arborea* with 26 eggs of deep-sea catshark (*Apristurus profundurum)* collected with bottom trawl at around 500 m depth in the Northeast Channel, Nova Scotia, 2002

however, the redfish can be observed up in the water feeding on larger zooplankton (Dons 1944, Buhl-Mortensen et al. 2015a).

Ray eggs are often found on gorgonian corals where they are firmly fastened and receive a high flow-through of oxygenated waters (see also ▶ Chap. 8, "Global Biodiversity in Cold-Water Coral Reef Ecosystems"). Figure 9 shows a colony of *Paragorgia arborea* with 26 eggs of deep-sea catshark (*Apristurus profundurum*). As mentioned previously, sea pens have been found with red fish larvae attached (Baillon et al. 2012). Juvenile fish have not been commonly observed in coral forests but there is a chance that this is an underrepresentation if the juvenile fish lives largely cryptically. There are many reports of juvenile basket stars (*Gorgonocephalus* spp.) amongst the branches of the so-called broccoli corals (Fig. 10) (Mortensen 1927; Buhl-Mortensen and Mortensen 2004a), hiding from predators in an elevated position from the seafloor and also benefitting from increased flux of suspended food particles.

Fig. 10 “Meadows” of cauliflower coral (*Drifa glomerata*) off Norway is a nursery habitat for juvenile basket stars (*Gorgonacephalus* spp.) (Photo courtesy MAREANO/Institute of Marine Research)

6 The Role of Symbionts

Symbionts are species that are restricted to association with certain taxa for their existence. These could be parasites, commensals, or mutualistic symbionts. The composition of associated fauna is in general not host specific but consists mainly of species also occurring in other habitats. Exceptions are a few highly specialized parasites. Most associated species use the corals as substratum or refuge with few utilizing the coral as a food source.

Polynoidae (Polychaeta) is the most common family of symbiotic polychaetes on CWCs. Many of the species are obligate to antipatharian and gorgonian corals (Buhl-Mortensen and Mortensen 2004a). One peculiar example of such symbiosis is the polynoid *Harmothoe oculinarum* living on *Lophelia pertusa*, often inside tubes of the polychaete *Eunice norvegica* (Jensen and Frederiksen 1992; Mortensen 2001). The polychaete is bright white and blends in with the coral. *Eunice norwegica* commonly feeds on food particles captured by the coral’s polyps (Mortensen 2001). However, it also exhibits behavior which is highly beneficial to the coral, by cleaning the coral surface and attacking invading mobile organisms (Mortensen 2001). Furthermore, it stimulates the coral’s calcification processes (Mueller et al. 2013). The enhancement of calcification is also thought to strengthen the coral skeleton. *E. pennata* and *E. dubiata* are reported as facultative kleptoparasitic commensals or mutualists on *Madrepora oculata* (Martin and Britayev 1998). Another example of obligate mutualistic symbiont is the polychaete *Haplosyllis anthogorgicola,* which is reported from the gorgonian species *Anthogorgia bocki* in the Japanese seas (Utinomi 1956). *Lumbrineris flabellicola* is perhaps the polychaete with the widest array of coral hosts in deep water. It is an obligate commensal on cnidarians, mainly scleractinians, but also occurs on unidentified hydroids and zoantharians (Zibrowius et al. 1975). It has been recorded on 22 scleractinian species in the Pacific and Indian Ocean (Miura and Shirayama 1992; Zibrowius et al. 1975; Cairns and Zibrowius 1997).

7 Coral Associates in Cold Versus Warm Waters

Corals in the cold deep are obviously lacking zooxanthella (symbiotic algae), which are so characteristic for warm shallow-water coral reefs. This also reflects a big difference in trophic structure with implications for the composition of functional groups of species. Obligate associations between species are rare among associates with cold-water scleractinians, a great contrast to the many examples of symbiotic associations between various taxa and reef-building corals in warm water. Interestingly, there are more examples of obligate association for octocorals than for hexacorals (the reef builders) in cold water. The fauna associated with CWC consists mainly of sessile suspension feeders. However, there is also a rich associated mobile fauna consisting of both deposit feeders and predators. For cold-water gorgonians, this fauna may be richer than what can be found on tropical gorgonians (e.g., Goh et al. 1999). This fauna is dominated by crustaceans both in abundance and number of species. The abundance and diversity of associated fauna is positively correlated to host morphology (e.g., number of branches and height of colony) both for warm-water gorgonians (Abele and Patton 1976) and cold-water gorgonians (Buhl-Mortensen and Mortensen 2005).

Buhl-Mortensen and Mortensen (2005) compared results on fauna associated between two species of cold-water gorgonians (*P. arborea* and *P. resedaeformis*) off Nova Scotia and 16 species of shallow-water gorgonians on coral reefs in Singapore (Goh et al. 1999). Characteristic for both warm- and cold-water-associated fauna was the dominance of amphipods and frequent occurrence of parasitic copepods. Interestingly, the associated fauna of the two cold-water gorgonians comprised more species and a higher abundance than of the warm-water associates.

While the peracarid fauna seems to be richer on cold-water gorgonians, the decapod fauna on the tropical corals is richer than observed on the cold-water gorgonians. Some of the differences in observed faunistic composition might be due to sampling methods (SCUBA diving vs. ROV). However, for the decapods fauna the high number of associates of shallow-water tropical gorgonians probably reflects the high diversity of decapods in general in these waters. As mentioned above, many of the species associated with tropical corals are obligate (Patton 1972, and references therein), while most species found on the deep-water corals are facultative symbionts (Buhl-Mortensen and Mortensen 2004a). However, many of the species associated with the corals are much less common in other habitats. Several conditions of the North Atlantic deep-water coral habitat can be used to explain this general pattern, including time needed for development of such relationships, frequency of disturbance, and variability of nutrient supply. In general, interspecific obligate relationships are less common for high-latitude biotopes, compared to the tropics (Karr 1971; Rhode 1978; Beaver 1979). At present, CWC ecosystems have been less studied for tropical areas than areas at high latitudes. It is therefore uncertain whether the lack of obligate relationships in CWC forests simply is a false impression or this remains a fundamental difference between the warm and the cold coral ecosystems.

8 Conclusion

The diversity of CWC forests is great with respect to species composition of habitat forming and associated species, habitat heterogeneity across spatial scales, and trophic ecology. Even though the trophic ecology of CWC is not fully understood, it is clear that they utilize a wide array of food sources, which partly explain the wide environmental range of their habitats. As the food supply to CWC forests rely largely on particulate matter transported by currents, the seabed topography is an important factor creating optimal conditions for particle concentration and retention for several types of CWC forests. Similarly, the morphology of CWCs and the habitats they develop is crucial for food supply for themselves as well as their associates. Tidal variation of current velocities seems to be important for creating "feeding windows" for species with different optimal current speeds for particle capture. The perceived image of cold-water coral ecosystems as less diverse, with few examples of obligate association between various species and their coral host, may not completely reflect the real picture. To reveal whether there is a fundamental coevolutionary difference between cold- and warm- coral ecosystems, more studies on CWC ecosystems in tropical waters are needed.

9 Cross-References

- ▶ Animal Forests of the World: an overview
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Energetics, Particle Capture, and Growth Dynamics of Benthic Suspension Feeders
- ▶ Filter-Feeding Zoobenthos and Hydrodynamics
- ▶ Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles

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Part III

Animal Forests Under Threat

Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems

33

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Abstract

Animal forests form the foundation of many important marine benthic habitats. However, a near ubiquitous lack of long-term scientific data raises significant challenges in assessing how these communities have changed over time in response to human impacts and how they might respond to future perturbations. To address these questions, alternative sources of data have to be gathered. Marine historical ecology is a rapidly growing field of research that uses historical sources to challenge our assumptions about what is natural in our marine environments. This discipline thus has the potential to fill some of the gaps in our understanding of animal forests through time. This chapter reviews how historical ecology research helps us to better understand the changes that have occurred in marine animal forests, focusing in particular upon oyster and shallow-water coral communities. The variety of data sources available and the methodologies that have been used to uncover past changes in these and related ecosystems are highlighted. The use of historical data to inform restoration efforts and emerging concepts in marine ecology, such as ecosystem service provision, is examined. Finally, the limitations of historical data and remaining knowledge gaps with regard to past animal forest communities are discussed.

Keywords

Benthic communities • Demersal trawling • Exploitation • Historical ecology • Marine fisheries

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Contents

1 Introduction

It is widely recognized that much of wild nature today is vastly altered as a result of human impacts (Barnosky et al. 2011; Jackson and Sala 2001). Yet many of these changes took place long before the advent of monitoring or rigorous scientific surveys (Jackson et al. 2001; Roberts 2007). The longer-term perspectives promoted by the study of historical data provide a greatly enhanced understanding of the scale and trajectory of changes undergone in natural environments, as well as what has driven these changes.

The animal forest is defined as a living three-dimensional structure made up of benthic, sessile marine species such as cnidarians, sponges, and molluscs (Rossi 2013). This structure is usually dominated by ecosystem engineers, species that physically create, modify, or maintain habitats upon which other species depend and, through which, the benthic community is formed and regulated (Jones 1997). Animal forests are particularly sensitive to change, both as a result of the destructive techniques often used to exploit these diverse structures and their often slow recovery times (Rossi 2013). Numerous drivers including pollution, land reclamation, mining, direct harvesting, and demersal trawling have contributed to the degradation and decline in animal forests (Rossi 2013). The impact of demersal trawls on sensitive benthic habitats is widely documented (Hutchings 1990; Jones 1992), and the frequency and scale of contemporary trawling activities, and available historical information (e.g., Kerby et al. 2012; Thurstan et al. 2010), indicates that these impacts are both large scale and severe. Certainly the exploitation of animal forests or the exploitation of their associated fauna has resulted in the global loss of large expanses of structured benthic habitats (Beck et al. 2011; Watling and Norse 1998). As a result, much of the trawled seafloor now has a low habitat complexity and diversity, and some areas formerly constructed of biogenic hard substrates, such as mussel beds, oyster reefs, and coral, have been converted to two-dimensional soft bottoms (Koslow et al. 2001). The impacts, however, are not restricted to the loss of solid structures; it is likely that even soft-bottom communities were once more complex, diverse, and productive (Bradstock and Gordon 1983). In all cases, the lack of baseline data represents a significant challenge both to our biological understanding of these habitats and our understanding of the environmental impacts of current management.

Our understanding of the important role of the animal forest in the ecology of the oceans remains limited, not only because of a poor understanding of our impacts upon them, but because by their subtidal nature, they are challenging to survey. While the mapping of benthic habitats has been the subject of increasing effort in recent years, the focus has been on the hydrological and geomorphological elements of habitats. Such work rarely includes information on the distribution of animal forests. Even where direct sampling of the benthos has allowed for detailed mapping of the distribution of animal forests, the potential changes that have likely occurred in marine habitats as a result of human impacts make it critical that contemporary maps are not accepted as a baseline for future management. Degraded habitats often exhibit low structural heterogeneity and tend to support a less diverse and less productive community (Heck et al. 2003). Therefore, to accept the current status as an ecological baseline would likely result in an undervaluing of our marine ecosystems relative to their potential.

While much still remains to be understood, the critical role of marine autogenic engineers was recognized as early as the nineteenth century. Möbius (1883), for example, not only described beds of the native European oyster, *Ostrea edulis* L., and associated species as forming a "biocönose," a rich biotic community dependent upon the structure of the oyster beds (as such embodying much of the concept of the animal forest), he also went on to use forests as an analogy for this habitat building bivalve. The primary motivation for this comparison was to draw attention to the widespread destruction of the oyster beds themselves:

> *As man has uprooted the greatest forests, so can he also annihilate the richest oyster beds* [...]. *The preservation of oyster beds is as much a question of statesmanship as the preservation of forests.* (Möbius 1883)

This destruction, however, continued more or less unabated, and as a result oyster beds are now extirpated throughout much of their original range (Beck et al. 2011). This widespread loss of oyster habitat presents three challenges, which we contend are representative of a whole host of formerly abundant animal forests. Firstly, the true historical extent of this habitat is exceedingly poorly known. While records of historical locations exist, there are few if any locations where the historical extent of beds of *O. edulis* is known. Secondly, the nature, e.g., natural density, size distribution, and population dynamics, of this habitat is largely unknown, which presents a real challenge for restoration and management. And, finally, the composition of the community associated with this once abundant animal forest is also unknown, making it challenging to set restoration or recovery goals or to present evidence of the likely biodiversity and ecosystem service benefits associated with such investments.

This chapter discusses how the field of marine historical ecology has the potential to address some of these challenges and, by improving our understanding of the species and communities that used to occur, provide novel insights for the future management of animal forest communities.

2 Using Historical Data to Understand the Past

Marine historical ecology is a field of research that aims to document and interpret long-term change in marine ecosystems (Lotze and Worm 2009). It provides an understanding of the species and communities that used to exist in our oceans, how these have altered over time, and what has driven these changes (Jackson et al. 2001). Historical ecology therefore has a critical role to play in the future management of the animal forests on our seafloor. Researchers use a range of approaches to unravel long-term change – often using data sources that are unconventional to marine resource management – to provide insights into past ecosystems. The timescale studied, resolution, and interpretation of data all vary depending upon the sources and methodologies used.

Historical data sources may provide information as simple as the past presence of a species, or they may present enough detail that we can observe nuanced shifts in community composition over time. Some of the most pervasive and earliest impacts upon marine ecosystems occurred through fishing (Jackson et al. 2001). While the majority of animal forest communities were rarely recorded in fishing statistics, a few habitats, such as oyster reefs, were both rugous and valuable enough to map and sample as early as the late 1800s in some regions (zu Ermgassen et al. 2012; Fig. 1). Occasionally, these data sources are able to provide quantitative estimates of what has been lost, such as along the United States coastline, where areal extent and density, as well as the size composition of historical oyster reefs has been calculated (zu Ermgassen et al. 2012). When compared with contemporary measurements, these historical data provided evidence for a 64% decline in the spatial extent of oyster habitat and an 88% decline in oyster biomass since the late nineteenth century.

While continuous time series of landings are not always available, even for these commercially important species, researchers have used fishery data together with other historical sources to evaluate the magnitude and timing of change. For example, Kirby (2004) used historical proxies derived from fishery records and legislative changes to evaluate the expansion and collapse of oyster fisheries throughout North America and eastern Australia. He showed that fishery collapse began in estuaries nearest to developing urban centers before spreading along the coast. Alleway and Connell (2015) synthesized fishery statistics, charts, and archival accounts to assess the historical distribution and abundance of oysters along the coast of South Australia. They found that prior to intensive fishing activities and coastal development oysters were distributed across more than 1,500 km of coastline. Today, these native oyster reefs no longer exist and little mention is made of them in contemporary records.

Marine sponges from the genus *Hippospongia* and *Spongia* are another benthic community that has long been targeted, this time for their skeletons that, once dried, are used in households, medical, and manufacturing industries. Sponge fishing has a

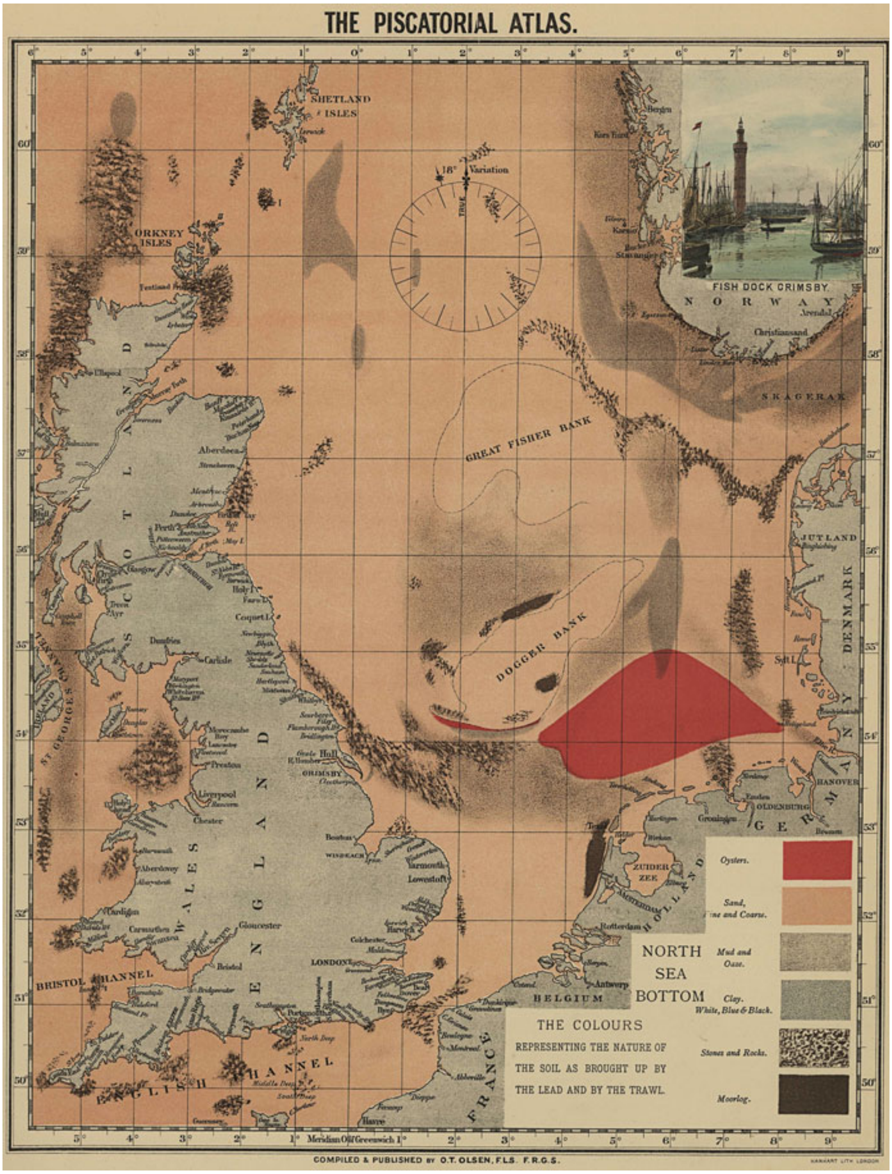

Fig. 1 The extent and location of oyster (*Ostrea edulis*) beds (shown in *red*) in the southern North Sea during the nineteenth century (Olsen 1883)

long history in the Mediterranean and the Caribbean (Josupeit 1990), and although their importance has declined since the advent of plastic, targeted fishing still occurs in these regions (Josupeit 1990). Despite their historical significance few early landings data exist, and researchers have instead had to synthesize disparate fishery and archival data sources to understand trends over time. For example, McClenachan (2008) used such sources to describe how high levels of fishing effort resulted in the overexploitation of sponges in the Florida Keys. While historical extent and density of the sponge beds can only be inferred from the data sources available, this research suggested that synergistic stressors, in this case, overexploitation in combination with disease outbreaks, led to declines in sponge populations from which they were unable to fully recover (McClenachan 2008).

While fishery records (however sparse) exist for some animal forest communities, many such communities were perceived to have little direct value as a resource and as such were never recorded in fishery or survey data. For example, North Sea fishery records exist for the last 100 years, but these rarely recorded the presence or abundance of noncommercial species. Likewise, changes to coral reefs and their associated communities were rarely monitored until the 1980s. As a result we have very little idea to what extent present-day benthic communities differ from those that existed prior to the intensification of fishing and other anthropogenic activities. In some cases, alternative sources of data have been sought by researchers to better understand these changes over time.

For example, Rumohr and Kujawski (2000) identified museum collections that housed specimens collected from scientific surveys undertaken in the North Sea at the beginning of the twentieth century and compared these with survey data sampled 80 years later, in 1986. Between these periods levels of fishing effort in the North Sea intensified greatly (Engelhard 2008). Analyses revealed some distinct differences in the types of species present in each of the two time periods. Over time significant declines were observed in virtually all species of bivalve, while scavengers and predators such as crustaceans and sea stars occurred more frequently in the latter period. The authors attributed this to fishery impacts, which are likely to have favored scavenging species. While these historical data do not present a pre-fished system, they do provide insights into North Sea ecosystems prior to the intensification of fishing activities and suggest that significant community changes have occurred (Lindeboom and de Groot 1997).

Although underwater photography has a relatively short history, precluding its use in historical studies of subtidal habitats, photographs of intertidal habitats exist for some locations from the late nineteenth century onwards. Photographs taken by Saville-Kent (1893) provide some of the earliest pictures of Australia’s Great Barrier Reef shallow-water coral communities. Over 100 years later, Wachenfeld (1997) recreated Saville-Kent’s photographs, with the aim to determine whether broad ecological changes had occurred over this period (Fig. 2). Although firm conclusions were unable to be drawn from these two snapshots in time, with trends differing for the 14 locations for which temporal comparisons could be made, these photographs nevertheless provide a rich and important source of historical data on a benthic community for which few other historical archival records exist.

Sediment cores and isotopic dating methods have also been used to understand long-term changes in benthic communities. Edgar and Samson (2004) identified

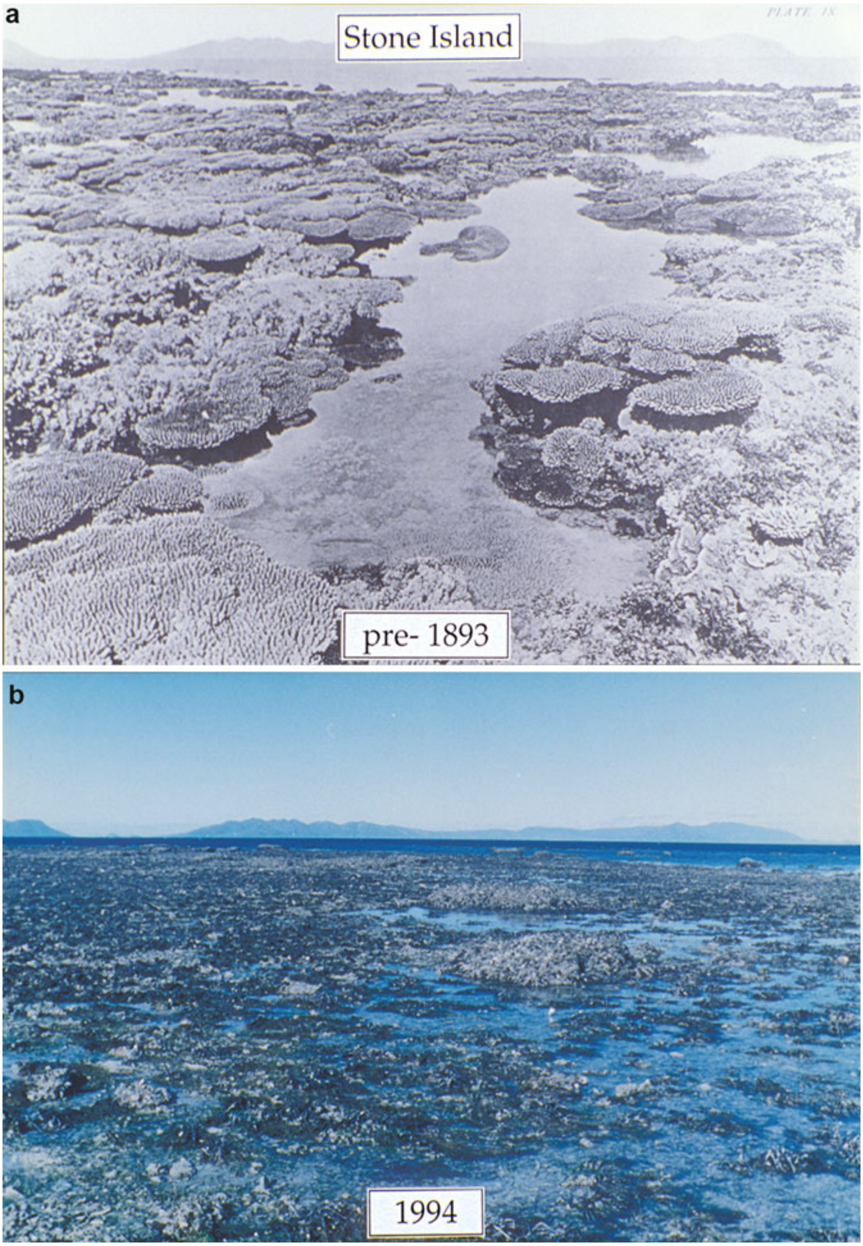

Fig. 2 A coral reef flat during low tide, at Stone Island, Queensland, Australia, in (**a**) 1893 and (**b**) 1994 (Copyright Commonwealth of Australia (Great Barrier Reef Marine Park Authority) (Photographers: W. Saville-Kent and A. Elliott))

mollusc shell remains collected from sediment cores in Tasmania. Using Pb-210 and Cs-137 isotope-dating analysis, they were able to show that species richness and abundance declined significantly over a period of 120 years and noted that the timing of decline correlated with the onset of a dredge fishery in the early twentieth century. Trawling and dredging have also been associated with bivalve declines in the northern hemisphere (Bradshaw et al. 2002; Thurstan et al. 2013).

Fossilized remains of coral reef communities have also been used to set more recently observed ecosystem changes into context. In the Caribbean, coral cover has rapidly declined in recent decades, and its composition was fundamentally altered in the 1980s by the virtual elimination of the once dominant elkhorn (*Acropora palmata*) and staghorn (*A. cervicornis*) coral species. However, sampling of fossil coral reefs suggests that large shifts in community composition are not representative of coral reef community dynamics over long timescales (Pandolfi and Jackson 2006). Rather, the fossil record shows that historical communities displayed remarkable persistence in their community structure over time, with the two *Acropora* species dominating shallow coral reef environments in the Caribbean for hundreds of thousands of years. This suggests that the changes occurring to modern Caribbean coral reefs are a novel response, most likely due to the cumulative effects of human impacts (Pandolfi and Jackson 2006).

While the drivers of change in many historical studies tend to be inferred by correlation, improved or more refined techniques can help us make stronger assertions regarding the most likely drivers. For example, high-precision dating tools have been used to determine the timing of change in east Australian coral reef communities and put forward strong evidence about the drivers of change. A study by Roff et al. (2013) uncovered a previously undocumented collapse of a once dominant species of coral in the central Great Barrier Reef. The accuracy of the dating techniques used enabled the authors to tie shifts in coral composition to land clearance and subsequent declining water quality following European colonization. Coral communities from earlier time periods showed no such shift, suggesting that this collapse was unprecedented in the historical record. Similarly, Lybolt et al. (2011) demonstrated that the composition of marginal coral reef communities present in a coastal embayment south of the Great Barrier Reef – while subjected to more natural variability as a result of changing sea levels – also significantly altered in the decades following European colonization. In the Caribbean, Cramer et al. (2012) used coral and molluscan death assemblages and radiocarbon dating to demonstrate that reefs near Bocas del Toro, Panama, which are known to have suffered from recent (post-1980s) regional episodes of bleaching and disease, were also heavily impacted by deforestation activities prior to 1960.

3 Using Historical Data to Set Restoration Goals

Ecological restoration (the assisted recovery of a past community) is an increasingly important conservation management intervention, especially where habitats are widely degraded and protection alone is not enough. One key conservation and

Fig. 3 Oyster shells outside a cannery at Baltimore, MD (year unknown). Pictures such as these help our understanding of the scale of oyster removal during the nineteenth and early twentieth centuries (Source: NOAA: Image ID: fish6863, NOAA's Historic Fisheries Collection)

policy use of historical information is to provide context against which restoration and conservation management goals can be set. The field of historical ecology therefore has a significant role to play in informing marine restoration efforts.

Marine ecosystems such as animal forests present a significant challenge to the practice of ecological restoration. As highlighted earlier, very few historical marine datasets allow for the quantitative delineation of benthic habitats such as animal forests. This makes estimating the extent of loss of animal forests near impossible, although exceptions exist (e.g., zu Ermgassen et al. 2012). Furthermore, the attributes (e.g., density, size distribution, community composition) of the degraded or lost animal forests are even more challenging to reconstruct with historical data. A lack of information on the absolute habitat extent and quality presents a challenge to setting restoration goals, but historical ecology can nevertheless inform restoration by highlighting the plight of threatened animal forests. Absolute or quantitative data are not required to help build a compelling case for investing in more of a highly threatened or near extirpated habitat type (Fig. 3). Relative abundance or perceived local declines can be used to communicate the status of animal forests and to engage with stakeholders. Fostering an understanding of the status of a habitat is often enough to gain the support of stakeholder champions, which are critical in progressing restoration efforts at all scales.

Quantitative or relative goals can nevertheless be more powerful than those based on a qualitative or perceived need to restore. Numerous oyster restoration goals in the United States have, for example, been based on regaining a given proportion of the historical extent. Management plans for Chesapeake Bay call to restore 10% of the historical oyster reef area (Chesapeake Research Consortium 1999). It could, however, be argued that such goals are nevertheless arbitrary; there is often no particular justification for setting the goal at, say, 10% of historical extent as opposed to 20%. Here again historical ecology can play a role. Historical ecology can provide a picture of the past ecological importance of degraded animal forests, thereby allowing modern stakeholders and decision-makers to better understand the opportunities and benefits different extents of restoration might yield.

Oyster reefs in the United States provide an example of an animal forest for which historical ecology is helping to set ecologically meaningful large-scale restoration goals. Oyster reef restoration is now commonly undertaken along all US coasts, and the scale of restoration has increased dramatically over the past decade as the science behind delivering successful restoration has developed (Schulte et al. 2009). As the size of restoration projects increases, so does the need to set large-scale goals. These goals are best set in the context of past extent, but given the high cost of restoration efforts, stakeholders are commonly seeking more justification for the expense. Understanding the historical ecosystem service delivery associated with a particular habitat type can provide an alternative metric for goal setting.

In the case of oyster reefs, one commonly cited impetus for restoration is to enhance water quality or clarity. Oysters are filter-feeding bivalves that draw particles from the water column to the benthos, hence increasing water clarity. By interpreting historical fishery survey data, scientists were able firstly to build up a quantitative overview of the historical abundance of oysters in US estuaries (zu Ermgassen et al. 2012) and then to estimate the historical large-scale ecological impact of these filter-feeding bivalves (zu Ermgassen et al. 2013a, b). This large-scale impact was assessed by estimating the rate of water filtration by the historic oyster population relative to the residence time of each estuary. Oyster populations that were capable of filtering a volume equivalent to or greater than the volume of the estuary within the residence time of the estuary were likely to have had an ecological impact on an estuary scale (Dame 2011). The oyster population in most estuaries today is too small to exert such a filtration pressure (zu Ermgassen et al. 2013a; Fig. 4). This analysis, however, allowed estuaries to be identified for which aiming to achieve such a large-scale impact of filtration may be appropriate. In this case, numerous estuaries on the Gulf of Mexico coast of the United States were identified as historically having been ecologically dominated by oysters in this way, whereas it was determined that restoring to achieve large-scale impact of water filtration would be an inappropriate goal in Pacific coast estuaries (zu Ermgassen et al. 2013b).

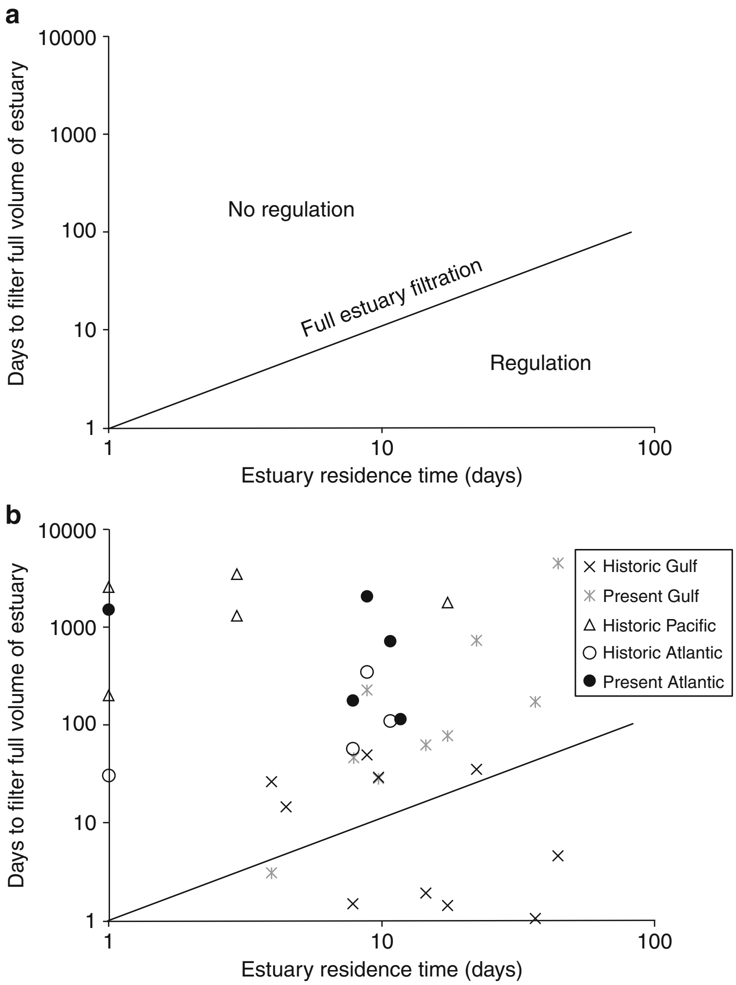

Fig. 4 The number of days both historic and present oyster populations requires to filter a volume of water greater than the volume of the estuary against the residence time of water in each estuary. The solid black line represents the point at which the number of days to filter the estuary volume is equal to the residence time of the estuary. Points falling above the line represent bays in which the oyster population would not be expected to have large-scale water quality impacts (Adapted from zu Ermgassen et al. (2013a, b))

Historical ecology of animal forests can therefore play an important role in their conservation and management. While for many animal forests the data required to undertake a quantitative assessment of the change in extent or associated ecosystem service delivery is lacking, there are a few exceptions. Even in the absence of such quantitative assessments, historical ecology can often offer a qualitative sense of the loss of not only extent but also the associated ecosystem services or biodiversity benefits, which can be used to communicate the importance of the remaining marine animal forests.

4 Using Historical Ecology to Plan for the Future

As the above examples show, historical ecology can provide data on the past presence and abundance of species, as well as the timings and drivers of change in marine communities. A greater understanding of past ecosystems and what drove them to change has advantages for management. As explored in the previous section, historical insights can help toward framing feasible goals for recovery of marine communities. In addition, managers also have to plan for what the future holds. For example, will benthic communities remain the same under climate change, and how will they respond to the intensification and accumulation of human impacts?

A short-term perspective often makes it difficult to know whether the changing composition of benthic communities is a novel occurrence caused by escalating human impacts or whether similar events have occurred in the past. Knowing this is important for alerting managers and scientists to potential changes in communities beyond levels of historical variability. Pushing systems beyond their known ecological boundaries leaves them at greater risk of crossing an ecological “tipping point,” beyond which it is unlikely to be able to recover to its former condition, even if drivers of change are reduced (Hughes et al. 2013).

During the 1980s, a series of episodic mortality events resulted in a marked reduction in Caribbean acroporid coral communities and a shift in community structure toward macroalgae dominance. While these events unfolded as an immediate consequence of bleaching and disease (Hughes et al. 2013), studies over longer temporal scales demonstrated that these coral communities had, in fact, been in decline throughout the twentieth century as a result of long-term anthropogenic stressors such as fishing and declining water quality (Cramer et al. 2012; Pandolfi et al. 2003). These long-term studies provide an additional perspective on the mechanisms of regime shifts and subsequent transitions to alternate stable states, and support an emphasis on understanding the cumulative impact of long-term disturbances, rather than focusing upon the impact of abrupt shocks to an already degraded system (Hughes et al. 2013).

Contemporary monitoring and historical data paint a concerning picture of the decline of Caribbean acroporid coral communities over the last century. However, paleoecological research demonstrates that the recent dramatic shift in community composition is unprecedented in the fossil record (Pandolfi and Jackson 2001, 2006). Moreover, while contemporary coral reefs commonly demonstrate large fluctuations in community composition, the fossil record shows that Pleistocene Caribbean coral communities demonstrated remarkable stability across tens of thousands of years (Pandolfi and Jackson 2006). The longer-term perspective of these studies shows that the changes witnessed in these coral communities over the last few decades really are unparalleled in the historical record.

A historical perspective can also help to determine whether animal forest communities observed today are already the result of a historical shift to an alternate stable state. In cases such as this and where the status of historical communities is unknown, contemporary management actions may even positively reinforce the maintenance of these stable states (Hughes et al. 2013), because we have come to perceive the contemporary state as natural. Understanding what has been lost thus enables societies to make more informed decisions as to the degree to which they wish to recover lost or degraded communities. In some cases full recovery may be difficult, impossible, or not desirable (i.e., we cannot get back to a past state emphasized in the historical record), but this does not mean that reductions in human impacts won't be beneficial in some way. For example, the Firth of Forth once held the most economically important oyster beds in Scotland, but increasingly intensive fishing activities alongside land-use changes meant that by the early twentieth century these communities had been extirpated (Millar 1961). However, contemporary surveys uncovered the presence of horse mussel (*Modiolus modiolus*) reefs which, if recovered, could potentially perform some similar functions to the extirpated oyster reefs, for example, filtration, consolidation of sediment, and the presence of a hard, three-dimensional substrate for other epifauna (Thurstan et al. 2013). Therefore, even if recovery of past communities looks impossible, some lost services may still be recovered via the restoration of alternative communities.

Finally, in some cases, the deep temporal perspective offered by historical studies may provide answers to some of our questions about what the future holds. For example, Greenstein and Pandolfi (2008) studied Pleistocene and modern coral reefs along the coast of Western Australia. They concluded that these reefs have long exhibited responses to changing climates and that past changes may provide clues as to how modern reefs will respond and shift as the oceans warm.

5 Limitations of Historical Ecology

Despite the range of data sources and techniques described here, fundamental limitations still exist in our ability to understand historical benthic animal communities. Even with the most detailed historical data, major gaps in information about benthic species that were either not of interest to fisheries (and hence not included in archival records), unable to be brought up in trawl surveys or whose remains do not persist over long time periods of time (and thus would not be recorded in fossilized remains or sediment cores), continue to exist. The lack of knowledge about these species, some of which will be included in the term "animal forests," is unlikely to change even as new data are discovered or techniques continue to be refined.

Historical data also usually contain some level of error or bias, impeding our ability to determine exactly what past communities looked like, although the comparative analysis of independent sources of data or improved techniques can reduce this uncertainty (Swetnam et al. 1999). Regions that are less impacted by human activities also provide valuable information on the composition of extant communities (e.g., Sandin et al. 2008), which may be able to fill in some of the knowledge gaps remaining after historical analyses have been conducted (Swetnam et al. 1999).

Furthermore, while historical data can reduce the occurrence of shifting environmental baselines, this does not mean that historical data are immune from this phenomenon, as many historical records only began to be collected after the advent of fisheries and other coastal impacts. For example, the impetus behind the mapping of oyster reefs was usually driven by observed declines in oyster catch, and as such represents a historical but nevertheless shifted baseline (zu Ermgassen et al. 2012). Fishery records also commonly began to be kept only many years after declines were first observed and calls were made for systematic data collection (e.g., Thurstan et al. 2014). Knowing the context of historical data – that is, not just *what* was recorded but *why* it was recorded – is thus critical to ensure accurate interpretation of historical ecology findings and to acknowledge the limitations of available historical data sources.

6 Conclusion

Compared to many other animal groups, much remains to be known about historical changes in marine animal forest communities. For those communities that were not directly targeted, or were too small or delicate to survive being hauled up in a trawl survey net, our state of knowledge is unlikely to change considerably. However, historical data sources do exist and are still being discovered. Their careful interpretation can provide an indication of the extent of changes that have occurred in some communities.

Along with the degradation or loss of animal forests, important ecosystem services have also been lost, for example, food sources, water quality control, and nurseries for other fished species. Historical ecology can elucidate the degree to which such services historically contributed to human well-being (e.g., zu Ermgassen et al. 2013a, b) and hence can provide a powerful communication tool for engaging with managers and stakeholders.

As knowledge of past marine animal forests increases, scientists must rise to the challenge of ensuring that managers and decision-makers acknowledge these data. A greater understanding of the potential but also the limitations of historical ecology is critical in fostering acceptance and the incorporation of such data into decision-making. Historical ecology allows us to communicate the historical importance of threatened or even extirpated marine animal forests and hence the critical role they used to play in providing for people and biodiversity. In this sense, the concept of an animal forest and the ecosystem services they provide to societies will be of great value in attracting stakeholder interest in the restoration and protection of these communities.

7 Cross-References

- ▶ Animal Forests of the World: an overview
- ▶ Conservation and Management of Vulnerable Marine Benthic Ecosystems
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest
- ▶ Harvesting and Collection of Animal Forest Species
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998
- ▶ Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral Transplantation

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Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest

34

Jake Rice and Anthony D. M. Smith

Abstract

The policy history of the Ecosystem Approach (EA) is first reviewed, from the perspectives of both intergovernmental agencies involved in resource management and agencies focused on conservation of biodiversity, focusing on how the agencies adapted the EA to the marine environment. This provides the general interpretation of "ecosystem approach," but at a conceptual level that needs to be substantially operationalized. To approach that operationalization, three case histories of applying the EA in the ocean forests of Australia are summarized. These include a place-based application, a threat-based application, and an attempt at an application simultaneously taking both components into the planning and implementation of an ecosystem approach. Building on those case histories the chapter explores how well the "ocean forest" analogy actually transfers into marine conservation and management. To do so, the chapter reviews the mature ecosystem approach and sustainable use frameworks from terrestrial forestry. The review summarizes the forest synthesis of ecosystem protection and management, and then evaluates the components of the synthesis in terms of applicability to marine rather than terrestrial ecosystems, and the forests of the ocean. The discussion concludes that the forestry operationalization as a useful basis for implementing an ecosystem approach in the ocean forests would require significant adaptations. These would change the focus from direct harvesting of the forest itself to the harvesting of resources found in the ocean forest. Thus, the analogy of an ocean forest may have limitations when viewed in a policy and management context.

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Ecosystem approach • Conservation and sustainable use • Ocean forests • Forestry • Biodiversity • Area-based management

Contents

1 Introduction

The precise origins of the concept of an ecosystem approach (EA) to conservation and sustainable use of living resources are unclear, as are the exact pathways by which it has entered the world of marine policy and management. However, two benchmarks are important for the establishment of an EA in policy and management. The first was the First Rio Convention on Environment and Development, where the EA was given a central place in the global commitments to sustainable development (UN 1992). The second was the Convention on Biological Diversity Principles for an ecosystem approach. These Principles, adopted just a few years later, were intended to provide guidance on interpreting how an EA should be applied (UNEP/CBD 1998; CBD 2004). Both of these benchmarks will be considered in detail in Sect. 3 of this chapter.

From these global policy foundations, the development of the EA has taken many paths. Probably every intergovernmental or nongovernmental organization (IGO and NGO, respectively) with a mandate that touches on the environment has endorsed some variant of the EA. The variants are partly disciplinary adaptations of the common policy roots to accommodate the special disciplinary or sectorial circumstances of each specific IGO or NGO. However, some aspects of the custom-tailoring of the meaning of the EA could be seen as efforts to either emphasize or downplay parts of the foundation, with the goal of targeting implementation efforts either towards or away from particular issues of importance to the IGO or NGO.

Even in the marine realm, the differences in how the EA is defined can be substantial. To illustrate:

The UN Food and Agriculture Organization (FAO) defines "An ecosystem approach to fisheries strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries." (http://www.fao.org/fishery/topic/13261/en. Accessed 2015/02/11)

To the International Union for the Conservation of Nature (IUCN) "The Ecosystem Approach is a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way." (http://iucn.org/about/union/commissions/cem/cem_resources/?373/The-Ecosystem-Approach-Five-Steps-to-Implementation. Accessed 2015/02/11)

These are not dramatically different definitions of an EA but neither are they identical. The fisheries definition explicitly mentions uncertainties and a balance of diverse objectives whereas the IUCN definition explicitly mentions conservation and equity. Both say that management should be "integrated." However, to fisheries the task is to integrate the management of fisheries, presumably across multiple fleets operating in the same ecosystems and across the diverse objectives for those fisheries. To the IUCN, the integration task clearly extends across multiple human uses and livelihood strategies – and across sectors operating both on land and in the water. In practice, these apparently minor differences in choices of words may have larger impacts on efforts at implementation. These issues will be revisited in Sect. 4 of this chapter.

Notwithstanding the differences raised above, with varying degrees of emphasis four different factors characterize most interpretations of an EA (Rice 2011):

- Giving greater consideration to how environmental conditions and variation may act as forcers of change in the ecosystem components being used or protected.
- Taking greater responsibility for the full ecological footprint of the use being managed or of the socioeconomic footprint of actions taken to conserve specific ecosystem components.
- Integrating decision-making about the use and protection of resources used or impacted by different industry sectors or communities. The integration takes account of interactions across multiple human activities in an ecosystem, to facilitate coexistence of the uses and protection effects.
- More participatory and inclusive approaches to governance of the resources themselves or of the places where the resources are found. The more inclusive governance extends to both policy decision-making and implementation of management and conservation measures.

The potential for differential emphasis to be given to each of these four factors has many consequences. The first is simply that there is no single way to characterize "the ecosystem approach." The attention given to each of the four factors will shape the nature of how the EA is implemented in various jurisdictions, so the EA can "look" different in different places, or even different for different uses in the same place. The potentially different emphases among the factors also mean that adopting an EA may have many different expected outcomes on all time scales. These differences in expected outcomes can cause communication problems between jurisdictions that have adopted different interpretations of the EA. They can also cause tensions and misunderstandings among sectors of society that may have different expectations of what was included in a decision to "implement an EA." However, these challenges mean that the EA should be viewed much more as a journey than a specific endpoint. It is the terrain that must be covered in the journey that determines what types of progress are made at what rates.

From this introduction, it is clear that if generalized statements are made about the EA they will have to be abstract and high-level. If more concrete statements are made, they will be qualified to specific times, places, circumstances, or jurisdictions. It is hard to draw a clear picture of progress or opportunities from statements that are either general but vague or else specific but heavily qualified. Hence we start the chapter with a set of carefully drawn case histories of the application of an EA in one jurisdiction, with a selectively benthic focus. Australia was chosen for several reasons. First, policy commitments to an EA were made some years ago. Second, resources were devoted to consolidating the science, assessing risks, developing options, making governance more inclusive, implementing new measures, and monitoring effects. Third, these efforts to implement an EA have been ongoing for long enough for lessons to be emerging from the experience. These case histories give a clear picture of one jurisdiction's journey on the EA, the challenges encountered, and the outcomes achieved to date.

2 The Ecosystem Approach in Practice: Case Histories from Australia

Australia made a policy commitment to an EA to marine issues early on and invested significantly in many aspects of its implementation. Right up-front we present a trio of case histories of different approaches that have been tried in one jurisdiction, building on the case made in the "Introduction" section that there is no single interpretation of what does and does not constitute "the" EA. The case histories illustrate both successes and failures in applying an EA to management of marine issues. Here we briefly review those initiatives, with particular consideration to management of ocean forests. The case histories were chosen to illustrate: first, a place-based initiative to give enhanced protection to a prime example of an ocean forest; second, an activity-based initiative to manage a threat that has potential to impact the ocean forest; third, an initiative to provide a policy foundation for integrating approaches to both protecting places and managing activities simultaneously in a coherent package rather than starting with one (a place or an activity) and working out towards the other.

2.1 Place-Based Protection: *Great Barrier Reef*

Australia's Great Barrier Reef (GBR) region stretches over 2,000 km along the Queensland coast, covers an area of about 346,000 km^2 and with close to 3,000 reefs is regarded as the largest coral reef ecosystem on earth (Day and Dobbs 2013). It contains one of the highest concentrations of biodiversity on the planet and represents an ocean forest par excellence, encompassing large areas of coastal mangrove and seagrass as well as coral reefs. Attempts to manage this area with enhanced protection commenced in 1975 with the Great Barrier Reef Marine Park Act. The Act came well before an EA was first formulated but embodied a number of the principles that came to define that approach. The main object of the Act is "to provide for the long-term protection and conservation of the environment, biodiversity and heritage values of the Great Barrier Reef Region," and consistent with this primary object to allow for sustainable use and enjoyment of the region. The GBR has been managed over the whole period by the Great Barrier Reef Marine Park Authority (GBRMPA) under joint authority from the Commonwealth (federal) and Queensland (state) governments.

From the outset, the Marine Park has been managed for multiple uses. Apart from tourism, other significant uses include commercial, charter and recreational fishing, and shipping. Land regions adjacent to the Park include over one million residents, and both mining and agriculture are significant economic activities. Ten major ports adjacent to the reef export mineral and agricultural products to the world. The Marine Park currently provides a direct benefit to the Australian economy of over AUD$5 billion annually, mainly from tourism, and was listed as a World Heritage Area in 1981.

The risk-averse management of threats to the GBR was integrated to some extent from the outset, with zoning as an important management tool. While the initial zoning plan fully protected a relatively small fraction of the area, a rezoning in 2004 resulted in high levels of protection to over a third of the Park. Governance of the GBR was also strengthened by widespread public interest in and involvement with the development of management plans. These in turn were supported by a strong monitoring and research effort, and over time more sophisticated tools for integrating decisions about the multiple uses have been employed in planning and management.

The Great Barrier Reef Marine Park is widely regarded as a model for multiple use management and the adoption of the ecosystem approach (Day and Dobbs 2013). Nevertheless, the environmental values of the Park are under threat from several current external drivers. These include climate change (ocean warming and acidification affecting coral growth and mortality), nutrient runoff from adjacent agricultural intensification increasing algal cover on reefs, port construction, dredging and shipping activity resulting from a major increase in coal and iron ore production, and export from the region. These threats are being taken seriously, and external scrutiny from the World Heritage process has resulted in changes by the Australian and Queensland governments to management of land use and shipping.

2.2 Threat-Based Protection: *Ecosystem Approach to Fisheries Management*

Australia was an early adopter of the ecosystem approach to fisheries (EAF; FAO 2003a) also referred to as ecosystem based fisheries management (EBFM; Pikitch et al. 2004). Moves towards EAF started in the early 1990s as part of a national response to international calls for sustainable development (UNCED 1992). In Australia, this approach was referred to as Ecologically Sustainable Development (ESD) and was adopted by the Commonwealth and all state and territory governments in 1992. ESD was developed for a range of resource sectors, including fisheries, and new fisheries legislation in the 1990s referred to it explicitly and made it a principle object of the Commonwealth and most state fisheries acts. This direction was given additional impetus by the passage of Commonwealth environmental legislation (EPBC 1999) that resulted in strategic assessment of fisheries to see that they met strict environmental standards. In general, Australia is seen as one of the leaders in implementation of EAF (Pitcher et al. 2009).

The adoption of EAF in Australia has been supported by a strong research effort with several important elements (Smith et al. 2007; Sainsbury et al. 2014). These included the development of a fisheries ESD reporting framework (Fletcher et al. 2005); of various methods for ecological risk assessment (ERA) specific to fisheries (Stobutzki et al. 2001; Fletcher 2005; Astles et al. 2006; Zhou and Griffiths 2008; Hobday et al. 2011); and in Western Australia, the development of regional integrated fisheries assessments (Fletcher et al. 2010). EAF has also been supported in some fisheries by whole-of-fishery management strategy evaluation (Sainsbury et al. 2000; Fulton et al. 2014).

While the risk assessment methods in particular have been useful in prioritizing issues for management response, and have indeed resulted in such responses, the focus to date has mainly been on species at risk rather than on habitats and communities. Nevertheless, some progress has been made in developing ERA to assess habitats (including ocean forests) at risk (Williams et al. 2011). A major impediment to date in adopting such approaches has been the lack of information on the distribution and location of vulnerable communities and forests, but progress is now being made on this front (Pitcher et al. 2007). The increasing use of spatial closures as a fisheries management tool (often to limit impacts of fishing on protected species rather than on habitats) is also helping to protect ocean forests, as is the recently declared National Representative System of Marine Protected Areas (NRSMPA) which more directly focuses on protection of biodiversity and habitats, including ocean forests.

2.3 Overarching Policy Approach to Protection: *Australia's Oceans Policy*

Australia was also an early adopter of attempts to establish integrated oceans management (IOM) considering all uses of the marine environment, with the announcement of Australia's Oceans Policy (AOP) in 1998. This followed Canada's Oceans Act (1997) but predated similar initiatives in the US and Europe. In Australia, IOM was established as a policy rather than through legislation. It was originally intended to be a national policy, including all levels of government, but in the event it only involved the Commonwealth government (with initial direction from the office of the Prime Minister) and so excluded coastal zone management which occurs in state waters out to 3 nm. A considerable governance structure was set up to support AOP, including a Council of Ministers and the establishment of a National Oceans Office (Vince 2011).

The main instrument to give effect to AOP was the development of Regional Marine Plans (RMPs). These were to be based around six bioregions previously identified across Australia's ocean territories. However, only one of these was ever developed and implemented, in the south-eastern bioregion. A review of AOP in 2004 led to a large change in direction, with the Council of Ministers replaced by a single minister (for the environment), the National Oceans Office being subsumed into the environment department, and RMPs being replaced by Marine Bioregional Plans, which, despite the similarity in name, focused almost entirely on environmental issues and on establishing the NRSMPA (which they did achieve in 2012). Even this success was potentially of short duration, with the newly elected federal government in 2013 announcing a review of the NRSMPA, and putting on hold the development of their management plans.

2.4 Contrasting the Experiences

Management of the iconic Great Barrier Reef is the first and arguably the most successful case considered. It focused on an iconic place, got the authority to manage several key threats to protect that place (including fishing and mining), and dealt with the threats as needed. It manifests all four elements of the EA, including considering environmental forcing, dealing with socioeconomic as well as ecological impacts, adopting an integrated approach to decision-making, and adopting a highly participatory governance structure. However, even with its widespread recognition of pioneering an ecosystem approach to multiple-use management of ocean forests, the GBR example also illustrates the challenges in such approaches, particularly where external drivers pose existential threats to the values of a region, and those drivers are outside the direct control of the relevant management agency.

Adopting an EA to fisheries management in Australia has met with mixed success. As with the GBR, the approach exhibits all four elements of the EA but, in this case, focuses on a single source of threat – from fishing. The approach has been particularly successful at identifying and managing species at risk. While it has also provided managers with the tools to manage impacts on ocean forests, including scientific tools such as ERA and management tools such as protected areas, it has in practice been constrained by limited knowledge of where to apply them.

The attempt to implement an Australian Oceans Policy has been the least successful of the cases considered. Several analyses have been undertaken of what went wrong with AOP and why (Tsamenyi and Kenchington 2012; Vince et al. 2015). Factors identified include failures of governance, science, funding, and nerve. Perhaps the main challenge was the enormity of the task and the way it cut across existing (sectorial) centers of power and authority. It is interesting to note that a very similar initiative within a state jurisdiction (South Australia) over the same time period resulted in an almost identical outcome, with an initial integrated multi-sector approach quickly reverting to a one sector (environmental) approach with a focus on establishment of marine protected areas. Comparison with similar moves towards embedding the EA in integrated ocean management in North America and Europe, including protection and management of ocean forests, suggests that jurisdictions will continue to struggle with application of the approach to such "wicked" problems.

3 Sustainable Forestry and the Ecosystem Approach

The case histories for Australia show alternative realizations of the EA. All three were shaped by characteristics of the coastal ecosystems of Australia, the legal regimes and governance processes of the country, and the mix of industries and lifestyles of Australia's coastal communities. As will be discussed in Sect. 4, there are important lessons to be learned from the case histories. That section will examine whether these lessons are sufficient to comprise a package that captures universal "best practices" to be exported to the rest of the world. Even if the lessons fall short of a comprehensive set of best practices for an EA, they at least provide a perspective on what can be accomplished with serious efforts to implement an EA from various starting points. They also highlight how both expected and unforeseen impediments can be encountered on the journey to more ecosystem-based approaches to policy and management. That perspective is invaluable in stepping back and looking at the EA in the context of the "ocean forest." However, lessons and perspectives are of greatest value when there is a framework in which to consider them. Here we examine if the "ocean forest" is such a framework.

3.1 The Socioecological Context of Uses of the Forests

The concept of the "ocean forest" has been developed throughout this book. Like all analogies, if it is based on real similarities rather than "parallel evolution" there should be an opportunity to borrow extensively from precedents in actual forestry. That would have many potential advantages, because sustainability and the "ecosystem approach" have been concepts investigated in terrestrial forestry for at least as long as they have been of interest in the marine realm. The many lessons already learned, and the best practices already developed in forestry, could be a foundation for solidifying an EA to the ocean forest as well.

Before looking for such lessons and practices as might transfer from terrestrial forests to ocean forests, it is important to be aware of the differences that need to be taken into account in the comparisons. The similarities and differences between terrestrial forest and ocean forest ecosystems are discussed in several chapters of this book. With regard to the EA, key similarities include:

- The crucial role of the forest in providing habitat for many other species partly or wholly dependent on those habitats (Part 1 of this book)
- The dependence of the characteristics of the forest on the substrate, topography, and related biophysical factors of an area (Part 3)
- The community-scale coherence of forest ecosystems as they progress through successional stages of development (▶ Chaps. 11, "Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems," ▶ 14, "Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests," and ▶ 20, "Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages")
- The high variability of time scales of recovery from disturbances, depending on the condition of the forest when disturbed and the extent of the disturbance, but time scales that can be very long for mature forests that experience extensive alteration (▶ Chap. 35, "The Impact of Anthropogenic Activity on Cold-Water Corals")
- Natural disturbance regimes that can affect the species composition and development stages of both terrestrial and ocean forests, with both species resistant to disturbance and species that are rapid colonists common in high disturbance areas

However, there are some important ecological differences as well that may be relevant to an EA:

- Terrestrial high-disturbance areas such as annually flooded areas may have more disturbance-resistant species (e.g., deep-rooted trees), whereas in coastal areas with high natural disturbance repeated recolonizations of the disturbed area may be more common.
- Airborne pollutants can strongly affect terrestrial forests, as waterborne pollutants can affect ocean forests. However, the currents of the oceans and freshwater plumes extending into coastal areas may channel the distribution of pollutants more than winds do on land, and water can carry heavier loads of depositional materials of more diverse types (toxic chemicals, silt, nutrients, etc.) leading to greater concentrations of transported materials.

Undoubtedly, a longer list of ecological differences could be constructed were one to drill more deeply into the two types of ecosystems. That is true of any analogy, including ocean and terrestrial forests. However, lengthening a list of differences would distract from more useful questions of how much can be learned from the similarities. Specifically, in terms of relevance to implementing an EA in the ocean forest, these ecological differences are greatly overshadowed by differences in the pressures imposed by human activities on those forests and in the governance of those pressures.

With regard to the pressures, of course two main pressures on terrestrial forests have been the direct harvesting of trees for lumber and other forest products and in the longer term, the conversion of forest land to agricultural uses or human habitation (Achard et al. 2002). The first pressure treats the forest as the product itself. There is only a need to transfer the form of the forest from living trees to lumber, wood pulp, biomass fuel, etc. The sustainability of the pressure was viewed in the context of the sustainability of the flow of forest products to market. The second pressure views the forest as something inconveniently "in the way," and the goal is actually to transform the landscape from one state (the forest) to a completely different state (a farm or community). When transformation of the landscape was underway, the forest products might be used locally or sent to markets, but the primary intent was the landscape transformation, not to obtain the forest products for use or markets. Concerns for sustainability in those cases focused on ecosystem services provided by the created landscape, not sustainability of landscape that was removed.

Neither of these pressures is expressed the same way in our ocean forests, except in rare circumstances. The ocean forest can be directly harvested for products, such as harvesting kelp for human consumption or corals for jewelry and decoration (▶ Chap. 36, "Harvesting and Collection of Animal Forest Species", Bruckner 2014). On quite local scales, these uses can be serious threats to the entity being harvested. However, where there is an enforcement capacity and will to manage the harvests, they can be managed sustainably. Unfortunately for our ability to transfer lessons learned from terrestrial forestry, such harvests comprise only a tiny fraction of the removals of the ocean forest by human harvesting. The vast majority of removals come as habitat "bycatch" when harvesting the fish that are using the ocean forest as a habitat. The "harvesting" of the ocean forest generally is incidental to harvesting the fish products to be taken to market. Correspondingly, the revenues from the harvesting are not based on the quantity and quality of the ocean forest being removed. Revenues are based on the quantity, quality, and value of the fish taken from that ocean forest.

Just as cases of directed harvesting of the ocean forest do occur, there are cases where the ocean forest is intentionally removed to transform the seascape from one state to another. That can occur when the seafloor is dredged for ports, shipping channels, etc., or when aggregates are removed for construction of human infrastructure. Intentional removals of the ocean forest also can occur when coastal vegetation such as mangroves is removed to accommodate mariculture or other uses by communities or tourists. When the seascape transformations involve mangroves there may be markets for the removed ocean forest but rarely otherwise. For some specialized coastal habitats this threat can reach serious proportions. For example, it is estimated that between 25% and 35% of mangroves have been lost through seascape conversion since 1980 (FAO 2005; Polidoro et al. 2010). However, the scale of these seascape conversions is still very small when compared to the amount of terrestrial forests that has been converted to agriculture and settlement in, for example, Europe or North America.

3.2 Sustainable Forestry and the Ecosystem Approach

Concerns for Sustainable Forestry were well established by the time of UNCED (1992), with Article 2b specifically devoted to the topic. "Forest resources and forest lands should be sustainably managed to meet the social, economic, ecological, cultural, and spiritual needs of present and future generations. These needs are for forest products and services, such as wood and wood products, water, food, fodder, medicine, fuel, shelter, employment, recreation, habitat for wildlife, landscape diversity, carbon sinks and reservoirs and for other forest products. Appropriate measures should be taken to protect forests against harmful effects of pollution, including airborne pollution, fires, pests, and diseases, in order to maintain their full multiple value." This statement, made nearly 25 years ago, was supported by 15 Principles of Sustainable Forestry, paraphrased by FAO (2003b) as per Table 1.

These Principles offer an important insight into how terrestrial forests are viewed in the world of global policy. Only two of the Principles are solely about the health of the forest. Principle 4 may be most directly relevant to forest health, highlighting the vital role of forests in maintaining ecological processes and balance. Principle 15 addresses an aspect of forest health, focusing on the protection of forests from pollution. Principles 2, 3, and 8 partially reference the conservation of forests. Principle 2 underscores the need for conservation, calling for ecological, cultural, and spiritual objectives, and Principle 3 calls directly for environmental protection. Principle 8 has several messages, but for this chapter the call that "protection of ecologically viable representative or unique forests should be secured" is particularly relevant. The other 10 of the 15 Principles are either about *use* of the forests or about governance of the uses and the sharing of benefits from those uses. The messages of the Principles for Sustainable Forestry are clear. Terrestrial forests are intended to be used to provide economic, social, cultural, and spiritual benefits, with full protection as the exception, not the rule.

Sustainable use may not be the same as the EA, but there are strong linkages. In addition to the groundings of the Convention on Biological Diversity (CBD) itself in the 1992 Rio Sustainable Development processes, the production of the CBD Principles for an ecosystem approach was a direct response to the language in UNCED. The FAO 2003b report contrasts the 15 Principles of Sustainable Forestry from UNCED with the 12 Principles of the ecosystem approach from the Convention on Biological Diversity (CBD 2004; Table 2). To the CBD the ecosystem approach is "a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way." It "encompasses the essential structure, processes, functions, and interactions among organisms and their environment. It recognizes that humans, with their cultural diversity, are an integral component of many ecosystems."

The CBD Principles of an ecosystem approach are more oriented to conservation than are the FAO Principles for Sustainable Forestry. Only CBD Principles 1, 2, 4, and 12 are predominantly about human uses of biodiversity, and the other Principles are exclusively or largely about how to approach its conservation. In

Table 1 Summary of the "Forest Principles" for sustainable use in an ecosystem approach (After FAO 2003b, where subparagraphs are separated by . . ., subparagraphs of the Principles have been shortened in the summary text)

No	"Forest Principles" for sustainable use in an ecosystem approach
1.	States have the sovereign right to use, manage and develop their own resources and ensure that activities do not cause damage to the environment of other States/areas.
2.	The incremental cost of achieving sustainable development should be equitable shared by the international community; . . . Forest resources and forest lands should be sustainably managed to meet the social, economic, and ecological, cultural, and spiritual needs of present and future generations and should be protected against the harmful effects of pollution, fires, pests, and diseases. . .. Timely, reliable, and accurate information on forests and forest ecosystems should be provided. Governments should promote and provide opportunities for the participation of all interested parties in the development and implementation of national forest policies,
3.	National policies and strategies should provide a framework for increased efforts for the management, conservation and sustainable development of forests and forest lands. . . . International institutional arrangements should facilitate international cooperation in the field of forests. Environmental protection and social and economic development should be integrated in SFM.
4.	The roles of all types of forests in maintaining the ecological processes and balance should be recognized.
5.	National forest policies should support indigenous people, other communities and forest dwellers. Participation of women in all aspects of SFM should be actively promoted.
6.	The role of forests in provision of bio-energy and industrial wood should be recognized, and aspects related to production, consumption and disposal of forest products taken into account. . .. Decisions should benefit from environmental cost-benefit assessments and methodologies for economic evaluations should be promoted. . . . Planted as well as natural forests play important roles for provision of goods and services, and SFM should be promoted.
7.	Economic incentives for SFM should be developed and a supportive international economic climate promoted.
8.	Efforts to maintain and increase forest cover and forest productivity should be undertaken. Implementation of national forest policies and programs should be supported by international financial and technical cooperation, . . . SFM should be based on sound national policies and guidelines, taking into account internationally agreed methodologies and criteria. . .. Forest management should be integrated with management of adjacent areas so as to maintain ecological balance and sustainable productivity. . .. Protection of ecologically viable representative or unique forests should be secured, including cultural, spiritual, historical or religious values. . . . Access to biological resources shall be with due regard to sovereign rights and sharing of technology and profits from biotechnology products shall be on mutually agreed terms. . ..

(*continued*)

Table 1 (continued)

No	"Forest Principles" for sustainable use in an ecosystem approach
	Environmental impact assessments should be carried out where actions are likely to have significant impacts on important forest resources.
9, 10, and 11.	Developing countries should be financially supported to enhance their capacity to implement SFM. Forest policies should take account of pressures and demands on forest ecosystems from outside the sector, and establish inter-sectorial means to deal with those. . . . Access to and transfer of environmentally sound technologies and know-how should be facilitated.
12.	Scientific research, institutional capabilities and knowledge-sharing should be strengthened. Benefits arising from use of indigenous knowledge should be equitably shared.
13.	Trade in forest products should be open and free. . . . Environmental costs and benefits should be incorporated into market forces and mechanisms.
14.	Unilateral measures to restrict international trade in forest products should be avoided.
15.	Pollutants that are harmful to forest ecosystems should be controlled.

Table 2 The 12 principles of the ecosystem approach, as adopted by the Conference of Parties to the Convention on Biological Diversity (Table from CBD 2004)

No	12 principles of the ecosystem approach
1.	The objectives of management of land, water and living resources are a matter of societal choice
2.	Management should be decentralized to the lowest appropriate level
3.	Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems.
4.	Recognizing the potential gains from management, there is usually a need to understand and manage the ecosystem in an economic context. Any such ecosystem-management program should: a) Reduce those market distortions that adversely affect biological diversity; b) Align incentives to promote biodiversity conservation and sustainable use; c) Internalize costs and benefits in the given ecosystem to the extent feasible.
5.	Conservation of ecosystem structure and functioning, in order to maintain ecosystem services should be a priority target of the ecosystem approach.
6.	Ecosystems must be managed within the limits of their functioning.
7.	The ecosystem approach should be undertaken at the appropriate spatial and temporal scales.
8.	Recognizing the varying temporal scales and lag-effects that characterize ecosystem processes, objectives for ecosystem management should be set for the long-term.
9.	Management must recognize that change is inevitable.
10.	The ecosystem approach should seek the appropriate balance between, and integration of, conservation and sustainable use of biological diversity.
11.	The ecosystem approach should consider all forms of relevant information, including scientific and indigenous and local knowledge, innovations and practices.
12.	The ecosystem approach should involve all relevant sectors of society and scientific disciplines.

addition, the CBD (2000) noted that implementation of these Principles should be guided by five points, all related to management actions and sharing of benefits. As the FAO (2003b) review concluded, the major differences between the Principles of Sustainable Forestry and the broader CBD Principles of the ecosystem approach are primarily because the former are developed specifically for the forestry sector, whereas the CBD Principles were intended to be much broader in scope. Thus the Principles of Sustainable Forestry contain many concerns specific to the sector. At the operational field level the review reports that there are Principles in both lists applicable to each aspect of forest management. These range from participation and benefit sharing to maintaining ecological balance and application of protective measures (Table 2).

Now we can return to the major difference between terrestrial and ocean forests that was highlighted earlier. The major pressures on the ocean forest are habitat impacts incidental to the act of harvesting fish, whereas in terrestrial forests the major pressures are directed harvest of the forest itself. How do each of the ecologically oriented CBD Principles of the ecosystem approach and the more usage-oriented FAO Principles of Sustainable Forestry actually play out in that contrasting pair of contexts? Initial insights can be gained by considering the arrangement of the two sets of Principles and their intended Goals, as these are set in parallel in FAO (2003b). These insights can be enriched by direct contrasts between the cases.

CBD Principle 3 addresses directly the consequences (actual or potential) of any managed activity on other ecosystems. Forestry has these considerations partitioned among several goals but primarily in Principle 8. In this principle, commitments are made to either maintain or increase forest cover and productivity and to conduct environmental impact assessments when there may be significant impacts on “forest resources.” For terrestrial forests, the “other ecosystems” of the CBD Principle clearly include other components of the ecosystems from which trees are being harvested. That is an interpretation that transfers very well to the ocean forests. If harvesting the fish or macro-invertebrate component of a marine ecosystem has impacts on other parts of the ocean forest ecosystem, those impacts must be considered by fisheries managers. Moreover, if the forestry model is applied to the ocean forests, the impacts must not only be “considered.” If they are likely to be “significant,” they should be subjected to environmental impact assessments.

“Significant impacts” are not defined, but the other parts of forestry Principle 8 give some guidance regarding what might be considered “significant.” Impacts would be significant if they fail to maintain or increase cover or productivity on appropriate space and time scales. If the forest model applies, ocean forest managers would not be expected to maintain the forest in an unaltered state. However, the level of cover and productivity of the ocean forest must be maintained in the medium term and on intermediate spatial scales, although local impacts are expected.

Environmental impact assessments of fisheries are uncommon, so we see already a major difference between current approaches to harvesting in the ocean forest and terrestrial forest ecosystems. However, there are activities in fisheries that look a great deal like environmental impact assessments. The first are the standards in the

Table 3 Risk assessment components for Deep Sea Fisheries; extracted from FAO 2009. Numbers refer to paragraphs in the guidelines

No.	Risk assessment components for Deep Sea Fisheries
1.	Flag States and RFMO/As should conduct assessments to establish if deep-sea fishing activities are likely to produce significant adverse impacts in a given area. Such an impact assessment should address, inter alia: i. type(s) of fishing conducted or contemplated, including vessels and gear types, fishing areas, target and potential bycatch species, fishing effort levels and duration of fishing (harvesting plan); ii. best available scientific and technical information on the current state of fishery resources and baseline information on the ecosystems, habitats and communities in the fishing area, against which future changes are to be compared; iii. identification, description and mapping of VMEs known or likely to occur in the fishing area; iv. data and methods used to identify, describe and assess the impacts of the activity, the identification of gaps in knowledge, and an evaluation of uncertainties in the information presented in the assessment; v. identification, description and evaluation of the occurrence, scale and duration of likely impacts, including cumulative impacts of activities covered by the assessment on VMEs and low-productivity fishery resources in the fishing area; vi. risk assessment of likely impacts by the fishing operations to determine which impacts are likely to be significant adverse impacts, particularly impacts on VMEs and low productivity fishery resources; and vii. the proposed mitigation and management measures to be used to prevent significant adverse impacts on VMEs and ensure long-term conservation and sustainable utilization of low-productivity fishery resources, and the measures to be used to monitor effects of the fishing operations.
2.	Risk assessments referred to in paragraph 47 (vi) above should take into account, as appropriate, differing conditions prevailing in areas where DSFs are well established and in areas where DSFs have not taken place or only occur occasionally.

FAO Deep-Sea Fishery Guidelines (FAO 2009), where the conditions of paragraphs 47–49 include many of the properties expected of an EIA (Table 3). Those fishery guidelines also contain an explicit definition of a “serious adverse impact” as “those that compromise ecosystem integrity (i.e., ecosystem structure or function) in a manner that: (i) impairs the ability of affected populations to replace themselves; (ii) degrades the long-term natural productivity of habitats; or (iii) causes, on more than a temporary basis, significant loss of species richness, habitat or community types. Impacts should be evaluated individually, in combination and cumulatively” (paragraph 17). The guidelines also state that in evaluating fisheries’ impacts on the seabed, the evaluations should consider, inter alia:

(i) The intensity or severity of the impact at the specific site being affected
(ii) The spatial extent of the impact relative to the availability of the habitat type affected
(iii) The sensitivity/vulnerability of the ecosystem to the impact
(iv) The ability of an ecosystem to recover from harm and the rate of such recovery

(v) The extent to which ecosystem functions may be altered by the impact
(vi) The timing and duration of the impact relative to the period in which a species needs the habitat during one or more of its life-history stages (paragraph 18)

If these guidelines were applied, and the standards met, the cover and productivity of the ocean forest should be maintained, even if its state is altered.

Another development in fisheries relevant to this CBD Principle and parallel forestry SD Goals is the increasing application of ecocertification of fisheries (Washington and Ababouch 2011). Under the Ecosystem Impacts part of such assessments, criteria require that fisheries demonstrate that "The [unit of assessment] does not cause serious or irreversible harm to habitat structure and function, considered on the basis of the area(s) covered by the governance body(s) responsible for fisheries management" (MSC 2015 P2, criterion 2.4.1). This criterion clearly allows local impacts, by defining the unit for assessing the criterion on a large spatial scale. However, it sets a similar standard that impacts must be reversible and not have "serious" consequences, noting that other Marine Stewardship Council (2015) guidance leads to an interpretation of "serious" similar to that in the FAO Deep-Sea Fishery Guidelines.

Consequently for this important EA Principle, the forestry model does transfer well to the ocean forest. However, such a transfer brings with it the expectation that the productivity of the forest and the functions it serves in the larger ecosystem will be maintained but not details of any specific state of the system.

This concept is reinforced by the 5th CBD Principle of the EA and its parallels in Principles 2, 4, 8, and 15 of the Forestry SD Goals. The major additions here are an equal focus on the structure as well as the function of the forest and the acknowledgement in SD Principle 4 that all types of forests have a role in maintaining healthy ecosystems. Both of these are important additions for the ocean forest. It brings into focus the need to maintain a mosaic of seafloor ecosystems, rather than increase the homogeneity of the seafloor. It also helps understand what serious harm may be, making alterations of the structure of an ocean forest serious even if functional consequences have not been conclusively demonstrated. Thus loss of species diversity would be a decrease in structure of the ocean forest. Responsible managers of harvests should avoid reducing diversity, whether the target of harvesting was the forests or the species using it for habitat. However, avoiding loss of diversity would not require that the entire species and size composition would have to persist in an unaltered state. Patches could be impacted substantially as long as this occurred on scales smaller than the processes responsible for ecosystem functions. A mosaic of patches of the ocean forest with different stages of disturbance could still ensure that the species and sizes comprising the structure of the ocean forest were present and undergoing normal ecological succession. Again the forestry model does transfer well to the ocean forest and fish harvesting but with the implication that disturbed ecosystems are acceptable within the bounds of rapid and secure recovery.

CBD Principle 6 is about functioning, as Principle 5 is largely about structure. Conceptually, the material discussed relative to Principles 4 and 5 lays out the implications for forestry clearly. The FAO 2003b document supports this interpretation by linking the CBD Principle 6 to the same Forest SD Principles as Principle 5. The phrase "within the limits" of the functioning of a forest ecosystem sets boundaries for acceptable perturbations. This boundary may be hard to quantify for most ocean ecosystems but at least focuses on an information need if use of the ocean forests is to be guided by the EA. Again, however, the Principles indicate that an ocean forest can be impacted by uses, whether direct or indirect. Some functions may be reduced and perhaps others increased, as long as the "limits" of these functions are not exceeded. This is consistent with the approach taken to species management in the oceans, which identifies and sets limits to acceptable impact. Particularly if functional redundancy among species (Rosenfeld 2002; Schindler et al. 2010) is found to be common in the ocean forest, this may permit a fair amount of perturbation of the exact configuration of the ocean forest.

CBD Principles 7 and 8 are about space and time scales and have no specific parallels in forestry implementation Principles. All the forestry Principles have explicit spatial scales set by the areas of the forests being managed for harvest, so they are likely to be on tens to even thousands of km^2. This is even more the case for all Principles which refer or indirectly allude to the function of the terrestrial forest as a source of habitat for other species. At least some of those species have large home ranges and even larger ranges for viable populations. Likewise, forest regeneration times are routinely thought to be decades. Consequently, the EA applied to terrestrial forests must be approached in large space and time scales, accommodating a mosaic of patterns of change within that scale. Success of management must also be evaluated on those large scales.

Applying this conceptual model to the ocean forest is somewhat more problematic than for some of the other Forestry Principles, especially with regard to spatial scales. As many chapters of this book document, although some habitats are widespread and large in scale, including some ocean forests of particularly high biodiversity value such as the Great Barrier Reef, many are local in scale. Considering management of the ocean forest, impacts of fishery harvests exclusively on large spatial scales may allow small patches of important habitat types to be lost. Likewise, there may be shortcomings to considering the sustainability of harvesting only on multidecadal temporal scales, in the context of ocean forest impacts. Forest harvesting can be rotated on multidecadal scales, with regrowth of the forest to conditions of high harvestable biomass and productivity between forestry harvests. Fish harvesting with its concomitant impacts on the ocean forest often occur at much shorter intervals, because mobile fish populations can return to a harvested area far faster than the ocean forest can recover its biomass and full productivity. Consequently, there is a risk of keeping large parts of the ocean forest at early stages of succession, comprised of species highly tolerant to disturbance. If the Principles already considered for ecosystem structure, function, and productivity are to be achieved in the ocean forest, both the space and time scales at which management is applied may have to be smaller than are used in an EA to forestry.

The ninth CBD Principle for EA is simply the acknowledgement that ecosystems are dynamic not static, and management cannot expect to maintain any single ecosystem state unchanged in the long term. Forestry's interpretation of this is to apply adaptive management. At its simplest, this adaptive management may consist of monitoring the forests on space and time scales that are informative about the outcome of management actions and evaluating the monitoring information against outcomes desired by management. If the discrepancy between the information from monitoring and the expected outcomes is too large then management measures are adapted to improve delivery of desired outcomes under the changed conditions. The ocean forests are no less dynamic than terrestrial ones, and the admonition not to try to manage to a static outcome applies equally well. Conceptually, the endorsement of adaptive management to the ocean forests should also transfer. In practice it will be more challenging than in forest harvesting. In that case, the forest harvests are adjusted to the changing state of the forest providing the wood products, yielding direct returns for effective adaptation. In the ocean forest, the mode of harvesting fish would have to be adapted to the changing benthos. If the changing state of the ocean forest directly changed the status of the fish populations, the links between ocean forest and fish yields would be demonstrable. It might be possible to justify the adaptive changes to management practices on the basis of the changes in the fish community being harvested. The fishery managers and harvesters could see direct reasons to accept the changes to management measures. However, if the fish population linkages to the state of the ocean forest are indirect or highly nonlinear, convincing fish managers to change fish harvests solely to accommodate changes to the seafloor may not be easy. Clearly, this is an EA Principle that is relevant, but it may be hard to gain support from fisheries managers and harvesters for applying the Principle.

Finally, CBD Principle 10 is the cornerstone of policy and management and picked up in aspects of Forestry Principles 2, 3, 6, and 8. The outcomes which management should strive to provide are a societal choice, balancing conservation and use of diversity, and through the Forestry Principles the ways that society may consider ecological, social, and economic outcomes are sketched broadly. Broad stakeholder engagement in setting objectives, cost-benefit analyses, and development needs are all important, as is acknowledgement that different sectors of society will bring different but strongly held value systems to the dialogue.

Of course this conceptual model of the governance aspects of the EA transfers well from terrestrial forests to ocean forests. Unfortunately, agreeing on the Principles is much easier than successfully implementing them. Societal debates about the desired outcomes of forest management are common and can be divisive. Just as much debate is expected in the dialogue on the proper outcomes for management of the uses of the ocean forest, as the long and complex debate about the United Nations General Assembly Resolution 61/105 on deep-sea fisheries and vulnerable marine ecosystems demonstrated. We don’t presume here to propose how governance processes should reach these societal decisions about objectives for management; it is far too complex an issue although many chapters of this book touch on aspects of those processes and outcomes. We simply stress that compromise as well as trade-offs will be needed from all parties in the dialogue. Those compromises can be guided by the governance objectives of the EA – equity of distribution of benefits, respect for diversity of values, and inclusiveness of stakeholders and their knowledge systems.

This analysis of the applicability of the interpretation of the EA guiding forestry practices to the ocean forest has focused on impacts of fishery harvesting. This focus was partly because of direct parallels of harvesting but also because bottom fishery impacts are often one of the greatest potential threats to ocean forests. Other threats to the ocean forest do warrant some discussion, however, such as the harvesting of predatory barrens-forming species. The forestry EA Principles note that harmful pollution should be controlled and that would certainly apply to the ocean forest as well. However, it is hardly a novel insight and the Principle itself gives no guidance on how harmful pollution should be controlled – just that it should be.

The other potential threat to coastal ocean forests is outright conversion of the area from a natural ecosystem to one allocated to an intensive human use – port development, channelization for navigation, mariculture, etc. For these coastal habitat conversions, the forestry EA Principles are silent, because areas converted from forests to agriculture, suburban expansion, etc., are no long the domain of forestry. To guide how to address the threat of seascape conversion, one must step back to CBD Principles. In this case, only general guidance is found. The objectives regarding protection of ecosystem structure and function (5, 6, 8, 9) are relevant but must be pursued in the context of the several Principles on societal choice and development (1, 4, 10, 11, 12). The latter group of Principles make the case that the benefits expected from the habitat conversion are a legitimate component of the governance dialogue. In that governance dialogue, the CBD Principles give potentially conflicting guidance. Spatial and temporal scales of management are certainly acknowledged as important (Principle 7). However, decentralizing decision-making to as low a level as possible (Principle 2) would move the dialogue to discussions at local scales and often single conversion projects. On the other hand, both taking account of the impact of each decision on other ecosystems (Principle 3) and the importance of viewing impacts on long time scales (Principle 8) argue for decision-making for coastal ocean uses on large scales. Marine spatial planning is a complex field and, like governance, is beyond the scope of this chapter (Ehler and Douvre 2009). However, the concepts captured in the CBD Principles for an EA are unquestionably a part of good marine spatial planning.

4 Syntheses of Case Histories and EA Principles

Section 3 has concluded that the FAO Principles for Sustainable Forestry are a workable representation of the CBD Principles for an ecosystem approach. The two sets of Principles partition the tasks for policy, management, and governance and the ecological, economic, and social aspects somewhat differently, but each Principle in the forestry framework has one or more parallels in the CBD framework and vice versa. Moreover, if the non-sector-specific CBD Principles are used as a method of "translation" of the subset of Forestry Principles focused wholly or in large part on ecological aspects of conservation, the majority of Forestry Principles seem to be transferrable at the conceptual scale from terrestrial forests to ocean forests. Aspects of the CBD Principles may also help in the translation of the Forestry Principles dealing with economic distribution of benefits from land to ocean forest as well, as explained below. The major potential challenges in transfer of the ecological aspects of the Principles appear to be related to scale, where the scale at which the forestry principles were designed to operate on land seems to be scores of hectares to perhaps a few thousands of km^2. In contrast, conservation of ocean forests often focuses on protection of ocean forest patches on quite small scales, as well as the larger scales more comparable to terrestrial forest management. The other consideration in the application of principles of sustainable terrestrial forests to ocean forests is the underemphasis of protection of terrestrial forests for other users of the forest, despite the important habitat provision functions of forest ecosystems. In practice, forestry Principle 2 does capture part of the role of forests as habitat for many species of animals, as the phrase "social, economic, ecological, cultural and spiritual needs of current and future generations" is being interpreted broadly. In addition, Principle 4 does focus on the general value of forests to biodiversity.

In most respects, there is good transferability of EA Principles from terrestrial forestry to ocean forests, and some clear messages emerge about the EA applied to forests, whether on land or in water. Above all, the EA is not about total protection of forests. It acknowledges that many ecosystem goods and services from forest ecosystems that are important to well-being of humanity cannot be used without altering those ecosystems. The goals of policy and management should be to ensure they are used at rates and in ways that are sustainable. Furthermore, the EA helps to understand "sustainable" to mean that the uses do not compromise the ecosystem's ability to continue to provide those goods and services, and recovery from those alterations would be secure and "rapid" (taking into account life histories of the species involved). This basic aspect of the EA emerges in a diffuse way from Forestry Principles 2, 3, 4, and 8 and more explicitly from the CBD Principles 3, 4, 6, and particularly 9 and 10.

The second key message to emerge from both sets of Principles is that decisions about how any forests – terrestrial or oceanic – are used should be made by very inclusive processes. The views of those pursuing economic activities in the forests and of the ardent conservationists are both legitimate in the dialogue, but so are the voices of civil society in general. Moreover, if anyone has a privileged place in that dialogue it is those whose traditional livelihoods are closely tied to the forests. This emerges from Forestry Principles 2 and 5 and is explicit in CBD Principles 2, 5, and 12.

This starting point of accepting change, as long as it is managed and reversible, and accepting that all of society has a role in decision-making, gives us the twin pillars of the EA. Thus the guidance for conservation and sustainable use of terrestrial forests may be a fertile source of lessons for ocean forests. As a test of this perspective, can we interpret the Australian experiences with applying the EA in marine ecosystems in a consistent way?

Unquestionably the experience with GBR was the most successful case history. It acknowledged multiple uses and the legitimacy of taking economic benefits from the ocean forests, paid close attention to scale and natural change, and prioritized conservation measures spatially while planning for the entire GBR. Its planning and Decision-making processes were broadly inclusive but were incremental as the participants learned and adapted. This characterization covers all the Forestry

Principles other than those involved in international trade and developing countries and maps fully onto every CBD Principle.

The Australian efforts at EAF had more mixed results. The focus on only some aspects of the ecosystem (especially species at risk) and at most tangentially on other aspects (especially habitats) has resulted in some ecosystem benefits being enjoyed. However, broad conservation benefits to the marine ecosystems did not progress as much as expected. On the positive side, several EA/Sustainability Principles were captured in these initiatives, particularly strong science and knowledge foundations (Forestry Principles 2 and CBD Principles 8 and 9), inclusiveness (several Principles of both), and acknowledgement of natural variation of the systems (Forestry Principle 10 and CBD Principles 8 and 9). For the EAF case history, setting limited objectives for ecosystem outcomes is fully consistent with the principles (Forestry Principle 2 and parts of 8; CBD Principles 1 and 12). However, the fisheries EAF did not fully adopt the guidance of Forestry Principles 3, 4, and parts of 8 and CBD Principles 3, 4, and 5 with regard to the full range of impacts of the activity (fishing) on the larger ecosystem, including the ocean forests.

Perhaps the most sobering message comes from the Integrated Ocean Management Policy initiative. Superficially it could be argued that this initiative drew on all the national-scale principles from both Forestry and CBD. It was inclusive, approached the challenges broadly both ecologically and socioeconomically, and was intended to be as integrative as possible. This is the ideal envisioned in Forestry Principles 3a and 8c and CBD Principle 10. However, perhaps it was just too ambitious to attempt in one piece, and did not sufficiently acknowledge that there are incremental costs that have to be internalized (Forestry Principle 2a, CBD Principle 4c). Sufficiently inclusive processes for high-level planning can skirt these costs and particularly avoid confronting how they will be distributed, until the process has progressed far down the pathway of planning. It appears that when the costs must be confronted, the choice may be to scale back implementing the plan, rather than paying the costs of what has to that point been considered ground-breaking progress.

5 Discussion

In this chapter, we have intentionally avoided presenting yet one more narrative on what the EA is and why the ocean forest would benefit from a policy and management approach that is inclusive of the broad biodiversity values of the ocean forest. The whole book makes the case for the potential benefits from such an approach. In addition, the EA has been such an integral part of environmental policy, management, and science for at least two decades, with a wide array of interpretations among jurisdictions and industry sectors. Hence no single, simple description of *the* EA would capture the diversity of experiences. This is particularly true because if an EA is truly attuned to the ecosystem being conserved and used, the concept of the EA would necessarily have to have as many variants as there are types of marine ecosystems.

Rather, we have taken a trio of initiatives to implement the EA in marine environments by a single country that made an early commitment to the EA, and two policy documents presenting Principles for sustainability and an EA, and discussed their relevance to the concept of an ocean forest. Although none of these initiatives nor policy frameworks were specifically developed using the current concept of the ocean forest, we conclude that the initiatives are illustrative of programs that could be designed for the ocean forest, and the policy frameworks are appropriate guidance for design of such programs.

From this experience and using this guidance it is clear that there is not a single way to design programs for the conservation and sustainable use of ocean forests. The overarching policy guidance can be followed with place-based approaches, with sectorial activity-based approaches, and with comprehensive policy-based approaches to filter down to places and activities. The Australian examples may suggest place-based approaches work best, which would be a welcome conclusion for many concerned about specific parts of the ocean forest, and that may be the case. However, the GBR success may be at least in part attributable to the long period of time over which it has developed and been allowed to evolve (40 years). It also may be hard to replicate, because place-based initiatives on such large scales are hard to motivate and harder to coordinate, but only on such scales is it possible to accommodate the full diversity of uses and protection that it takes to gain and keep the support of all sectors of society. It should also be noted that place-based approaches have to contend with the issue that places and the ecosystems they contain cannot be isolated from outside impacts – such as warming and acidification of the oceans. Activity-based initiatives could have equal potential for success, if they think broadly enough about all the parts of the ocean forest affected by the activity. Activity-based initiatives do not ensure the ocean forest is protected from impacts of other sectors, of course, but that does not diminish the value of making pressures like fisheries or mining fully sustainable within their own sector. The case histories also suggest that policy frameworks for integrated management may have the best chance of fully implementing the guidance from the forestry or CBD principles. One just needs to be aware of the scale of commitments of money, time, and effort from a wide spectrum of society that are required not just for the process of planning the integration of management and conservation but the even greater demands on money, time, and effort for implementing the plan once developed.

The last message is the generally positive analysis of the relevance of the Principles of sustainable (terrestrial) forestry for application in the ocean forest. The acceptance of impacts from use and the goal of keeping them sustainable through the types of actions consistent with the principles give a foundation for conservation and sustainable use of the ocean forest as well. There may be benefits from pursuing this forest analogy more seriously in future.

6 Cross-References

► Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
► Conservation and Management of Vulnerable Marine Benthic Ecosystems

▶ Ecosystem Functions and Services of the Marine Animal Forests
▶ Harvesting and Collection of Animal Forest Species

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The Impact of Anthropogenic Activity on Cold-Water Corals

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Abstract

Various human activities can have an impact on cold-water coral (CWC) habitats. Bottom trawling has been shown to degrade these habitats and, in some cases, to cause extensive damage. Among static fishing gears, bottom longlines and gillnets can be set directly on coral grounds. Intensive fishing with these gears, while having much less impacts compared to bottom trawls, may over time cause damage to CWC habitats. Current plans to begin mineral mining activities in the

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deep sea will pose a risk to CWC habitats due to substrate removal and smothering by toxic particulate waste material. The by-products of oil exploitation, including drill cuttings, drill mud, and wastewater discharge, can impact CWC habitats, for example, causing reduced polyp activity and growth. Effects of accidental oil spills, if occurring in the vicinity of CWC habitats, include partial tissue loss and ultimately death. Litter may affect CWC colonies in a variety of ways, e.g. smothering and entanglement in discarded plastic and lost fishing gear. Submarine cables can exert localized impacts on CWC habitats particularly during their installation, repair, and removal. Potential impacts of CWC exposure to radioactive waste are unknown, but leakages in their vicinity would represent a threat. The impact of increasing CO_2-induced global warming and ocean acidification is species-specific. While accurately predicting future effects is difficult, reduced availability of suitable habitats and weaker skeletal strength of reef-forming species are to be expected. Evaluating the risk posed by human activities to CWCs remains a challenge, given the remoteness of these habitats.

Keywords

Marine animal forests • Cold-water corals • Anthropogenic impact • Trawling • Mining • Oil production

Contents

1 Introduction

Cold-water corals (CWCs) are widely distributed in deep water (below 200 m) worldwide along the margins of continental shelves, offshore banks, and seamounts. Increasing anthropogenic activity in offshore areas, in particular fishing, and the exploration and the exploitation of oil, gas, and mineral resources, are increasing the potential for impacts in coral areas. CWC ecosystems are long lived, slow growing, and fragile, which makes them especially vulnerable to anthropogenic impacts (Roberts et al. 2009). This chapter reviews the human activities that can impact cold-water corals and the animals that depend upon them.

1.1 Cold-Water Corals as Animal Forests

Reef-building and habitat-forming corals in cold waters belong to several systematic groups. The most important of these are the colonial stony corals (Scleractinia), true soft corals (Octocorallia), black corals (Antipatharia), and calcifying lace corals (Hydrozoa). Several species of these groups create reefs and three-dimensional, forest-like structures on the seafloor, comparable to their warm-water cousins in size and complexity (Roberts et al. 2009). These cold-water reefs and structures act like woodland in a grassland landscape, providing structural complexity in areas that are usually flat and featureless. This distinct and rich ecosystem provides niche and nursery grounds for a rich variety of species, including commercial fish species (Roberts et al. 2009). Fishers and marine biologists have been pulling up pieces of CWC from the depths of the sea for several centuries, without realizing their importance. With the advent of modern technology, such as remotely operated vehicles (ROVs), it has become possible to obtain images of living coral reefs hundreds of meters below the surface of the sea. The initial images of thriving CWCs had a profound effect upon the scientists and managers who observed them. As a result, conservation measures were put in place that influenced where oil companies laid gas pipes (Hovland and Thomsen 1997; Armstrong and van den Hove 2008).

The presence of commercial fish species, such as monkfish, hake, and orange roughy, in the vicinity of CWC reefs, unfortunately means that some degree of impact from fishing activities is inevitable. While coral may destroy fishing gear due to abrasion and entanglement, the temptation to fish ever closer to reefs to try to increase catches can result in accidental damage to CWC habitats. Much worse, however, is the documented destruction of reefs by trawlers in pursuit of redfish off Norway (Armstrong and van den Hove 2008; Henry et al. 2013) and orange roughy off the west coast of Ireland (Foley et al. 2011).

In Norway, Armstrong and van den Hove (2008) described how, in 1994, static gear fishers alerted the authorities of their worry that trawlers were destroying cold-water coral habitats where the static gear fishers had previously experienced good fishing. The Norwegian fishers described how CWC areas that previously functioned as natural marine reserves were being turned into "marine deserts" due to trawling. Armstrong and van den Hove (2008) further explained that:

> . . .trawling was seen as precarious near coral, as trawl nets and other gear were easily damaged. Stock depletions, leading to reduction in quotas with resulting economic pressures, have induced fishers to develop fisheries in previously unutilized areas. This has led to the development of so-called rock hopper gear, which to some degree bulldozes the ocean floor, protecting the trawl net, while destroying coral reefs, and allowing for trawling activity on rocky and coral based substrates earlier left alone.

Video footage showing coral destroyed by trawling was subsequently obtained by the authorities. This video when shown to the public caused an outcry that led to rapid implementation of conservation measures, especially bottom trawl-free areas, for the protection of CWC off the Norwegian coast.

Off the coast of Ireland, a boom and bust trawl fishery targeting the long-lived deep-sea fish, orange roughy, similarly resulted in collateral damage to reefs at a number of locations (Foley et al. 2011). Again, video footage of trawl-damaged coral (Grehan et al. 2004) helped to convince the authorities (both Irish and European Commission) that conservation measures were necessary to protect coral, leading to a subsequent ban on trawling for orange roughy and the establishment of cold-water coral reef marine protected areas (Special Areas of Conservation) under the EU Habitats Directive.

Bottom fishing, especially bottom trawling, is considered to be the human activity causing the most serious threat to cold-water coral reefs all over the world. Drawing on our earlier analogy of coral reefs resembling woodlands amidst grassland, it is easy to understand how the American scientist, Elliott Norse, having previously published two books on forest conservation and the impacts of forest clear-cutting and associated practices, together with his coauthor Les Watling, was able to compare the type of bottom trawling described above to forest clear-cutting (Watling and Norse 1998). Various other human activities can affect CWC habitats directly or indirectly. These include current and future hydrocarbon exploration and production, cable and pipeline laying, bioprospecting, destructive scientific sampling, pollution and waste dumping, global warming, and ocean acidification (Armstrong and van den Hove 2008).

To understand whether cold-water corals can recover from anthropogenic impacts, it is important to determine how sensitive CWCs are to the different pressures resulting from each of the human activities occurring in their vicinity. For example, trawling causes pressures that include loss of habitat and species and smothering due to increased sedimentation. Sensitivity assessments are now used to try to better understand the environmental impacts caused by human activities and natural events such as climate change, on marine species and habitats. In these assessments sensitivity is defined as the product of:

- The likelihood of damage (termed intolerance or resistance) due to a pressure
- The rate of (or time taken for) recovery (termed recoverability or resilience) once the pressure has abated or been removed

Table 1 Knowledge of CWCs and their value. Cell colors indicate the state of knowledge on the contribution of CWCs to the provision of goods and services. Color code: green, some knowledge; yellow, little knowledge; gray, no knowledge; white, irrelevant. Symbols indicate monetary value, as present (+), not present (0), and unknown (?) (Adapted from Armstrong et al. 2012)

Services		*Cold-water corals*
Supporting services	*Nutrient cycling*	▒ ?
	Habitat	🟩 +
	Resilience	▒ ?
	Primary production	🟩 ?
	Biodiversity	🟨 +
	Water circulation and exchange	0
Provisioning services	*Carbon capture and storage (artificial)*	0
	Finfish, shellfish, marine mammals	🟩 +
	Energy: oil, gas minerals	🟩 ?
	Chemical compounds–industrial/pharmaceutical	🟨 +
	Waste disposal sites	0
Regulating services	*Gas and climate regulation*	0
	Waste absorption and detoxification	0
	Biological regulation	▒ ?
Cultural services	*Educational*	🟩 +
	Scientific	🟩 +
	Aesthetic	🟨 +
	Existence/Bequest	🟨 +

Applying the above definition, it is evident that CWCs are very sensitive because they are easily adversely affected by a number of human activities (i.e., have low resistance) and recovery is only achieved after a prolonged period, if at all (i.e., low resilience or recoverability).

1.2 Economic Activities with Potential to Impact Cold-Water Corals

To understand the full impact of human activities on CWC habitats, it is necessary not only to characterize their direct impacts at the species and ecosystem level but also to understand how the delivery of ecosystem goods and services of benefit to man may be affected (Table 1). Although in its infancy, the mapping and assessment of ecosystem goods and services will become a cornerstone of marine spatial planning, including the assessment of impacts. Knowledge about the services provided by CWC habitats is still limited, although this topic is receiving more attention in recent years. Ecosystem services are classified into provisioning, regulating, cultural, and supporting services. As of today, CWCs have little direct human use and therefore provide limited provisioning services. CWCs have been collected for the purpose of making jewelry in many parts of the world, including the Pacific and the Mediterranean (Roberts et al. 2009). Populations of some species belonging to precious octocorals (genus *Corallium*) and black corals have been impacted by this activity. The collection of cold-water corals for jewelry is now widely banned (Roberts et al. 2009). Cold-water corals can provide potential future provisioning services because of their potential as reservoirs of novel biocompounds for use by the medical, pharmaceutical, and biotechnology industries. CWC habitats may hold existence values regardless of their direct or indirect uses to society, but monetary valuation exercises have not succeeded in eliciting a willingness to pay for protection of these habitats from the public. Regarding supporting services, CWC habitats have been shown to harbor high biodiversity, and in some cases they attract large concentrations of some fish species. This co-occurrence suggests the existence of functional relationships between CWC habitats and fish (Armstrong et al. 2014). Though not conclusive, recent research indicates that corals may play an important role in the early life history of some fish and shark species, acting as nursery grounds, as well as providing shelter and feeding opportunities (e.g., Henry et al. 2013).

2 Human Activities with Potential Impacts on Cold-Water Coral Habitats

2.1 Bottom Trawling

Bottom trawls are mobile fishing gears in which a net is dragged over the seafloor. These include beam trawls, which consist of rigid frames mostly used in relatively shallow waters (<100 m), and otter trawls (Fig. 1), in which the mouth of the net is held open by two otter boards (Martín et al. 2014). Otter trawls are one of the most commonly used fishing gears in offshore waters, and because of the lack of a rigid frame, they can be used over rougher and steeper terrains than other types of bottom trawls and are towed at higher speeds covering more ground (Martín et al. 2014). To enable trawling over rough bottoms, the footrope is equipped with large rollers and rock hoppers, molded from steel or compacted rubber and weighting up to several hundred kilograms each. Otter boards can vary in size and weight. In the Icelandic trawl fleet, for example, otter boards can reach up to 11 m^2 and weight up to 5 tons. The wing ends of the net are attached to otter boards by wires known as bridles and sweep lines. The otter boards are in turn attached to the vessel by wires known as warps. Otter trawls are dragged over the seabed at speeds of between 2 and 5 knots. During fishing operations, the trawl is kept open in the horizontal direction by the boards and the tension from the towing lines. At the same time, the combined effect of the floats is placed on the headrope, and the weights on the footrope keep the mouth of net open in the vertical direction. Because of their design, the area swept by the moving net is not defined by the distance between wing ends but by the distance between the otter boards which is larger (Martín et al. 2014). The width of the swath of seabed in contact with the gear depends on the size of the gear and on specific gear settings such as bridle length and water depth. Assuming a distance between otter boards of 100 m and a towing speed of 4 knots, an otter trawl can potentially impact an area of 0.7 km^2 per hour of trawling. During trawling, most parts of the fishing gear, including the otter boards, footrope, and the net itself, are more or less in constant contact with the seafloor, while the bridles have much less impact. This means that the effects of these gear components differ. The otter boards scour the sediment surface, forming tracks that can be tens of centimeters deep but are quite narrow (generally <1 m in width), while the footrope and the net affect a much larger area (the area between the wing ends), but impacts are confined to the upper sediment layers.

Bottom trawls, and in particular otter trawls, deliver 22% of the global fish catch (Kheller 2005). In some areas like the Argentinean shelf, the North Sea, and off New Zealand, the proportion of reported catches associated with bottom trawls exceeds 50%. In the high seas, bottom trawl fisheries are estimated to contribute up to 80% of the total catch. Until the 1950s, bottom trawling was generally restricted to the continental shelf, usually at depths above 200 m. The 1960s witnessed an expansion of bottom trawling into deeper water, driven by the decline of several major coastal fish stocks, the adoption of exclusive economic zones (encompassing deeper water), and the development of large factory trawlers capable of spending long periods of time at sea. Today bottom trawls, and otter trawls in particular, are used in many regions of the world's continental shelf and slopes (Puig et al. 2012).

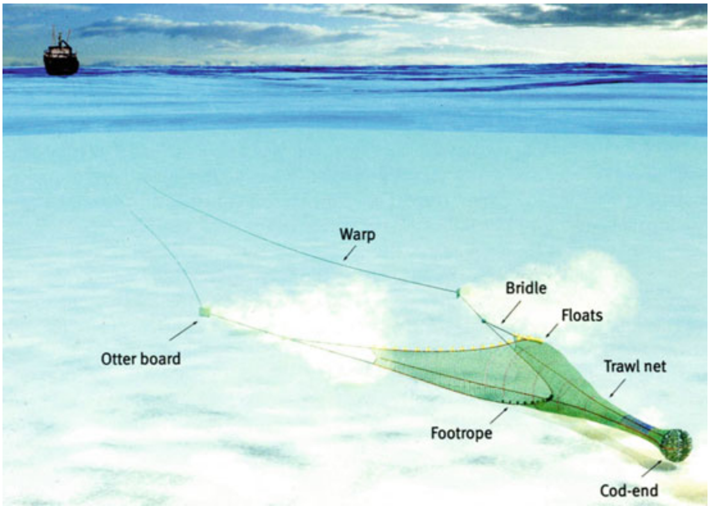

Fig. 1 The typical configuration of a demersal otter trawl (Courtesy of Galbraith et al. 2004, ©Marine Scotland)

Within fishing grounds, the same area of the seabed is often fished repeatedly. Off Northern California, for example, the continental shelf is trawled on average up to three times per year, while the continental slope (below 200 m water depth) is trawled 1.5 times per year (Friedlander et al. 1999). Nevertheless, the spatial distribution of bottom trawling activity can be very patchy, depending on the suitability of the bottom for trawling, the distribution of the target species, and the individual preferences of vessel operators. As a result, some areas can be impacted by trawls at much higher frequencies than others. Gerritsen et al. (2013) estimated that some areas on the shelf break off the south coast of Ireland can be trawled over ten times per year, and there are reports of greater fishing intensity from other locations. Analysis of high-resolution fishing effort data from Icelandic waters shows that some locations along the southern shelf break may be fished more than 40 times per year. High fishing effort also takes place around topographic features on the seabed such as seamounts and ridges where target fish species concentrate. In these locations, trawling effort can be intense, with hundreds or thousands of otter trawl tows located on and around these habitat features (O'Driscoll and Clark 2005).

Otter trawling is the main source of human impact in the deep sea (Benn et al. 2010). Deep-water bottom trawling has the potential to cause significant adverse impacts on seabed ecosystems, in particular on CWCs and other vulnerable biogenic habitats, as they are fragile, slow to recover, and have a limited spatial extent. Direct impacts include the damage and removal of habitat-forming species. The movement of trawl components through the benthos generally causes dislodgment or crushing of individuals, particularly of large organisms that are anchored to the seabed. Damage caused by bottom trawls on CWCs has been reported in many locations. On the Darwin Mounds, for example, side-scan sonar images have revealed trawl damage on the seabed, including scraping marks left by the different components of the otter trawl, including the doors, net, and the footrope, with trawled coral patches showing reduced backscatter suggesting decreased coral abundance (Wheeler et al. 2005). The observed damage to *Lophelia pertusa* reefs off Norway has been related to different levels of fishing intensity. Hall-Spencer et al. (2002) analyzed two reef areas off Norway. The Iverryggen area, exposed to intensive trawling in the 1990s, was characterized by widespread damage to CWC reefs, i.e., containing sparse living colonies that were often broken, dislodged, or buried in mud. The area was littered with coral rubble and trawl marks, and boulders and corals that had been dragged by trawl gear were identifiable. Trenches (5–10 cm deep) had been left by the otter boards. In contrast, in the coastal reef at Nordleksa, where no trawling had occurred, no trawl scars were visible, and prominent expanses of erect, live *L. pertusa* reefs were observed. In a recent extensive study, Buhl-Mortensen et al. (2013) explored 15 *L. pertusa* reefs off Norway exposed to variable otter trawl effort. Offshore reefs, exposed to high effort, showed a greater level of damage, including crushed and dislodged *L. pertusa* colonies and broken and overturned colonies of the bubblegum coral *Paragorgia arborea* than coastal reefs where trawling was not permitted. Even a low number of bottom trawl passes can have a considerable impact. Studies on small seamounts off New Zealand showed that coral coverage was around 10–15% on seamounts where fishing effort was low, whereas it was only 0–3% where fishing effort was high (Clark et al. 2010). Off Alaska, a single otter trawl pass (using a rock hopper with 40–60 cm discs) damaged 67% of sponges and 55% of gorgonians within the trawl path, as well as damaging other large epifaunal invertebrates and displacing boulders (Freese et al. 1999). On seamounts off Tasmania, *Solenosmilia* thicket coverage was two orders of magnitude less on seamounts where trawling was still active, compared to seamounts that had not been trawled. The reduction of *Solenosmilia* thicket was linked to significant changes in the structure of the benthic community (Althaus et al. 2009).

The study of the distribution of fishing effort at small spatial scales also demonstrates the impact of bottom fishing on CWC habitats. In many cases, thriving, complex coral habitats are only observed in locations where bottom trawlers do not operate. Within Icelandic waters, locations with complex bathymetry, e.g., lava fields, steep ridges, and slopes, restrict the use of bottom trawls and have protected CWC habitats (Fig. 2). It is also evident that the impacts of trawling in locations, where corals consist of low-relief colonies, can be particularly severe (Fig. 3). In the Morgue Seamount on the Chatham Rise, dense colonies of scleractinian corals are only found on a ridge where the seabed is too rough for bottom trawling (Clark et al. 2010). The physical disturbances caused by bottom trawling can be significant. In the most extreme cases, coral reefs may be totally destroyed. Buhl-Mortensen et al.

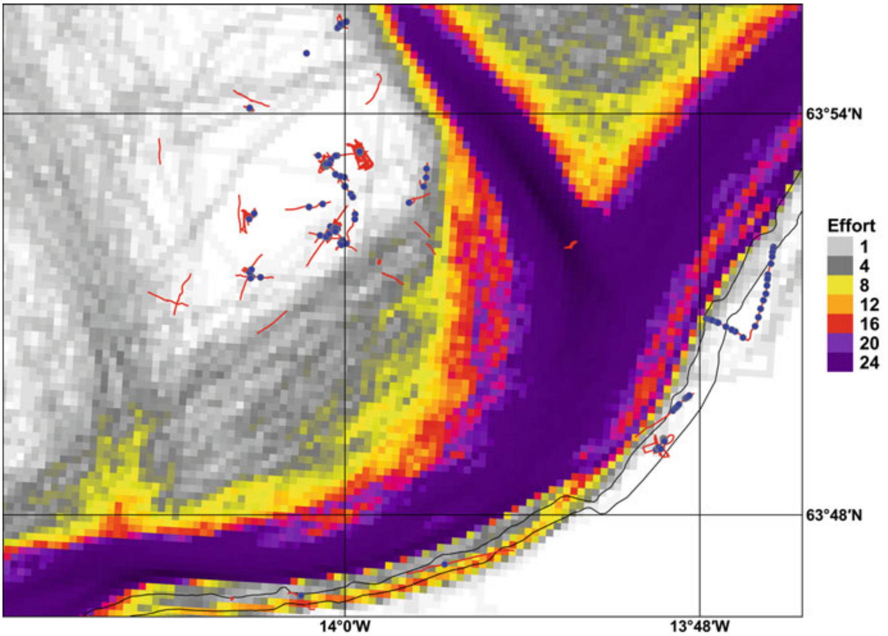

Fig. 2 Trawling effort (tows per year) in the Lónsdjúp trough (300–450 m), Southwest Iceland, derived from electronic logbook data. *Red lines* show underwater video survey tracks. *Blue circles* indicate records of *Lophelia pertusa*. Note the limited overlap between fishing effort and *L. pertusa* distributions, but reefs were found on ridges where trawling was not possible

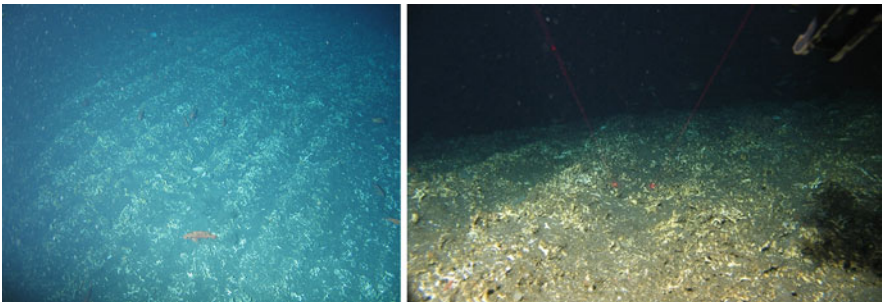

Fig. 3 Destroyed coral grounds in the Skeiðarárdjúp trough (*left*) and on the Öræfagrunn shelf (*right*) off Southeast Iceland. The depth at both sites ranges from 200 to 300 m. The parallel marks on the seabed and the littering of coral rubble on the sediment surface are caused by the passage of otter trawls. Live coral habitat was observed in close proximity (<1 km) to the Skeiðarárdjúp site. Photographs courtesy of Marine and Freshwater Research Institute

(2013) described a completely dead coral reef north of the Korallen area where the seabed was covered with crushed coral fragments, trawl marks, and remains of fishing gear, with no signs of coral regeneration. Off Iceland, similar observations were obtained in the Öræfagrunn and Skeiðarárdjúp areas, where logbook data indicated that the area was heavily fished during the 1990s (Fig. 3).

In addition to direct physical impacts, CWCs can be affected when smothered by suspended sediments. Bottom trawlers are capable of suspending large amounts of sediments when trawling occurs over muddy or sandy bottoms. These suspended sediments are eventually deposited on the seabed and may cause smothering of organisms, e.g., by clogging feeding mechanisms of filter feeders. In shallow water environments, sediments are suspended during storms, and thus the fauna is often sufficiently adapted to such natural disturbances to withstand trawl-induced sediment disturbances. The deep-sea fauna is however more sensitive to such smothering events, as natural disturbances are rare. Several studies have shown how bottom trawlers can generate resuspension and redistribution of sediments in coastal environments and on the continental shelf. For example, Palanques et al. (2001) studied the effect of bottom trawling on the inner shelf of the Northwestern Mediterranean. They observed that the passage of trawlers generated a thick layer of suspended sediments up to 15 m above the seafloor that persisted for 4–5 days after trawling had ceased. This suspended sediment is redistributed by currents and tides. In submarine canyons and steep slopes, bottom trawling can even generate sediment gravity flows (Martín et al. 2014). Palanques et al. (2006) recorded frequent events of increased near-bottom turbidity at 1200 m depth in the La Fonera submarine canyon that were caused by the activity of otter trawlers operating on the northern wall of the canyon at depths of 400–600 m. The impact of smothering on benthic organisms is poorly known. Larval settlement may be impaired in areas where colonies have been smothered with sediments (Rogers 1999). The level of impact is likely to be related to the degree of smothering. As an example, *L. pertusa* appears to survive a light sediment load, but polyps start to die when covered by thicker sediments (Larsson and Purser 2011).

The recovery of CWC habitat that has suffered structural damage is very slow (Althaus et al. 2009; Williams et al. 2010). Reef-forming species can have low growth rates. For example, growth rates of between 5 and 25 mm $\mathrm{yr.}^{-1}$ have been reported for *L. pertusa* (Roberts et al. 2009 and references therein), and slower growth has been reported for species like *Desmophyllum dianthus* (0.5 mm yr^{-1}) (Adkins et al. 2004). Large reefs may take hundreds of years to mature and can be several thousand years old (Rogers 1999). Data on the recovery of coral habitats after fishing impacts are available from some areas. Carpets of uniformly sized *L. pertusa* have been observed in some locations in Norwegian waters that had been trawled 10 years previously (Buhl-Mortensen et al. 2013). On the other hand, the coral matrix formed by *Solenosmilia variabilis* and associated megabenthos removed by bottom trawls on Tasmanian seamounts did not show any sign of recovery 5 years after the bottom fishing activity had ceased (Althaus et al. 2009).

2.2 Bottom-Set Longlines

Bottom-set longlines are used to target demersal fish species, such as gadoids, skates, rays, and various flatfish. A longline consists of a groundline and short branchlines (also called snoods or gangions) that are attached at regular intervals to the groundline using a clip or a swivel. Each branchline holds a baited hook. Gear configurations can be extremely variable in terms of line length, number of hooks, and bait type. As an example, Norwegian and Icelandic autoliners set longlines that are typically 40–50 km long and contain 30–45,000 hooks. In comparison, the longlines set in the Eastern Mediterranean are generally less than 20 km in length, and the number of hooks used rarely exceeds 2000. The longline is generally highly species and size selective, but the selectivity is mainly determined by the hook size and bait type. In some cases the lines are weighted in order to reduce the displacement of the line while on the seabed and to reduce seabird bycatch. The fishing effort by demersal longlines has increased in some parts of the world. For example, the fishing effort by longlines within Icelandic waters was on average roughly twofold greater in 2000–2014 compared to 1991–2000. In the waters around the Azores, all bottom fishing with trawls and gillnets have been banned since 2005, with only longlines and handlines now allowed.

Longlines can be set on seabeds that are too rugged for trawling, but it is in these habitats that the probability of damaging vulnerable benthic organisms, such as cold-water corals, is highest. Longliners sometimes target coral grounds as they have been shown or are perceived to provide higher fish catches. In some locations off South Iceland, there is a high overlap in the spatial distribution of longline fishing effort and cold-water coral habitats (Fig. 4). It is not uncommon that lines that are snagged in coral habitats sometimes snap and long segments are left on the seabed. Several studies have reported the occurrence of derelict lines in coral habitats, but few have attempted to estimate their frequency. Orejas et al. (2009) estimated the density of

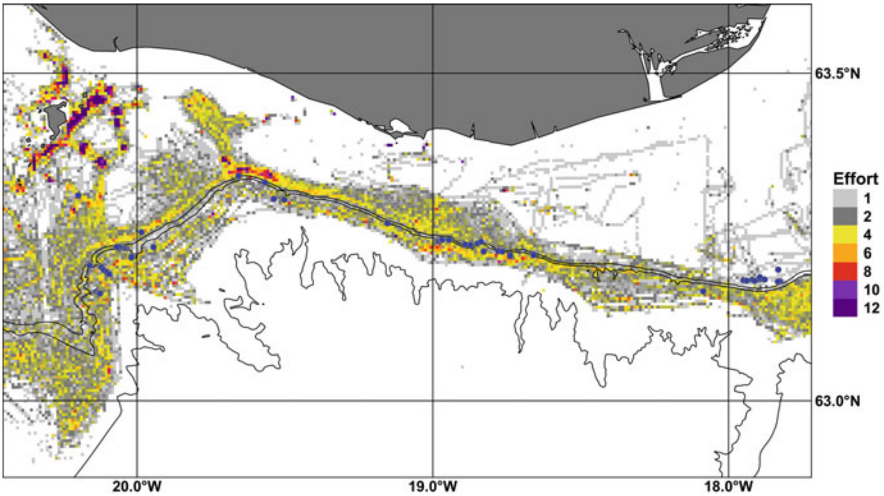

Fig. 4 Longline fishing effort based on vessel monitoring data for the period 2007–2011 off South Iceland. Effort is defined as the number of VMS transmissions identified as fishing per cell (200 × 200 m) per year. *Blue circles* indicate the presence of *Lophelia pertusa*. Note the overlap in fishing effort and coral distributions in some locations

lost lines in three video transects to range between 0.06 and 0.22 items m^{-1}, in the Northwestern Mediterranean. Large et al. (2009) estimated that the total length of retrieved longlines was up to 0.083 km per km transect in the Porcupine coral grounds off Ireland.

Little is known about the impacts of longlines on coral habitats. Some studies have evaluated impacts of longlining by analyzing coral bycatch or the extent of damage viewed *in situ* with video observations. D'Onghia et al. (2012) reported that between 0.4% and 2.2% of longline hooks deployed in the Santa Maria di Leuca coral grounds (Italy) contained coral bycatch. In the Hatton Bank area, the capture rates ranged from 0 to 9.3 kg per 1000 hooks (Muñoz et al. 2011). In the Lónsdjúp coral grounds off Southeast Iceland, the proportion of hooks with coral fragments ranged between 0% and 2.5% (Ragnarsson unpublished observation). Most of the coral bycatch consisted of small fragments of *L. pertusa* colonies, while only 0.025% of hooks contained large pieces of *L. pertusa* colonies and entire individuals of the sea fan *Primnoa resedaeformis* (1–16 kg). The average coral bycatch in a study carried out in the Azores was 32 coral fragments per 1000 hooks, but their study was based on observer data from the commercial fishery and thus not limited to coral areas (Pham et al. 2014a). Higher rates of removal and damage were observed among coral species with high structural complexity.

The amount of coral bycatch may be a poor indicator of the actual magnitude of the damage caused by the longline. While Pham et al. (2014a) reported low coral

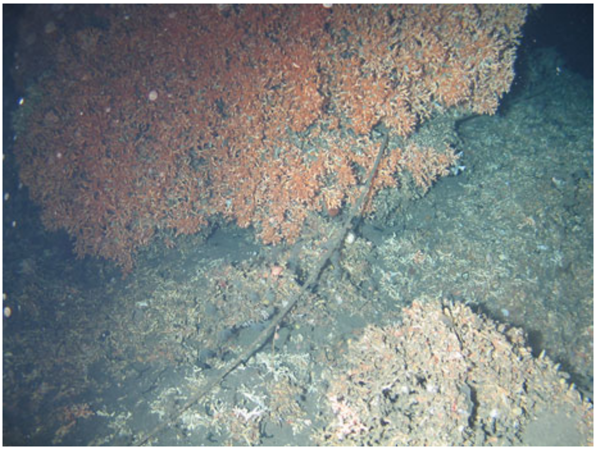

Fig. 5 Lost longline in coral ground on the continental shelf south of Iceland. This longline damaged the *Lophelia pertusa* colony by abrading into the living part of the colony. Photograph courtesy of Marine and Freshwater Research Institute

bycatch rates, video observations from a case study area within a fished ground revealed that 38% of all individuals of *Dentomuricea* aff. *meteor* exhibited major structural damage. Stone (2006) found damage to coral habitats in 76% of video transects carried out in the Aleutian Islands, Alaska, although the disturbance was highly localized. Lines set in coral habitats inflict damage during hauling, and in some cases trails of broken corals can be seen on the seabed where the longline was set. Lines can move laterally across the seabed, during hauling or by the action of strong bottom currents. At times, the line can become snagged on coral structures causing the longliner to encircle the site in an attempt to disentangle it. Recovery of the line can lead to the damage or destruction of fragile coral habitat (Fig. 5).

Providing an assessment of the impacts of longlines on coral habitats is difficult. Data on coral capture by longlines is likely to underestimate their impact on coral habitats, while data to accurately estimate the spatial overlap between longline fishing effort and coral habitats is generally lacking. However, it is likely that the catchability of octocorals will be higher than that of scleractinian corals. In comparison to otter trawls the impact of longlines per unit area appears to be much smaller (Pham et al. 2014a). However, the fact that longliners can target grounds that are largely avoided by trawlers, many of which are known to contain CWC habitats, means that intensive longline fisheries can over time cause significant adverse impacts.

2.3 Bottom-Set Gillnets

Bottom gillnets are nets that are placed to hang vertically above the seabed. The construction of bottom gillnets can be very variable, but they are generally suspended by a topline with regularly spaced floats. At the bottom of the net, a weighted line is used to keep the net in place on the seabed. Various types of gillnets exist, including trammel and tangle nets and true gillnets. In many cases, up to several hundred nets are attached to each other. Gillnetting is one of the oldest fishing practices and is used worldwide, usually in shallow waters. Some fisheries that target deep-water species, such as sharks, deploy gillnets in deeper waters, even below 1000 m. In the North-East Atlantic, a deep-water gillnetting fishery in various locations along the continental slope west and northwest of the British Isles existed but has now ceased. The rate of fishing gear loss could be high in intensively fished areas. For example, Large et al. (2009) reported that the total length of gillnets that were retrieved from the Porcupine Bank ranged from 0.025 to 0.059 km per km transect. In response to significant loss of gillnets, and reports of high incidence of ghost fishing, and to aid protection of several shark species, gillnets were banned in the North East Atlantic Fisheries Commission (NEAFC) and South Pacific Regional Fisheries Management Organisation (SPRFMO) regulatory areas. Information about the effects of gillnetting on CWC habitats is very limited. Gillnets placed within coral habitats may cause considerable damage, for example, by entangling corals in the nets (Hourigan et al. 2007).

2.4 Pots and Traps

Baited pots and traps with aluminum and steel frames are designed so that prey species can enter into them easily but have difficulty escaping. Bait is selectively added to attract the desired crustacean or fish species. Although most fisheries using this gear are carried out in inshore waters, there are some offshore fisheries operating down to 1000 m which may potentially affect vulnerable benthic habitats. The size and weight of each pot used in offshore fisheries can be several times greater than those used in inshore fisheries. For example, in the Alaskan king crab fishery, each boat typically carries 150–300 pots, each covering roughly 4–5 m^2 of the seabed and weighing over a ton when full. During retrieval and handling of pots, these are dragged over the seafloor, thus increasing the area of seabed that is impacted. Impacts are increased still further when multiple pots are attached to each other. Data on the spatial distribution of the offshore potting fishery is scarce.

The few studies that have examined impacts of these fishing gears on benthic communities have been carried out in inshore waters and have demonstrated relatively minor impacts. There is little data available on the effects of potting and trapping in deep waters, but the fact that these are larger and heavier compared to those used in inshore waters suggests that they have greater impacts. If deployed in coral habitats, they are likely to cause physical damage during setting or when dragged over the seafloor during retrieval. Risk et al. (1998) reported that a pot fishery caused damage to gorgonian corals (*Primnoa* spp.). Derelict pots and traps may increase sedimentation and continue fishing (Arthur et al. 2014). It is reasonable to assume that fisheries targeting coral grounds can cause some degree of impact, although further research is required to verify that.

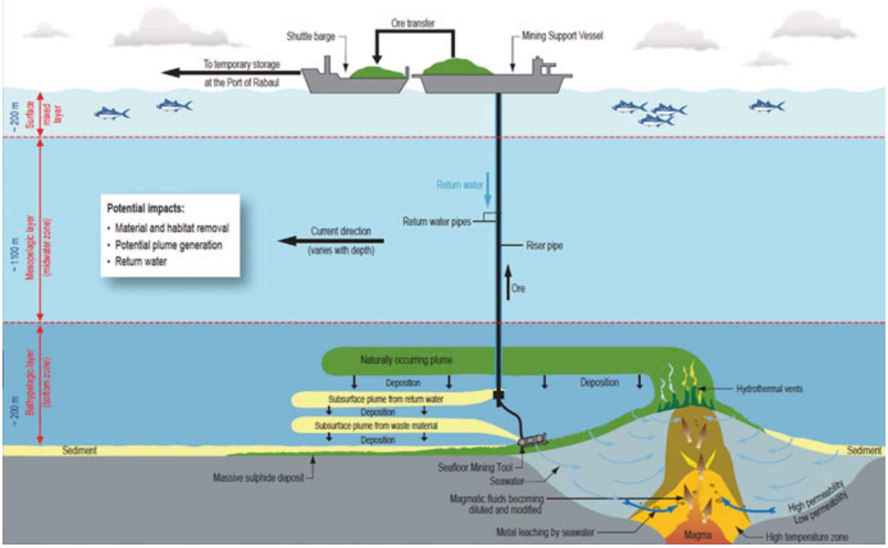

Fig. 6 Schematic diagram showing a proposed mining process and perceived potential impacts. Reproduced from Fig. 3 in Collins et al. 2013 (with permission from Elsevier)

2.5 Deep-Sea Mineral Mining and Disposal of Tailings from Land-Based Mines

Massive sulfides in hydrothermal vent systems, and polymetallic nodules on abyssal plains, can contain highly concentrated deposits of nickel, copper, cobalt, lithium, gold, manganese, and rare earth minerals. These deposits, in addition to cobalt-rich seamount crust, are coveted by the mining industry. Deep-sea mining is, however, in its infancy. Apart from the mining of diamonds at <300 m depth on the continental shelf off South Africa, there is no large-scale commercial extraction of minerals in the deep sea today. Since 2001, however, the International Seabed Authority has granted 26 contracts worldwide to carry out mineral exploration within a combined area covering a total of 1 million km^2 in Areas Beyond National Jurisdiction. Furthermore, the state of Papua New Guinea has granted permission for the excavation (mining) of massive sulfides from hydrothermal vent systems located in the Bismarck Sea. Deep-sea mining will be carried out using giant remotely operated seafloor mining tools equipped with a cutter suction head that can grind rock to a slurry that allows pumping up to a mining support vessel (Fig. 6) or using nodule collectors that will plow through surface sediments to collect nodules. Preliminary processing of the slurry will occur onboard a support vessel and sediment will be discharged back to the sea along with processed seawater (Fig. 6). Deep-sea mining will generate substantial amounts of particulate waste material that can contain toxic substances with the potential to affect marine life either during suspension in the water column or when settled out on the seafloor. Furthermore, the activity will result in a complete removal of physical structures, substrates, and epifauna. While hydrothermal vent systems are generally small in spatial extent, nodule fields can cover large areas of the seafloor. The potential mining of polymetallic nodules in the Clarion-Clipperton Fracture Zone alone is predicted to affect 100s to 1000s of km^2 of seafloor each year. Nodule mining will remove relatively rare hard substrate from the abyssal seafloor, causing severe habitat loss and a drastic reduction in epifaunal densities (Smith et al. 2008; Vanreusel et al. 2016).

In a handful of locations worldwide, including France, Greece, Indonesia, Norway, Papua New Guinea, and Turkey, disposal of tailings from land-based mines takes place in the deep sea instead of the usual practice of using land-based storage (Ramirez-Llodra et al. 2015). Disposal of the tailing material typically takes place by producing a deaerated slurry which is then piped to a disposal site. Chemicals may be added to the slurry to improve particle flocculation and to increase the rate of settlement at the deposition location. Turbidity clouds are created when these tailings are disposed. Field measurements have demonstrated the enormous potential depositional footprint that may result from the release of small suspended particles into the water column.

There are no published studies documenting the effects of pollution from deep-sea mineral mining or disposal of mine tailings on deep-sea corals. It is however expected that the activity may severely affect suspension feeding organisms (such as corals, bivalves, and sponges) due to the increased toxicity and the sharper edges of the mined suspended particles. A long-term laboratory exposure study demonstrated that the physiological response of deep-sea sponges to increased suspended particle loads was highly dependent on particle type. Exposure to ground rock particles with sharp edges has a more negative impact on sponge respiration than when individuals are exposed to natural bottom sediments (Kutti et al. 2015).

2.6 Oil Exploration and Production

Hydrocarbon exploration represents a time-limited source of contamination to deep-sea ecosystems, generally lasting from 1 to 2 months (Tenningen et al. 2011; Møskeland et al. 2012). Discharges are composed mainly of drill cuttings (broken bits of solid material removed from a drilled well) and drill muds (water, oil, or synthetic-based fluids mixed mainly with weighting agents and minor amounts of viscosifiers, emulsifiers, deflocculants, pH, and shale control agents) (see Neff 2005; Bakke et al. 2013, Fig. 7). Releases to the seafloor occur mainly during the drilling of the two top-hole sections. For example, an average well drilled on the Norwegian shelf disposes of roughly 300 tons of cuttings (Møskeland et al. 2012). Larger particles and flocculated solids, which represent approximately 90% of the discharges, settle quickly, forming a cutting pile restricted to a radius of approximately 50 m around the well head (Neff 2005). Smaller, unflocculated particles can stay in suspension for a long time and disperse to wider areas. The degree of dispersion depends on local hydrodynamics and the size and density of the particles. Turbidity levels can be twofold higher compared to natural background levels up to 500 m away from the discharge locations (Møskeland et al. 2012), while significantly

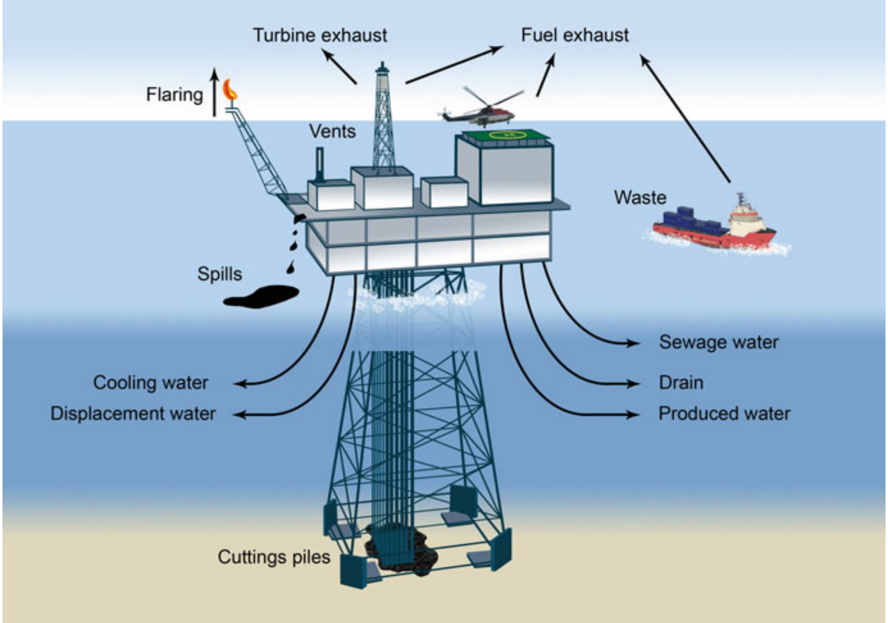

Fig. 7 Release of substances from a range of sources during routine offshore oil and gas production (©OSPAR 2010a)

elevated levels of barium in the sediment originating from the drill mud can be found up to 600 m from the well (Tenningen et al. 2011). The drilling of an exploration well at Trændjupet on the continental shelf of Norway left traces of barite in the sediment 4 km away from the location of the well. Furthermore, it was shown that *L. pertusa* colonies had incorporated barite particles into their calices as far away as 600 m down-current from the drill site (Lepland and Buhl-Mortensen 2008).

Hydrocarbon exploitation impacts deep-sea ecosystems through the disposal of drill cuttings and mud during drilling, along with wastewater discharge from rigs and platforms (Fig. 7). Historically, disposal of all drilling waste was done at sea; however, nowadays, discharge is limited to those drilling muds, cuttings, and wastewater that meet local regulatory requirements. When cuttings are unsuitable for discharge in the ocean, they are either re-injected into a nearby, suitable water-filled reservoir or transported ashore for disposal. Re-injection of wastewater into the hydrocarbon-filled reservoir is routinely done to maintain pressure in the reservoir as oil or gas is removed. Wastewater can be released into the ocean after it has gone through a cleaning process; however, even after cleaning, the wastewater still contains remnants of dispersed oil, aromatic hydrocarbons and alkylphenols, heavy metals, naturally occurring radioactive material, organic particles, organic acids, sulfur, and sulfite (Neff et al. 2011). After decades of oil activity in the North Sea, elevated concentrations of barium (originating from barite drill muds) have been measured in depositional areas of the Skagerrak (Lepland et al. 2000) more than 100 km away from the nearest oil field supporting the theory that the small particles from the drilling mud can be dispersed over a very large area by bottom currents. During hydrocarbon exploitation, there is also a risk of accidental spills of oil and chemicals. Furthermore, mechanical damage to CWCs can occur during anchoring operations of rigs.

Exposure to drill cuttings, and mud and oil contamination, can affect coral behavior, fitness, and survival. The responses are, however, both species and life history dependent. Laboratory studies have shown that adults of the scleractinian coral *Lophelia pertusa* are relatively tolerant to sediment exposure. However, some individuals exhibit reduced polyp activity and increased mucus production when exposed to increased levels of suspended particles and sedimentation of drill cuttings (Larsson et al. 2013). Over prolonged periods, exposure to suspended drill cuttings and mud at ecologically relevant concentrations results in slightly decreased growth (Larsson et al. 2013). Increased larval mortality of the same species has been shown, with younger larvae being more susceptible to lower levels of drill cuttings than older ones (Järnegren et al. 2016). Complete burial in drill cuttings results in 100% adult *L. pertusa* mortality within days due to insufficient oxygen (Allers et al. 2013).

Tropical corals have been reported to exhibit a range of responses to oil contamination such as reduced growth, tissue damage, and impaired settlement. Knowledge of the effects of hydrocarbon releases on deep-sea corals is limited with most knowledge resulting from studies of coral communities around the Macondo well in the Gulf of Mexico. The blowout of this well resulted in an unprecedented release of petroleum hydrocarbon and hydrocarbon dispersants into deep water. Studies following the incident showed that effects were highly site specific. At several locations gorgonian corals appeared not affected while at others close to 50% of the corals observed bore evidence of impacts caused by exposure to the oil plume (Fisher et al. 2014). Visual indications of coral stress included partial tissue loss, excessive mucus production, retracted polyps and coverage on the branches of a brown flocculent material containing petroleum residues, and, in some cases, recent death. Overall, coral recovery was slow. After a few months, gorgonian corals had lost >20% of their tissue and had become heavily colonized by hydroids on the bare skeleton patches (Fisher et al. 2014). The long-term effects of hydrocarbon pollution incidents on coral health and longevity are not known. Mortalities in deep-sea coral populations can cause long-lasting changes in benthic ecosystem structure and function as the corals are generally slow growing and have very low recruitment rates. Hydrocarbon exploration and exploitation in vicinity of deep-water coral ecosystems should always be carefully managed and monitored.

2.7 Litter

Marine litter is defined as “any persistent, manufactured or processed solid material discarded, disposed of, or abandoned in the marine and coastal environment” (UNEP 2009). The presence of marine litter in the deep sea is being reported with increasing frequency. Plastics are the most commonly observed items, including plastic bags and bottles (e.g., Galgani et al. 2015), and items originating from the fishing industry, such as lost longlines and nets (Pham et al. 2014b).

Densities of litter can reach thousands of items per km^2 (e.g., van den Beld et al. 2016), although their distribution can be very patchy. Environmental factors play an important role in the circulation, distribution, and accumulation of litter (Pham et al. 2014b). Plastics can be transported far from their entry point, for example, by rivers, and can be present in the deepest and the most remote parts of the oceans. Once in the sea, litter is transported by ocean currents. The hydrological regime within submarine canyons, including up- and downslope currents, causes litter to accumulate within these geomorphological features. Submarine canyons act as conduits for litter, transporting items from the continental shelf to the deep sea (Mordecai et al. 2011). At the local scale, litter tends to accumulate within structurally complex features on the seafloor, including rocky outcrops and corals (van den Beld et al. 2016).

Litter can impact marine fauna, for example by causing entanglement and smothering (Kühn et al. 2015). CWCs can be covered by macro-litter, including plastic bags and longlines. There are reports of partial necrosis of *L. pertusa* and gorgonians, caused by the entanglement of coral colonies with longlines, plastic, and other marine debris (Kühn et al. 2015). Marine debris can also induce sediment hypoxia or anoxia (Kühn et al. 2015). As a counterpoint, litter can provide new substrate for colonization by cold-water corals. *Lophelia pertusa*, *Madrepora oculata*, and solitary cup corals have been observed growing on plastics, fishing gear, and other litter items. Although it is known that litter impacts marine organisms in different ways, the exact spatial extent and its impact at the population and organism level remain largely unknown.

2.8 Submarine Cables

During the last two decades, there has been a remarkable growth in the capacity of the world's communication cables, from less than 1 Tbps (terabytes per second) in 1997 to over 45 Tbps in 2012. The total length of fiber-optic cables in the world's oceans is now close to 1 million km, and they carry over 95% of transoceanic voice and data traffic. Modern fiber-optic cables are between 17 and 21 mm in diameter in the deep ocean, while they are much thicker on the continental shelf (40–50 mm) because they are covered by a protective armoring. Submarine cables (up to 15 cm in diameter) are also used for the transmission of electrical power, e.g., to link shore-based power grids and to power offshore installations like oil platforms and scientific observatories. As an example, the NorNed cable is 580 km long and connects Norway and the Netherlands (OSPAR 2009). The number of submarine power cables is expected to grow in the future, in particular with the development of offshore energy sources such as wind farms and tidal power plants (OSPAR 2009).

Submarine cables may cause impacts during installation, repair, and removal, as well as during their operational phase. Submarine cables can be laid down to depths of between 1500 and 2000 m. They are buried in the seafloor to prevent damage from bottom fishing gear and anchors. Burial is commonly done by a sea plow which digs a trench into the seabed, sometimes assisted by a powerful water jet, before guiding the cable into the trench. Cable burying causes disturbance of the seabed, including impacts on benthic habitats, increased turbidity, and release of contaminants. These effects are generally considered temporary, and their spatial extent is restricted to the cable corridor, which is around 10 m in width along the cable route (OSPAR 2009).

Few studies have examined the effect of underwater cables on benthic organisms. Studies carried out in shallow waters have found no impacts or only minor impacts on marine biota during cable laying (Andrulewicz et al. 2003). Nevertheless, in vulnerable habitats, underwater cables may cause substantial local impacts. Sultzman et al. (2002) reported significant and long-lasting damage to sponges, gorgonians, and scleractinian corals in the path of an array of communication cables laid on the surface of a nearshore coral reef off Florida. Dunham et al. (2015) examined the effect of the deployment of submarine power cables connecting Vancouver Island to the Canadian mainland on a glass sponge reef (phylum Porifera, class Hexactinellida) and observed 100% glass sponge mortality within the cable footprint and 15% mortality in the 1.5 m-wide corridor surrounding the cable, 3.5 years after installation.

2.9 Radioactive Waste

Anthropogenic radioactive materials in the oceans originate from several sources. The largest inputs are linked to fallout from past nuclear weapons testing (in the order of 10^8 TBq, IAEA 2015) and controlled discharges from land-based nuclear facilities (4×10^5 TBq). Dumping of low- and medium-level radioactive waste in the sea was an accepted practice from 1946 onward. Concerns about the harmful effects of radioactive waste led the contracting parties of the Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter (the London Convention) to impose a moratorium on dumping of high- and low-level radioactive waste in 1975 and 1982, respectively, and a total prohibition of dumping of all radioactive waste in 1994. Radioactive waste originating from research, medicine, and nuclear industry activities were dumped in more than 80 sites in the Atlantic, Arctic, and Pacific oceans by 14 nuclear capable nations between 1946 and 1994 (Fig. 8, IAEA 2015). The total amount of radioactive waste disposed of was approximately 8.5×10^4 TBq. Of this amount, 53.4% was associated with the disposal of low- and intermediate-level, packaged solid waste, most of which (93.5%) was disposed of at dumping sites in the North-East Atlantic by eight countries, but principally by the Great Britain. An additional 43.1% of radioactive waste came from the dumping of reactors with spent nuclear fuel by the former USSR in the Arctic Sea, some of which was high-level radioactive waste (IAEA 2015). The waste was generally packaged in metal drums that were designed to remain sealed during the descent but would gradually disintegrate as a result of corrosion (expected lifetime between 15 and 150 years) and thus slowly release the radionuclides into the surrounding waters (IAEA 2015). It has been

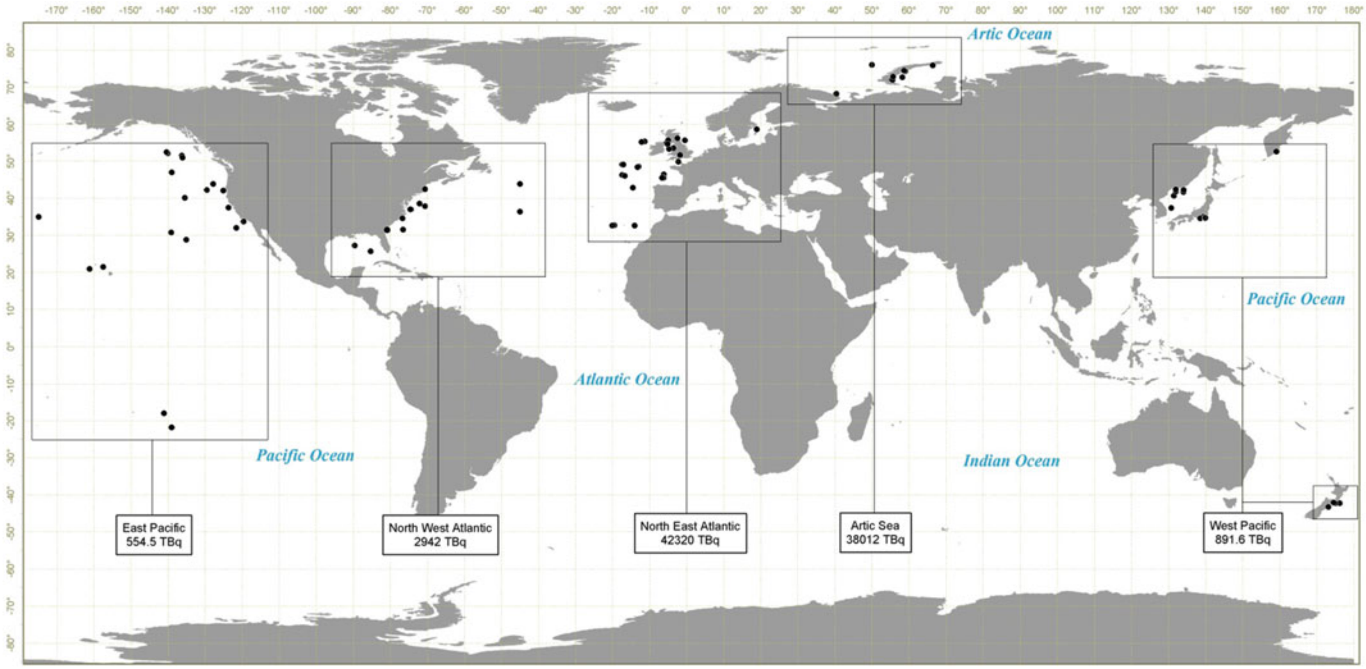

Fig. 8 Inventory of radioactive waste dumping worldwide, in terabecquerels per region (IAEA 2015)

estimated that 225,732 drums containing 114,726 tons of radioactive waste have been dumped in the North Atlantic (Thiel 2003).

Elevated concentrations of radioactive isotopes (including cesium, plutonium, and americium isotopes) have been observed locally in the vicinity of some dump sites (OSPAR 2010b). Increased radionuclide levels have been recorded in a variety of marine organisms, including sea anemones, holothurians and asteroids, and some fish and decapods on both sides of the Atlantic. While numerous laboratory experiments have shown the impacts of radiation on a range of marine and freshwater organisms, especially during the embryonic stage, it is difficult to use these findings to evaluate radiation impacts in the field (Dallas et al. 2012). Following the Fukushima nuclear plant accident, the initial radionuclide exposure was locally high but fell rapidly back to background levels and thus is unlikely to impact marine biota at the population level (Batle et al. 2014). Hall-Spencer et al. (2002) showed that *L. pertusa* specimens collected from deep waters off the west coast of Ireland were not contaminated by ^{14}C from atomic bomb testing in the 1950s, while this type of contamination was found in corals from Norwegian waters. It was suggested that this was due to the fact that the corals off Ireland were located in water masses that had not been in contact with the ocean surface since bomb testing had taken place. On the basis of current knowledge, it is difficult to evaluate the impacts of radioactivity on CWCs. Localized leakage of radioactive waste from drums located on or near coral grounds is however likely to cause some degree of impact.

2.10 Elevated Carbon Dioxide in the Atmosphere and Oceans

The rate at which carbon dioxide (CO_2) is increasing in the atmosphere can present a threat to marine biodiversity through global ocean warming and acidification. Ocean warming has been reported in deep-sea environments, especially along continental margins which are home to many CWC habitats. Elevated temperatures can directly affect physiological processes in corals, but temperature changes may also affect corals indirectly, for example, through lowering the concentration of dissolved oxygen in seawater. A third of the CO_2 emitted into the atmosphere due to anthropogenic activities since the industrial revolution has been absorbed by the world's oceans. This has resulted in a decrease in seawater pH and calcium carbonate saturation state (Ω_{CaCO3}). Seawater pH can directly influence biochemical processes (e.g., enzyme activity) in marine organisms. The Ω_{CaCO3} is specifically important for calcification processes and thus exclusively affects calcifying organisms, including many CWC species. Although elevated CO_2 in the atmosphere and ocean results in concurrent changes of multiple environmental parameters that are of importance for CWC species, the decrease in Ω_{CaCO3} is a particular threat to scleractinian reef-forming species (Roberts and Cairns 2014).

The Ω_{CaCO3} generally decreases with depth due to the effect of pressure on calcium carbonate solubility. The depth below which aragonite dissolves in seawater is called the "aragonite saturation horizon." Above this depth there are enough carbonates present in the water to support coral communities. It is estimated that up to 70% of CWC reefs, which currently live at low saturation states, will be in aragonite-undersaturated water by the end of the century due to the projected shallowing of the aragonite saturation horizon (Hennige et al. 2015).

Experimental evidence suggests that the effects of $\Omega_{\text{Aragonite}}$ on CWC species are complex and species specific and should be investigated in conjunction with other stressors and over relevant time scales. For example, calcification in *L. pertusa* was negatively affected after short-term (1 week) exposure to acidified conditions, but after 6 months the corals had acclimatized to the experimental conditions through sustained growth and calcification rates with no increases in metabolic rates (Form and Riebesell 2012). In general, CWC species have shown varying responses to ocean acidification and decreased pH/$\Omega_{\text{Aragonite}}$, with little or no significant negative effects reported (e.g., Maier et al. 2013; Movilla et al. 2014). Resilience to elevated CO_2 could be significantly related to a species-dependent pH-buffering capacity (McCulloch et al. 2012). For example, upregulation of pH (and subsequently $\Omega_{\text{Aragonite}}$) at the site of calcification has been shown in *L. pertusa* (Wall et al. 2015) and warm-water coral species (McCulloch et al. 2012), but this is an energy-demanding process that may be restricted under finite food availability. However, the skeletal framework precipitated by the corals in low $\Omega_{\text{Aragonite}}$ conditions has been shown to be weaker, which means that these become more susceptible to bioerosion and mechanical damage (Hennige et al. 2015).

The scarce data available on the physiology and ecology of CWCs at different life history stages and the complexity of studying the effects of multiple stressors simultaneously makes it more difficult to predict what the future holds for solitary and reef-forming species in response to elevated CO_2. Based on available data, future changes in the distribution and biodiversity of CWCs will likely reflect species-specific responses to ocean warming and acidification together with other environmental changes. Unless CO_2 emissions are successfully curbed, the continuing rise in atmospheric and oceanic CO_2 could result in a severe reduction in the availability of suitable habitat for CWC globally.

3 Discussion

A number of human activities are known to or can potentially impact CWC habitats, including deep-water fisheries, drilling for oil and gas, mineral extraction, and ocean acidification. Measuring the impacts of anthropogenic disturbances on CWC habitats requires information on (1) the spatial distribution (footprint) of human activities that can impact CWCs, (2) the magnitude and intensity of the impacts of these human activities, (3) the distribution of vulnerable coral habitats, and (4) the sensitivity of coral habitats to human activities.

3.1 Spatial Extent of Human Activities

Over the twentieth century, there has been a gradual trend for fishing effort to extend into deeper waters in response to the depletion of fish stocks in shallower waters. Watson and Morato (2013) estimated that the mean trawling depth in 1950 and 2004 was around 170 and 520 m, respectively, and the trend over time was linear. Data on temporal trends for other human activities in the deep sea that could impact CWC habitats is generally quite limited. Overall, there have been few attempts to evaluate the relative spatial extent of human activities for large maritime areas such as in the high seas. Benn et al. (2010) made a first attempt at estimating the spatial footprint of all human activities within the North-East Atlantic in a single year (2005). They demonstrated that the human activity with the greatest footprint was bottom trawling. Their estimates of the total size of the trawl fishing footprint ranged from 548 to 37,160 km^2 depending on their assumptions about trawling speed and gear width. The authors were unable to obtain fishing effort data from all nations carrying out fishing activities in the area under study, and thus this estimate of fishing footprint is likely to be an underestimate. In comparison, the total spatial footprint from all other human activities, e.g., pipelines and cables on the seafloor, waste disposal, and scientific research, was estimated to be about 150 km^2. The maximum total area impacted by human activities in 2005 was estimated at 27,932 km^2 which is small compared to the total size of the area studied (8,517,010 km^2 deeper than 200 m). It is not known to what degree the spatial footprint of the different human activities recorded by the study in the North-East Atlantic overlap spatially with CWC habitats.

Evaluating spatial interactions between human activities and CWC habitats requires data on the spatial distribution of the human activity at the highest spatial resolution possible. Considering the small spatial extent of most CWC habitats, the spatial resolution of anthropogenic pressures needs to be sufficiently high to accurately estimate spatial overlaps in human activity impacting the seafloor where corals occur. With respect to commercial bottom trawl fishing effort, the accuracy of the information submitted to enforcement agencies can be highly variable, depending on how it was collected. The data provided by conventional paper logbooks generally does not provide information at the spatial and temporal resolution required to examine in detail spatial overlaps in the distribution of fishing and CWC distributions. Data on fishing effort patterns obtained with satellite surveillance systems, such as the Vessel Monitoring System (VMS) and Satellite Automatic Identification System (S-AIS), provide data on fishing effort at much greater spatial resolution and thus are better suited to support evaluation of spatial overlaps. The use of VMS is currently compulsory for a large number of flag states (generally large vessels only) and also in Areas Beyond National Jurisdiction (ABNJ) regulated by regional fisheries management organizations. Over recent years, the proportion of vessels with satellite AIS (S-AIS) has gradually increased. Vessels using VMS and S-AIS systems have a transmitter installed which sends information on vessel identity, location, course, and speed. For vessels operating offshore, VMS systems usually require ship location information to be sent every hour or two, while S-AIS systems have a polling rate of less than a minute. This means that the mapping of vessel tracks is more accurate when based on S-AIS data than for VMS data. The main limitation of VMS and S-AIS data is that it does not record when the vessel is fishing, and locations corresponding to fishing activities therefore need to be identified by indirect methods (e.g., using vessel speed intervals as a proxy for fishing). Electronic logbooks overcome this limitation as they record the geographical position of the vessel only during fishing operations at relatively high polling rates (Natale et al. 2015). It should be noted that some human activities exert pressures for which the spatial extent is difficult to delineate, e.g., smothering caused by resuspension of sediments by demersal trawling and drill cuttings.

3.2 Magnitude of Human Impacts

The nature and relative magnitude of impacts caused by different human activities on cold-water habitats is highly variable. Ramirez-Llodra et al. (2011) assessed the severity of all major human activities for a range of deep-sea habitats, including CWCs, based on scientific expert judgment. As in the present review, they identified bottom trawling as being associated with significant impacts on CWC habitats. Compared to bottom trawls, there has been less concern about the impacts of static gears. Pham et al. (2014a) estimated that between 4,000 and 23,000, longline deployments would be needed to remove 90% of the initial density of branched and unbranched corals on slopes and seamounts, while only 13 tows by bottom trawlers would have the same impact. Nevertheless, longliners often set lines in areas of complex bathymetry which can contain CWCs as these are considered to produce high fish catches. Trawlers tend to avoid fishing in such locations to alleviate fishing gear damage, although there is some evidence of deliberate destruction of reefs. Intensive longline fishing on coral habitats may over time gradually damage these habitats. Several studies have investigated the impacts of longlining based on capture of corals. However, this approach is likely to underestimate the impact of longlining as the efficiency of this gear to capture coral organisms is not known. Knowledge of the impacts of other human activities aside from fishing on CWCs is limited. Ramirez-Llodra et al. (2011) concluded that some of the more serious threats to CWCs in the future are the large-scale changes in oceanographic variables associated with climate change, i.e., ocean acidification, warming of the oceans, and changes in deep-sea current regime and productivity. There is currently evidence of decadal changes in abyssal temperatures in the Pacific Ocean, Caribbean, and Antarctic bottom waters. Glover et al. (2010) found some evidence, although not conclusive, that three deep-sea sedimentary ecosystems had undergone changes that could be linked with climate change. There is currently high uncertainty as to how climate change can impact deep-sea benthic communities. With respect to ocean acidification, the consequences of gradual shoaling (shallowing) of the aragonite saturation horizon on many calcareous forming organisms are not well understood. As an example, it appears that some calcareous forming CWCs can survive to some extent in undersaturated waters. Ramirez-Llodra et al. (2011) evaluated the present and future impacts of mining, drilling for oil and gas, underwater cables and pipelines, and dumping of waste (e.g., radioactive and litter) to be of less concern than bottom trawl fishing and climate forced changes. It is clear that oil exploration and mining can have an impact if they occur in close proximity to CWC habitats. For example, accidental oil discharges have the potential to cause significant impacts in CWC habitats, as was the case after the Deepwater Horizon spill in the Gulf of Mexico (White et al. 2012).

Bottom trawling, mining, and oil exploration cause the resuspension of sediments that can smother organisms. Sediment smothering by drill cuttings produced by the oil industry can have impacts on the fauna in close vicinity to where drilling takes place (Gates and Jones 2012), while the impacts of plumes of resuspended waste sediments that are spread over much larger areas are less well known. There is evidence that intensive trawling can modify the shape of underwater landscapes over large spatial scales such as by causing gravitational flows of sediments to deeper waters (Puig et al. 2012; Martín et al. 2014) and resuspension of large amounts of sediments (Palanques et al. 2014). Oberle et al. (2016) estimated that, within a bottom trawling footprint of 11,516 km^2 (with some locations towed more than 80 times a year), an average of 13.5 MT of sediments were resuspended annually. Storms causing sediment resuspension in waters deeper than 120 m are rare, and thus it could be expected that deep-sea organisms, especially suspension feeders, would be highly sensitive to large amounts of deposited sediments. There is limited knowledge on the effects of smothering on deep-sea organisms, including CWC habitats, but further research may reveal that it has a greater effect than is currently thought.

3.3 Measuring Spatial Distribution of Cold-Water Coral Habitats

CWCs often have a highly patchy distribution with individual patches being of limited spatial extent. Data on spatial distribution of CWCs therefore needs to be at a very high spatial resolution (<1 km^2) to enable evaluation of possible spatial conflicts from overlapping human activities. However, good data coverage on CWC habitat distribution is lacking for many maritime areas. Martin et al. (2015) estimated the global distribution of areas of importance for biodiversity, including CWC habitats. They classified 13 million km^2 (3.7%) of coastal and marine areas as highly or potentially, high biodiversity habitat. The remaining 349 million km^2 (96.3%) could not be evaluated, mainly due to lack of data. Only 1% of Areas Beyond National Jurisdiction (ABNJ) could be classified.

Potential locations where reef-forming species like *Lophelia pertusa* and *Madrepora oculata* are likely to be found can be identified based on analysis of high-resolution bathymetry data. Currently, about 10–15% of the total seafloor has been mapped at a 100 m resolution, which enables the detection of large reef structures. To detect smaller reefs, mapping at a resolution of a few meters is necessary. However, less than 0.05% of the seafloor worldwide has been mapped at this resolution. In comparison, 60% of the surface of the Mars has been mapped at

20 m resolution. The most direct method to investigate the distribution and composition of CWC habitats is the use of unmanned or manned underwater vehicles to obtain visual data (video and photographs). Given the financial and logistical constraints of sampling in the deep sea, the size of the area of seafloor that can be surveyed using this approach is extremely small. Some countries have established ambitious habitat mapping programs based on multibeam survey and ground truthing with video and other methods. Two good examples are the INFOMAR project (http://infomar.ie) in Ireland and the MAREANO project in Norway (Buhl-Mortensen et al. 2015). Another approach that provides data about the distribution of CWCs is to analyze coral bycatch recorded during demersal fish survey assessments and from commercial fisheries (Kenchington et al. 2014). However, it is not possible to know exactly where corals were caught during fishing operations, so this approach provides semiquantitative information at best on the distribution of key coral habitats. Species distribution models are often used to predict the distribution of CWC habitats based on their association to environmental parameters such as bathymetry, substrate type, currents, temperature and primary productivity.

3.4 Evaluating Sensitivity to Human Activities

Assessment of the potential impact of human activities on CWC habitats requires evaluation of the sensitivity of coral organisms or habitats to different human pressures. Quantitative data (e.g., experimental work) measuring responses of coral organisms to human pressures is only available for a few well-studied species or for more data-rich shallow water settings (e.g., Hinz et al. 2009). Studies that have evaluated the sensitivity of various cold-water coral species have therefore relied on expert judgment to create sensitivity matrices that determine the potential magnitude of impact for all pressures generated by a suite of human activities. One recent example of this approach is the Marine Evidence based Sensitivity Assessment (MarESA) framework (http://www.marlin.ac.uk/). This framework considers a large range of pressures classified into four groups: physical (e.g., habitat loss and smothering), chemical (e.g., heavy metal contamination), biological (e.g., removal of target species), and hydrological (e.g., temperature changes). For each organism or habitat, the responses to each pressure are evaluated on the basis of their resistance (i.e., ability to tolerate disturbance) and their recoverability or resilience. The sensitivity of a particular organism to a particular pressure is scored qualitatively from “not sensitive” to “high.” The confidence in the evaluation is ranked from low confidence to high. The MarESA and other similar approaches have been applied to evaluate the sensitivity of a wide range of species and habitats, including CWCs.

Another approach used to evaluate the sensitivity of CWC habitats is to apply the Food and Agriculture Organization of the United Nations (FAO) habitat criteria. This provides a list of habitat descriptors that are used to evaluate the quality of habitats. These include uniqueness or rarity, functional importance, and structural fragility. Recently, the ICES Working Group on Deep-water Ecology (ICES WGDEC 2016) used these FAO habitat criteria to evaluate the sensitivity of

13 invertebrate groups, based on expert judgment, that were considered indicators of vulnerable marine ecosystems. Among these, stony corals received the highest score, followed by black corals and large sponges (ICES WGDEC 2016). Coupling sensitivity scoring of different human activities with other information, such as the spatial distribution of human activities, enables production of sensitivity maps (e.g., Agbayani et al. 2015) which can be used to identify areas at risk and in need of management.

3.5 Cumulative Impacts

Measuring the cumulative impacts of human activities on marine habitats, including CWC habitats, has proven challenging as there is limited understanding of how impacts caused by two or more stressors interact. With respect to CWCs, most cumulative impacts are predicted to be caused by climate change-related pressures (e.g., ocean warming, changes in primary production, hypoxia, and ocean acidification) and deep-water bottom fishing (Ramírez-Llodra et al. 2011). Increased temperatures can lower oxygen thresholds and reduce the tolerance of species to acidification, while, in turn, hypoxia and acidification can reduce thermal tolerance. In addition, the physical disturbances caused by bottom trawling, deep-sea mining, and oil and gas extraction can increase the effects felt by organisms experiencing physiological stress due to climate change factors (Smith et al. 2008; Ramirez-Llodra et al. 2011). Ocean acidification, for instance, may impair skeletal growth, resulting in CWCs having a weaker skeleton (Hennige et al. 2015), which in turn makes them more sensitive to physical disturbances caused by bottom fishing gears. Another source of physiological stress may be disruption of the topographically enhanced carbon pump by enhanced stratification and lower surface productivity caused by higher temperatures, as described by Soetaert et al. (2016). Both will have a negative impact on the energy balance of cold-water corals. Changes in deep-water circulation and ocean stratification may also have an effect on the transport and accumulation of litter and other pollutants.

There remains a great need for more experimental studies to quantify the response of deep-sea organisms to anthropogenic stressors, in particular to oil drilling discharges, smothering events, exposure to pollutants, and organic enrichment associated with dredge spoil dumping and to the disturbances associated with deep-sea trawling (Smith et al. 2008). Cumulative impacts can be either synergistic or antagonistic when the combined effects of multiple pressures are greater (synergism) or less than (antagonism) the sum (additive) of the impacts of individual pressures. Current understanding of antagonistic and synergistic impacts is limited, and most studies therefore assume that cumulative impacts are additive (e.g., Agbayani et al. 2015). This includes studies where the expert-based sensitivity scores from two or more activities impacting a particular habitat are summed together. Weighing the potential impacts based on expert judgment of a vast range of disparate human activities such as bottom trawling and ocean acidification will always be challenging and have a high degree of subjectivity.

3.6 Mitigating Human Impacts on Cold-Water Coral Habitats

Measures to mitigate the impacts of human activities on CWCs have been mostly confined to bottom fishing and include the establishment of marine protected areas (MPAs). Currently, MPAs are established both within national waters and also in Areas Beyond National Jurisdiction (ABNJ) to protect vulnerable marine ecosystems. As an example, bottom trawling is now banned in 30% of the New Zealand's exclusive economic zone (Helson et al. 2010), and large MPAs have been established in ABNJ within the North-East Atlantic (Johnson et al. 2014). In the ABNJ, fisheries are regulated by various regional fisheries management organizations, and fishing activity mostly takes place within existing footprints. Within the fishing footprint, the "move-on" rule has been established which requires vessels to move a minimum distance when the bycatch of several types of highly sensitive organisms, including corals and sponges, exceeds a threshold level during fishing (Auster et al. 2011). For CWCs, the threshold levels vary between regulatory areas. For example, if the weight of CWCs caught in a trawl exceeds 60 kg in the Northwest Atlantic Fisheries Organization (NAFO) regulatory area, the move-on rule is triggered. In June 2016, the European Union agreed to implement a general ban on bottom trawl fishing within the North-East Atlantic below a depth of 800 m (around 4.9 million km^2), with the objective of protecting vulnerable benthic habitats. Fishing is also banned in areas below 400 m if the quantity of vulnerable species caught exceeds threshold limits. Finally, trawling is only allowed within an existing footprint based on the fishing effort between 2009 and 2011. While these are clearly major steps toward the protection of vulnerable marine habitats, several advocacy groups have demanded a general ban on fishing below 600 m depth, which would ensure protection of a much larger proportion of vulnerable deep-sea ecosystems. There are also measures in place to mitigate the impacts of other human activities. As an example, the Norwegian oil and gas industry has regulations governing the minimum safe distance required between drilling locations and coral habitats.

3.7 Final Remarks

This review shows that CWC habitats are impacted by a number of human activities. However, evaluating the impacts of human activities on CWC habitats is often difficult due to lack of baseline data on CWC distribution and functioning and on the nature of pressures that impact these habitats. Over recent years, there have been successful attempts to restrict the spatial distribution of bottom trawl fishing effort, which reduces the risk that remaining pristine coral grounds will be impacted and allows recovery of those coral grounds that have already been degraded. The consequences of other human activities may be more difficult to manage. An improved understanding of the cumulative effect (both through direct and indirect pressures) of multiple activities in a given area is needed. The greatest risk to CWC habitats may be changes in ocean hydrography associated with climate change.

Arresting these changes requires a global effort to significantly reduce emission of greenhouse gases. The investigation of climate-driven impacts on CWC communities should be given a high priority.

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4 Cross-References

- ▶ Conservation and Management of Vulnerable Marine Benthic Ecosystems
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest
- ▶ Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998

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Harvesting and Collection of Animal Forest Species

36

Alison M. Jones, Daniel J. Thornhill, and Anthony J. Roelofs

Abstract

The harvest and trade of corals and other benthic organisms from the world's shallow tropical reefs is a lucrative industry that can have positive socioeconomic benefits for communities while supplying the increasing demand specimens for aquaria and curios. For most countries, this trade has historically been almost entirely unregulated. More recently, in response to concerns about the rapid decline of some reefs in the face of anthropogenic and natural pressures, as well as indications of depletions and even localized extinctions of some species caused by harvesting, there have been attempts to improve the sustainability of the industry. Both developing and developed countries face different impediments to this reform, the most pressing and common of which is the lack of reliable data on world trade through CITES. Thereafter, differences in the processes through which reform can be implemented are based principally on the length of the supply chain from collection to export, the degree of industry stewardship, and resourcing. The coral collection fishery in Queensland, Australia, provides an example where continual improvements in reporting and risk assessments and adopting a comanagement approach are delivering better adaptive management of the resource, although the on-ground sustainability

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benefits of this approach are still to be tested. A simpler approach to sustainable use of coral is to favor the replacement of wild harvested specimens with those bred or grown entirely in an aquaculture facility (as opposed to merely collected and then grown out in culture). Yet there are major impediments to this change, including the dependence of many public aquaria on the same sources as the hobbyist community, difficulties of culturing some species in captivity, and infrastructure costs. Nevertheless, this approach will likely play an important part in reef conservation efforts in the future.

Keywords
Aquarium harvest • Aquarium trade • Aquaculture • Aquarist • CITES • Coral collecting • Coral harvest • Coral reef • Wild harvest • Wildlife trade • Precious coral

Contents

1 Introduction

Coral reefs are among the world's most ancient ecosystems, rivaling old-growth forests in their longevity. Sometimes called rainforests of the sea (Knowlton et al. 2010), modern reefs have evolved through extreme climatic changes including several extinction events (Kiessling et al. 2007). In total, coral reefs occupy less than 0.1% of the world's ocean surface or 5% that of the world's rainforests, yet they are the most diverse marine habitat per unit area and house 25% of all the known marine species. Reefs are of immense social and economic value, providing food and income to millions of people. Estimates show that coral reefs provide nearly US$ 30 billion each year in net benefits in goods and services to world economies, including tourism, fisheries, and coastal protection for 39% of the world's population (Cesar et al. 2003). In Florida, the loss of almost all of the reef-building coral species as a result of bleaching and poor water quality has led to efforts to replenish the reefs with aquacultured corals (Fig. 1, Fitt et al. 1993). With about 28% of world reefs now showing signs of decline (Knowlton et al. 2010), further loss of coral reefs could be devastating for world economies.

Fig. 1 An aquacultured coral nubbin is transplanted in the Florida Marine Sanctuary following catastrophic bleaching. Image on the *right* shows a diver cleaning algae from the bases of transplanted cultured corals to prevent overgrowth (Photos courtesy of A. Jones)

Coral reefs are living, three-dimensional structures made of corals and other benthic, sessile marine species and those organisms that depend on them for habitat (Rossi 2013). Surprisingly, most of the diversity living on coral reefs lies not in the species that make up the three-dimensional structure (there are, in fact, fewer than 1000 species of stony corals (Veron 1995)) but in the multitude of small organisms living with corals, much like the insects found in rainforests. These organisms are responsible for the ecosystem services such as bio-erosion, filter feeding, waste recycling, and a plethora of other essential activities that support life.

The healthy state of many of the world's coral reefs is vulnerable to both global (climate) and local pressures (harvesting and water quality). The more specific threat of climate change to coral reef biodiversity has only been recognized in the recent past (Carpenter et al. 2008) with the Center for Biological Diversity successfully petitioning the United States Government to list 83 species of corals under the Endangered Species Act. This lack of attention to biodiversity in the oceans may be attributed to a lack of information about many marine species (Knowlton et al. 2010) and also to the difficulty in measuring change in marine communities in general.

2 The Issue of Sustainability for a Growing Marine Aquarium Trade

One of the main causes of coral reef decline comes from overharvest, particularly on reefs close to coastal human communities. Trade in coral reef wildlife provides an important source of income for the coastal communities of many developing nations. In addition to the harvest of fish for food, this includes the harvest of corals and other benthic species for trade as ornamentals. Globally, trade in marine organisms has increased over the last decades to a point that it is now considered a threat to the world's coral reefs (Wabnitz et al. 2003; Rhyne et al. 2012). Stony corals (Scleractinia) are targeted for their value as ornaments in reef aquaria, and many of the associated invertebrate organisms are collected for their role in cleaning and filtration in domestic and public aquaria. Stony corals form the structural framework of reefs through the accretion of elaborate calcium carbonate skeletons. Just like overharvest of trees from terrestrial forests and rainforests, overexploitation of stony corals may affect the structural integrity of the reef itself, while removal of invertebrates such as mollusks, crustacea, anemones, and sea horses can result in the loss of essential ecosystem services that support the reef's function.

In addition to the stony corals that inhabit tropical reefs, the much rarer and less well-understood precious corals have also been commercially exploited for making jewelry for many centuries. Precious coral is the common name given to *Corallium rubrum* and several related species of marine coral. The distinguishing characteristic of precious corals is their durable and intensely colored red or pink skeleton, which is used for making jewelry. Commonly known as red, pink, black, gold, blue, and bamboo corals, precious corals can be found in deeper waters where, like the stony corals of shallow reefs, they form a habitat for a plethora of other marine organisms, thus promoting biodiversity. Precious corals are slow growing (Grigg 1984), and because of their value, their harvest is typified by overexploitation of discovered stocks (Tsounis et al. 2010) followed by local depletion and has led to population declines.

The removal of corals and other benthic invertebrates from the world's tropical reefs to supply the global ornamental wildlife trade is a controversial and heavily debated subject. Of the approximately 6000 known species of corals, over 140 species are collected for use as live specimens in domestic aquaria or dead as jewelry or for curios (Wabnitz et al. 2003). Historically, the ornamental coral trade primarily targeted a small suite of species with attractive skeletons for sale as curios (Fig. 2, Ross 1984; Oliver and McGinnity 1985; Green and Shirley 1999). While this practice is sometimes regarded as potentially sustainable for relatively fast-growing species like the acroporids (i.e., ~15 cm yr^{-1}, Harriott 2001), curios collection can be destructive as large individual specimens and large volumes of small-polyp species of corals are often taken. For the live aquarium trade, along with corals, most harvesters also now collect other benthic invertebrates, including anemones, to include in mini-reef aquaria as curios or as pets. Many detrital cleaners such as mollusks, crustaceans, and live rock (coral reef substrate that includes living microbes and various invertebrates such as borers and filter-feeders and sometimes juvenile corals) are also collected to maintain the health of aquaria (Tissot et al. 2010; Rhyne et al. 2012; Wood et al. 2012). An estimated 500 species of invertebrates and over 1800 species of fish are now collected to service this market, raising justified concern for the impact on the sustainability of the practice for targeted reefs (Wabnitz et al. 2003), while the collection of living rock raises concerns for the loss of potential settlement substrate for new coral recruits.

In the case of the precious coral trade, improved technology such as scuba diving, remotely operated vehicles, and manned submersibles have been a two-edged sword. On the one hand, technology has improved understanding of population dynamics and ecology of these key species (Grigg 1976) but, on the other hand, has permitted more efficient exploitation (Rossi et al. 2008). Because they are rare and restricted in

Fig. 2 Examples of the dead, dried, and artificially colored ornamental "curios" sold by the aquarium harvest trade in pre-1990 (Photos courtesy of A. Jones)

distribution, poor management of the precious coral fisheries could have long-term and possibly permanent consequences that could change the entire ecosystem.

3 A Shift in the Marine Aquarium Trade

The steady shift in the marine aquarium trade since the 1990s has been driven, until recently, by increasing demand for mini-reef ecosystems in domestic aquaria (Wabnitz et al. 2003; Tissot et al. 2010; Rhyne et al. 2012; Wood et al. 2012). Visually pleasing, slow-growing genera with larger, colorful polyps such as *Trachyphyllia*, *Euphyllia*, *Goniopora*, *Acanthastrea, Plerogyra*, *Scolymia*, and *Catalaphyllia* sp. are now among the most popular coral specimens with marine aquarists (Fig. 3). These genera typically are brooders as opposed to the more widespread broadcast spawners

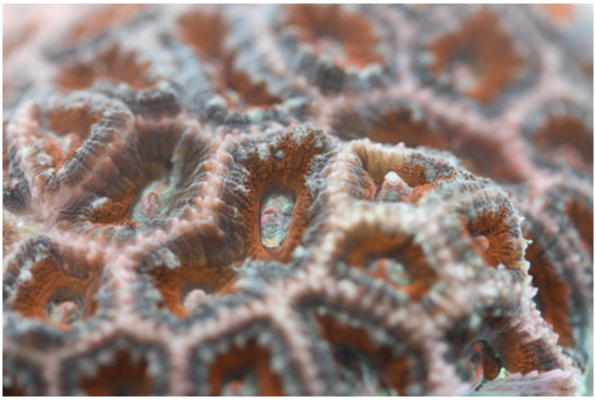

Fig. 3 Examples of pieces of live, large polyp species of coral collected by the aquarium trade *Acanthastrea lordhowensis*. Corals are chiseled from the reef and then fragmented before shipment or sale. The corals often have other organisms attached to their skeleton (Photos courtesy of D. Brighton)

like the acroporids. This makes them easy to collect but risks localized depletion as the size of the global trade grows, outstripping sustainable supply from the wild (Fig. 4, Jones et al. 2008; Tsounis et al. 2010; Jones 2011; Thornhill 2012). Management of aquarium harvest fisheries has generally failed to keep up with the shift in demand, potentially placing heavily targeted genera at risk. A recent shift by aquarium hobbyists toward even smaller "nano"-reef tanks raised hope that the need for fewer organisms to stock these smaller tanks might lessen the coral reef wildlife trade's demand on reef ecosystems globally (Rhyne et al. 2012). However, the inherent difficulty in maintaining adequate water quality for a healthy system without the buffering effect of a larger volume of water, and the tendency for these tanks to "crash" much more easily and frequently, has now led to further concern for an increase in the demand for replacement specimens.

The history of the precious coral trade is vastly different to that of the marine aquarium trade. Precious corals have been used for jewelry-making since antiquity, but the official trade is thought to have started about 5000 years ago in the Mediterranean (Grigg 1984). The trade peaked in the 1800s when collecting methods were industrialized by the Kingdom of Naples but varying in response to world politics (e.g., WWII), discoveries of new stocks, and market forces. The boom and bust nature of precious coral exploitation resembles mining rather than a typical fishery with stable yields.

4 Case Studies of Aquarium Harvest Damage to Reefs

In some locations, the harvest of corals to supply the global aquarium trade has been accompanied by population depletions, localized extinction, destructive fishing practices, and demographic shifts (Bruckner and Bruckner 2006; Knittweis and Wolff 2010). For example, Ross (1984) compared locations in the Philippines where corals were heavily collected for the curio trade to low- or no-collection

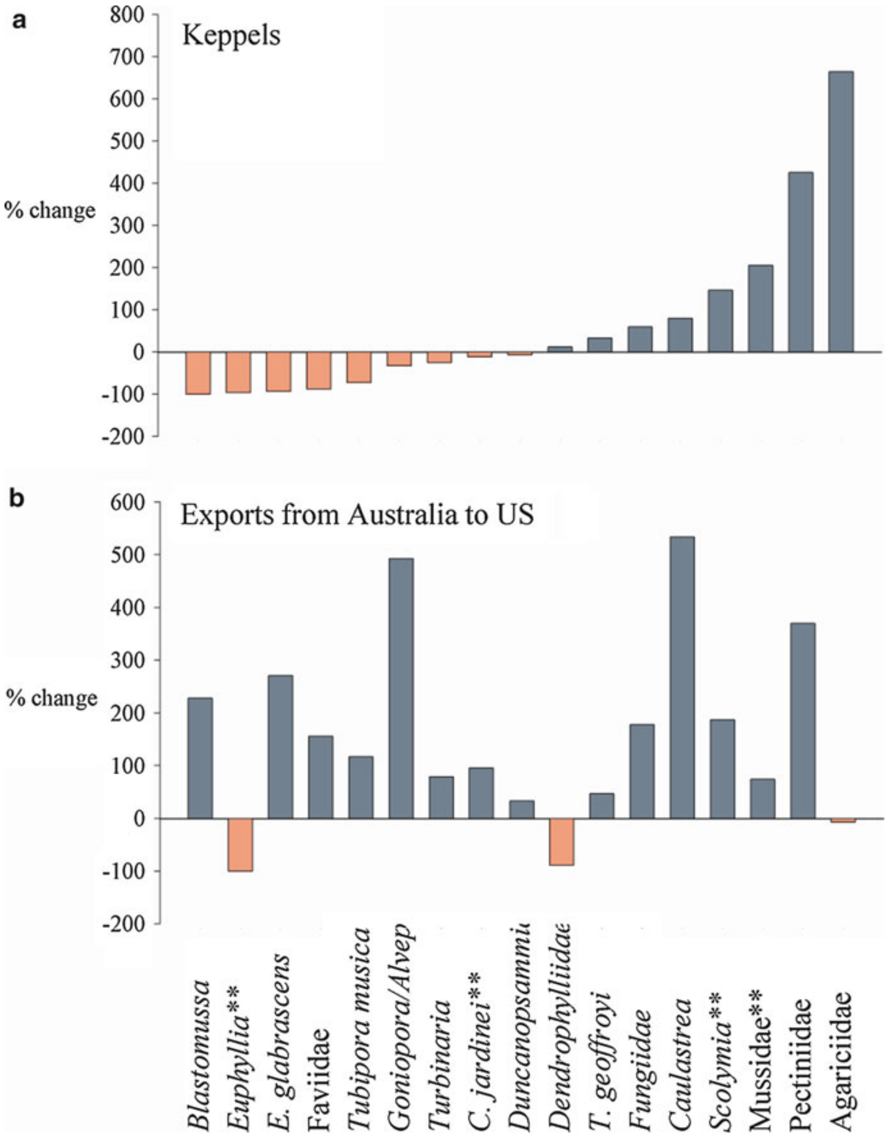

Fig. 4 Percentage change in (**a**) the number of specialty coral specimens collected in the Keppel Islands region and Southern Great Barrier Reef and (**b**) exported from Australia to the USA between 2006/2008 and 2009. Bars represent the percentage change in harvest for 2009 compared to the average for 2006/2007–2007/2008. Data were sourced from the Fisheries Queensland CFISH database and Convention on the International Trade in Endangered Species (*CITES*) database, respectively. Only a subset of the 28 taxa reported by the Queensland Coral Fishery for the Keppels for which CITES export data were available are shown. Taxa marked with ** are listed as at risk of local depletion (Figure is a reproduction from *Raiding the Coral Nurseries* by Jones (2011))

sites. For 25 out of 28 targeted species, collection reduced coral density and cover. Reductions were most extreme in the upper reef crest, with a 77.8% decline in density and 86.3% reduction in the cover of collected species. Demographic shifts toward younger coral colonies were also observed. Likewise, the collection of the coral *Heliofungia actiniformis* in Indonesia decreased the species' abundance, with an absence of corals in the size range preferred by aquarium hobbyists and a shift to less attractive color forms, which suggested localized depletion of particular color morphs (Knittweis and Wolff 2010) and raises questions about the ecological impact that this might have on functional diversity (Takabayashi and Hoegh-Guldberg 1995; Hoegh-Guldberg and Jones 1999). On fringing reefs in Bolinao (McManus et al. 1997), coral-grabbing anchors resulted in a 30% reduction in coral recovery rates with reduced resilience to natural disturbances.

For the precious coral trade, the widespread practice of dredging was largely abandoned for selective harvest by divers in helmeted suits in the late 1800s (mainly because dredging recovered only about 40% of corals). Divers were finding corals at ever-increasing depths up to 100 m in the 1900s, indicating a depletion of stocks at lesser depths (Tsounis et al. 2010). Similarly, in the Pacific Islands off the coast of Japan, fleets of fishing vessels that employed dredges were making every more distance trips for precious corals at depths up to 1500 m as newly discovered stocks were slowly depleted. As late as the 1980s, France still reported tonnage production of precious corals by both divers and dredging (5:1). In 1991, an all-time low < 3 t of precious coral production was recorded in the Pacific indicating the depletion of all known stocks (Grigg 1984). Age-frequency distribution of some precious coral populations (Hawaii) were beginning to decline (Tsounis et al. 2010), indicating biomass loss (Grigg 2004). The past problems of destructive wild harvest practices like dredging and the removal of entire colonies, ineffective management and lack of regulation, poor quality data, and demand exceeding supply continue to be concerning aspects of the trade in ornamental and precious corals.

5 Past Attempts at Improved Sustainability of the Marine Aquarium Trade

Over the past decade, there have been attempts to improve the sustainability of the aquarium trade for corals and for other species, particularly as the world's ocean ecosystems face increasing pressures from a range of natural and anthropogenic processes. These include international agreements, marine protected areas, rotational closures, banned-species lists, quotas, cyanide detection, gear restrictions, specimen size limits, licensing and limited entry into the fishery, and regulations on imports (reviewed in Dee et al. 2014).

Selected examples include:

- Improved integrated and adaptive management practices (e.g., in Australia, a new voluntary operational code in response to the impacts of thermal bleaching and floods on the inshore regions of the Great Barrier Reef)

- A coalition of four US nonprofit organizations – Environmental Defense Fund, World Wildlife Fund, Defenders of Wildlife, and the Humane Society International – that sought improved US import standards for coral reef wildlife
- Grassroots, legislative, and legal campaigns by activists in Hawaii to limit or ban the collection of fish and invertebrates for the ornamental trade (e.g., For the Fishes; the Humane Society, USA; and Earthjustice)
- Various voluntary partnerships between industry and conservation organizations; initiatives to identify species that are appropriate for home care and can be collected with limited environmental impact (e.g., Reef Protection International, Sustainable Aquarium Industry Association)
- Efforts at sustainable aquaculture and sustainable collection practices (e.g., the Marine Aquarium Council in the USA, Olazul, Rising Tide Conservation) (Amos and Claussen 2009; Tissot et al. 2010)
- In 2006 the state of Hawaii returned to the minimum size limit of 1.2 m for black corals in response to a decreased biomass of 25% and began setting up an inventory tracking system using bar codes to gather data on the harvest and trade (Tsounis et al. 2010). A good understanding of the ecology of black corals targeted by the trade, their relatively faster growth rate, and a 20-year history of response leading to a steady state for the industry have led to successful adaptive management approach for Hawaiian black coral trade.

The success and viability of these efforts have varied tremendously due to social, political, and economic impediments. Issues such as the number of countries involved in trade, the sometimes remote locations involved, the wide diversity of taxa targeted, and the difficulty of identifying specimens accurately for reporting purposes have to be taken into account. Traditionally, stock assessment and quotas on total catch have been employed as management tools, but these approaches are not often feasible for invertebrate and ornamental and precious coral fisheries due to the limited availability of data on the population dynamics of targeted species, lack of accurate stock and collection assessments, as well as the prevalence of black market fishing (Dee et al. 2014). Attempts at sustainability policies that employed market power to help drive marine aquarium industry reforms have failed (Amos and Claussen 2009). Among the most successful approaches have been moratoriums on certain species, no-take reserves, tiered quota systems, tightly regulated size restrictions, and import and export restrictions.

6 Lack of Data Availability and Quality: A Challenge for Managers and Fishers

Other impediments are the limited data available to make informed sustainability decisions, the voluntary nature and lack of accountability or enforcement of sustainability certification programs (e.g., Marine Aquarium Council in the USA and the Stewardship Action Plan in Australia), weak enforcement, and economic as well as biological impediments to shifting to aquaculture (Amos and Claussen 2009; Tissot et al. 2010;

Rhyne et al. 2012; Dee et al. 2014, Thornhill pers. obs.). Issues of data availability and enforcement are particularly relevant in developing countries where coral harvest can represent a significant economic benefit to local communities, and there is a reluctance to change the status quo. A shift to aquaculture may be slowly occurring (Wood et al. 2012); however, problems with the reporting standards of collected data also hamper validation of this trend. Accurate reporting of collection remains one of the biggest challenges facing fishery managers and scientists in making informed decisions on the development of responsible and sustainable collection practices.

The global nature of the market for marine ornamental products makes compliance and reporting increasingly stringent and complex. As aquarium products move from one country to another, they must comply with national laws to implement the United Nations Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). CITES is an agreement between 175 governments that was created in 1975 to ensure that international trade does not adversely affect global biodiversity and establishes permitting and monitoring requirements for CITES-listed species. However, there are differences in the capacity and efficacy of developed and developing countries in ensuring sustainability of coral harvest. In developed countries, less destructive fishing practices, greater transparency (Murray and Watson 2014), the implementation of marine protected areas, better enforcement, and socio-ecological pressure mean that management has a higher chance of being effective (Dee et al. 2014). On the Great Barrier Reef in Australia, for example, there has been steady progress toward clearer and more accurate reporting by collectors about their harvest through changes in management policy, but it remains to be seen whether this results in ecological outcomes.

Despite these positive developments, there remains a real risk of systemic breakdown in the managing and policing of the global trade in coral-derived products. This is in part due to widespread inconsistent skill levels in identifying corals and the complex nature of coral taxonomy. Collectors in Australia are concerned that coral products will be rejected at the importing country because of misidentification and are now using the highest level of identification (e.g., *Acropora* spp.) even though they may be confident they know the species and genera they are exporting. There is a need to raise the identification skill levels of collectors, reef managers, and trade officials to ensure the trade is managed appropriately and that the assessment of harvest risk to populations be based on facts. Further, a lack of data that can confirm whether species are threatened can prevent listing in the CITES Appendix II (species not necessarily threatened by extinction but in which trade must be regulated to protect declining populations and ensure sustainable exploitation). The use of smaller coral specimens in manufacture of reconstituted coral for beads and jewelry combined with the continuing threat of mass mortality events makes the risk of predicting extinction even more difficult to predict.

Coral research and monitoring efforts to date generally have not focused on the current target coral species in the trade or their habitats. This has created a large gap in our scientific understanding of the large polyp species of corals (LPS) in particular. Knowledge of the basic life history characteristics of the LPS corals, their productivity potential, and their required habitats is fundamental to develop appropriate management policies and strategies to ensure sustainable harvest. Improvements in this knowledge are essential for resource managers and government decision-makers to maintain pace with the global coral trade.

Another gap in data quality relates to differences between the type of data required to sustainably manage coral fisheries and those of other marine fisheries. Size-class estimates of a population rather than numbers of colonies or percentage of total reef cover could be more effective at identifying population decline in colonial animals because the polyps, not the colonies, are the reproductive units (AW 2009; Bruckner 2014); however, it is not practical to routinely collect these data. This type of data requires a time series comparison or a comparison with unfished populations (Tsounis et al. 2010). The other issue can be a lack of local, decentralized management that can actually be the most effective for less developed countries. In those contexts, problems occur when outside forces come in (international development, roving collectors) and disrupt the social agreements that were in place to manage resources sustainably. Therefore, trade control through CITES remains an increasingly important tool in coral and invertebrate fishery management, supported by strong local management and enforcement.

7 Successes in Improving Management of Coral Harvest Fisheries

A wide range of measures has been implemented to manage the trade and protect reefs from overexploitation (reviewed in Dee et al. 2014). For example, despite being the world's largest consumer of corals, the USA has prohibited stony coral collection under most circumstances within its jurisdictions. This has been implemented through a patchwork of state-level bans and US Endangered Species Act protections for several species. Some other countries permit collection at levels ranging from tightly controlled harvest to open access and unmanaged fisheries, while others attempt harvest management through legislation, the limitation of levels of harvest through total annual catch, and local compliance monitoring.

8 Coral Fishery Management in Developed Countries

The coral fishery that harvests on the Great Barrier Reef in Queensland, Australia, provides one example of an industry that is managed by regulation aimed at ensuring sustainable levels of harvest. Listed as a World Heritage Area, the Great Barrier Reef is the world's largest barrier reef ecosystem. The Great Barrier Reef Marine Park is managed jointly by the Commonwealth of Australia and the state of Queensland. The Queensland Coral Fishery is managed under a system of total annual allowable catch for the entire industry. Within the fishery, there is a single level of state management for policy, regulation, monitoring, and enforcement with an overarching Commonwealth of Australia management of biodiversity impacts and control of live trade exports through the Environment Protection and Biodiversity

Conservation Act as well as the regulations for the sustainable trade of wildlife exports through CITES. Recently, following concerns about harvest sustainability in this World Heritage Area following thermal bleaching and devastating flood impacts on inshore reefs targeted by the fishery, progress has been made toward improved data collection (Jones and Berkelmans 2008, 2014; Jones et al. 2008; Jones 2011). An expanded targeted species list was implemented and catch reporting changed from estimated to actual weights to improve decisions about quota- and species-level risks (Table 1). These changes refined the risk assessment process for the levels of harvest for this fishery through species- and location-specific catch triggers (although triggered levels of harvest are only identified a year or more after reporting). Identified ecological risks are further mitigated by direct in-water industry action. For example, following the review of fishery ecological risk levels in 2013, the Queensland aquarium industry revised a voluntary code of conduct in response to reef disturbance events like floods, bleaching, and cyclones to include specimen size limits for "at-risk" coral species. The data generated by improvements in catch reporting can be used to test whether these new measures will translate into more sustainable harvest of rare species and control localized depletion of targeted species (although without population structure assessments over time, it is difficult to ascertain how localized depletions will be identified, as catch reporting rates could reflect low demand, reduced effort, or a poor market).

9 Coral Fishery Management in Developing Countries

In developing countries, highly dispersed supply chains combined with limited and often decentralized management of coral harvest decrease the likelihood that fishing controls will have their intended effect on sustainability (Dee et al. 2014). Perhaps as a result, various studies and reports have documented overharvest of target species in the Philippines, Indonesia, and elsewhere (Ross 1984; Bruckner and Borneman 2006; Knittweis and Wolff 2010). Establishing effective management of wild harvest of corals in developing countries is difficult. For example, although species-specific quotas are now in place in Indonesia (Green and Shirley 1999), they are not based on a total allowable catch and are often misaligned with the population sizes of the targeted corals (Bruckner and Borneman 2006). Similarly, despite licensing and marine protected areas being in place, weak enforcement, corruption, and inadequate resourcing limit effectiveness (Dudley and Ghofar 2006). Management resources are similarly difficult in places like the Philippines and Solomon Islands. The Philippines, for instance, once had problems with over-collection and destructive practices (Ross 1984). As a result, the Philippines banned the collection and export of most corals after they were listed under Appendix II of CITES.

Despite the difficulties posed by collection practices in decentralized and largely unregulated coral harvest fisheries, there are examples of successful management at the local level. For instance, in the Maldives and Tonga, no-take zones and tiered quota systems represent steps toward reforming the trade. In Fiji, exclusive community-based fishing zones and benefits-sharing hold promise (Manoa 2008). Similarly, controls on the

Table 1 Reported taxa harvested from the Keppel region of the Southern Great Barrier Reef classified as either (**a**) large polyp corals (LPS) or (**b**) small-polyp corals (SPS). Taxa marked with ** are listed as at risk of local depletion (Jones 2011)

A. LPS				B. SPS			
Class Anthozoa	Subclass Hexacorallia	**Order Scleractinia (stony corals)**	*Blastomussa*	**Class Anthozoa**	Subclass Hexacorallia	**Order Scleractinia (stony corals)**	Agariciidae
			*Catalaphyllia jardinei***				Pocilloporidae
			Caulastrea				*Montipora*
			Dendrophylliidae				Oculinidae
			Dendrophylliidae (*Duncanopsammia***)				Poritidae
			Euphyllia glabrescens			**Order Actiniaria (solitary sea anemones)**	*Heteractis crispa*
			*Euphyllia***			**Order Zoanthidea (clonal sea anemones)**	*Entacmaea quadricolor*
			Faviidae			**Order Corallimorpharia**	Corallimorphs
			Fungiidae		Subclass Octocorallia	**Order Alcyonacea (soft corals)**	Nephtheidae
			Goniopora/*Alveopora* spp.		Subclass Alcyonaria	**Order Alcyonacea (gorgonians)**	Gorgonacea
			Mussidae**			**Order Alcyonacea**	Paralcyoniidae
			Pectiniidae			**Order Alcyonacea** (*Tubipora*)	*Tubipora musica*
			*Scolymia***			**Order Stolonifera**	Tubiporidae
			Trachyphyllia geoffroyi	**Class Hydrozoa**		**Order Capitata**	Milleporidae
			Turbinaria			**Order Stylasterina**	Stylasteridae

importation of vulnerable species, such as the EU's Wildlife Trade Operation and Hawaii's "http://www.reef2rainforest.com/2013/12/16/west-hawaii-fisheries-white-list-of-legal-aquarium-fishes/" could improve sustainability of the trade.

10 Coral Aquaculture: A Sustainable Future for Coral Fisheries?

Aquacultured corals – which are propagated by fragmentation or reproduction of specimens in captivity and are not simply fragments grown in culture after being taken directly from the wild – offer one promising means of achieving a sustainable future for the aquarium industry. A shift to aquaculture seems a logical way forward but there are several major challenges to widespread adoption of this approach. Changing the perception of aquarists toward the aesthetics and value of aquacultured specimens, as well as improving knowledge about the sustainability of their hobby in the face of what are now globally considered as overwhelming pressures on tropical reefs, could help facilitate a shift in demand. Somewhat surprisingly, public aquaria consider a wholesale shift to aquaculture as undesirable, as many aquariums depend on the same supply lines and the diversity of aquacultured stock often does not match their needs. There are obvious potential benefits of trade between countries, but there remains the problem of damaging collection practices and localized over-collection.

Further impediments to shifting to aquaculture include motivation within the industry in general to improve practices, especially if changes detrimentally affect profit; however, it is not only industry reluctance that is impeding progress. In Australia, for example, there is growing interest by commercial collectors in "farming" coral fragments on structures in the open sea; however, negotiations between collectors and the state and federal regulators to allow this activity within the marine park that borders most of the Queensland coastline have not commenced. In contrast, in Western Australia, an aquaculture policy has been developed, and there is now a steadily growing trend toward sustainability through aquaculture. Overcoming challenges such as government restrictions on mariculture, developing cost-effective methods of identifying wild versus aquacultured specimens, and developing systems and policies to manage potential exotic pests, disease, and genetic quarantine issues could help move the industry in Australia from principally wild capture to sustainably aquacultured products.

11 Conclusion and Future Directions

It is beyond doubt that the unregulated harvest of structurally important species of the marine animal forests has led to degradation of large expanses of the world's oceans (Rossi 2013). Unsustainable removal of ecosystem engineers – sponges, bryozoans, cnidarians, and other animals – can undermine the structural integrity of these marine forests by simplifying what is otherwise a highly complex system. Humans have utilized these coastal and offshore benthic systems since antiquity for building materials, ornaments, jewelry, and now, domestic aquaria. There are examples where this wild harvest is relatively well managed such as in Australia; however, more improvements in research, monitoring, and management at the local and global scale are required. The world will continue to rely on marine animal forests for a variety of needs, not the least of which is as an important source of food. It is vital for the survival of the marine animal forests that the damaging effects of human interference are controlled. With greater transparency and public acceptance, minimally destructive wild coral harvest methods of abundant species and brood stock, combined with a gradual shift to aquaculture, could cultivate a sustainable industry that preserves ecosystem services while supporting socioeconomic goals in coastal communities. However, moving away from wild harvest to aquaculture requires substantial infrastructure and training costs, business risk, as well as a considerable shift in public perception and management policy, industry perception, and day-to-day work practices.

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37

Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management

Hilmar Hinz

Abstract

Negative impacts of fishing activities on marine animal forests have been documented from around the world. Besides climate change, fishing poses the greatest global threat to these often very vulnerable and slow-recovering habitats. The impact of fishing on animal forests in shallow water ecosystems is relatively well studied, while for deeper waters, due to logistical constraints and scale, the true extent of fishing impacts still needs to be adequately described. Scientific efforts should be intensified to identify potential conflict zones between fishing and the location of animal forests to identify priority areas for conservation efforts. For this purpose, the use of new technological advances such as Vessel Monitoring Systems (VMS) and acoustic habitat mapping techniques, e.g., multibeam, will be essential. Preserving these vulnerable habitats will be a scientific, political, and social challenge and will require the collaboration of all stakeholders, in particular the involvement of fishers. Scientific studies will not only have to concentrate on identifying and describing impacts, but it will be essential that science also focuses its efforts on identifying the goods and services these habitats provide with respect to ecosystem health and the production of fish. Understanding the importance of these habitats will be crucial in securing the support, compliance, and acceptance of management measures aimed at conserving animal forests.

Keywords

Fishing impacts • Bottom trawling • Static fishing gear • Scallop dredging • Fishing experiments • Observational studies • Comparative impact studies • Shelf seas • Deep sea • Seamounts • Vulnerable marine ecosystems (VME) • Ecosystem approach to fisheries management • Stakeholder engagement • Vessel

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Monitoring Systems (VMS) • Automatic Identification System (AIS) • Habitat suitability modeling • Recovery potential • Sedimentation • Human food production • Buffer zones • Spatial management

Contents

1 Introduction

The majority of fishing methods employed for the exploitation of marine animal protein use fishing gear that during its operation comes in direct physical contact with the seabed. In particular, the exploitation of demersal fish species or benthic invertebrates mostly requires the towing or dragging of nets over the seabed. Equally, other more static fishing methods, such as the setting of nets or traps, also have seabed contact, although these methods tend to have a smaller areal footprint compared to the towed fishing gears. Intrinsically complex animal structures that emerge from the seabed, embodied within this book by the term "animal forests", stand in direct conflict with most fishing practices. The effect of towed fishing gear on benthic communities in general has been widely demonstrated, and an overwhelming scientific consensus exists about the negative environmental impact of these practices (Kaiser et al. 2006). Nevertheless, it needs to be recognized that the severity of the fishing impacts and the potential for recovery of benthic habitats is context dependent (Jennings and Kaiser 1998). Thus, some habitats may be able to tolerate a certain intensity of fishing by specific fishing gears, while other habitats are highly sensitive to even small amounts of disturbance. In general habitats that are frequently disturbed by natural events (e.g., by storms) tend to be inhabited by more opportunistic or ephemeral species that also appear to be more resilient to fishing disturbances (Sciberras et al. 2013). Such habitats may therefore tolerate some degree of disturbance without the loss of ecological structure and functioning. On the other end of the spectrum are benthic communities that are highly sensitive and show the least resistance and resilience to fishing disturbance. These benthic communities in general are composed of species that are long lived, have fragile structures, and live within the first few centimeters or are emerging from the seabed. The most sensitive habitats are thus precisely those habitats that have been defined as “animal forests” within this book. Nevertheless, even within the “animal forest” group of habitats, distinctions with respect to their vulnerability and likely severity of impacts on the ecosystem as a whole need to be made, depending on their species composition, similar to the terrestrial system where one would also distinguish between shrubs and ancient oak forest (see ▶ Chap. 23, “The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep”). This is particularly important to remember when prioritizing on conservation goals, and the idea of “one glove fits all” should be avoided with respect to the consequences of fishing disturbance. Thus, for example, a brittle star bed (e.g., *Ophiothrix fragilis*) in the Irish Sea or a *Lanice* bed (emergent bed of tube worms) in the North Sea could both be categorized as “animal forests”; yet the impact and wider ecological consequences of fishing disturbance cannot be compared to the impact on a cold water coral (CWC) reef (e.g., *Lophelia pertusa*) in the deep sea. Both *Ophiothrix* and *Lanice* are highly common species with fast reproduction cycles that recover relatively quickly from trawling events, while *Lophelia* reefs are rare and slow growing and have a relatively low reproductive output and thus have been estimated to take decades to centuries to recover from a trawling event (Fosså et al. 2002). Also the ecological roles between these example habitats differ significantly with *Lophelia* representing a foundation species, due to its structural properties and long-life-sheltering high biodiversity levels (see ▶ Chap. 32, “Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems” in this book), compared to both *Lanice* and *Ophiothrix* beds which harbor one or two associated ephemeral polychaete and bivalve species.

It is clear that an unlimited exploitation of natural resources is not desirable due to the negative implications on the functioning of our ecosystems and the loss of biodiversity. Like land-based ecosystems, marine ecosystems need to be exploited in a more sustainable way that limits the loss of species and that allows natural processes to prevail. This way of thinking has already rooted in form of the idea of an “ecosystem approach to fishing” (Garcia et al. 2003), but in many ways this approach is still a work in progress and is far from being implemented on a global scale (for more information please also read the ▶ Chap. 34, “Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest”). Overall, the most pressing issue has to be to increase efforts to locate and describe our most vulnerable marine ecosystems (VME) of which “animal forests” form an important part. These ecosystems need subsequently immediate effective protection to prevent further damage or destruction by fishing and other anthropogenic stressors. The current chapter aims to introduce the reader to the subject of fishing impacts on “animal forest” habitats and to provide an overall picture of the topic as well as providing a vision for future research and the conservation of “animal forests”. This chapter’s stated aim, however, is not to deliver a complete review on this subject.

2 Fishing Impacts Studies: Their Strength and Limitations

In the early 1980s with clear signs of overexploitation of many fish stocks, the impact of fishing on bottom dwelling fauna surfaced as an important ecological issue and received increased scientific attention. Fishing impacts have been the focus of studies since then globally, concentrating primarily on the impacts of different fishing gears on different habitat types including "animal forests". Research studies that have focused on the impact of fishing on benthic habitats can be broadly categorized into *experimental fishing experiments* and *observational studies* (Hinz et al. 2009). Both study types have their distinct advantages and limitations of which readers should be aware when evaluating results and conclusions drawn from these papers. Within fishing experiments, scientific trawls are towed over a previously set experimental area, and the effect of trawling is monitored before and after the impact (e.g., see Thrush et al. 1995; Kaiser and Spencer 1996; Prena et al. 1999). In contrast, observational studies rely on some knowledge of where and at what intensity fishing occurred in order to compare impacted versus non-impacted areas (e.g., see Collie et al. 1997; Koslow et al. 2001; Althaus et al. 2009). The advantage of fishing experiments is that the times a trawl passes over a particular habitat type can be experimentally set and damage rates quantified accordingly. Equally, these experiments allow the monitoring of recovery from a known amount of fishing pressure (Kaiser and Spencer 1996). However, the limitations of these studies are that the impact of real fisheries will tend to be chronic and not punctual, as in most fishing experiments, with varying amounts of impacts and recovery processes occurring through time. Thus, the estimates obtained from experimental studies may differ considerably to impact and recovery processes on real fishing grounds (Hinz et al. 2009). In this context also, the estimated recovery rates from these studies need to be considered here. In fishing experiments only a small corridor of impact is created with large areas of intact habitat surrounding it. On real fishing grounds, fishing impacts will be chronic and will have occurred over large spatial scales with no or limited areas of intact habitat available that may supply larvae and emigrating fauna to aid recovery. Chronically impacted fishing grounds are therefore expected to recover far slower than estimated by fishing impact experiments (Hinz et al. 2009). Comparative fishing impact studies in contrast have the advantage that they describe and evaluate the impact of real fisheries. These studies, however, require that the fished and unfished areas are really comparable with respect to their habitat composition. Furthermore, proving that the areas did not differ prior to the onset of fishing is often not possible due to the lack of historical records. Thus, the conclusions drawn from many comparative fishing impact studies tend to hinge on circumstantial evidence. Moreover, many past studies were not able to quantify fishing effort due to the lack of high-resolution spatial data on the movement of fishing vessels. Thus, impacts often have been assessed as present but not quantified with respect to fishing intensity. More recent comparative fishing impact studies have overcome this limitation by using VMS Information (VMS) to quantify trawling intensities over real fishing grounds and appear to deliver the most accurate and comparable method of assessing fishing impacts (Hiddink et al. 2006; Lambert et al. 2011; Buhl-Mortensen et al. 2015).

3 Fishing Impacts on “Animal Forests”

3.1 Direct Impacts

Experimental fishing studies on “animal forest” habitats are rare and are principally limited to investigations on the effect of trawling impacts on sponge and soft coral communities in shallow shelf seas. Van Dolah et al. (1987), for example, investigated the impact of trawling on a hard bottom community dominated by sponges and corals in Georgia (southeastern USA). A single pass resulted in the significant reduction of barrel sponges by 32%, while other sponge species and corals did not show significant reductions in density. Van Dolah et al. (1987) also investigated recovery trajectories and found that within 12 months, no difference could be found between trawled and non-trawled areas. A similar study by Freese et al. (1999) in the Gulf of Alaska found significant reductions and increase in damage in sponges and anthozoans following a single trawl pass. Removal rates of barrel sponges were reported to be considerably higher with 62% compared to the previous study by Van Dolah et al. (1987). This difference between the two studies was linked to the heavier trawl gear used by Freese et al. (1999). A more recent experimental study by Wassenberg et al. (2002) in Australia on a sponge- and gorgonian-dominated habitat found that about 14% of sponges and 3% of gorgonians were removed by a single pass, while a great majority of sponges and gorgonians passed under the net. The study found that larger sponges in particular were susceptible to being damaged or dislodged by a single pass. From these three example studies and other similar studies (e.g., Moran 2000; Burridge et al. 2003; Pitcher et al. 2009; Boulcott et al. 2011), four main conclusions on the impact of trawling on sponge and soft coral communities in shelf seas environments can be drawn: (i) all habitats showed significant damage to “animal forest” components; (ii) a single trawl pass did not remove all “animal forest” and associated fauna, and their vulnerability was dependent on their respective growth forms and skeletal and tissue characteristics, i.e., large ridged organisms being more susceptible and low-growing flexible species less susceptible; (iii) the extent of removal and damage to “animal forest” components was largely determined by the weight and rigging of the fishing gear used with heavier gear causing considerably more damage; and (iv) sponge and soft coral habitats within productive shallow shelf seas have a recovery potential most likely on the scales of years.

The majority of knowledge from the impacts of fishing on “animal forest” habitats originates from comparative fishing impact studies. In general, these studies compare areas impacted versus non-impacted areas of seabed. In many instances a true evaluation of the fishing intensities of the fished sites is not reported. As such the reported damage rates are relative and specific to the situation of each study. Cross comparisons of studies to examine the relationship between fishing intensity and faunal responses are thus very difficult to make. More recent studies on soft bottom communities have made use of VMS data and these studies show promising results in ascertaining pressure gradients (e.g., Hiddink et al. 2006; Lambert et al. 2011; Buhl-Mortensen et al. 2015). Studies using this type of background data are to date still relatively rare but mark the future direction of fishing impact studies. Nevertheless, past comparative studies on "animal forests" give a good indication of what fishing impacts of working fisheries look like for different types of fisheries and habitats which can be seen as a guide to scale potential impacts. For shallow shelf seas, impacts on sponges, gorgonians, and *Modiolus* reefs from towed fishing gears have been investigated (e.g., Collie et al. 1997; Magorrian and Service 1998; Heifetz et al. 2009; Boulcott et al. 2011; Hinz et al. 2011; Lambert et al. 2011). Similar to the experimental studies above, comparative studies have all found significant reductions in density or damage for some but not all species of the "animal forest" component, comparing impacted versus non-impacted areas. Furthermore, most studies on shelf habitats do not report on a complete absence of these species from trawled sites, but in general these areas tend to contain lower abundances and smaller-sized animals. This would suggest that, at least for shallow shelf seas (<150 m), many of these species have the potential to withstand some degree of fishing impact damage. Certainly, there will be a difference between a fully grown "animal forest" with respect to its ecological functioning and an impoverished patchy forest. Nevertheless, the good news is that this observation demonstrates that if protected, there is the potential for recovery as remnant populations will have the potential to reseed shallow water forests. That this is indeed the case can be seen from the recovery reported following the exclusion of towed fishing gears from sensitive areas. For example, Sheehan et al. (2013) reported on the recovery of a temperate reef fauna (principally an erect branching bryozoan *Pentapora fascialis* and a large tunicate *Phallusia mammillata*) following the implementation of a marine protected area (MPA) excluding all towed fishing activities in the southwest coast of the UK after 4 years. Furthermore, comparative studies in general, as the ones selected below, demonstrate that the morphology of the "animal forest" species (size, flexibility, etc.) as well as the fishing gear type predominantly used determines the severity of fishing impacts. Three example studies from continental shelf environments illustrate these general observations. Collie et al. (1997) compared trawled and un-trawled areas on the Georges Bank (northeastern USA) using underwater video observation and found that structuring epifauna were less common or absent from trawled areas. In particular, reef-forming polychaetes as well as bryozoans and hydroids were less abundant at trawled sites. Heifetz et al. (2009) compared the encounter rate of damaged "animal forest" components, i.e., gorgonians, hydrocorals, and sponges, in trawled versus un-trawled areas using underwater video footage in Alaska. They found that in highly trawled areas, the damage rate for "animal forest" species varied between 14% and 59% compared to 5% and 10% of damage in un-trawled areas. Hinz et al. (2011) studied the impact of scallop dredging on temperate reef fauna in the south of the UK. Despite the fact that scallop fishing gear is most likely one of the most damaging fishing gears, differences between fished and unfished sites were evident for some but not all "animal forest"

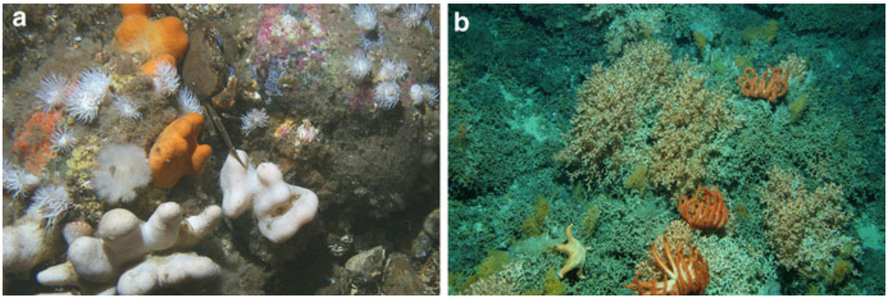

Fig. 1 Examples of animal forest communities in (**a**) shallow shelf seas in the UK at 40 m depth (Copyright Hilmar Hinz) and (**b**) in the deep sea (Image provided by Malcolm Clark, NIWA), seamount off New Zealand at approx. 1000 m depth. Both habitat types show considerable vulnerability to fishing impacts; however, their potential for recovery is distinct; with recovery trajectories on a scale of months within productive shallow systems and decades or even centuries in deep-water system

species. While there was a notable difference between fished and unfished sites for a species of soft coral, *Alcyonium digitatum* (67%) and an erect bryozoan *Pentapora fascialis* (73%), no significant difference could be detected for the resident sea fan species *Eunicella verrucosa*. The reasons for the lack of difference in the sea fan species was linked to two factors: one being the inefficiency of scallop dredges fishing over uneven complex hard substrates that are the preferred attachment sites for this sea fan species and two being the morphological flexibility of the sea fan itself that most likely allowed it to bend and erect itself again if not uprooted by the impact. That scallop dredges are not able to remove all “animal forest” components on morphologically complex rocky hard substrates due the bouncing of the fishing gear was further confirmed by an experimental study conducted off Scotland (Boulcott et al. 2011) (Fig. 1).

The impact of towed fishing gear on “animal forests” of deep sea environments stands in stark contrast to the impacts and consequences reported above from shelf sea habitats. Fishing experiments have to date not been carried out on “animal forests” in the deep sea. This is nor should they. Such studies would be morally highly questionable considering the fragile nature of these habitats and unnecessary given the considerable science base that exists. Furthermore, ample opportunities to study fishing impacts on deep sea habitats exist within a comparative framework utilizing preferably nondestructive sampling methods such as underwater cameras, Remotely Operated Vehicles (ROVs), or manned submersibles. Comparative fishing impact studies in the deep sea thus far have shown that the damage to “animal forest” habitats can be detrimental, in instances resulting in the complete destruction of structure-forming species in areas that have been intensively fished, leading to a complete change in overall faunal composition and ecosystem functioning of the affected areas (Clark et al. 2016). The main difference between shallow shelf habitats and the deep sea is that ecological processes in deep waters are generally much slower due to the generally lower food availability and low temperatures. As a result, filter feeders that make up the majority of deep sea “animal forest” are frequently extremely slow growing and have a lower reproductive output compared to species living in shallower waters. Some deep-water coral reefs can be several hundred or even thousand years old with radial growth rates of 0.36–0.5 mm per annum (Clark et al. 2016). Furthermore, some of the larger species are reef-forming species whose morphological characteristics do not withstand the physical disturbance of towed fishing gear. Thus, the biological configuration of deep sea “animal forests” make them highly vulnerable to fishing disturbances and lower their recovery potential after a disturbance event. On this basis recovery potentials of deep sea “animal forests” following fishing disturbance have been estimated to be on a decadal to century scale (Clark et al. 2016). Five example studies are presented here to illustrate the impact of towed fishing gears on “animal forests” in the deep sea. Readers who want a more complete review of the available literature of fishing impacts on deep sea ecosystems should consult the extensive review on the subject published by Clark et al. 2016. Hall-Spencer et al. (2002) reported on damage to deep sea coral reef communities by a trawl fishery of the west coast of Ireland and off Norway and brought into focus that European cold water coral (CWC) ecosystems are under increased threat. The study examined bycatch composition of trawlers and reported the fishing of large coral fragments. C^{14} dating of the coral pieces revealed that the coral community had a minimum age of 4550 years. Similarly around the same time Fosså et al. (2002), studying *Lophelia* reefs in Norwegian waters by underwater video surveys documented extensive damage by trawl fisheries at five locations. From the impact observed, the study estimated that between 30% and 50% of Norwegian reefs may be damaged or impacted with wide-ranging consequences for associated species including commercially exploited fish. Similar reports of fishing impacts on deep-water coral reef systems have been documented from other areas of the world. Koslow et al. (2001) studying the impact of fishing on seamounts south of Tasmania (Australia) found that trawl operations had removed all reef aggregate from the most heavily fished seamounts. Benthic biomass of unfished seamounts was 106% greater compared to fished seamounts. A more recent study on seamounts off Tasmania appears to provide a similar picture. Althaus et al. (2009) examining underwater still images found that on trawled seamounts images of stony coral cover (*Solenosmilia variabilis*) were absent compared to 50% of images showing coral cover on un-trawled seamounts. In trawled areas whip-like soft coral (*Chrysogorgonia*) was, however, evident, and its presence was most likely related to the higher resistance/resilience of this species to trawling. Overall, species diversity and abundance were three times lower on trawled seamount compared to un-trawled seamounts. Furthermore, the study investigated the recovery of a seamount where fishing had ceased 5 years earlier and found no signs of recovery with respect to coral cover and faunal assemblages. Clark and Rowden (2009) studying seamounts off the New Zealand coast report similar impacts of trawling on seamounts; the study found that 21–41% of the still images analyzed from un-trawled seamounts showed colonies of habitat-forming corals (*Solenosmilia variabilis* and/or *Madrepora oculata*), while trawled seamounts only showed corals in of 1.4–1.8% of still images taken. Similar to the Tasmania seamounts, clear differences in the community structures of trawled and un-trawled seamounts could be found.

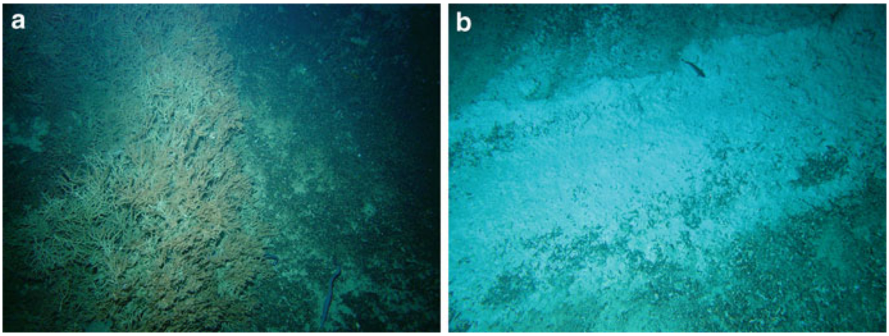

Fig. 2 Images of (**a**) unfished (*Madrepora oculata*) and (**b**) fished seamounts off the New Zealand coast at depth of approximately 1000 m. Image **b** is showing a trawl door gouge with a width of approximately 2 m. Photos originate from the study by Clark and Rowden (2009) on the impact of fishing on seamount habitats (Image provided by Malcolm Clark, NIWA)

The example studies given above clearly demonstrate the fragility of deep sea "animal forests" and the associated loss of biodiversity and productivity. Additionally, the age and slow recovery potential are highlighted by the examples (Fig. 2).

Most studies on fishing impacts on "animal forest" species have focused on the impact of towed fishing gears, while the impact of static fishing gear, such as longlines, gillnets, and traps, has not been the focus of many studies up to date (but see Mortensen et al. 2005; Sampaio et al. 2012; Pham et al. 2014). Static gears may come in direct contact with erect and emergent fauna through snagging or lateral movement of the fishing gear while being retrieved, with subsequent damage and/or dislodgment of fauna. Sublethal damage to gorgonians and corals may cause infection or encourage growth of epiphytes that may later lead to the death of damaged colonies (Mortensen et al. 2005). The loss of fishing gear in this context is also seen as a source of considerable impact as, e.g., drifting long lines may continue to damage sensitive species for considerable time (Mortensen et al. 2005). Again the same principles of vulnerability as for the towed fishing gear impacts will apply here, with branching brittle species being more fragile while species with a sturdier stout and/or more flexible morphology being less susceptible to impacts. Eno et al. (2001), for example, studied the impact of crab pots on sea fans and sea pen species in the shallow UK waters and found no detectable effects from static gears. The lack of effect was mainly explained due to the flexible morphology of the sea fans and sea pens, bending and reerecting itself even if a pot was directly dropped on top of the animal. Similarly, in the deep sea Heifetz et al. (2009) found that impacts from static gears where indistinguishable from natural background disturbance with respect to damage to corals and sponges. Nevertheless, noticeable impacts on highly complex habitats by static gears have been reported. Mortensen et al. (2005) demonstrated damage on gorgonians and corals from long-lining off Nova Scotia (Canada). Likewise, Sampaio et al. (2012) investigating the bycatch of longline fisheries in the Azores found that CWC and gorgonian were extremely common bycatch species. While the damage from long-lining on "animal forests" species appears to be indisputable, its effect on a population level appears thus far to be low, especially when compared to mobile fishing gears. Pham et al. (2014) found that despite high intensities of long-lining over a period of over 20 years, slow-growing vulnerable CWC species were still common over a fishing ground in the Azores. This study further concluded that if long-lining was managed correctly, it could be seen as an alternative to towed fishing methods, due to its lower environmental impact coupled with selectivity and low fuel consumption of this type of fishery. To compare the magnitude of impact between the two fishing methods, the study estimated that one single trawl deployment would have the equivalent impact to 296–1719 long-line deployments. Summarizing, it appears that while static fishing gears have the potential to do damage, the considerably smaller areal footprint of this type of fishing appears to make it less of a problem compared to the towed fishing gears. This said, the amount of damage static gears may cause will ultimately depend the fishing intensities and the faunal composition of the habitat they fish over. Thus, when scaling potential impacts on "animal forests", static fishing gears should nonetheless be carefully considered within a conservation and management context.

3.2 Indirect Impacts

The main indirect impacts of fishing on "animal forest" species may arise from the resuspension of sediment particles by towed fishing gear. Trawling and dredging on soft substratum mobilizes sediments resulting in a sediment plume behind the trawl gear (Churchill 1989). Such trawl or dredge plumes can consequently increase sedimentation over large spatial areas depending on local hydrographic conditions. Especially in the outer-shelf and deep sea environments where storm-related sediment resuspension is generally weak, trawling can become one of the primary drivers of sediment transport (Churchill 1989; Martín et al. 2008; Puig et al. 2012). Sediment resuspension and transport from trawling-induced disturbance can be severe modifying natural sedimentation processes. Thus, it has been demonstrated that trawling on fishing grounds near continental shelf slopes can affect sedimentation processes in the deep sea by triggering gravity flows (Martín et al. 2008). Many "animal forest" species are filter-feeding organisms and may therefore be impacted by either smothering or sediment particles interfering with suspension feeding efficiency, potentially reducing growth or in extreme circumstances causing death. While there are few studies on the effect of sedimentation on animal forest species, it may be assumed that shallow water species are evolutionarily better adapted to tolerate high sediment loadings (e.g., storm-born disturbance events) compared to deep sea species that tend to be less frequently exposed to high sediment disturbance. However, recent studies from CWC have demonstrated that they can effectively remove deposited material from the coral surface even after repeated exposures, indicating an efficient cleaning mechanism (Larsson and Purser 2011). Furthermore, CWC species have shown that they are able to survive light smothering (Allers et al. 2013); however, the impacts of sedimentation on feeding efficiencies are still unknown. In contrast to this deep sea sponge respiration appears to completely shut down as a result of heavy sedimentation (Tjensvoll et al. 2013) although respiration is able to recover quickly after exposure ceases. How growth and the longevity of sponges would be affected in a chronic sediment disturbance event is currently unknown.

4 Fishing Impacts, Scaling Up the Problem

While a considerable number of studies describe the nature of change following fishing disturbances on “animal forest” for specific locations, there is thus far no full inventory of the status of these habitats on larger geographical scales. Getting a more global picture about the extent of the disturbance is mainly hampered by a lack of knowledge on the precise location of these habitats and on the state they are in. While on land habitats can be mapped and monitored with ease and high spatial precision, mapping habitats in the sea is logistically challenging and associated with high financial costs. Underwater cartography requires considerable time on research vessels and highly sophisticated equipment such as multibeams and underwater camera systems. This is particularly true for offshore and deep sea areas. Within coastal and shelf seas, habitat mapping is currently progressing, especially in seas surrounding industrialized countries with sufficient financial capacity. But still large amounts of seabed remain unsurveyed even here. For example, in the European context seabed habitat mapping is highly advanced in UK waters, parts of the North Sea, and the Baltic, while few surveys have been conducted in the Bay of Biscay and the Iberian coast. Similarly, great parts of the Mediterranean have remained unsurveyed, and information on seabed habitats is relatively scarce (see http://www.emodnet-seabedhabitats.eu/). While knowledge on the location of habitats is patchy on shelf seas, the extent of knowledge we have on the location of vulnerable deep sea “animal forests” is at best punctual. On a global scale, it has been estimated that only 0.0001% of the deep sea floor have been the focus of scientific studies (Gjerde 2006). Due to the high financial cost of habitat mapping, it is foreseeable that this information will not be available in the short term and that filling in the large gaps in our maps will be a decadal task. On the other hand, knowledge about where fishing is occurring and at what intensities is increasingly becoming available with the advent of VMS being introduced by many countries to monitor and police fishing operations in territorial waters. This type of data opens up possibilities that may help estimate impacts on larger scales (e.g., see Benn et al. 2010). While VMS data from fisheries protection agencies have yet no global extension and access to this data can be hampered due to legal constraints (Hinz et al. 2013), other similar data systems such as AIS (Automatic Identification Systems) that are open access and have a global reach may hold enormous potential for future monitoring of fishing effort also in remote offshore areas (Natale et al. 2015). Spatially detailed fishing effort information from such systems may allow the study of fishing impacts along fishing intensity gradients to assess the relationship between fishing intensity and ecological impact on “animal forest” habitats that up to now have been lacking from many fishing impact studies. Such studies subsequently allow scaling the fishing effort to a sustainable level of impact, considering impact, resilience, and recovery potential of the species comprising these habitats (Hinz et al. 2013). Such fishing intensity studies have thus far been successfully conducted on soft sediment habitat types (e.g., see Hiddink et al. 2006; Lambert et al. 2011; Buhl-Mortensen et al. 2015). Also, VMS and AIS data will allow, in combination with modeled habitat suitability maps for “animal forest” species (e.g., like García-Alegre et al. 2014), the estimation of likely maximum impacts. Corresponding modeled habitat suitability maps of “animal forest” species and real fishing effort distributions could also serve to highlight specific conflict zones to direct research and conservation efforts to conflict hotspots between fisheries and conservation.

5 Direct Management Implications from Fishing Impact Studies on “Animal Forests”

There are several management implications for “animal forests” that result from the knowledge gained from fishing impact studies. The vulnerability of “animal forests” in the deep sea, their slow recovery potential, and their role as ecosystem engineers (see Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems) make it a primary conservation goal. To prevent further loss of these slow-growing habitat types, they need to be adequately protected. This also implies that research efforts should be increased to map these habitats and start integrating these in spatial management plans (Davies et al. 2007; Benn et al. 2010). The closure of these areas to fishing from damaging gear types will be essential and fine-tuned management strategies will be required. While habitats in national waters may be relatively easily protected, the challenge will be to win international agreements to protect these species in international waters (Davies et al. 2007; Clark et al. 2016).

With the same logic applied above, less vulnerable habitats may rank lower in the need for protection, and in some instances fisheries may be allowed to continue if regulated to levels that do not impair the functioning and reproduction potential of these habitats. This may be particularly true for productive shelf habitats that predominantly show growth forms that are relatively resilient to trawling impacts due to their common occurrence and fast growth rates, such as dead man’s fingers, for example, *Alcyonium* spp. Obviously, the need for protection versus the continuation of fishing will have to be a case-by-case decision-making process by fisheries and conservation managers alike. At least within Europe, there is a legal framework in the form of the Water Framework and Habitat Directive (WFD 2000/60/EC and HD 92/43/CEE, respectively) to foster such a decision-making process to ensure seabed integrity and good environmental status habitats. In general, greater efforts need to be made to reduce the physical impacts from bottom-contact fishing gears. It is evident from fishing impact studies that the design of the fishing gear and the way of fishing can greatly reduce the impact upon benthic communities in general. The positive news is that scientists and the fishing industry alike have woken up to this challenge, and initiatives are being pursued to develop lighter and less habitat impacting fishing gears (e.g. see Soetaert et al. 2013). However, it will need to be seen if these more environmentally friendly designs are being voluntarily accepted or need to be legislated for.

Fishing impact studies of static fishing gears appear relatively inconclusive. On the one hand, it is evident that damage from static gear occurs (Mortensen et al. 2005; Sampaio et al. 2012; Pham et al. 2014); on the other hand, the spatial impact these gears have appeared in most reported instances small and below the detection level of studies conducted thus far (Heifetz et al. 2009; Sampaio et al. 2012). However, ultimately the amount of damage from static gears will depend on the fishing intensities and the faunal composition, and therefore also static gears should be considered within a conservation and management context.

The fact that trawl fisheries can resuspend large amounts of sediments affecting “animal forest” habitats even if they themselves are not directly impacted by the physical contact of the fishing gears (Martín et al. 2008) suggests that if “animal forests” are being protected by fisheries exclusions, a buffer zone around these areas would be recommended. The size of such a buffer zone will be dependent on local hydrodynamic conditions and should be set following reasonable assumptions or studies about the drift of the plume and sedimentation rate.

6 Trawling and the Comparison to Forest Clear-Cutting: Should Trawling Be Banned “Outright”?

Fishing disturbances have frequently been compared to cutting down forests in order to catch one or two desired fish species for human consumption (Watling and Norse 1998). Considering the consequences for many marine benthic species, this comparison certainly appears appropriate and has understandably conjured up images of fishing, and in particular trawling, causing catastrophic seabed destruction. This very visual comparison has frequently led to the call of banning trawling “outright.” If we are making an analogy with land-based systems, we should think this land-marine comparison through to the end. Food production on land has led to the cutting down of forests on an enormous scale to make place for agricultural monocultures replacing the initial flora and associated fauna. Humans have in this way modified almost all accessible land habitats, yet despite this immense environmental modification, we are not calling for an outright ban on agriculture practices and land-based food production. We know that these artificial agriculture landscapes we live in are necessary for maintaining our modern societies. Thus, in many ways, food production on land is not unlike food production in the sea when considering environmental consequences. Trawling grounds are also modified landscapes that have been kept in a modified state for decades if not centuries. The majority of current fishing occurs over established trawling grounds, and thus impacts are far removed from the image of continuously cutting down marine forests. A more appropriate comparison would be if one would compare trawling to plowing of fields, which also prevents the reestablishment or recovery of the original flora and fauna on land.

Additionally, one needs to consider that the majority of fish protein is caught by trawling and that other fishing techniques are far less effective and economically less viable to catch sufficient fish to satisfy current human demand. Banning trawling outright appears like a very drastic solution to the problem, and as such a ban is highly unlikely to find great support due to a large economical, socioeconomic, and food security interests (Kent 1997). There are many ways to achieve greater sustainability of fisheries and to secure the protection of vulnerable marine habitats. The negative consequences of fishing practices should thus be seen and evaluated in the context with other food production systems, and society should make an informed decision about how to address the resulting dilemma of food production versus environmental protection.

Similar to the use of land, we need to regulate where and when fishing occurs and this is where the two systems are fundamentally different. While there is private land ownership, the sea belongs to the public. As such, there is a need to regulate more strictly marine food production and its consequences including the prohibition of trawling over sensitive areas and a serious attempt to mitigate the consequences of fishing as much as possible, e.g., through innovation and tighter fishing gear regulations. Furthermore, spatial management strategies are essential, as is the continuation of moving toward an ecosystem approach to fishing. These ideas are increasingly being implemented by environmental and fisheries regulations in Europe, e.g., Habitat Directive, Water Framework Directive, and the Common Fisheries Policy. Furthermore, other Non-governmental Organisations (NGO's) initiatives such as the Marine Stewardship Council (MSC) accreditation scheme of fisheries have increased the awareness about environmental issues related to fishing to consumers as well as to fishers themselves. There may be associated problems and weaknesses within accreditation schemes like the MSC, with respect to the criteria used and their application to certify specific fisheries as sustainable (Froese and Proelss 2012; Christian et al. 2013), but it needs to be recognized that through this mechanism, for the first time fisheries themselves are looking at the problem of fishing impacts and are forced to think about mitigation measures and solutions. This is a positive development, but we need to ensure that this does continue, and we do need to ensure that all is done to protect vulnerable habitats now, in particular in the deep sea where recovery of animal forest habitats would take generations.

7 Leaving the Blame Game: The Importance of Stakeholder Engagement

Conservation-minded groups and fishers often tend to be on a confrontational course especially when both groups adhere to a black and white view on the world. NGOs appear to claim the moral high ground, while fishers see these groups as hypocritical, blinkered, and a threat to their existence. In such circumstances, both fishers and conservation groups fail to see that they are really interested in the same thing, that is, a healthy productive sea with plenty of fish. So how come there appears to be such a large drift between these two groups? Ultimately it appears that both groups need to increase their understanding of each other's experiences, knowledge base, and motivations. Fishers can be highly knowledgeable about the sea, and they tend to have a good idea of how and where to encounter certain target species. Their view of the sea is, however, mainly shaped by their personal observations and experiences of things that land on their decks, while most have very limited knowledge of ecological processes. Personal observations made by fishers are often subsequently linked to plausible but sometimes incorrect explanations. A personal experience while working with scallop fishers in the UK may illustrate this. One of the fishers ensured me that scallops grow like plants out of the ground and that there were several layers on top of each other that could be harvested. These ideas where shaped by the experience he made that if he fished the same ground several times over, the number of scallops first increased for a time until he only fished empty shells and very small individuals. To him it appeared that he was harvesting several layers with the young scallops living in the last layer but in reality what he observed was an increase in catch efficiency of scallop dredges following the first pass of the dredges. With the first dredge pass, stones and other debris are pushed aside allowing the dredge to be in closer, uninterrupted contact with the seabed increasing fishing efficiency. Ecological processes, such as the reproductive ecology of his target species, were alien concepts to him; neither had he ever seen the species he dredged up, day after day, in their real environment. After showing him underwater video footage of his own fishing ground, he became increasingly interested in the scientific aspects of the fishery, and in the end he became one of the greatest supporters for progressive management strategies to conserve vulnerable habitat types. Often the things that appear on fishers decks and that we scientist and conservationist get excited about don't look very appealing once they are out of the water, and for a fisher they often just represent some kind of nuisance material without any value. As scientists, we therefore need to engage fishers far more and provide far more knowledge transfer with respect to the ecological importance of key species and habitats for the functioning of ecosystems. If we can make fishers aware of the fact that they are really sawing off the branch they sit on, we have come a long way. This means that we also should not only study the impacts of fisheries, but it is also essential to continue baseline research that demonstrates the functional importance of these key habitats on overall production including benefits to fisheries (e.g., determination of nursery value). If we can manage to transmit these values, we will find that fishers will be far more susceptible to agree to conservation plans and more likely to comply with new regulations. This aspect will be especially important with respect to compliance to regulations in offshore and deep sea areas where policing fisheries is challenging and where the conservations of features often rely upon fishers compliance. Overall we need to ensure that all relevant stakeholders have the same level of knowledge to come to the best possible management solution.

Sadly, there are always groups that are not interested in communication and fishers that are only interested in short-term economical gain without respect for the environment they exploit. Often no amount of talking will sway these people into joining the process of solution finding. In these instances, the only option is that the people that do talk with each other create suitable legislation, enforcement, and fines to protect sensitive ecosystems.

As from the impacts listed above, it is essential that scientists and conservation groups do distinguish between different fishing sectors. Putting the blame on fishers in general and dealing with them as a unified group is neither helpful nor does it reflect reality. In many instances, fishers are the first to notice environmental change (Willison et al. 2001) and may be sensitized to the conservation of ecologically important features. For example, the studies about the trawling impact on *Lophelia* reefs off Norway were in part initiated after concerns raised by static gear fishers about the status of the reefs (Fosså et al. 2002). They, in correspondence with the loss of *Lophelia* habitats, noted a sharp decline in their catches of nets set adjacent, but not on the reefs. Thus, in this case, the static fishers were monitoring reef health and alerting scientist to the problem caused by a different fishing sector. Within this example it could even be imagined that static fishers may form part of an early warning system monitoring the health of such reefs in the future. Rather than thinking of a blanket ban of fishing near "animal forest" habitats, fisheries and conservation managers should think creatively about the engagement of fishers in spatial management plans.

Fishers may also have their part to play in locating "animal forest" habitats and aiding in the process of mapping these. Most fishers have a good understanding of where certain features are located, and equally most fishing vessels are nowadays equipped with highly sophisticated echo-sounding equipment which could be used to identify potential reef habitats as well as trawling areas that have a low ecological vulnerability. Spatial management is seen as one of the key elements for the conservation of "animal forest" (Davies et al. 2007), and to succeed the integration of stakeholders in the process will be vital. This will also require that the decision and management process is fair and transparent and that knowledge limits are clearly identified and addressed wherever possible with evidence-based approaches.

It is furthermore vital that society does accept that if we all want to eat fish, fishers need to be able to pursue their activities. It is clear that these activities need to be regulated, but we need to find the best possible compromise between food production and the protection of vulnerable habitats and ecosystem functioning. Often the best way of solution finding is to involve all stakeholders and try to achieve the greatest possible consensus. The more stakeholders feel ownership and believe in the process, the greater the likelihood of success in protecting vulnerable habitats.

8 Conclusion and Further Direction

It is evident that animal forests due to their role as foundation species (The Builders of the Oceans. Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep) contribute extensively to ecosystem functioning processes. At the same time they rank among the most vulnerable habitats in particular in relation to fishing disturbances, and thus their protection and preservation have to be a paramount goal for the future (Measuring the Impact of Anthropogenic Activity on Cold-water corals). While continuing science into fishing impacts, research efforts into the functional importance of these habitats for ecosystem services should be increased. Such knowledge will be essential in winning over stakeholders, the general public, and politicians, which altogether hold the key to the future protection of these habitats. The more sensitized these groups are about the importance of "animal forests," the more likely is the implementation of science and management plans that further the mapping and protection of these very special habitats. The science basis is there to act; the challenge now lies in the political arena to devise legal frameworks and spatial management plans that ensure the sustainable use of marine resources and the conservation of marine animal forests.

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Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals

38

Federica Costantini, Anna Maria Addamo, Annie Machordom,
and Marco Abbiati

Abstract

Recent explorations of rocky habitats from 40 to about 6,000 m depth disclosed the role of gorgonian and scleractinian corals as habitat formers in tropical, temperate, and polar deep waters. Deep biogenic habitats host high species richness and complexity and their conservation requires a profound understanding of biological and ecological features of sessile species inhabiting them, such as the habitat-forming corals. In sessile species, earliest life history stages and larval processes (e.g., reproduction mode, larval development, behavior, and feeding mode) ensure the exchange of individuals within and among subpopulations, supporting species and habitat resistance and resilience. Genetic studies allow investigating larval processes when direct observations cannot be used. Parameters such as genetic connectivity, gene flow, and levels of genetic diversity are essential to monitor health and resilience of populations under current and future scenarios of anthropogenic environmental changes. In this chapter a review

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of studies on genetic connectivity of temperate and cold-water habitat-forming corals and associated invertebrate species will be presented. Among them, two case studies, *Desmophyllum dianthus*, a deep-sea worldwide-distributed scleractinian, and *Corallium rubrum*, a harvested Mediterranean and Eastern Atlantic alcyonacean with a wide bathymetric distribution, will be discussed in detail. This chapter will also show how these studies contributed to develop, implement, and recommend future conservation strategies and management plans. Existing gaps in literature on genetic connectivity of habitat-forming corals and other invertebrates have been also stressed and discussed. Finally, a conceptual framework for optimizing and planning effective studies on genetic connectivity is provided, including general recommendations on sampling design, key species and new molecular markers to use with a special emphasis on the "next-generation" DNA sequencing technologies.

Keywords
Biogenic reefs • Scleractinia • Alcyonacea • Larval dispersal • Population genetics • Mediterranean Sea

Contents

1 Introduction

In recent years, the development of effective tools for a visual survey of deep-water habitats (e.g., Remotely Operated Vehicles and Autonomous Underwater Vehicles) allowed the extension of marine investigation (below the common SCUBA diving depth), leading to the discovery of widely distributed biogenic reefs characterized by the formation of three-dimensional forest-like habitats mainly generated by cnidarian species (Kahng et al., ▶ Chap. 6, "Mesophotic Coral Ecosystems," this volume; Gori et al., ▶ Chap. 7, "Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea," this volume). Being largely neglected in the past, these formations are widely distributed in tropical, temperate, and cold-water seas where shallow water zooxanthellate coral reefs do not occur (Lesser et al. 2009). Similar to tropical coral reefs, temperate and cold-water biogenic reefs host some of the most productive benthic assemblages, supporting huge species richness. Moreover, they are exposed to threats similarly to tropical reefs (e.g., diseases, thermal stresses, pollution, fisheries, and tourism; Grehan et al., ▶ Chap. 35, "The Impact of Anthropogenic Activity on Cold-Water Corals," this volume). Habitat-forming sessile species are ecosystem engineering and directly or indirectly modulate the availability of resources to other species, causing changes to the abiotic or biotic features (see Rossi et al., ▶ Chap. 1, "Animal Forests of the World: An Overview," this volume for an overview). Moreover, they provide habitat, feeding grounds, recruitment, and nursery areas for a variety of invertebrate and vertebrate species. The high diversity of these species, together with their ecological functions has promoted extensive studies investigating biological and ecological features as well as their vulnerability.

1.1 Larval Ecology: From Dispersal to Connectivity

Population's recovery and resilience of habitat-forming sessile species strongly depend on their early life history processes: dispersal, settlement, and recruitment. Life history traits and environmental factors may affect these processes, influencing directly the population structure and dynamics, and therefore the structure of the biological communities (Fig. 1). Adjeroud et al., ▶ Chap. 20, "Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages," in this volume discuss the relevance of recruitment and of pre- and post settlement processes in the resilience of corals. Here, we focus on the relationships between dispersal and connectivity.

In habitat-forming species with sessile adults, dispersal potential is necessarily influenced by reproductive mode (broadcasting vs. brooding), larval development (sedentary vs. pelagic larval phase), nutritional mode (lecithotrophic vs. planktotrophic), duration (planic vs. aplanic), and behavior (benthic vs. planktonic) (Gleason and Hofmann 2011; Table 1). All these features determine the dispersal capability and the exchange of individuals within and among populations. Whether individuals after dispersal are able to contribute to the gene pool of the receiving populations (i.e., "effective migration" in population genetics) and impact their demographic rate, then we can refer to *population connectivity* (Cowen and Sponaugle 2009). Population connectivity is measured when individuals recruit, grow, and are able to reproduce. Therefore, population connectivity plays a fundamental role in intrapopulation and metapopulation dynamics, community dynamics, and structure. In particular, connectivity may improve the persistence of a metapopulation after disturbances, by enhancing their recovery in size and/or recolonization. Investigating levels of population connectivity contribute to (1) define ranges of effective larval dispersal, (2) predict and ensure persistence

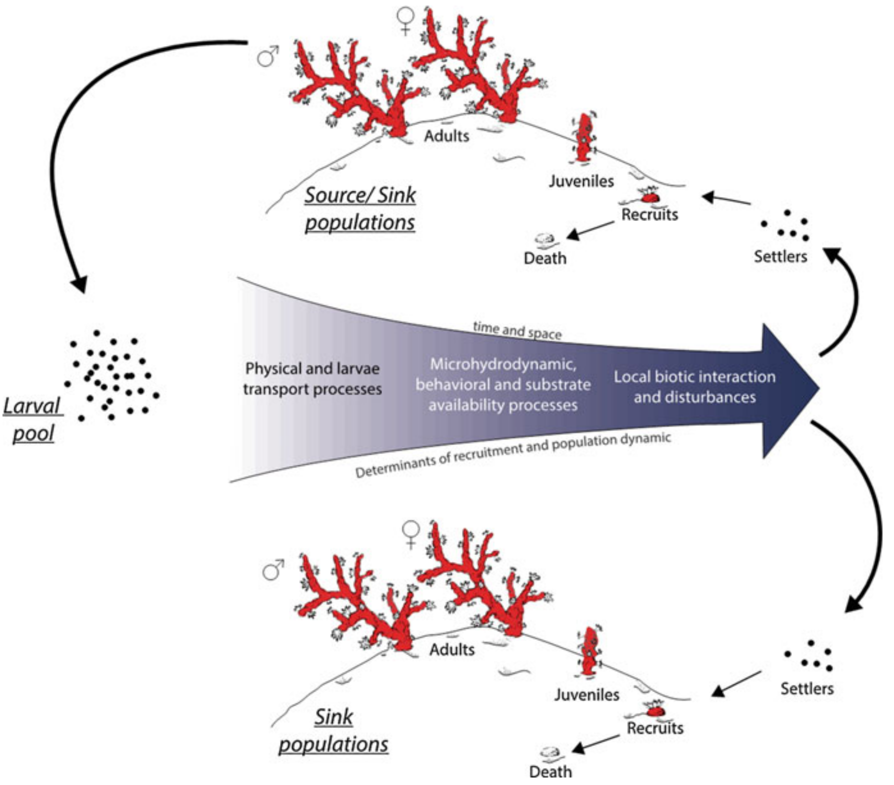

Fig. 1 Schematic representation of the life history of the habitat-forming corals. A myriad of larvae are released on the water column from a source/sink population. Then, larvae are exposed to several abiotic and biotic processes through time and space. All these processes influence larval dispersal reducing the number of larvae that are able to settle. In a metapopulation model, larvae may settle in the source population (self-recruitment) and/or in a sink population. Once larvae are settled, other postsettlement processes can act reducing again the number of recruits that can grow, became juveniles and able to reproduce (Drawing made by Mancuso FP and modified from Pineda (2000))

and resilience of populations under current and future scenarios of environmental changes, (3) manage commercial and harvested species, and (4) conserve populations through the establishment of reserve networks.

Different methods can be used to measure connectivity, and each method is best suited depending both on species life history and spatial and temporal scales of variation. Direct methods, such as visual observation and mark-recapture, provide the most accurate information on animal movement over demographic timescales, but not over evolutionary timescales, being affected by small spatial or seasonal variations in recruitment. Moreover, these methods can only rarely be used in marine species. When scientific knowledge about species biology is limited or totally absent and/or when it is difficult to track larvae in the field (e.g., deep-sea organisms),

Table 1 Larval development patterns of habitat forming species

I. Reproductive mode
Broadcasting
Species that release both eggs and sperm into the water column
Brooding
Species that release only sperm and house the eggs within the polyp until the fully mature larval stage is reached
II. Type of reproduction
Gonochorists
Separate sexes
Hermaphrodites
Produce both female and male gametes either simultaneously or sequentially
II. Larval development
No pelagic larval phase
Species with no intermediate stage of development
Pelagic larval phase
Development that includes free-living larval stages
III. Nutritional mode
Lecitotrophic
Pertaining to developmental stages (e.g., larvae) that feed on a yolk reserve
Planktotrophic
Pertaining to developmental stages that feed on plankton
IV. Duration of planktonic period
Planic
Actaeplanic
Larvae that develop in the plankton for 1–6 weeks
Brachiplanic
Larvae that develop in the plankton from hours to days
Aplanic
Larvae with no free-living dispersal stages
V. Behavior of the larvae
Benthic/Demersal
Larvae that develop on close association with the substratum
Planktonic
Larvae that spend a significant portion of their development time swimming freely in waters

Modified from DiBacco et al. (2006) and Gleason and Hofmann (2011)

indirect approaches (e.g., chemical fingerprint and genetic techniques) should be employed as complementary tools. Genetic methods allow inferring pattern of genetic structuring and connectivity among populations, which represent essential information for the development of effective management strategies and species and/or population conservation plans.

1.2 Genetic Connectivity as a Conservation and Management Tool

1.2.1 Population Genetics and Its Quantitative Descriptors

Population genetics investigates the structure of genetic variation, analyzing and modeling the changes in allele frequencies and genotypes within and between populations over time. The field of population genetics came into being in the 1920s and 1930s as a vital ingredient in the emergence of the modern evolutionary synthesis thanks to the works of R. A. Fisher, J. B. S. Haldane, and S. Wright. A population is subjected to four main evolutionary processes: natural selection, genetic drift, mutation, and gene flow. The alleles are different versions of the same gene that might be expressed as different phenotypes, and their appearance is based on the random and natural process of mutation, whereas their frequency of occurrence changes regularly as a result of mutation, genetic drift, gene flow/migration, and selection. Since changes in gene frequencies are at the heart of evolution and speciation, population and evolutionary genetics are often studied together. New approaches to population genetic studies arose in the 1980s applying the coalescent principle (i.e., the retrospective approach), which relates the genetic diversity in a sample to the demographic history of the population from which it was taken. On the contrary, the prospective (classical) population genetics approach predicts changes in the frequencies of alleles forward in time and describes patterns of genetic variation in an entire population.

Several statistical measures of population genetics – such as Hardy-Weinberg equilibrium (HWE) test, effective population size, inbreeding, and relatedness – are used to elucidate the genetic variability, structure, and dynamics at individual and population levels. Genetic variation is essential for the survival and adaptability of populations to a changing environment. The measures of the amount of allele richness and heterozygosity across all genes can be used as a general indicator of the amount of genetic variability and genetic "health" of a population. In fact, migrants may carry new alleles that will be integrated into the population through reproduction, creating new gene combinations on which selection can potentially act. Furthermore, gene flow increases genetic diversity of the population, enhancing the ability to counteract the effect of rapid random changes in allele frequencies from one generation to the next through drift. Small and isolated populations are subject to genetic erosion, with alleles being rapidly fixed or lost through drift, while selection and mutation generally play a less important role than drift in populations with small effective population size.

1.2.2 Genetic Connectivity

Genetic connectivity allows (1) to discriminate the spatial scales at which populations can be differentiated into discrete units and (2) to provide a proxy of the number of larvae migrating between populations. Successful migrants leave the genetic signature of their movements in a population, and population-genetics methods allow inferring information on species biology, such as reproductive strategy, prevalence of asexual reproduction, and effective larval dispersal. Moreover, these methods permit to infer patterns of genetic connectivity that represent the degree to which gene flow affects evolutionary processes among populations. When this information is combined with local demographic rates, data on movement behavior, or estimates of reproductive success of immigrants, we are able to provide insight on demographic connectivity (Lowe and Allendorf 2010).

At the sea, genetic connectivity studies have been used to address a variety of conservation and management issues such as (1) identification of genetically isolated populations of protected or endangered species that should be monitored as individual conservation units; (2) optimization of the size and location of protected areas; (3) monitoring of genetic variability loss and changes in population structure through empirical observation of genetic variation over time or before and after a major disturbance, such as harvesting; (4) identification of shifts in the range of geographic distribution in species affected by climate changes; and (5) detection of invasive species and reconstruction of invasion histories. Moreover, recent studies exploring the third dimension (i.e., depth gradients) provided important data about the potential role of deep-water populations as refugia for the recovery of disturbed shallow populations (van Oppen and Gates 2006; Costantini et al. 2011).

2 Genetic Connectivity in Temperate and Cold-Water Habitat-Forming Corals

In the scientific literature, connectivity and genetic diversity studies have been mainly carried out in the context of genetic conservation of tropical coral reef ecosystems (van Oppen and Gates 2006, and references therein) where a range of genetic structures varying from extremely local-scale patterns of self-recruitment to ecologically significant connectivity among reefs at scales of tens of kilometers (and in some cases, hundreds of kilometers) have been found. Scarcity of studies on biogenic temperate reefs is mainly related to the low information on their spatial distribution and to the paucity of knowledge of species biology and ecology inhabiting them. Indeed, although several studied have been developed on biodiversity hot spots in the Mediterranean Sea and in temperate Australian waters, only recently limited efforts have been devoted to investigate patterns of spatial genetic structuring in other regional areas, like Eastern Atlantic and temperate deep ecosystems.

2.1 Population Structure and Connectivity in Scleractinian Corals

So far, hundreds of species of the Scleractinia order have been described and classified as Cold-Water Corals (CWC, e.g., azooxanthellate cnidarians living at water temperatures between 4° C and 12 °C), representing half (~700 species) of all known scleractinian species. However, only few taxa, including endemic and cosmopolitan species inhabiting shallow and deep waters, have been the subject of genetic connectivity studies such as *Astroides calycularis*, *Cladocora caespitosa*, *Desmophyllum dianthus*, and *Lophelia pertusa*,[1] *Madrepora oculata* and *Solenosmilia variabilis* (e.g., Le Goff-Vitry et al. 2004; Morrison et al. 2011; Casado-Amezúa et al. 2012, 2014; Becheler 2013; Addamo et al. submitted; K. Miller, personal communication 2011).

Nuclear (ITS) and mitochondrial (16S, COI) genes have been used as molecular markers to determine genetic differentiation and phylogeographic patterns among CWC populations. Nevertheless, these markers were not very informative in terms of clustering individuals, that is, grouping a set of individuals based on their genetic similarity (see Le Goff-Vitry et al. 2004; Miller et al. 2011; Addamo et al. 2012; Becheler 2013). On the contrary, nuclear microsatellite sequences have been demonstrated to be the most revealing DNA markers available for inferring population genetic structure and dynamics (e.g., Le Goff-Vitry et al. 2004; Morrison et al. 2011; Casado-Amezúa et al. 2012, 2014; Becheler 2013; Addamo et al. 2015, submitted; K. Miller, personal communication), also providing a finer resolution at different spatial scales in deep-sea coral species (e.g., Dahl et al. 2012).

Cladocora caespitosa is an endemic Mediterranean shallow water reef-forming zooxanthellate scleractinian species. According to the fossil record, it is considered a relict species from the subtropical late Pliocene and Quaternary periods. Currently, the overall abundance of the species is decreasing and it has been included in the list of marine endangered species. Patterns of genetic differentiation among populations in the Western Mediterranean Sea have been related to high levels of self-recruitment, supported by egg-retention mechanisms and sporadic dispersal events driven by regional surface currents during the spawning period (Casado-Amezúa et al. 2014).

Similar population structure and connectivity have been found in the Mediterranean colonial scleractinian coral *A. calycularis* (Casado-Amezúa et al. 2012). Microsatellites revealed a high level of connectivity among localities separated by as much as 1 km and moderate levels of genetic differentiation among more distant localities, somewhat corresponding to a stepping-stone model of gene flow and connectivity. Its brooding reproductive mode, the demersal and sinking behavior of planula larvae, together with local hydrodynamic processes and its distribution of rocky substrate along the coastline could drive the genetic connectivity pattern among investigated populations.

Regarding to a deep and cosmopolitan CWC species, such as *L. pertusa*, the patterns of connectivity and gene flow found to date among populations strongly depend on the molecular marker used. Ribosomal Internal Transcribed Spacers (ITS) used in population genetics studies of *L. pertusa* in the North Western Atlantic (Le Goff-Vitry et al. 2004) suggest that some gene flow occurs over large geographic distances. Conversely, studies using microsatellites reported differentiation and even

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[1] *Lophelia pertusa* is a junior synonym of recently reassigned scientific name of *Desmophyllum pertusum* (see Addamo et al. 2016). Although it should be consistent with using the species name *D. pertusum*, authors decide to maintain the name *L. pertusa* in the main text in order to be coherent with other chapters and do not confuse the reader.

genetic discontinuities among populations of this species in the North Eastern (Morrison et al. 2011) and North Western Atlantic Ocean (Le Goff-Vitry et al. 2004).

In other cases, both nuclear ITS and mitochondrial DNA regions have proved to be potentially informative for distinguishing between geographically and bathymetrically isolated populations, suggesting depth as an important physical factor that can determine isolating mechanisms for eurybathic scleractinian species (see Miller et al. 2011, for *D. dianthus* population genetics). According to these results, microsatellites also provided evidence that population structure of the solitary coral *D. dianthus* in the South Pacific is strongly linked to depth, supporting the existence of three depth-related groups (see Miller et al. 2011, K. Miller, personal communication). Nevertheless, depth do not seem to be an important structuring force in the matrix-forming colonial coral *Solenosmilia variabilis* that appears to have differentiated gene pools even within the same seamount. Such results provide empirical evidence that groups of seamounts can function either as isolated islands or as stepping-stones for dispersal for different taxa (K. Miller, personal communication).

2.2 Population Structure and Connectivity in Gorgonian Corals

In gorgonians, mitochondrial DNA is not a good candidate for population-level analyses at ecological time scales due to its extremely low evolution rates compared to scleractinian corals. The low evolutionary rate has been attributed to the presence in gorgonians mitochondria of an apparent homolog of the bacterial mismatch repair gene (*mtMutS*, Pont-Kingdon et al. 1995). Nevertheless, several authors have recently shown that mitochondrial markers could give some information on the genetic structure of deep-water gorgonian populations at different depth/geographic extents, being able to explain patterns at evolutionary time scales (e.g., Liu et al. 2005; Thoma et al. 2009; Pante and Watling 2011; Herrera et al. 2012). These studies, regarding Atlantic species, showed a wide geographic distribution of haplotypes reflecting high dispersal capabilities and/or ancient connections between ocean basins (Thoma et al. 2009; Pante and Watling 2011; Herrera et al. 2012).

Population genetic studies on gorgonian corals are mainly based on microsatellites data. Most studies are dealing with Mediterranean species, even if recently microsatellite markers have been developed for several Atlantic species (e.g., *Eunicella verrucosa*, *Alcyonium palmatum*, *Paragorgia arborea*, *Junceella juncea)*. Out of approximately 20 gorgonian species inhabiting the Mediterranean Sea, extensive studies are available only on *Corallium rubrum*, *Eunicella singularis*, and *Paramuricea clavata*. Pey et al. (2013) experiments explored the thermal threshold of the white gorgonian *E. singularis*, as well as possible links between thermal sensitivity and host/symbiont genotypes. Although the main focus of the study was not the analysis of the genetic structure of the populations, they observed that host populations from different depths (15 and 35 m depth) were genetically homogenous within a geographic location, while genetic differentiation was found between locations hundreds of kilometers apart (Riou and the Medes Islands).

Observed geographical differentiation could be related to the contrasting environmental conditions of the two sites and/or to the low dispersal potential of the species. Conversely to Pey et al. (2013), Costantini et al. (2016) found in Cap de Creus (Spain) a break at 30–40 m depth in gene flow between populations, supporting the pattern of morphological variability observed at different depths by Gori et al. (2012). Moreover, Costantini et al. (2011) found a threshold in genetic connectivity in *C. rubrum* between 40 and 50 m depth (see Sect. 4.2), suggesting that environmental features associated with depth have an important role in determining patterns of genetic structuring in Mediterranean gorgonians.

The genetic structure of *Paramuricea clavata* populations have been analyzed at a local and broad range of spatial scales (Mokhtar-Jamaï et al. 2011, 2013; Arizmendi-Mejía et al. 2015; Pilczynska et al. 2016), and strong genetic differentiation among patches separated by distances ranging from thousands of kilometers to 20 m was found. A pattern of isolation by distance was observed at global, as well as at regional scales (Mokhtar-Jamaï et al. 2011, but also see Arizmendi-Mejía et al. 2015 for Balearic Islands and Pilczynska et al. 2016 for Ligurian Sea). A clear distinction between southern, north-western, and eastern Mediterranean populations was revealed. In the north-western Mediterranean Sea, three clusters were found: Medes (Catalan Sea), Marseille (Gulf of Lion), and North Corsica (Ligurian Sea) (Mokhtar-Jamaï et al. 2011), and at local-scale hints of possible effects of distance (Pilczynska et al. 2016) or depth were also found in populations sampled at 20 and 40 m depth (Mokhtar-Jamaï et al. 2011). Downscaling the analysis within an area of 2 m^2, Mokhtar-Jamaï et al. (2013) observed a strong level of self-recruitment (25%), unveiling the occurrence of a complex family structure at a small spatial scale, consistent with the limited larval dispersal of this species. However, no evidence of small-scale spatial genetic structure (SGS) was revealed.

3 Genetic Connectivity in Invertebrates Associated to Temperate Biogenic Reefs

The population structure of other habitat-forming invertebrates (e.g., sponges, bryozoans) has been recently analyzed using microsatellite loci (e.g., Johnsons and Woollacott 2012; Pérez-Portela et al. 2014). Moreover, several studies have been carried out on species living in close association with habitat-forming corals (see Costantini et al. in prep. for a review). Among them, four major taxonomic groups have been examined: Cnidaria, Echinodermata, Tunicata, and Porifera, with a prevalence of studies on Porifera. Among all the analyzed species, few have a commercial value (e.g., *Spongia lamella* and *Spongia officinalis*), while the others are ecologically relevant (e.g., ascidians are habitat formers and an important component of the fouling assemblages).

Despite the broad and patchy distribution of benthic assemblages, in most species very low dispersal capability of larvae and gametes has been detected. Significant deviations from Hardy-Weinberg equilibrium, as well as heterozygosity deficits, have been observed. Deficits of heterozygotes is a frequent trait in marine invertebrates (see Addison and Hart 2005 for a review) and may be the result of biological factors, such as mixing of differentiated gene pools (Wahlund effect) and high levels of consanguineous mating (inbreeding). In invertebrates associated to temperate reefs, heterozygosity deficits may reflect life history traits, reproductive features (gonochorism vs. hermaphroditism), and restricted (e.g., *Crambe crambe*, Duran et al. 2004) or null larval dispersal (e.g., *Amphipholis squamata*, Boissin et al. 2008). The great majority of these species showed a genetic structuring at scales of tens of kilometers, suggesting that a dispersal range of up to few kilometers may be common (Costantini et al. in prep.). Nevertheless, a poor correlation between pelagic larval duration (PLD) and population genetic structure was observed, suggesting that patterns of connectivity in the marine realm are difficult to predict based on life history characters alone (Riginos et al. 2011). In fact, other biotic and/or abiotic variables may act in shaping the genetic structuring of populations. At larger scales, the hydrodynamic and geomorphologic characteristics of habitats contribute to explain common patterns of genetic structuring across the main biogeographic transitions (Villamor et al. 2014).

4 Case Studies

As case studies, two habitat-forming cnidarian species, that is, *Desmophyllum dianthus* (Hexacorallia: Scleractinia) and *Corallium rubrum* (Octocorallia: Alcyonacea), with contrasting spatial and depth distribution and differing in biological and ecological features, have been selected. Both of them are long-lived, slow growing, and fragile corals, which makes them especially vulnerable to human damage. Large banks of *D. dianthus* have been recently discovered worldwide, creating three-dimensional forest-like structures on the sea floor. Conversely, *C. rubrum* is a Mediterranean and Eastern Atlantic species that has been harvested for thousands of years for the use of its calcareous skeleton in jewelery, traditional medicine, and tribal rituals. Its current distribution reflects this long history of harvesting and human pressures, especially in shallow water.

4.1 The Deep Cold-Water Coral *Desmophyllum dianthus*

Desmophyllum dianthus (Esper, 1794), or its frequently used synonym *D. cristagalli* (Milne Edwards and Haime, 1848), is the type species of the genus *Desmophyllum* Ehrenberg, 1834, within the family Caryophylliidae Dana, 1846 (Fig. 2a). *D. dianthus* is one of the few cosmopolitan species of Scleractinia, widely distributed across the Atlantic, Pacific, and Indian oceans. However, it is not present in the northern boreal Pacific and off Antarctica. This solitary and azooxanthellate species mainly dwells on hard substrates occurring from the continental slope to the upper bathyal zone, commonly associated to scleractinian reef framework-forming cold-water corals *Lophelia pertusa* and *Madrepora oculata* (Roberts et al. 2009). Although solitary, it often produces pseudocolonial clumps of specimens, acting as the

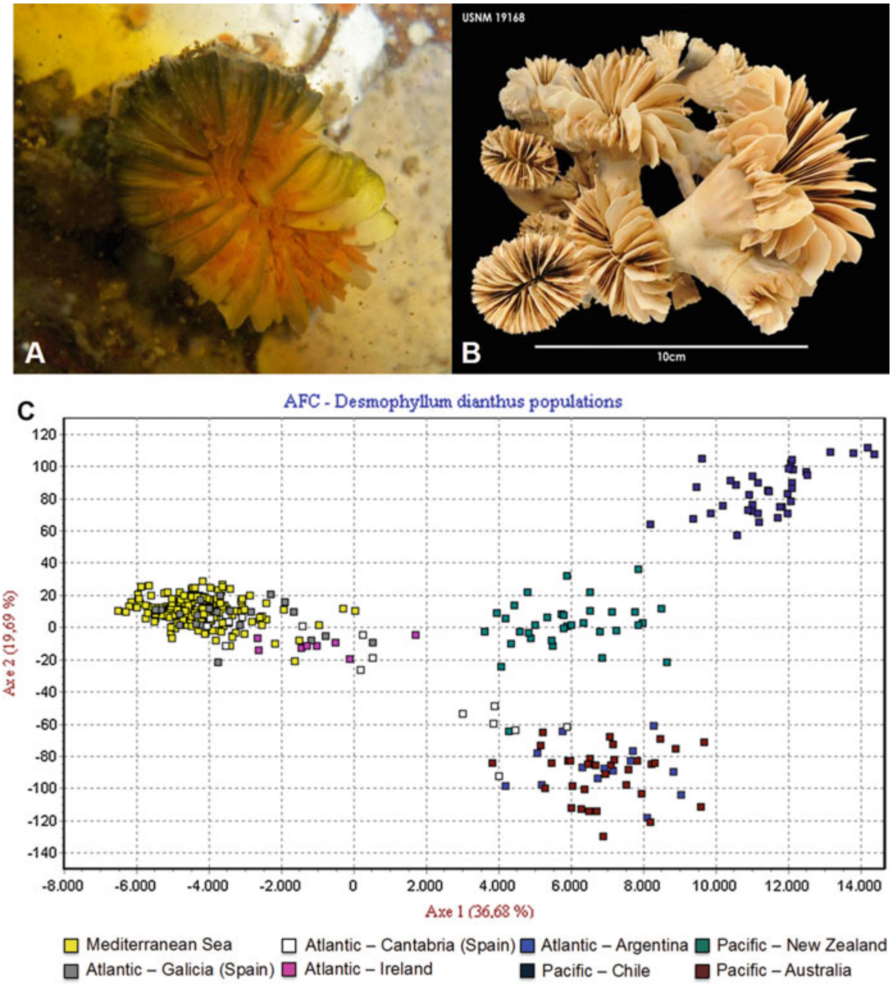

Fig. 2 (**a**) *Desmophyllum dianthus* (Pitipalena Fjord, Chile, −17 m. Photo: Addamo AM). (**b**) Example of pseudocolony of *D. dianthus* (USNM 19168. Photo: NMNH Smithsonian). (**c**) Factorial correspondence analysis (AFC) based on allele frequencies from 30 microsatellite loci genotyped in *D. dianthus* populations from northern and southern hemispheres. Colors represent sample locations; percentage explains the correspondence contribution per each axis

framework coral for deep-water coral banks (Fig. 2b). Its worldwide depth range is 80–2,460 m, exceptions made when environmental conditions are favorable, namely, cold upwelled waters associated with fjords, as it occurs both in New Zealand, where shallowest records are reported at 25 m depth, and in Chile, where single individuals are found as shallow as 8 m depth, though larger accumulations are generally found below 20 m depth (Roberts et al. 2009 and references therein; Haüsserman et al., ▶ Chap. 10, “Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters,” this volume).

Except for taxonomic studies, earliest scientific works related to *D. dianthus* are dated to the late 1970s and were mainly focused on geological analyses, such as skeletal microstructure and ontogenetic development, lifespans and growth pattern, and the potential paleo-climatic proxies of the species (Freiwald and Roberts 2005, and references therein). Only in the last decade has the scientific attention moved to other disciplines, and studies to obtain insights about the biology, physiology, and ecology of *D. dianthus* have been conducted (Freiwald and Roberts 2005, and references therein). These studies have revealed that *D. dianthus* displays an average growth rate of 0.5–1 mm/year, with a long lifespan of up to 200 years and that it is an exceptional proxy for pH and temperature of water masses in marine ecosystems (Freiwald and Roberts 2005, and references therein). It seems to be a species with low acidification and moderate thermal tolerances (Gori et al. 2016), and survival and growth of specimens have been documented from 12 °C (environmental temperature of its natural habitat) to up to 17 °C in the Mediterranean Sea (e.g., Naumann et al. 2013). Studies about demography, population structure, and reproduction of *D. dianthus* are rather scarce and, only recently, a genetic study using the internal transcribed spacers (ITS), the 16S mitochondrial ribosomal subunit (16S) and the control region (MtC), was conducted to determine levels of gene flow within and among populations of *D. dianthus* in the Southern Pacific Ocean and to assess the ability of these corals to disperse into different regions and habitats (Miller et al. 2011). This study showed slight, but significant genetic subdivision among geographic sites (Australia, New Zealand, and Chile), as well as among different depths, indicating isolation and limited contemporary gene flow with limited vertical larval dispersal. Therefore, it was hypothesized that the reproductive traits of *D. dianthus* might be similar to those of other deep-water corals, that is, broadcast spawner with lecitotrophic larvae, which display a low larval dispersal (e.g., Miller et al. 2011).

Surprisingly, when the network analysis was performed including individuals from the Mediterranean Sea, shared haplotypes were found among the northern and southern hemispheres (Addamo et al. 2012). Such an occurrence could indicate historical patterns of genetic connectivity (current or recent gene flow, incomplete lineage sorting or retention of ancestral polymorphism), methodological bias (using genes or regions with an inadequate substitution rate to show divergence) or both (differences in the coalescence of these genes combined with populations divergence) (Addamo et al. 2012). Markers with higher evolutionary rates – such as microsatellites – have been developed for *D. dianthus* (Addamo et al. 2015) to assess connectivity among populations from different oceans and dwelling at different depths and to infer biological (e.g., reproduction strategy or larval dispersal) and oceanographic (e.g., bathymetry or water circulation) factors driving isolation. Statistically significant levels of genetic differentiation have been found among populations from the northern and southern hemispheres, consistent with limited gene flow and isolation by distance (e.g., North Atlantic-Mediterranean Sea vs. South Pacific, Fig. 2c). Nevertheless, depth (combined with water circulation) was a major component of differentiation among populations from the South Pacific (e.g., Chile vs. Australia-New Zealand, Fig. 2c, Addamo et al. submitted).

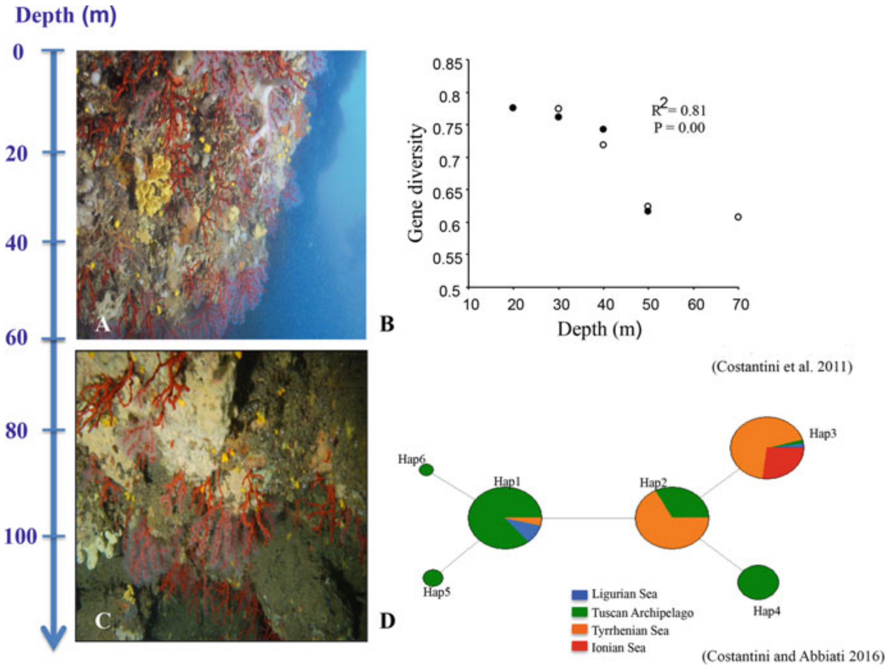

Fig. 3 (**a**) Picture of red coral population in Portofino (30 m depth; Courtesy of Palma M). Results of regression analysis between gene diveristy and depth in *Corallium rubrum. White circles*: Portofino samples, *black circles*: Cap de Creus samples (Costantini et al. 2011). (**b**) Picture of red coral population of Giglio Island (Tuscany, 100 m depth; Courtesy of Canese S). Median-joining network depicting relatedness and geographic distribution of mitochondrial control region haplotypes of *Corallium rubrum. Circle* size is proportional to the number of colonies with the corresponding haplotype (Costantini and Abbiati 2016)

4.2 The Precious Coral *Corallium rubrum*

The red coral *Corallium rubrum*, Linnaeus 1758 is a gonochoric long-lived octocoral, endemic to the Mediterranean Sea and its neighboring Atlantic rocky shores. It can be found on vertical cliffs, caves, and in crevices from 20 to 100 m depth, though it also occurs in deeper waters (roughly down to 1,000 m depth) where it dwells on scattered boulders, rocky outcrops, submarine canyons, and seamounts. Three typologies of red coral populations related to the depth distribution have been described (Costantini et al. 2010; Angiolillo et al. 2016): (i) shallow-water populations, occurring at 15–60 m depth, made by small, short-lived colonies; (ii) intermediate-water populations at 60–300 m depth, made by larger, sparse, long-lived colonies; and (iii) deep-water populations, which are poorly known and dwell below 300 m depth (Fig. 3a, b).

Natural (e.g., smothering by sediments, infection by parasites, and invasion by alien species) and anthropogenic stressors (e.g., harvesting, habitat loss and fragmentation, and threats arising from climate change and ocean acidification) affect

C. rubrum populations along its entire bathymetrical distribution (see also Rossi et al., ▶ Chap. 19, "Demography of Animal Forests: the Example of Mediterranean Gorgonians," this volume). For instance, in summers 1999 and 2003, mass mortality events, linked to natural stressors and thermal anomalies, impacted shallow water populations. Moreover, historical exploitation has lead to the present structure of shallow water populations affected their demographic structure, and nowadays they are made by young and fragile colonies (less than 10 years old) with low economic value. However, the main target of professional harvesting now shifted to populations occurring between 80 and 130 m. Regarding these deeper populations, they are threatened by destructive fishing, that is, bottom trawling and entanglement in lost long lines and netting (Bo et al. 2014).

Given its ecological, economical, social, and cultural value, red coral has been protected by different International Conventions (Barcelona, Berne, and the European Habitat Directive). In recent years, a growing number of scientific studies on reproductive biology, feeding, distribution, and population dynamics, as well as on manipulative experiments exploring processes driving the ecology of this species in shallow water, have been published. Several studies have also addressed the genetic structure of the species in different habitats, at a variety of geographical scales, and at different depth ranges. In shallow water populations, strong genetic structuring was observed at the Mediterranean scale down to patches separated by 10 m (Costantini et al. 2007a, b). In the Western Mediterranean, a pattern of genetic structure, reflecting a combination of regional clustering and isolation by distance, was found at a scale of hundreds of kilometers (Ledoux et al. 2010a). However, marked chaotic structuring was detected when downscaling the studies to very small patches (distances of 1 m) with a significant spatial genetic structure observed between colonies within a 0.5 m^2 square (Ledoux et al. 2010b). Based on these results, the mean dispersal range was estimated between 20 and 30 cm, suggesting that breeding units are restricted in space and are composed by related individuals.

Regarding depth, a consistent reduction in genetic variability was observed between shallow and deep colonies, with a threshold at 40–50 m, suggesting isolation between shallow and deep sublittoral red coral populations (Fig. 3a; Costantini et al. 2011). Several explanations may be provided for the reduced genetic variation of deeper populations, among which physical forcing, environmental factors and/or biological processes (e.g., reproductive biology, recruitment, and selective mortality). Experiment in aquaria and reciprocal transplant experiments acts to evaluate the response of *C. rubrum* to thermal stress, suggesting that this genetic isolation could also be related to differences in adaptive abilities (Torrents et al. 2008; Ledoux et al. 2015). In fact, differences in fitness traits (measured as grow rate, polyps activity, calcification rate) were observed between shallow and deep colonies. Shallow populations showed a capacity to cope with the expected increase in sea temperature under different climate change scenarios, contrary to deep populations (Ledoux et al. 2015). While shallow red coral populations may act as reservoir of adaptive genetic variation (Costantini et al. 2011; Ledoux et al. 2015), deep ones cannot act as refugia for shallow water populations, as hypothesized for some tropical species. Indeed, genetic analyses of red coral colonies collected below

600 m depth suggest that the deep refugia hypothesis is unlikely for this species. Differences in ITS-1 and *mtMutS* sequences between deep- and shallow-water colonies reinforce this suggestion (Costantini et al. 2010), as well as the results obtained by Costantini et al. (2013) and Costantini and Abbiati (2016), who investigated genetic spatial structuring and variability of *C. rubrum* intermediate populations dwelling at 55–120 m along ~1,500 km of coastline from the Ligurian to the Ionian Sea. In these studies, mitochondrial and nuclear markers showed high genetic structure between Northern (Ligurian Sea and Tuscan Archipelago) and Southern (Tyrrhenian and Ionian Seas) populations (Fig. 3b, Costantini et al. 2013; Costantini and Abbiati 2016). The common genetic discontinuities observed between Northern and Southern Mediterranean deep red coral populations seem to be mainly related to vicariant events or local adaptation. Differences in adaptive skills, together with the limited connectivity both in shallow and deep populations, open a question concerning the ability of *C. rubrum* to face future global environmental changes.

5 Conservation and Management Applications

Previously described studies provide background knowledge to be integrated in future policies for the management and conservation of marine animal forests. The high genetic structuring observed in all the species analyzed represents a challenge for the conservation of temperate habitat-forming corals. Indeed, an increase of mortality due to natural and anthropogenic impacts, such as harvesting, trawling, or water temperature anomalies, could lead to deep changes in the specific composition and structure of these communities. Evidence of genetically differentiated populations at scale of kilometers suggested that conservation plans have to be based on local or regional approaches. Nevertheless, since networks of MPAs are widely acknowledged to be an important tool for ensuring the long-term health and conservation of ecological processes in the marine environment, not only a regional approach has to be considered. Collaborations among countries are needed to have a global view of species connectivity patterns.

In general, the results from these studies provide scientific knowledge to support policy implementation, such as the European Union Marine Strategy Framework Directive (MSFD), the main aim of which is to achieve Good Environmental Status (GES) of the EU's marine waters by 2020 and to protect more effectively the marine environment, and resources upon which marine-related economic and social activities depend. For example, studies related to *D. dianthus* populations have been used to build a set of guidelines to establish networks of MPAs and off wind farms in the Mediterranean Sea. Specifically, results from studies on genetic connectivity contributed to characterize and define the novel concept of Cells of Ecosystem Functioning as conservation and managements units, a key concept for the definition of the networks of MPAs and for the identification of suitable areas for off wind farms (see www.coconet-fp7.eu, CoCoNet EU project).

Another relevant example is given for *Corallium rubrum*: the General Fisheries Commission for the Mediterranean enforced a ban on precious red coral harvesting down to 50 m depth (FAO, GFCM 2010) based on the breakdown in genetic connectivity found across this depth. Furthermore, FAO stressed the need to increase the knowledge on deep populations to better understand the impact of new harvesting technologies (e.g., Remoted Operated Vehicles) on both the resource and the ecosystem. In fact, from a conservation point of view, considering the extension of the fishing to deeper water where populations are genetically structured, the creation of new deep-sea and offshore reserves is pivotal. Deep-sea and offshore marine protected areas have been recently recognized by international and national organizations as efficient tools for protection of the deep habitats. In the Mediterranean, conservation was recently promoted with the establishment of three MPAs for the conservation of the cold-water coral ecosystems in the Gulf of Lion and with the establishment of two sites of community interest (SCI) in the Ligurian Sea and in the southern Tyrrhenian Sea.

6 Conclusion

Despite the relevant implication of connectivity for conservation, only few studies have been developed to address patterns of spatial genetic structuring in temperate and deep seas habitat-forming species. This scarcity of data could be partially due to the fact that species that are the easiest to sample are the most difficult to analyze using traditional molecular methods and to constrains in sampling deep marine environments. However, nowadays, development of new and sophisticated technologies has proven to be a turning point for nondestructive sampling of deep rocky reef species.

Despite the complex, broad, and patchy distribution of deep rocky habitats in temperate seas, the species studied so far have shown limited dispersal capability of larvae. This main result is an important point to take into account in conservation strategies, as species generally consist of an array of metapopulations structured both geographically and by depth. Observed patterns of genetic divergence mainly result from the interaction between the biological characteristics of species and the hydrodynamic and geomorphologic characteristics of the investigated regions. Moreover, other evolutionary processes as vicariance events, incomplete lineage sorting or retention of ancestral polymorphism could contribute in explaining the genetic structuring observed.

Guidelines for the implementation of an effective framework for spatial conservation plans should incorporate genetic approaches that bridge the fields of population genetics and conservation genetics. They should take in consideration genetic diversity among a wide spectrum of habitat-forming corals, in order to represent major parts of overall biodiversity and functions. Species living across environmental gradients, encompassing a variety of life history strategies and with peculiar ecological distributions (e.g., the gold coral *Savalia savaglia* and black corals of the Order Antipatharia), should be analyzed. Moreover, guidelines should clearly define the conservation goals, and the data required to define the best approach in terms of sampling design, temporal and spatial scales of analysis, and molecular markers (Marti-Puig et al. 2013).

7 Future Directions

Future studies must fill the gaps existing in the field of genetic connectivity and conservation. Such gaps are mostly related to two aspects of the current studies: habitat-forming corals and conceptual and technological frameworks. Most studies have focused on tropical coral species; this is the first bias with respect to species that live in the temperate seas. A second gap, which is revealed by the richness of shallow versus deep population genetic datasets, is due to the difficulties in sampling deep-sea species. Moreover, studies on population connectivity have to be based on an effective sample size (at least 30 individuals) and, possibly, on replicated populations. However, most oceanographic campaigns to explore the deep sea have not been designed to achieve the effective sample size and replication. These gaps have to be taken in account in future studies.

Concerning conceptual and technological gaps, integrative studies and collection of large datasets will be the frameworks fulfilling the current lack of knowledge. Global change-related challenges and conservation policies could be addressed on a solid knowledge of the patterns and processes responsible for population structure and connectivity. Multidisciplinary studies, including oceanography, geology, ecology, and other fields, together with genetic connectivity, are needed to tackle these goals. Seascape genetics could be a relevant approach to address these issues by coupling parameters (both abiotic and biotic) affecting the population genetic structure and connectivity data arising from molecular studies. Projects as the “Integrated Ocean Observing System” led by NOAA, or similar initiatives led by the European Commission, will provide valuable data essential for priming models with the goal to disentangle complex patterns observed at the species level.

From a technological point of view, the advent of the Next Generation Sequencing (NGS) seems to have opened the doors to the “Library of Alexandria” of genomes, where the entire life history is written, recognizable and available. This noteworthy increase of genomic data is fundamental and provides a potential source of informative markers, useful for population conservation and management. Nevertheless, as Shafer et al. (2015) clearly stated, “under the premise that assisting conservation of the world’s biota is its ultimate purpose, the emerging field of conservation genomics must openly and pragmatically discuss its potential contribution toward this goal. While there are prominent examples where genetic approaches have made inroads influencing conservation efforts, it is not immediately clear that the conservation community and society more broadly have embraced genomics as a useful tool for conservation”.

One of the reasons why stakeholders and end-users hesitate to adopt genomics as a core methodology for conservation studies is the complexity of data processing and interpretation. Indeed, the analytical pipelines are often tight and no user-friendly.

NGS is advancing at a rate that is not achieved yet by bioinformatic tools, leaving a relevant gap between the available and attained knowledge. Furthermore, the historical gap between fundamental and applied research also needs to be bridged. Filling this gap might lead to answer several important questions, which are essential to face the challenge of avoiding the currently important loss of biodiversity. For instance, the comparison of gene expression in different habitats (e.g., through RAD-sequencing and transcriptome analyses) would address adaptation of species to changing environmental conditions. Having the possibility of finding more and better genetic markers would permit scientists to provide quick and accurate answers at the molecular level. The design of networks of MPAs has been largely discussed, and usually based on the study of few species, that could not represent, as previously mentioned, the complexity of ecological systems (Villamor et al. 2014). Metagenomics analyses can be a step towards addressing this point.

8 Cross-References

- ▶ Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters
- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests of the World: an overview
- ▶ Demography of Animal Forests: The Example of Mediterranean Gorgonians
- ▶ Global Biodiversity in Cold-Water Coral Reef Ecosystems
- ▶ Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages
- ▶ Mesophotic Coral Ecosystems
- ▶ The Impact of Anthropogenic Activity on Cold-Water Corals

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Contrasting Effects of Ocean Acidification on Coral Reef “Animal Forests” Versus Seaweed “Kelp Forests”

39

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Abstract

Ocean acidification is the sustained absorption of anthropogenically derived CO_2 and is a major threat to marine ecosystems. Ocean acidification results in the decline of seawater pH (increase in protons) and carbonate ions and increased CO_2. Added CO_2 could benefit terrestrial forests, but changes in the concentration of any one of aspect of the carbonate system could affect various marine organisms both positively and negatively. One ecosystem under particular threat from ocean acidification is tropical coral reefs, formed predominately by scleractinian coral species that are predicted to be negatively impacted by ocean acidification. In contrast, temperate shallow rocky reefs are dominated by seaweed that forms extensive kelp/seaweed forests; these noncalcareous seaweeds are not predicted to be as negatively impacted by ocean acidification. Tropical coral reef “animal forests” and temperate “kelp forests” both provide three-dimensional habitat for tens of thousands of species, but are characterized by vastly different environmental regimes. The present chapter outlines differences in key environmental parameters (such as nutrients, water motion, and temperature) in these two habitats that could dictate the relative magnitudes of the effects of ocean acidification within them. The vulnerability of key habitat-forming organisms within these habitats and the potential mechanisms behind specific responses to ocean acidification are also discussed.

Keywords

Calcification • Photosynthesis • CO_2 concentrating mechanisms • Coralline algae • Climate change • Environmental variability • Light • Water motion • Nutrients • Warming

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Contents

1 Introduction

Ocean acidification is the sustained absorption of anthropogenically derived CO_2 by surface seawaters (Caldeira and Wickett 2003). Ocean acidification is named for its effects on seawater pH, whereby proton concentrations increase, moving alkaline seawater toward a more neutral state. This “acidification” changes the speciation of dissolved inorganic carbon (DIC), decreasing carbonate ions (CO_3^{2-}), increasing dissolved CO_2, and increasing bicarbonate ions (HCO_3^-). These changes in seawater chemistry have dramatic physiological effects on some marine species, as all components of the carbonate system can be related to the metabolic function of various species (Hepburn et al. 2011; Comeau et al. 2013a; Wittmann and Pörtner 2013). The clearest physiological impacts of ocean acidification are on calcification rates, which generally decline as pH is reduced (Ries et al. 2009; Comeau et al. 2013b; Kroeker et al. 2013). Changes in CO_2/pH resulting from ocean acidification could also disrupt acid-base metabolism in many marine invertebrates and fishes, having negative consequences for many of these organisms too (Pörtner and Farrell 2008; Wittmann and Pörtner 2013). However, the negative effects of ocean acidification are not universal (Ries et al. 2009, Comeau et al. 2014a), and, inversely, there has been much speculation regarding whether photosynthetic or growth rates of marine autotrophs could actually benefit from elevated CO_2 concentrations (Hepburn et al. 2011; Connell et al. 2013; Kroeker et al. 2013), as some species may be capable of utilizing additional CO_2 (Raven 1997; Hepburn et al. 2011; Cornwall et al. 2015). Together, these direct effects of ocean acidification could have dramatic consequences for marine ecosystems when scaled up. However, assemblages comprised of different organisms will display varied responses to ocean acidification, with assemblages dominated by calcifying species likely more affected

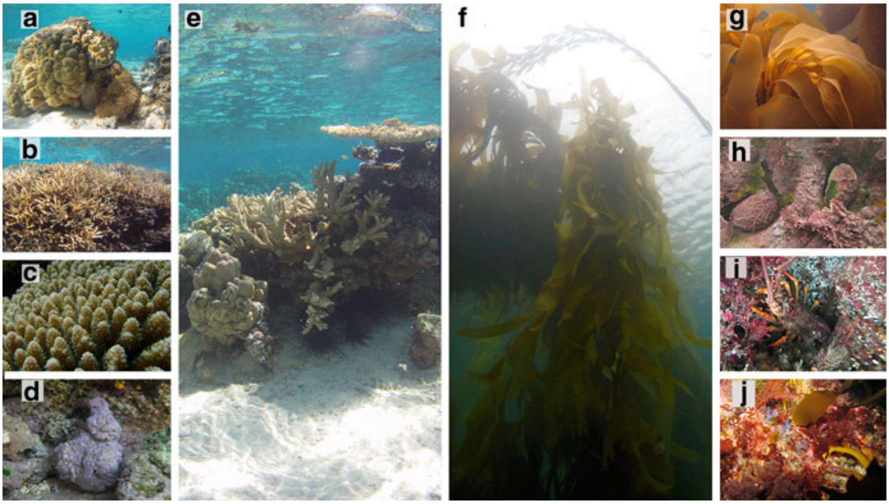

Fig. 1 Key organisms within both coral reef animal forests and kelp forests ecosystems. The left panels show examples of the main reef builders in a typical coral reef: **a**) Massive *Porites* spp., **b**) the branching coral *Acropora pulchra*, **c**) a close-up view of the coral *Acropora hyacinthus*, and **d**) the coralline alga *Hydrolithon reinboldii*. The panel **e**) shows the back reef of Moorea, French Polynesia. Kelp forests are characterised large biomasses of macroalgae, such as the giant kelp *Macrocystis pyrifera* (**f**). The right panels show organisms leaving typically in kelp forests: **g**) canopy-forming kelp (*Macrocystis pyrifera*), **h**) crustose coralline algae and abalone (*Haliotis australis*), **i**) lobster (*Jasus edwardsii*), and **j**) a diverse mixed assemblage of understorey seaweed, including juvenile kelp (*Ecklonia radiata*)

than the ones dominated by noncalcareous species such as fleshy seaweeds (Hall-Spencer et al. 2008; Fabricius et al. 2011; Enochs et al. 2015). Additionally, environmental conditions will largely mediate the magnitude of responses to ocean acidification (Russell et al. 2009, 2011; Comeau et al. 2014b, c; Cornwall et al. 2013a, 2014). The following chapter presents the potential effects of ocean acidification on habitat-forming marine organisms from two very different, but highly diverse shallow water marine ecosystems: warm water shallow scleractinian coral reef "animal forests" and cooler water seaweed "kelp forests" (Fig. 1). The potential mechanisms behind specific responses to ocean acidification and the role played by key environmental parameters such as temperature, nutrients, water motion, and light to modulate the observed responses in these two habitats are also discussed. Terrestrial forests share similarities with both kelp forests and coral reefs. All three habitats provide food and shelter for tens of thousands of species globally. However, their responses to anthropogenic CO_2 emissions are predicted to vary greatly. Terrestrial forests could benefit from elevated CO_2 (Norby et al. 2005), whereas organism responses to elevated CO_2 in kelp forests will be mixed, and organism responses within coral reefs to elevated CO_2 are expected to be largely negative.

2 Summary of the Effects of Ocean Acidification

2.1 Effects of Ocean Acidification on Seaweed "Kelp Forests"

Here we discuss the effects of ocean acidification on shallow water (>15 m) cool temperate habitats with rocky substrate dominated by seaweed. These regions are characterized by seawater that does not generally range outside 5–22 °C. Ocean acidification will affect many resident species within kelp forests. It is not the goal of this chapter to be an exhaustive review, as there are already many adequate reviews concerning the effects of ocean acidification on key kelp forest biota (e.g., Wittmann and Pörtner 2013; Brodie et al. 2014). Most calcifying organisms will be negatively affected by ocean acidification, particularly coralline algae, mollusks, and echinoderms, whose calcification rates and development may be inhibited (Kroeker et al. 2013; Wittmann and Pörtner 2013). Fishes and crustaceans could also be impacted, though to a lesser extent, mostly by changes in behavior for the former and declines in calcification for the latter (Kroeker et al. 2013; Wittmann and Pörtner 2013). Impacts on keystone species within these groups, such as on lobster or predatory fishes, could have disproportionately large ecological effects resulting in changes in food web dynamics, as numbers of current prey species increase or decrease (Cornwall and Eddy 2015; Gaylord et al. 2015). However, arguably the most important species within kelp forests (at least in those that lack strong top-down control) are the seaweed themselves (Steneck et al. 2002).

The effects of ocean acidification on kelp, kelp equivalents (such as fucoids) (Fig. 1), or on understorey seaweed could directly influence the composition, size, and function of the habitat itself. Within these kelp forest habitats, seaweeds form the base of the food web (Mann 1988) and provide three-dimensional habitat to potentially thousands of resident species (Steneck et al. 2002; Bennett et al. 2015). The wide range in their possible responses to ocean acidification (Hepburn et al. 2011; Koch et al. 2013) means that it is difficult to predict the response of seaweed assemblages to ocean acidification. Calcareous seaweed, particularly those that are obligate calcifiers (e.g., coralline algae; Borowitzka 1987), will generally respond negatively to ocean acidification, as demonstrated mostly through reductions in their calcification rates and abundance (Comeau et al. 2013b; Cornwall et al. 2013a, 2014; Kroeker et al. 2013; Johnson et al. 2014; Fabricius et al. 2015); few species might not be affected (Martin et al. 2009; Comeau et al. 2014a). Increased CO_2 concentrations could benefit noncalcareous (hereafter "fleshy") seaweed, but unlike terrestrial plants, the effects of elevated CO_2 on the photosystem of seaweed are less certain. There have been a range of studies examining the direct effects of ocean acidification on fleshy seaweed; however, most studies focus on single-species responses, and though some studies find positive (Gao et al. 1991; Connell and Russell 2010; Bender et al. 2014b), neutral (Bender et al. 2014b; Brown et al. 2014; Fernández et al. 2015; Gordillo et al. 2015) and negative (Bender et al. 2014a; Gutow et al. 2014; Britton et al. 2016) responses to ocean acidification, there are no clear trends in responses.

The clearest trends are that some opportunistic turf assemblages respond positively to the effects of ocean acidification – more mechanistic understanding of these responses are now required (Connell et al. 2013). It is possible that these turf assemblages are comprised of species that are DIC limited, probably due to either the relatively thicker diffusion boundary layer around turf assemblages than around less densely packed macroalgal assemblages that would limit CO_2 flux to the turf (Raven 1991; Hurd et al. 2011; Cornwall et al. 2013b), or due to possessing CO_2 concentrating mechanisms (CCMs; that allow active uptake of HCO_3^-) that are not sufficient to support maximum rates of growth under ambient CO_2 concentrations (Raven 1991; Raven and Beardall 2014).

It has been proposed that seaweed without CCMs and those with less efficient CCMs could respond positively to elevated CO_2 concentrations (Kübler et al. 1999; Hepburn et al. 2011; Cornwall et al. 2015), similar to changes observed in aquatic ecosystems (Raven 1991; Maberly et al. 2014). Although this would explain some of the positive responses to ocean acidification (Young and Gobler 2016), this hypothesis has not yet been adequately tested. Therefore, the direct effects of ocean acidification on fleshy seaweed could be expected to range between positive and neutral depending on their physiology (Hepburn et al. 2011) – the role of the CCM and its interplay with the environment will be expanded on in sections below.

Ocean acidification will not only affect habitat-forming kelp species directly through changes in carbonate chemistry but also indirectly through its potential to alter species interactions (Cornwall and Eddy 2015; Gaylord et al. 2015). Three important interactions between habitat-forming kelp species will be with their competitors, facilitators, and species at higher trophic levels (i.e., herbivorous species and their predators). No research to date has empirically examined how complex trophic interactions within kelp forest communities will change due to ocean acidification, though it is logical to expect that top-down interactions could be altered. This will depend both on the current relationship between kelp and organisms at higher trophic levels and the identity of the organisms in the upper trophic levels and their expected responses to ocean acidification. For example, in ecosystems where keystone species are directly impacted by ocean acidification (such as lobsters), changes in food web dynamics could be large (Cornwall and Eddy 2015). Similarly, in ecosystems without the presence of keystone predators, but with large numbers of calcareous herbivores that have strong effects on ecosystem structure (such as barrens forming sea urchins), indirect effects of ocean acidification on kelp could also be large (Ghedini et al. 2015).

Phase shifts between kelp forests and other impoverished ecosystem states could also occur due to changes in competitive interactions between foundation species (Connell et al. 2013). One of the most important foundation species in temperate kelp forests (and in other ecosystems, including coral reef animal forests) are coralline algae (Nelson 2009). Coralline algal calcification rates will likely decline due to ocean acidification (Cornwall et al. 2013a, 2014), which could enable fleshy understorey species that are currently DIC limited to proliferate in areas with canopy gaps that coralline algae once inhabited (Raven 1991; Russell et al. 2009; Hepburn et al. 2011; Connell et al. 2013; Cornwall et al. 2015). A myriad of other indirect effects between kelp and resident species are also possible, such as changes in mutualistic or parasitic calcareous epiphytic species that either enhance or reduce the supply of nutrients or DIC to kelp (Hepburn et al. 2006). Therefore, unlike terrestrial forests, the impacts of elevated CO_2 concentrations will be mixed in kelp forests, and though some benefits are probable, CO_2 will not universally "fertilize" kelp forests with additional CO_2. In coral reef "animal forests" that are abundant in shallow warm water regions, the effects of elevated CO_2 will likely be even more negative.

2.2 Effects of Ocean Acidification on Coral Reef "Animal Forests"

Corals are ecosystem engineers, capable of constructing the largest coastal structures made of calcium carbonate; this process will likely become more challenging in the future more neutral ocean (Silverman et al. 2009). Ultimately, ocean acidification could lead to a drastic reduction of coral reefs cover as shown by the contraction or disappearing of reefs during geological intervals of high $p\mathrm{CO}_2$ (Veron 2008; Pelejero et al. 2010). Thus, the effects of ocean acidification on coral reefs have received a large amount of attention from the scientific community. Ocean acidification will affect coral reefs both by directly decreasing the capacity of calcifiers (mainly corals and coralline algae) (Fig. 1) to precipitate new calcium carbonate and by increasing the dissolution rates of calcium carbonate structures and sediment already present on the reef (Andersson and Gledhill 2013). Initially, predictions for the future of coral reefs were bleak, with studies showing strong decreases in net calcification and increased bleaching and mortality for coral and coralline algae under ocean acidification (Anthony et al. 2008; Jokiel et al. 2008; Silverman et al. 2009). Recently, however, it has been demonstrated that the effects of ocean acidification will be subtler, with some species being resistant to decreasing pH (e.g., *Pocillopora damicornis* and massive *Porites* spp.), exhibiting only a slight decrease or no change in either net calcification rates or abundances (Fabricius et al. 2011; Comeau et al. 2014a). Aside from calcification, the impact of ocean acidification on other physiological parameters appears to be limited. A meta-analysis, performed on studies published before 2011, showed that coral calcification decreased on average by 32% when ambient $p\mathrm{CO}_2$ doubled (Kroeker et al. 2013). Given the more nuanced results published in the last 4 years, this number might be overestimated.

Predicting the effects of ocean acidification on corals is complicated by the fact that the dinoflagellate symbiont hosted in scleractinian coral tissues (*Symbiodinium*) can react differently than their host to a shift in carbonate chemistry. The coral host generally suffers reduced calcification rates with ocean acidification (see the following section for mechanisms) (Jokiel 2011; Comeau et al. 2013b, Hoey et al. 2016). Conversely for the symbiont, the increase in CO_2 available in seawater could also increase photosynthesis (also see Sect. 2 and following sections). An increase in photosynthetic rates of *Symbiodinium* could mean more energy available for corals to offset any energetic costs associated with calcification under ocean acidification, which could explain why some corals appear to be resistant to decreasing pH. However, while such a hypothesis is appealing, most research has shown no increase in photosynthetic rates of corals incubated in elevated $p\text{CO}_2$ conditions (Anthony et al. 2008; Kroeker et al. 2013, Takahashi and Kurihara 2013).

Tropical coralline algae could also be potentially impacted by ocean acidification to a greater degree than corals. These organisms are key for coral reef functioning as they act as a cement for dead calcium carbonate structure and favor coral larval settlement (Nelson 2009; Doropoulos et al. 2012; Doropoulos and Diaz-Pulido 2013). In some reefs they replace corals as the main contributors to reef growth and substrate (Solihuddin et al. 2016). Ocean acidification can have a broad range of effects on tropical coralline algae, ranging from no effect to a 50% decrease in calcification when incubated in elevated $p\text{CO}_2$ conditions (Anthony et al. 2008; Diaz-Pulido et al. 2012; Comeau et al. 2013b). There are many possible reasons for this variability in responses of coralline algae to ocean acidification; these will be discussed in their own sections below.

Ocean acidification is expected to increase the dissolution rates of the existing and newly formed structures, rather than just the living reef organisms themselves. Ocean acidification causes an increase in sediment dissolution (Andersson and Gledhill 2013), an increase in bioerosion, and an increase in reef pavement dissolution (Comeau et al. 2016b). The rates of dissolution of sediment and pavement are tightly linked to other parameters such as the structure composition (e.g., aragonite vs calcite) or the availability of organic matter necessary to enhanced bacterial activity in the sediment (Andersson 2015). This is of concern because increasing dissolution and bioerosion could lead to a weakening of entire reefs that would lead among other issues to a reduction of the complexity of the three-dimensional structures that provide habitats for thousands of species (Fabricius et al. 2014). In this regard, calcareous "animal forests" (including coral reefs) are likely unique, as they are one of the only habitats where increasing $p\text{CO}_2$ will affect the structure already formed; as a comparison, on land this would correspond to an increase in decomposition and a decrease of available substrate with increasing atmospheric $p\text{CO}_2$.

Future reefs will be transformed into states unlike those we currently observe as a result of species-specific decreases in net calcification rates and increases in reef dissolution. Indirect effects of ocean acidification are likely to be important within coral reef animal forests (Fabricius et al. 2014; Gaylord et al. 2015) and make projections of future reefs highly challenging (Edmunds et al. 2016). Species-specific sensitivities to ocean acidification could lead to a shift in competitive interactions among coral species. Ocean acidification was shown, for example, to modulate the spatial competition between scleractinians by affecting linear extensions of corals in competition (Evensen et al. 2015), which could be caused, among other reasons, by modifications of the carbonate chemistry within coral aggregates (Evensen and Edmunds 2016). In addition to affecting adults, increasing $p\text{CO}_2$ has the potential to modify reefs by reducing coral fecundity (Albright and Langdon 2011; Albright and Mason 2013) and recruitment (Doropoulos et al. 2012), which would ultimately affect the long-term trajectories of coral populations (Mumby and

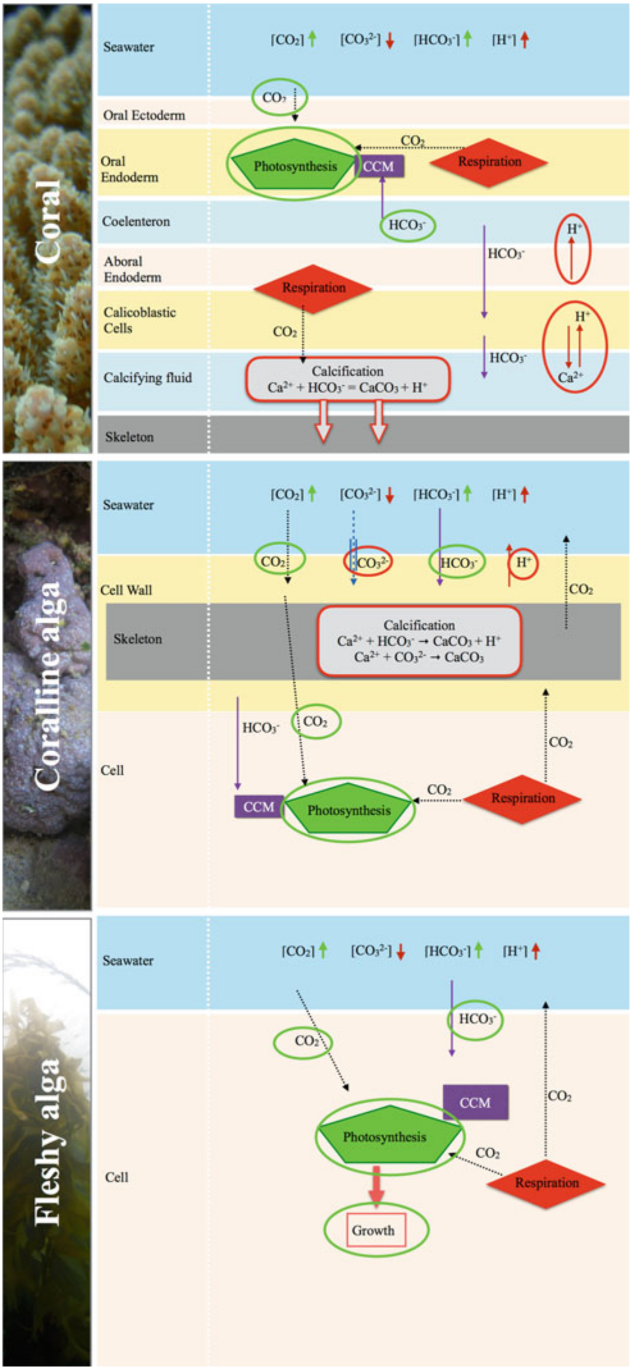

Fig. 2 (continued)

van Woesik 2014; Edmunds et al. 2016). Ocean acidification has been proposed to favor a shift in the balance between macroalgae and coral competition toward macroalgal-dominated reefs (Hoegh-Guldberg et al. 2007; Diaz-Pulido et al. 2012). Competitive interactions between corals and macroalgae will be influenced by the potential fertilization effect of pCO_2 for coral reef seaweed (see previous section on kelp forests, relevant also here for coral reef seaweed and section below regarding seaweed with CCMs) and by local effects such as overfishing of herbivorous that favors macroalgae expansion (Hughes et al. 2007). The increased dissolution and fragility of the reef will likely lead to reefs with reduced three-dimensional and slower growth reducing their roles as habitat providers and protectors against coastal erosion.

3 Effects of Ocean Acidification on Photosynthesis and Calcification

Increasing absorption of anthropogenically derived CO_2 will result in increased [DIC], increased [H^+], and changes in the speciation of DIC (increased dissolved [CO_2], slight increase in [HCO_3^-], and decrease in [CO_3^{2-}]). Changes in all of these components can have physiological impacts on the species within animal and kelp forests. The two metabolic processes that could be impacted the most by changing carbonate chemistry for benthic habitat formers in coral reef "animal forests" and kelp forests are photosynthetic use of DIC (usually via a CCM) and calcification (Fig. 2). Below we discuss both processes in the context of ocean acidification.

Fig. 2 Simplified conceptual model of the effect of ocean acidification on calcification and photosynthesis mechanisms in coral, coralline algae, and fleshy seaweed. The first row represents a schematic view of a cross section of coral tissue, the second row a cross section of a coralline algal cell, and the third row a cross section of a fleshy seaweed cell. The processes that will be potentially enhanced by ocean acidification are circled in green while the processes that will be negatively affected by ocean acidification are circled in red. In seawater, under ocean acidification, the concentration of dissolved CO_2 [CO_2], bicarbonate ions [HCO_3-], and protons [H^+] will increase, in contrast the concentration of carbonate ions [CO_3^{2-}] will decrease. For corals, increasing [HCO_3-] and [CO_2] might favour photosynthesis and the transfer of HCO_3- (purple arrows) to the site of calcification. In contrast, the increase of protons in seawater could render the export of proton with the Ca^{2+}/H^+ pump (red arrows) more difficult, which would limit the capacity of corals to maintain elevated pH in the calcifying fluid. For coralline algae, the increase in [CO_2] and [HCO_3-] could favour photosynthesis, while the decrease in [CO_3^{2-}] (potentially transported with seawater in the cell wall, blue arrow) and [H^+] will likely impact calcification; note that HCO_3- is also actively transported across the cell. For fleshy algae, increasing [CO_2] could favour increased photosynthesis and growth for some species

3.1 DIC Uptake via CCMs

The effects of ocean acidification on the CCM activity of photosynthetic organisms within coral reefs and kelp forests are relatively unknown. Ocean acidification could benefit photosynthetic organisms, but these benefits will likely be tied in with the CCM activity of the organism. Rather than all being limited by CO_2 concentrations, many marine autotrophs have effective CCMs that allow them to actively concentrate CO_2 at the site of Rubisco by actively transporting HCO_3^- (and possibly CO_2) across the plasmalemma and possibly through other internal membranes (Giordano et al. 2005; Hepburn et al. 2011). CCMs are more energetically costly than CO_2 uptake via diffusion alone however (Raven et al. 2014). The photosynthetic species most likely to directly benefit from elevated CO_2 are (1) DIC-limited species without CCMs or with inefficient/inactive CCMs and (2) species whose CCM activity decreases due to elevated $[CO_2]$ (Fig. 2). There is a chance that ocean acidification could exert other physiological changes in the photosystem of marine organisms (e.g., lowering nutrient costs of utilizing DIC, changing the internal pH, etc.; see Raven 1991 for an excellent review), though we view the two scenarios above as being the most likely.

For species in group 1, ocean acidification could alleviate any species which are currently DIC limited to a certain extent. This would occur for both organisms that do not possess CCMs or whose CCM activity is currently low, and would be more likely in low light habitats both where CCM activity is lower and where species lacking CCMs are more abundant (Hepburn et al. 2011; Cornwall et al. 2015). Any species who is DIC limited could have higher growth rates under elevated CO_2 conditions, though it is currently unknown whether species without CCMs are actually limited by CO_2 and light in situ (Kübler and Dudgeon 2015). For smaller rhodophyte (red) algae, any increase in productivity may relate to minor changes in species distributions as competitive ability increases (Hepburn et al. 2011; Kübler and Dudgeon 2015). However, for larger chlorophyte (green) algae without CCMs that can create more extensive and taller canopies, increases in their production and/or competitive ability could have disproportionately larger effects on ecosystem function and food web dynamics in some locations (Cornwall et al. 2015). The ecological effects of benefits to species in group 1 may manifest by the movement of these species from regions that are currently marginal for their survival into either regions of higher light where CCM species currently dominate or movement into either deeper habitats where light is limited (Kübler and Dudgeon 2015). The replacement of algae the replacement of algae with CCMs with those without CCMs under higher $[CO_2]$ occurs in freshwater ecosystems (Maberly et al. 2014), so it is also possible in marine ecosystems (Hepburn et al. 2011).

For species in group 2, energetic savings from lower CCM activity (i.e., downregulation) could result in increased growth rates or competitive ability. The total energy saved by downregulation due to elevated seawater $[CO_2]$ has not been calculated for either coral or seaweed species, but this has been calculated for diatoms as representing a 3–6% saving in total energetic budget (Hopkinson et al. 2011). It is unknown for fleshy macroalgae how much energy would be saved due to CCM downregulation (Raven et al. 2011, 2014) and how this would manifest if savings were to occur. Changes in macroalgal growth rates due to CCM downregulation would be difficult to detect using conventional experimental approaches. For example, power analysis reveals that 60 experimental units would be required to guarantee a 6% increase in growth rates is detected statistically given the variability associated with many species of macroalgae. Calcifying photosynthetic organisms such as coral and coralline algae could also receive some benefits from ocean acidification, though these would be weighed against offsets from declines in net calcification and would be even more difficult to detect in traditional laboratory experiments.

The effects of increasing CO_2 on DIC uptake are not straightforward for corals because of the interaction between the host and the symbiont. *Symbiodinium* possess a form II Rubisco with low affinity to CO_2, which necessitates the presence of a CCM (Whitney et al. 1995). DIC for photosynthesis mostly comes from seawater (~80%, Furla et al. 2000), while the rest is directly provided by the respiratory CO_2 from the host. S*ymbiodinium* are maintained in the host tissues between membranes where the pH is decreased relative to seawater (Laurent et al. 2014), which further facilitates the conversion of HCO_3^- into CO_2. Therefore, it is less likely that *Symbiodinium* are as strongly DIC limited as kelp forest seaweed; this is confirmed by the general lack of enhancement of photosynthesis with increasing pCO_2 measured in corals (Kroeker et al. 2013). Also, this provision of respiratory CO_2 from the host would also mean the benefits of CCM downregulation could be lower. Any potential benefits from CCM downregulation or DIC alleviation are not likely to fully offset declines in net calcification rates for coral.

3.2 Calcification

The response of calcification to ocean acidification has received considerable attention in the literature, but there are still many uncertainties regarding the mechanisms involved in the precipitation of calcium carbonate. Among other questions, the sources of carbon used for calcification, the composition of the calcifying fluid (CF), and the role played by the organic matrix are still under debate, and answering to these questions is critical to correctly assess the effect of modifications of the carbonate chemistry in both corals and coralline algae. Three main hypotheses have been put forward to explain reductions in calcification due to ocean acidification for both coral and corallines: (1) increased dissolution purely due to chemical effects of lower saturation sate/higher proton concentrations at the organism surface or internally, (2) increased energy expenditure due to impacts on either internal gradients in pH or on influx/efflux of DIC/protons, (3) increased substrate limitation due to reduced saturation state internally or combinations of the above (Erez et al. 2011; Jokiel 2011; McCulloch et al. 2012b; e.g., Comeau et al. 2013a; Cornwall et al. 2014).

3.2.1 Calcification in Corals

For coral, the combined effects of processes 1–3 could all be responsible for declines in net calcification. Increased dissolution under ocean acidification has been reported in several coral taxa (Erez et al. 2011), but whether dissolution is occurring internally or in exposed skeleton is unknown. Even at pH 7.2 there are no signs of dissolution on the skeleton covered by tissues for at least one species of coral (*Stylophora pistillata*) (Tambutté et al. 2015), meaning that forces acting on gross calcification likely explain at least part of the decline in net calcification of coral under ocean acidification.

Modification of the carbonate chemistry at the site of calcification, within the calcifying fluid, could explain some of the responses of coral calcification to ocean acidification. As an example of the effects of seawater chemistry changes on the calcifying fluid, when external seawater pH declines, pH at the site of calcification also decreases, though this decrease is species specific and offsets from the seawater pH decrease (McCulloch et al. 2012a, b). Understanding of the composition of the calcifying fluid has grown rapidly during the last years with the use of various tools such as pH-sensitive dye (Venn et al. 2013), microprobes (Cai et al. 2016), and stable isotopes (McCulloch et al. 2012a). Results obtained with these various techniques have shown an active control by the corals of the composition of the calcifying fluid where calcium carbonate is precipitated (McCulloch et al. 2012b; Venn et al. 2013). It is now well established that shallow water scleractinian corals mostly maintain pH at their site of calcification at levels (generally pH = 8.4–8.9) well above the seawater pH (McCulloch et al. 2012a). Corals have been shown to be able to maintain elevated pH in the calcifying fluid, though pH decreased slightly, when maintained in experimentally acidified seawater mimicking the conditions expected by the end of the century (McCulloch et al. 2012b; Venn et al. 2013). Maintaining such elevated pH at the site of calcification requires the export of protons (H^+) from the calcifying fluid (through an H^+/Ca^{2+} pump) and the import of dissolved inorganic carbon to the calcifying fluid (Allison et al. 2014; Cai et al. 2016). By this mechanism corals are able to create a chemical environment that favors the precipitation of calcium carbonate, with an estimated aragonite saturation state of ~15 in the calcifying fluid (McCulloch et al. 2012b; Cai et al. 2016). In addition to modified internal chemistry, organic matrices catalyze the precipitation of calcium carbonate; these are comprised of lipids, sugars, and proteins (for a review, see Tambutté et al. 2007) that have been shown to favor precipitation of calcium carbonate even at ambient and acidified pH (Mass et al. 2013).

Overall, calcification in corals is an active process that requires about ~13–30% of the total energy expenditure of corals (Allemand et al. 2011). Under ocean acidification it has been hypothesized that calcification will become more energetically costly because it will be potentially more challenging to maintain elevated pH in the calcifying fluid and the calcifying cells (Erez et al. 2011). For example, the export of proton with the Ca^{2+}/H^+ pump will be done under an increasingly negative gradient as seawater pH decreases, rending this process potentially more costly (Jokiel 2011; Fig. 2). However, it is important to note that any increased energy expenditure for calcification under ocean acidification has not been shown empirically for corals

(Edmunds 2011; Schoepf et al. 2013). This could be due to either a lack of compensation from corals (i.e., calcification decreases to compensate the increasing cost for calcification), the technical difficulties associated with detecting small changes in energy allocation, or the relatively small theoretical change in energy expenditure for some species (i.e., <1% of total energy) (McCulloch et al. 2012a).

3.2.2 Calcification in Coralline Algae

Many of the same physiological pathways and mechanisms that involve changes in coral calcification in responses to ocean acidification are also somewhat relevant to coralline algae. The main difference is the fact that coralline algae precipitate calcium carbonate primarily within the cell wall (also mediated by an organic matrix), within the protected cell membrane, and secondarily in the interfilament region between cells (Borowitzka 1987; Fig. 2). The second main difference is that coralline algae obviously contain their own photosynthetic apparatus without symbionts. This has led to some speculation that the dissolved inorganic carbon pools could be jointly split within them between calcification and photosynthesis/respiration more so than in coral (Borowitzka 1987). Circumstantial evidence has shown that dissolved inorganic carbon derived both from seawater and respiration could be used during calcification depending on the degree of photosynthetic activity of the organism/region (Lee and Carpenter 2001) and that regions within coralline algae are highly separated, as these effects can be very local. This has led to support that metabolic alteration of pH through photosynthesis could support calcification, either through altering pH at the surface of the organism (Borowitzka 1981; Cornwall et al. 2014) or at the DIC pool location internally (Comeau et al. 2013a; Fig. 2). Regardless, coralline algae also undergo rapid dissolution and re-precipitation processes at night and during the day, respectively (Bradassi et al. 2013), and enhanced dissolution at night could exacerbate effects of ocean acidification more on coralline algae than corals. A greater effect of dissolution on coralline algae has also been predicted due to their higher Mg content, which makes their calcite more prone to dissolution than coral aragonitic skeleton (Ries 2011). As a result, some corallines precipitate calcium carbonate with less Mg incorporated under ocean acidification (Cornwall et al. 2013a; Roleda et al. 2015).

4 Mediating Role of the Environment: Temperature, Water Motion, Nutrients, pH Variability, and Light

4.1 Temperature and Ocean Acidification

Kelp forests and coral reef animal forests are markedly different environments, with vastly different environmental regimes; the biggest difference is the separation of temperature regimes in these habitats. The effects of global warming on coral reef animal forests reef and kelp forests are expected to be severe and could lead to both the disappearance of some corals due to repeated bleaching events and reductions in kelp forest habitat in the future (Hoegh-Guldberg 1999; Johnson et al. 2011; Wernberg et al. 2011, 2013). While temperature will have a large effect on marine organisms, the following discussion will focus only on studies looking at the combined effects of ocean acidification and temperature. The fact that coral reefs lie in low latitudes, and kelp forests in high, means that the interacting effects of temperature with ocean acidification could vary between the two ecosystems.

One theory is that ocean acidification could act to narrow many calcifying species' thermal optima (Pörtner and Farrell 2008). So rather than acting as additive stressors, the consequences of interacting stressors could be complex with synergistic effects likely common (Crain et al. 2008; Harvey et al. 2013). In the coral reefs living close to their thermal maximum, the effects of temperature are likely to be most extreme, particularly for coral species, where only the most thermal tolerant species will be able to survive in shallower waters. Movement to higher latitude regions or deeper waters may be possible for some species. However, generally less favorable environmental conditions for calcification (lower saturation states, lower light) are found in higher latitudes and deeper regions, which might reduce the competitive advantage of these species. Furthermore, adding the stress of reduced net calcification rates and/or increased energetic demands on species as a result of ocean acidification could mean much reduced cover and reproductive success of coral in these regions in the future. In temperate environments, the movement of kelp/fucoid species is not possible in many locations in the southern hemisphere (Johnson et al. 2011); therefore, the impacts here would also be great, resulting in the extinction of species or great reductions in their ranges. In the northern hemisphere, movement of kelp and fucoids to higher latitudes is possible (Brodie et al. 2014), but changes in species ranges will still have large impacts on ecosystem function within kelp forests.

The alternative view to ocean acidification acting to narrow organisms' thermal optima is that it will have subtle or limited effects on organisms; under this premise only a given physiological parameter such as net calcification rate is impacted, and effects would be largely additive with increased temperature. As a result, negative effects will still be greatest, for example, on reef organisms living close to their thermal maxima, but more in terms of reduced net calcification rates of resident organisms that are capable of persisting under elevated temperatures.

There is currently an urgent need to acquire more data on the combined effects of decreasing pH and increasing temperature on marine organisms in order to assess the probability of these two scenarios. So far, there are no conclusive patterns for coral and coralline algae, with either synergistic effects or no interaction of warming and ocean acidification observed (Anthony et al. 2008; Diaz-Pulido et al. 2012; Comeau et al. 2016a). For fleshy macroalgae, effects are as uncertain. When temperature and acidification have been combined, there has been a gamut of responses, ranging from negative antagonistic to positive synergistic responses (Connell and Russell 2010; Vaz-Pinto et al. 2013; Bender et al. 2014b). This lends support to the fact that responses to both warming and temperature will likely be species specific and difficult to predict. Future research should focus on constructing frameworks by which we can predict generalized responses to the interaction between both global stressors.

4.2 Nutrients and Ocean Acidification

Coral reefs are largely oligotrophic, in contrast to kelp forests which have highly variable nutrient concentrations (Kleypas et al. 1999; Hepburn et al. 2007); within any region where nutrients limit calcification, additional limits to calcification or increases in dissolution/energetic demand will have disproportionately adverse effects. Corals rely both on autotrophy and heterotrophy (zooplankton, bacteria, organic matter) to thrive in oligotrophic tropical waters. Heterotrophy can represent between 15% and 35% of the metabolic requirements of corals, with this proportion increasing during bleaching events up to 100% (Houlbreque and Ferrier-Pagès 2009). Heterotrophy is the main pathway for corals to acquire essential nutrients such as nitrogen and phosphorus, which are used by both the host and the *Symbiodinium*. The effects of increasing food supply or dissolved nutrient on the response of corals to ocean acidification are poorly understood (Edmunds 2011; Comeau et al. 2013c). Few studies looking at the effect of enrichment in nutrient or feeding have led to contradictory outcomes, with enrichment in nutrients or feeding either alleviating or not affecting the response of calcification to ocean acidification (Holcomb et al. 2010; Comeau et al. 2013c). However, for tropical and temperate coralline algae, the interaction between nutrient concentrations and response to ocean acidification has not been explored, with minimal interactive effects being observed in one study (Russell et al. 2009). It is possible that during periods of low nutrient concentration (such as in summer at the height of seaweed productivity) temperate coralline algae also would be expected to respond in a similar way to ocean acidification as tropical coral species.

4.3 Light and Ocean Acidification

Light is one of the most variable environmental factors within both habitats, and it has the capacity to heavily modulate the effects of ocean acidification on both calcification and CCM operation (Hepburn et al. 2011; Suggett et al. 2013). As detailed in the CCM section above, light levels often dictate the activity of the CCM; when light is low, CCM activity is lower, and in habitats with lower mean light, the prevalence of organisms with active CCMs declines (Hepburn et al. 2011; Cornwall et al. 2015). So any beneficial effects of ocean acidification on photosynthetic organisms would be expected to be higher under lower light levels, as the operation of the CCM will be more restricted (Raven 1991). Light also has a strong effect on calcification rates, potentially via several mechanisms. Firstly, increased energetic supply could aid in alleviating negative effects of ocean acidification that increase the energy needed for calcification, such as through increased pumping of protons outward or bicarbonate inward. Secondly, increased light would equate to higher flux of $CO_2/(HCO_3^- + H^+)$ into the organisms during the day via photosynthesis. This would equate to higher pH levels at the surface of the organisms, which could further alleviate any negative impacts of ocean acidification on the calcification of individuals under high light (Cornwall et al. 2014). Though simplified, the combined effects of light on CCM activity and calcification would mean that in high-light habitats the effects of ocean acidification would be lower than under low light; under low light benefits from increased CO_2 alleviation of photosynthesis and CCM downregulation would be larger, and negative impacts from declines in net calcification would be higher. The few studies looking at the crossed effect of light and ocean acidification on adult corals partially confirm this theory, with either stronger effects of $p\mathrm{CO}_2$ on corals incubated at low light (Suggett et al. 2013; Vogel et al. 2015) or no interacting effects (Comeau et al. 2013c). Therefore, the possible effects of ocean acidification could vary greatly across habitats (at macro- and microscales) with varying light levels within both coral reefs and in kelp forests.

4.4 Water Motion and Ocean Acidification

The interactive effects of water motion and ocean acidification could be vastly different between coral reef animal forests and kelp forests. In coral reefs, limitation on calcification through limited nutrient delivery during periods of low water velocity (i.e., mass transfer limitation) is common (Bilger and Atkinson 1992). Mass transfer limitation is expected to not be as important in more nutrient-rich temperate kelp forests (Hurd 2000). In nutrient-poor coral reefs, increased water motion could provide three hypothetical benefits: (1) increased provision of DIC/CO_2 for photosynthesis and calcification, (2) increased nutrient uptake, and (3) removal of protons created by calcification in corals (Jokiel 2011; Comeau et al. 2014c). Experimentally, reduced calcification rates under high CO_2 and low flow have been shown for coral communities comprised of corals, coralline algae, and sediment (Comeau et al. 2014c). For temperate coralline algae, it is probable (based on $\delta^{13}C$ evidence) that they possess an active CCM (Cornwall et al. 2015); therefore, elevated CO_2 uptake via increased water motion could have comparably less benefits than for coral. Additionally, increased provision of nutrients would have comparably limited benefits in many regions/at most times due to relatively higher nutrient concentrations in kelp forests compared to coral reef animal forests. Lastly, the role of proton export in coralline calcification has not been fully explored to date, but it is still possible that elevated water motion could provide benefits, particularly at night when respiration drives pH within the diffusion boundary layer lower than pH in the surrounding seawater (Cornwall et al. 2014). In contrast, temperate coralline algae could also receive some buffering from ocean acidification under slower flows, if not nutrient limited during the day; this is largely because photosynthesis increases pH as DIC is taken from seawater (Fig. 3; Cornwall et al. 2014). This too has been shown experimentally

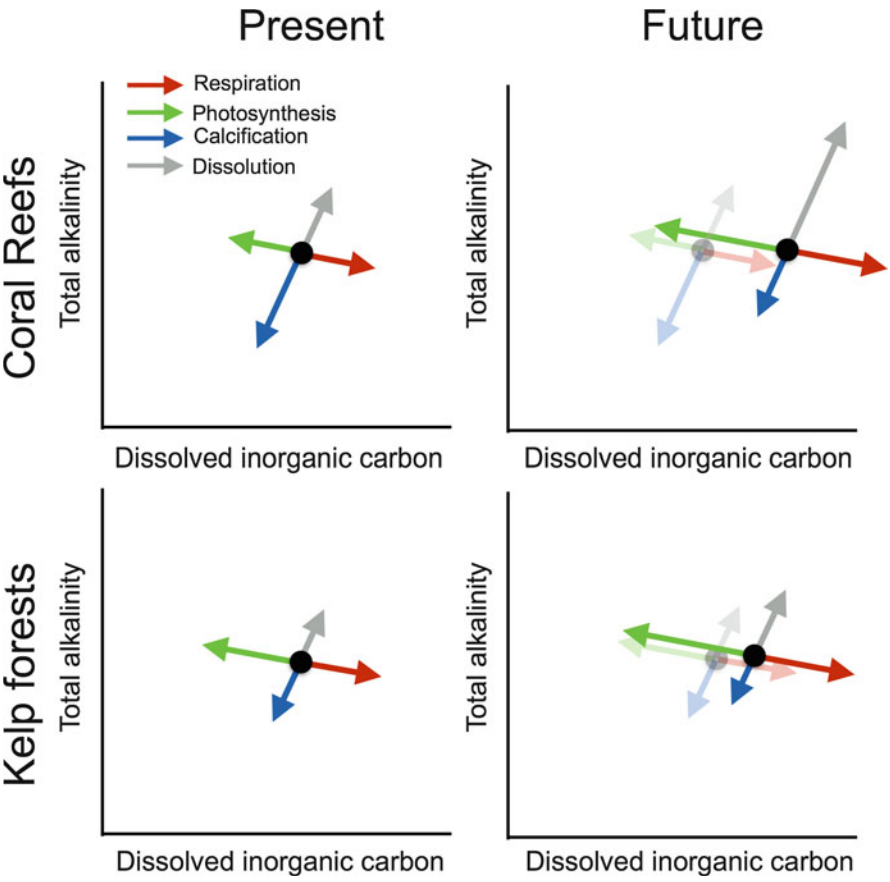

Fig. 3 Present and future metabolic forces acting on total alkalinity [TA] and total dissolved inorganic carbon [DIC]. Photosynthesis and respiration mostly affect [DIC], while calcification and dissolution mostly affect [TA]. Note, pH would lie on the diagonal here, where both photosynthesis and dissolution increase pH, and respiration and calcification decrease pH. The left column represents the conceptual metabolic forces acting on the carbonate chemistry in the present coral reefs (first row) and kelp forests (second row), and the right column the conceptual metabolic forces acting on the carbonate chemistry in the future. Under ocean acidification, [DIC] will increase while [TA] will remain constant. In future coral reefs (top-right panel), photosynthesis is expected to increase (i.e., reefs dominated by macro-algae), calcification is expected to decrease, and dissolution is expected to increase (due to ocean acidification). In kelp forest, photosynthesis is expected to increase due to the increasing availability of dissolved CO_2, and, due to ocean acidification, calcification of coralline algae will likely decrease, and bioerosion and dissolution will increase

(Cornwall et al. 2014). Tropical coral reef corallines, on the other hand, may experience both positive and negative effects of increased water motion under ocean acidification, with higher flow favoring nutrient uptake and limiting the positive effect of higher pH in the boundary layer.

4.5 pH Variability and Ocean Acidification

The degree of pH variability in habitats could influence responses of those habitats to ocean acidification. Metabolic variability in pH recorded in kelp forests is usually greater than that in coral reefs (Boyd et al. 2016). This could be because of greater retention of seawater and a large ratio of photosynthetic organisms to calcifying organisms within kelp forests. In contrast to calcification-dominated coral reefs, pH changes are limited because during the day photosynthesis drives the pH up and the DIC down, while calcification drives the pH and the total alkalinity down (Fig. 3). The region-specific impact of biological activities on the carbonate chemistry will likely be modified under ocean acidification because of modifications in species abundances (i.e., reefs dominated by macroalgae) and individual responses to increasing $p\mathrm{CO}_2$ (increasing photosynthetic rate) (Fig. 3). In both ecosystems, regions with higher pH variability could provide two benefits for resident organisms: (1) under ocean acidification, higher pH during the day could allow them windows of time where pH conditions are elevated compared to locations with more stable pH; (2) organisms currently exposed to greater variability in pH could be more plastic in their responses to ocean acidification (Comeau et al. 2014d), where populations in variable pH environments could contain more organisms with the potential to cope with declining pH (similar to levels at or higher than what they already encounter at night). However, both hypotheses have evidence for and against (Boyd et al. 2016); therefore, it is difficult to explicitly state whether more variable pH environments will be more resistant to the effects of ocean acidification than less variable ones. More research on this topic is clearly required.

5 Conclusions and Future Directions

The effects of increasing CO_2 concentrations will be vastly different in marine environments compared to terrestrial forests. In terrestrial forests, benefits may outweigh negative impacts. In the oceans, the response of different ecosystems will vary greatly as a function of the dominant organisms. Coral reef animal forests will likely be one of the ecosystems to be most negatively impacted by ocean acidification, either directly (decreasing calcification and increasing dissolution) or through increased competition with fleshy macroalgae which can change ecosystem stability and function (Diaz-Pulido et al. 2016). While kelp forests may be better off than coral reefs, ecologically crucial coralline algae will likely have much reduced abundances due to ocean acidification; this will have dire consequences for the myriad of species which rely on them as habitat and settlement substrates.

Environmental variables will be key in dictating responses of both ecosystems to ocean acidification. In regions with higher nutrient concentrations, effects of ocean acidification are expected to be less severe than when nutrient concentrations are low. Additionally, nutrient concentrations will interact with water motion, where under low flow and low nutrient concentrations the effects of ocean acidification will be exacerbated relative to when flow or nutrient concentrations are higher. Light will also act in a similar way, under combined high light and slow flow; given no nutrient limitation the effects of ocean acidification will likely be reduced, where metabolic alteration of pH in higher light could alleviate the effects of ocean acidification to some degree. A simplified summary of how the effects of multiple environmental variables discussed in the previous sections would manifest would be that deeper and more wave-exposed habitats in temperate kelp forests would be expected to be more impacted than wave-sheltered, shallow habitats. Conversely, in coral reef animal forests, the most impacted locations would be expected to be slow flow regions of low light in more oligotrophic areas. These are generalizations though, as micro-gradients in light and water motion will result in different impacts on individuals within close geographic proximity. More research is required that targets interactions between large numbers of key environmental variables and ocean acidification in logical frameworks. Additionally, species-specific responses and the presence and absence of other key mediating species (such as seaweed in coral reefs) will be key to determine the future of those critical ecosystems.

6 Cross-References

- ▶ Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes
- ▶ Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean
- ▶ Living in the Canopy of the Animal Forest: Physical and Biogeochemical Aspects
- ▶ Where Seaweed Forests Meet Animal Forests: The Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem

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Octocoral Diseases in a Changing Ocean

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Ernesto Weil, Caroline S. Rogers, and Aldo Croquer

Abstract

Octocorals (Cnidaria, Octocorallia) constitute a geographically widely distributed and common group of marine invertebrates commonly referred to as "soft-corals," "sea fans," "horny corals," "sea feathers," and "sea plumes." They are found from shallow coastal habitats to mesophotic and abyssal depths. Octocorals are important members of most Atlantic-Caribbean, Indo-Pacific, and Mediterranean coastal and mesophotic reef communities; however, information about their susceptibility to diseases, predation, and competition, and their relationship with changing environmental conditions is limited. At least 19 diseases have been observed in at least 42 common octocoral species throughout their range. Twelve of these have been reported in the wider-Caribbean (CA), one in Brazil (BR), two in the Mediterranean (ME), one in the Eastern Pacific (EP), and three in the western Pacific (WP). Pathogenic and/or environmental causes have been identified for eight diseases, including viruses, terrestrial fungi, protozoans, bacteria and cyanobacteria, filamentous algae, parasitic copepods, and high temperature. Only a few of the suspected

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pathogens have been tested with Koch's postulates. At least eight disease outbreaks have led to extensive octocoral mortalities in the CA, ME, BR, and EP with detrimental ecological consequences. The fungal disease Aspergillosis has produced the highest mortalities in the CA and the EP. Other fungi, protozoans, and the bacterium *Vibrio coralliilyticus* were identified as potential causes of the death of millions of colonies in two Mediterranean disease outbreaks. Bacterial and fungal agents seemed to be responsible for the mass mortalities in Brazil and the WP. Most outbreaks in all regions were linked to high thermal anomalies associated with climate change, which seems to be the major driver. Other biological stressors such as predation and/or competition produce injuries that may contribute to the spread of infections and mortality. Overfishing of common predators could lead to population explosions of octocoral-feeding species that produced mass mortalities in some Caribbean localities. Our lack of knowledge of causes and pathogenesis of octocoral diseases parallels that of hard corals. New diseases are being described almost every year concomitant with increasing seawater temperatures. The ecological and economic consequences could be significant, with drastic changes in the seascape of shallow coral reefs and other coastal marine habitats and reduction of their ecological services. Given our limited knowledge, our best options for recovery of octocorals and coral reefs in general include sound management of coastal fisheries, development and tourism; reduction of land- and sea-based pollution; and abating effects of climate change.

Keywords

Diseases • Biological stressors • Gorgonian octocorals • Soft octocorals • Mass mortalities • Prevalence • Caribbean • Mediterranean • Indo-Pacific • Climate change • Thermal anomalies

Contents

1 Introduction

Over the last few decades, disease outbreaks have affected an expanding range of marine organisms worldwide. Environmental changes associated with climate warming have been proposed as major drivers explaining the rising rates of emergence, incidence, prevalence, and virulence of new marine diseases, with drastic consequences to marine biota and human economies. Thermal anomalies are now more frequent, widespread, and intense, and many marine taxa, including foundation, keystone, and commercially important species, have been affected by disease outbreaks in tropical and temperate coastal environments (Harvell et al. 2004, 2007; Rosenberg and Loya 2004; Carpenter et al. 2008; Weil and Rogers 2011; Altizer et al. 2013; Lafferty et al. 2015; Lafferty and Hoffman 2016). The most recent examples include mass mortalities of colonies of diverse scleractinian species due to a new outbreak of white plague disease (WPD) off the southeastern coast of the USA (Precht et al. 2016), the mass mortalities of many species of sea stars along the northwest and northeast coasts of the USA (Fuess et al. 2015), and several other disease outbreaks affecting oysters, lobsters, crabs, and other important economic species (Burge et al. 2014; Groner et al. 2016).

Coral reefs have the highest biodiversity of all marine ecosystems and provide important ecological services to other marine communities and to humans. Coral reefs aid in the establishment and protection of productive seagrass beds and mangrove forests and provide habitat, refuge, and resources to millions of species, including commercially important species. Humans exploit these communities for food, building materials, active pharmacological compounds, tourism, and other commercial products. Reefs also provide protection to coastlines from storms, and areas for research, recreation, and education. Unfortunately, coral reefs are rapidly declining worldwide, mostly as a consequence of mass mortalities of many foundation species caused by disease outbreaks, frequent intensive bleaching events, increasing frequency and intensity of storms, and ocean acidification associated with global climate change (GCC), all of which are compounded by local/regional anthropogenic stressors such as pollution, coastal development and overfishing (Hoegh-Guldberg et al. 1997; Bruno et al. 2003; Harvell et al. 2004, 2009; Burge et al. 2014; Lafferty and Hoffman 2016). Major losses in live coral cover, coral abundances, and diversity have produced changes in coral reef composition, structure, and function (Hughes 1994; Hughes et al. 2004; Aronson and Precht 2001a; Gardner et al. 2003; Bruno et al. 2007; Ward and Lafferty 2004; Carpenter et al. 2008; Wilkinson and Souter 2008; Miller et al. 2009; Weil et al. 2009; Dubinsky and Stambler 2011; Jackson et al. 2014; Woodley et al. 2016 and references therein).

Most reports of coral reef decline are focused on scleractinian corals. Much less is known about the other important foundation groups in the community, such as the Octocorallia, one of the most abundant taxa in shallow and temperate coral reefs and coastal, mesophotic (40–120 m), and deep water (>1000 m) benthic communities (Figs. 1 and 2). According to the most recent classification (World Register of Marine Species, WoRMS), Octocorallia is a subclass of the Anthozoa in the Phylum

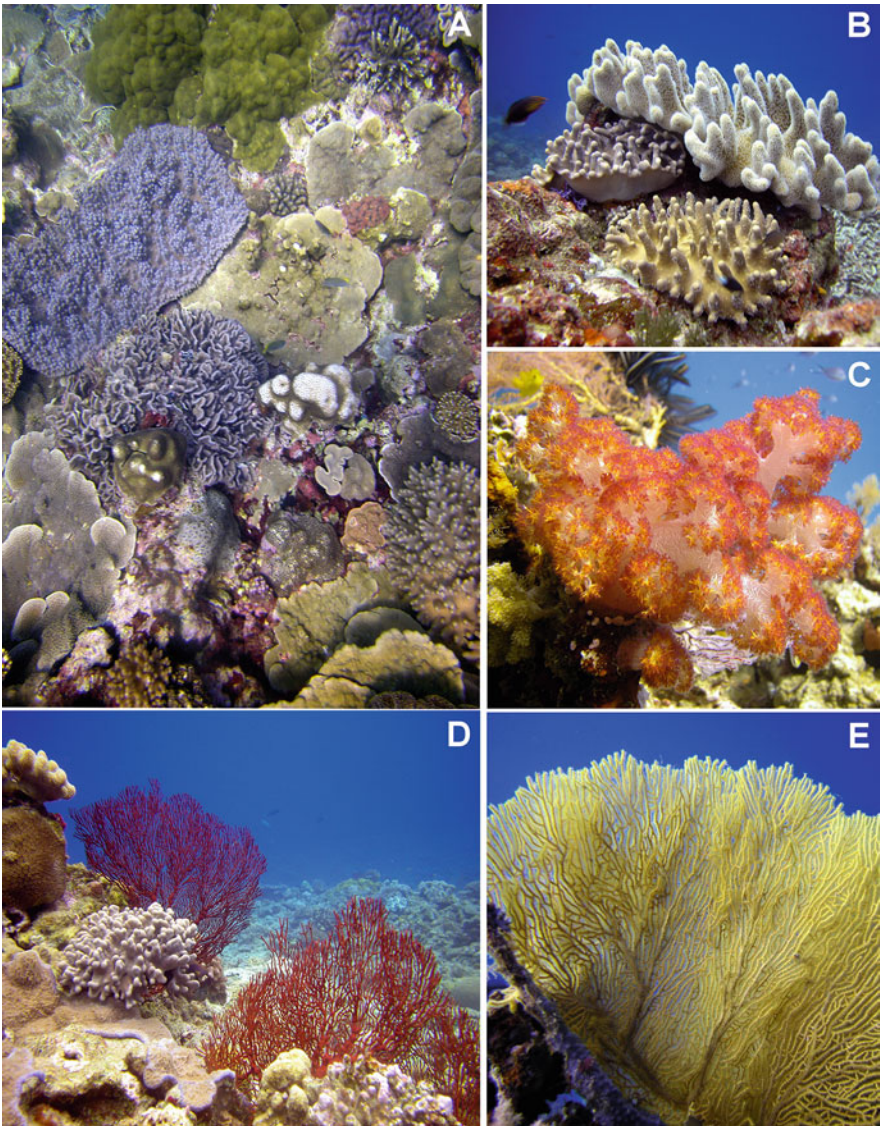

Fig. 1 Soft octocorals (**A**–**C**) and gorgonian octocorals (**D**–**E**) from the western Pacific. Typical view of a reef community with scleractinian corals and soft octocorals in Palau (**A**). Soft octocorals in Okinawa, Japan (**B**), and Palau (**C**). Two red gorgonians in a shallow reef at the Kerama Islands, Japan (**D**) and a golden gorgonian from Palau (**E**) (Photos EW)

Cnidaria. It comprises around 3,500 species worldwide of mostly modular (colonial) marine organisms, characterized by an eightfold body symmetry (eight mesenteries and eight tentacles, or replicates of eight, in each polyp, hence Octocorallia) invariant within the clade and therefore diagnostic. The order Alcyonacea includes

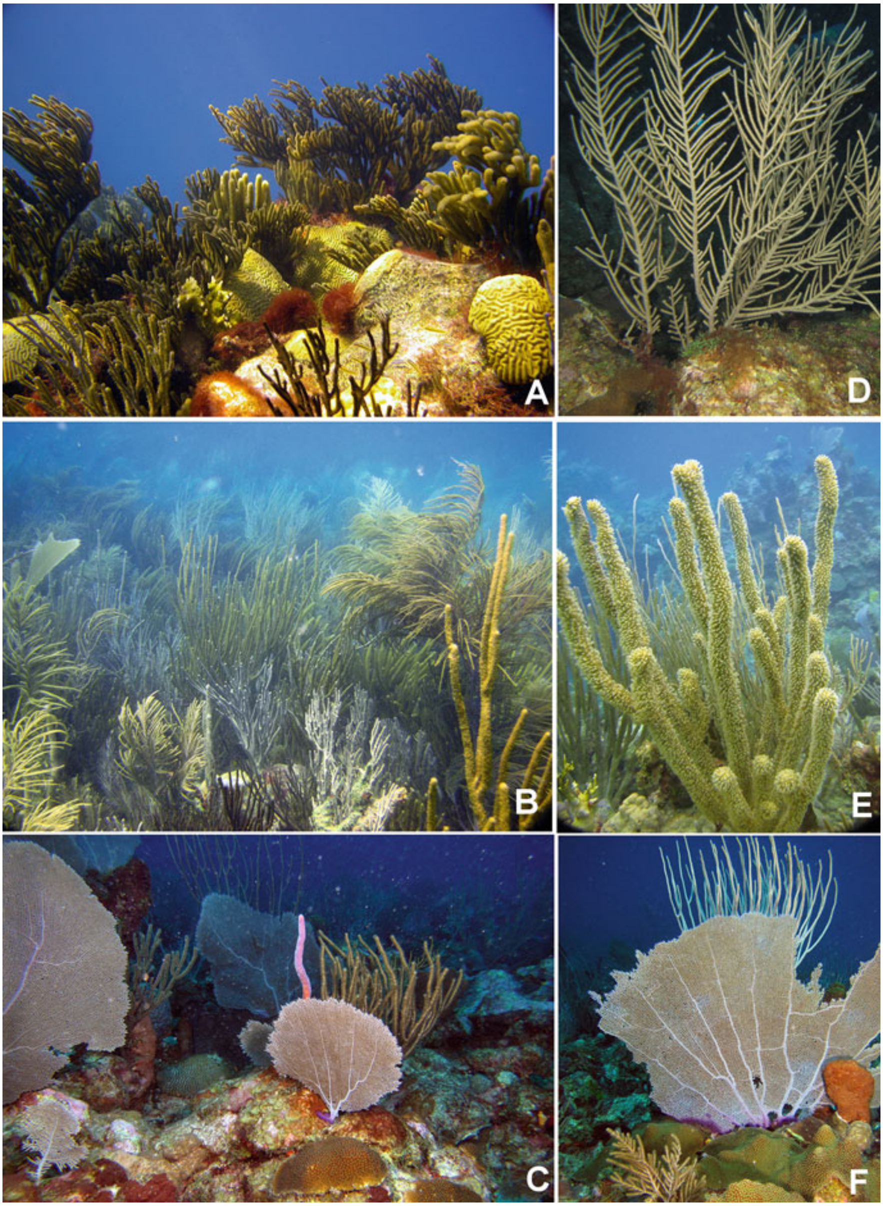

Fig. 2 Typical shallow and exposed Caribbean reef habitats dominated by gorgonian octocorals in Bermuda (**A**) and Puerto Rico (**B**). A deep (20 m) reef habitat with abundant gorgonians in Grenada (**C**). Examples of common gorgonian species in Caribbean reefs, the feather-like Pseudoterogorgia acerosa (**D**), the candelabra-like Plexaurella nutans (**E**) and the sea fan Gorgonia ventalina (**F**) (Photos EW)

30 families in two suborders, the Alcyoniina with around 1145 species without a supporting skeletal axis here referred to as “soft octocorals” that are more abundant in the Indo-Pacific, and the Holaxonia with 1561 mostly branching species with a supporting skeletal axis of scleroproteinous gorgonin and/or calcite spicules, here referred to as “gorgonian octocorals“. This group includes the sea fans, sea plumes, sea whips, horny corals, and branching octocorals, which are more abundant in the Atlantic-Caribbean, Eastern Pacific, and Mediterranean Sea (Bayer 1961; Daly et al. 2007). The Subclass Octocorallia has long been considered a monophyletic group based mostly on morphologic characteristics, a conclusion now supported by molecular analyses (Sánchez et al. 2003; Daly et al. 2007).

As with all other cnidarians, octocorals have a complex life history dominated by a sessile polyp phase and a motile, planktonic dispersal phase, the planula-larva, produced by sexual reproduction and generally short-lived (days to weeks). The larva sinks and attaches to the substratum, goes through a short metamorphosis resulting in the primary polyp which starts the long sessile, asexual growing phase. Geographically and ecologically, Alcyonacea constitute an important group found in all oceans, from shallow coastal to mesophotic and even abyssal habitats. In the Atlantic-Caribbean, the Eastern Pacific, Brazil, and the Mediterranean, gorgonian octocorals usually dominate exposed, shallow reef and coastal habitats with good water circulation where they form “forest-like,” three-dimensional complex habitats (Fig. 2) providing essential ecological services (protection, energy, nutrients, nursery habitats, etc.) to many other members of the community. Despite their importance, octocorals have received relatively little attention, mostly due to the greater research focus on hard corals (scleractinians) and their still confusing taxonomy, which is limiting our understanding of octocoral biology, ecology, evolution, and biogeography. Numerous alcyonacean species remain either unidentifiable or undescribed, and many families and genera require extensive taxonomic revision (Daly et al. 2007).

Octocorals produce biologically active compounds that help defend them against predators, competitors, fungi, microbes, and fouling organisms (Sammarco et al. 1987; Pawlik and Fenical 1989; Harvell and Fenical 1989; Kim et al. 2000a, b). For example, sea fans produce compounds that in high concentrations are effective bacterial and/or fungal inhibitors (Mydlarz et al. 2008). Some of these compounds, including hormones, have extensive pharmacological applications. Eight percent of the wet weight of the common Caribbean octocoral *Plexaura homomalla* is prostaglandins, a potential fish predation deterrent and an important regulatory hormone in mammals (Gerhart 1991). Populations of this octocoral were overexploited on many Central America reefs to extract the hormone for the pharmaceutical industry. In the Bahamas, the feather-like *Pseudoterogorgia elizabethae* have been harvested with few regulations since the late 1990s. The species produces pseudopterosins, compounds that exhibit anti-inflammatory and analgesic properties that are used by the cosmetic industry (Goffredo and Lasker 2008). *Telesto riisei,* a Hawaiian octocoral, produces punaglandins with anti-inflammatory and anti-tumor properties (Baker and Scheuer 1994). Furthermore, microorganisms living in association with octocorals are known to produce secondary metabolites with promising pharmacological applications (Wei et al. 2004). Octocorals are also susceptible to diseases and

Fig. 3 Map showing the approximate location of the major disease-induced mass mortalities of octocorals reported and other areas where high prevalences of diseased octocorals have been observed. *Red* = Caribbean and Bermuda; *Orange* = Brazil; *Green* = Mediterranean and south-west coast of England; *Pink* = Great Barrier Reef, Australia and the Okinawa area in Japan; *Yellow* = the eastern Pacific

environmental degradation (Weil et al. 2002; Rosenberg and Loya 2004; Raymundo et al. 2008; Kim and Rypien 2016), and several mass mortalities caused by disease outbreaks associated with thermal anomalies have been reported around the World (Fig. 3; Table 1).

Disease is here considered as *"any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxicants, and climate; infectious agents; inherent or congenital defects or combinations of these factors*" (Wobeser 2006; Rogers 2010). Diseases involve an interaction between a host, an agent (i.e., pathogen/parasite) and the environment (Burge et al. 2014). These three components must interact in a precise way for a disease to occur. The host is the organism affected by the disease (e.g., octocorals, corals, and humans), and the agent is the factor that directly or indirectly causes the physiological dysfunction. The environment is usually the driver that affects the physiological status (resistance and/or susceptibility) of the host and/or the agent (virulence), and facilitates the development of the disease (Wobeser 2006; Work et al. 2008). Not all Infectious agents are transmissible between hosts. Most diseases are infectious but not all are contagious. Transmission could happen through different mechanisms (contact, air, water, vectors, etc.). Noninfectious agents include diverse biotic agents, extreme environmental conditions, malnutrition, genetic mutations, etc.

Studying diseases in the marine environment is not an easy task. For example, survey and sampling logistics are difficult and costly, and identifying putative

Table 1 Chronology of octocoral disease epizootics and mass mortalities around the World, their geographic location, type of disease, agent, number of species affected, potential impact, and environmental correlates

Year	Locality	Disease	Agent	Species affected	Impact	Environmental Correlate	Source
1977–1981	Bonaire, Colombia	Growth Anomalies (GAN)	Endolithic algae *(Entocladia endozoica*) and other unidentified agents	*Gorgonia ventalina* and 9 other spp.	No tissue or colony mortalities	?	Morse et al. (1977); Goldberg and Makemson (1981); Botero (1990); Peters (1997)
1983–1984	Central America, Florida, Trinidad	Aspergillosis (ASP) ??	*Aspergillus* spp. ?	*Gorgonia flabellum*, *G. ventalina*	Thousands of dead colonies. Tissue loss. Loss of ecological services	High temperature	Guzman et al. (1984); Garzon-Ferreira and Zea (1992)
1983–1984 and 1992–1994	Florida	Red Band Disease (RBD)	*Oscillatoria* sp. and other bacteria	*Gorgonia ventalina*	Many diseased colonies. High levels of tissue and colony mortality	High temperature	Rutzler et al. (1984); Richardson (1998)
1996–2002	Florida, Bahamas, and 11 more Caribbean countries	Aspergillosis (ASP)	*Aspergillus sydowii*	*Gorgonia flabellum and G. ventalina*	Thousands of dead colonies. Tissue loss. Loss of ecological services	Possibly linked to high temperatures	Nagelkerken et al. (1997a, b); Smith et al. (1996); Geiser et al. (1998); Harvell and Kim (2004)

1998–1999	Florida, Bahamas	*Briareum* Bleaching Necrosis (BBN) and *Briareum* Wasting Syndrome (BWS)	High temperatures and other unidentified agents	*Briareum asbestinum*, *B. polyanthes*	Extensive tissue and colony mortalities (>68% of affected colonies)	High temperature	Harvell et al. (2001)
1998–1999	Great Barrier Reef – Australia	Bleaching and Tissue wasting syndrome	High temperatures and other unidentified agents	Many soft-coral species (*Sinularia* spp., *Lobophyton* spp. and *Sarcophyton* spp.)	Tissue and colony mortalities	High temperature	Strychar (2005); Willis et al. (2004)
1999–2004	Great Barrier Reef – Australia	Black Necrotic Syndrome (BNS)	Unknown pathogen (*Penicillium* fungus ?)	*Isis hippuris* and other octocoral spp.	Moderate loss of tissue and colony mortalities	High temperature	Morrison-Gardiner (2001); Willis et al. (2004)
1999	Ligurean Sea, Mediterranean	Fungal-protozoan syndrome (FWS)	*Trichoderma*, *Clodosporium* and *Penicillum* spp. plus protozoans	*Paramuricea clavata*, *Eunicella verrucosa* and many other octcoral and invertebrate spp.	Large numbers of dead colonies. Loss of productivity and ecological services	High temperature	Cerrano et al. (2000)
2001–2016	Wider Caribbean	Aspergillosis (ASP)	*Aspergillus sydowii,* other *Aspergillus* spp.?	*Gorgonia ventalina* and at least 9 other spp.	Large numbers of dead colonies. Loss of productivity and ecological services	Chronic epizootic – increasing prevalence associated with thermal anomalies	Kim and Harvell (2004)

(*continued*)

Table 1 (continued)

Year	Locality	Disease	Agent	Species affected	Impact	Environmental	Source
2003	Ligurean Sea, Mediterranean	Octocoral *Vibrio* Syndrome (OVS)	*Vibrio coralliilyticus*	*Eunicella singularis, Paramuricea clavata* and other spp.	Large numbers of dead colonies. Loss of productivity and ecological services	High temperature	Coma et al. (2006); Bally and Garrabou (2007)
2005	Lundi's Lane, south west England	Fungal-protozoanl syndrome (FWS)	Fungal-protozoan co-infection ? *Vibrio* sp. ?	*Eunicella verrucosa* and other spp.	High tissue and colony mortalities	High temperature	Hall-Spencer et al. (2007)
2005	Puerto Rico, Caymans, Grenada, Bermuda, Curacao	Bleaching, Aspergillosis, Red Band Disease and other diseases	High temperatures, *A. sydowii*, *Oscillatoria* spp. and other unidentified agents	23 octocoral spp. *Muricea* spp., *Briareum* spp., *Erythropodium* sp. and *Plexaurella* spp. were the most affected	Extensive tissue and colony mortalities in crustose species. >90% mortality in *Muricea* spp.	High temperature	Prada et al. (2010); McClanahan et al. (2009); Weil et al. (2009); Croquer and Weil (2009)
2005–2016	Puerto Rico, Curacao, Grenada, Caymans, Bermuda	Aspergillosis, Red Band Disease, *Briareum* Bleaching Necrosis (BBN) and *Briareum* Wasting Syndrome (BWS), *Erythropodium* Wasting Syndrome (EWS)	*Aspergillus sydowii*, *Oscillatoria* spp. and other unidentified agents	*Gorgonia ventalina*, *G. mariae*, *P. americana*, *P. porosa*, *Briareum asbestinum*, *B. polyanthes*, *E. caribaeorum*	Extensive tissue and colony mortalities (>68% of affected colonies)	High temperature	Harvell et al. (2001)

2005–2016	Puerto Rico, Curacao, Grenada, Caymans	*Erythropodium* Bleaching Necrosis (EBN) and *Erthropodiun* Wasting Syndrome (BWS)	High temperatures and other unidentified agents	*Erythropodium caribaeorum*	Extensive tissue and colony mortalities	High temperature	Weil et al. (2014); Weil unpublished data
2005–2016	Caribbean	Multi focal purple spots (MFPS) and Gorgonian Labyrinthulomycosis (LABY)	*A copepod Sphaerippe* sp. and protozoans	*Gorgonia ventalina*	Low tissue loss and no colony mortality	High temperature	Weil and Hooten (2008); Burge et al. (2012); Ivanenko et al. (2015)
2008–2010	Colombian Eastern Pacific	Aspergillosis (ASP)	*Aspergillus sydowi*i, other *Aspergillus* spp.?	*Pacifigorgia adamsi*, *P. rubicunda*, *P. eximia* and other spp.	High tissue and colony mortalities (70% colonies dead between 12 and 20 m)	High temperature	Sánchez et al. (2011; 2014); Barrero-Canosa et al. (2013)
2011–2016	Puerto Rico	Gorgonian Wasting Syndrome (GWS)	Unknown pathogen	*Gorgonia ventalina*	High tissue and colony mortalities (11% prevalence)	High temperature	Weil et al. (2014); Weil unpublished data
2013–2014	Brazil	*Phyllogorgia* Wasting Syndrome (PWS)	Unknown pathogen	*Phyllogorgia dilatata* and other spp.	High tissue and colony mortalities (48% of affected colonies)	High temperature and local pollution	Cassola et al. (2016)

pathogens is complicated. It is almost impossible to collect samples without contamination from the surrounding water and the microorganisms suspended in it. Most marine bacteria, including pathogens, are still unknown or are difficult or impossible to culture, making their identification, laboratory manipulation, and testing of Koch's postulates difficult (Work and Meteyer 2014). This process requires collecting diseased and nondiseased tissue samples and describing the lesion at the gross and cellular levels. Then, laboratory tools are used to culture, isolate, and identify suspected causative agents. These putative pathogens are then used to infect nondiseased hosts under controlled experimental conditions, and the response of the host is observed. If lesions similar to the original ones develop, they are sampled and the introduced microbe is cultured and reisolated. If it is the same one, then it can be classified as a causal agent for the disease (Raymundo et al. 2008).

Even if a putative pathogen is identified, knowing which environmental driver is responsible for its emergence is not straightforward (Randall and van Woesik 2015). Furthermore, octocorals are holobionts (communities), harboring high diversities and abundances of bacteria, *Symbiodinium* zooxanthellae, endolithic algae, fungi, viruses, and other mutualistic invertebrates interacting in complex ways (Knowlton and Rohwer 2003; Ritchie 2006). These intricate and complex relationships, the result of millions of years of coevolution, allow for their efficient biological and ecological function under particular ranges of environmental conditions and provide protection against foreign pathogens. Changes in one or several environmental conditions (i.e., high/low thermal anomalies) could disrupt this complex physiological equilibrium leading to changes in the resident microbial community composition and function, which could enhance virulence of particular agents and/or affect the immune mechanisms of the host, increasing susceptibility to new or old pathogens, or as in the case of bleaching, loss of *Symbiodinium* cells (Porter 2001; Rosenberg and Loya 2004; Harvell et al. 2007; Wooldridge and Done 2009). The identification of diseases affecting scleractinians, octocorals and other important community members has improved over the years, probably aided by the increasing number of researchers in the field and new microbiological technologies, which have improved our knowledge and understanding of the problem.

The compromised-host hypothesis (sensu Rosenberg and Ben-Haim 2002) suggests that rising ocean temperatures may increase the number and prevalence (proportion of diseased individuals in a population) of coral diseases by making octocorals (and other marine invertebrates) more susceptible to ubiquitous pathogens or by causing shifts in resident microbial communities making some of them pathogenic. Very little is known about the composition and dynamics of the natural microbial communities living in association with most marine organisms, including scleractinian corals and octocorals. This microbiota changes quickly (hours to days) when conditions/locations change (Rosenberg et al. 2007), even when moving colonies from the field into aquaria for controlled experiments (Ritchie 2006). A definitive disease pathogen or cause is therefore difficult to determine.

Few quantitative studies have attempted to relate the emergence (new diseases), prevalence (proportion of diseased individuals in the population at a given time), incidence (number of new infections in the population per unit time), and/or virulence (rates of tissue and/or individual mortality in the population) of coral reef diseases with deterioration/change in environmental quality (Wooldridge and Done 2009). Either large spatial and/or long temporal scales are required to produce reliable results and/or testable epizootic (epidemiological) models. Relatively long-term studies (many decades) are missing, but some shorter studies have shown significant correlations between the onset of disease outbreaks and increasing sea-water temperatures providing a clearer understanding of the role of sea water temperatures associated with climate change as a potential driver in the dynamics, host resistance, and epidemiology of diseases in shallow marine environments (Bruno et al. 2003, 2007; Weil and Rogers 2011; Altizer et al. 2013; Maynard et al. 2015; Lafferty and Hoffman 2016; Woodley et al. 2016, and references therein).

Ideally, consistent observations and field data over time are needed to properly characterize and name a disease condition, to differentiate it from other diseases, and to reduce the confusion produced by proliferation of names and terminology (Rogers 2010; Weil and Rogers 2011). Careful microbiological and histopathological research and testing of Koch's postulates as well as field and molecular approaches are needed to characterize pathologies, transmissibility patterns, reservoirs, and vectors (Work and Meteyer 2014). Long-term field data on disease prevalence, incidence and virulence, their local and regional variability, as well as host susceptibilities and environmental correlates are needed to characterize and model epizootic events. Long-term studies are also essential to evaluate ecological impacts of particular diseases in different marine ecosystems, model their dynamics, and develop well-conceived management programs.

Octocorals constitute an important foundation group in tropical and subtropical coastal communities that provide services to humans, and they are susceptible to many diseases and environmental degradation. It is important to improve our knowledge and understanding of their biology, ecology, and disease dynamics (etiology, pathologies, etc.) and impact (Weil et al. 2002; Weil and Rogers 2011; Kim and Rypien 2016). In this chapter we provide a comprehensive and synthetic review of the major diseases affecting octocorals worldwide. After the brief historical perspective, we present the information available about the disease agents, etiology, octocoral species affected, environmental drivers and ecological impact in the Caribbean, the Eastern Pacific, the Mediterranean, and other geographic regions. The chapter concentrates on one of the three Octocorallia orders, the Alcyonacea, which is the most widely distributed, most diverse, and most abundant in shallow tropical and subtropical habitats and the most affected by diseases in coral reefs and other tropical and temperate shallow water coastal communities. The chapter ends with a brief discussion of management priorities and options in a changing ocean and some recommendations.

2 Historical Perspective

Diseases affecting coral reef organisms have likely been around for millions of years and may have produced significant population mortalities with changes in community structure and function (community shifts) in the past. The fossil record does not provide evidence of infections, but rapid changes in community composition (disappearance of populations/species in particular areas), not clearly linked to a major environmental driver, might have been produced by epizootic events. The current emergence of new diseases affecting major Caribbean coral reef taxa (scleractinians, octocorals, sponges, etc.) appears to be unprecedented in the recent geological record (Aronson et al. 1998), but past warming events probably induced similar bleaching responses and/or disease outbreaks. Limited paleontological evidence suggests that the white band disease (WBD) outbreak in the early 1980s, one of the most extensive and ecologically important disease-induced mass mortalities ever recorded, was unparalleled on a timescale of at least three millennia (Aronson and Precht 2001a, b). This outbreak almost eliminated the acroporid scleractinians throughout their geographic range. Comprehensive historical reviews of scleractinian diseases and important recommendations can be found in Peters (1997, 2015), Richardson (1998), Porter (2001), Rosenberg and Loya (2004), Weil et al. (2006), Raymundo et al. (2008), Work et al. (2008), Rogers (2010), Weil and Rogers (2011) and Woodley et al. (2016).

The first recorded abnormal anthozoan condition was bleaching (BLE) (the loss of coloration due to the loss of *Symbiodinium* symbionts) in scleractinian corals. A few undetailed reports date back to 1876 (see Oliver et al. 2009), but the earliest confirmed record of reef-wide bleaching due to thermal stress was in the Great Barrier Reef in 1929 (Yonge and Nicholls 1931). Then, growth anomalies (GAN = tumor-like structures) were observed in octocorals and scleractinians in the early 1960s and 1970s in the Caribbean (Morse et al. 1977). Histological work suggested that endolithic algae might cause some of the tumors (Peters 1997). The first infectious disease producing extensive and rapid tissue loss in anthozoans was black band disease (BBD) affecting scleractinians in Belize, Bermuda, and Florida in the early 1970s (Antonious 1973; 1981; Garrett and Ducklow 1975).

Later, three disease outbreaks impacted a range of common scleractinians in a few localities around the wider Caribbean between 1975 and 1980 (Weil 2004). The situation worsened in the early 1980s when three more concurrent and geographically widespread disease outbreaks affected foundation and keystone species in coral reefs across the Caribbean. The white band disease (WBD) outbreak spread quickly throughout the region in 3 years killing up to 95% of the acroporids, the most abundant and dominant genus in shallow water environments (Aronson and Precht 2001b; Randall and van Woesik 2015). Then an unknown pathogen almost eliminated (up to 99% mortality in some localities) the black sea urchin *Diadema antillarum*, an important grazer controlling algal biomass and diversity, and likely affecting reef growth over their geographical distribution (Lessios et al. 1984, 1988). Finally, a widespread epizootic (presumably Aspergillosis) killed thousands of colonies of the sea fan *Gorgonia flabellum* between 1982 and 1983 in Central America and elsewhere in the Caribbean (Guzman and Cortes 1984; Garzon-Ferreira and Zea 1992). The pathogenic agents and/or environmental drivers of the acroporid, sea urchin, and sea fan disease outbreaks were never clearly determined, but all were associated with unusual increases in seawater temperatures during and after an intense El Niño event (1982–1983) that also produced localized bleaching but without any significant scleractinian mortalities across the region (McClanahan et al. 2009).

The disappearance of the large stands of acroporids and the keystone urchin *Diadema* had unprecedented ecological and economic consequences we are still seeing today. Essential fish habitat, biomass, and energy sources were lost, biodiversity declined, communities shifted from coral-dominated to algal-dominated, and coastal protection declined (Carpenter 1990; Hughes 1994; Jackson et al. 2014). Octocoral habitats provided refuge and energy to fish and invertebrates and reduced surge impacts in shallow communities. Disease effects were increased by local anthropogenic factors such as overfishing and environmental deterioration, affecting ecological services provided throughout the wider Caribbean (Aronson and Precht 2001b; Weil et al. 2003; Weil and Rogers 2011; Kim and Rypien 2016).

Throughout the 1980s and 1990s, many octocorals, scleractinians, and other important members of the community [i.e., hydrocorals, zoanthids, sponges, and crustose coralline algae (CCA)] succumbed to local outbreaks of single or multiple diseases, further indicating that this phenomenon was an expanding problem (Rosenberg and Loya 2004; Bruckner and Hill 2009). White band disease became a chronic problem, local white plague disease (WPD) outbreaks continued killing colonies of major reef building species in Florida and elsewhere around the Caribbean, and the unidentified disease affecting sea fans continued to expand in the region.

A new and fast-killing, reddish cyanobacterial-mat disease called red band disease (RBD), similar to BBD, was observed affecting mainly sea fans and a few scleractinians in the Florida Keys in the early-mid 1990s (Richardson 1998). A second, and more widespread, mass mortality of sea fans associated with signs similar to those of the die-off in the early 1980s was observed in 13 Caribbean countries in 1995–1996 (Nagelkerken et al. 1997a, b). The putative pathogen was finally identified as the terrestrial fungus *Aspergillus sydowii* and the disease was termed Aspergillosis (ASP) (Smith et al. 1996; Geiser et al. 1998). ASP produced extensive mortalities in the three sea fan species and in the other six common octocorals in the wider Caribbean (Smith and Weil 2004; Kim and Rypien 2016) (Table 2). In 1998, the strongest El Niño event ever recorded produced extensive bleaching and mortalities in scleractinians and other invertebrates across the Pacific. In the Caribbean, bleaching and associated tissue loss were observed in large numbers of colonies of three common octocorals, *Briaerum asbestinum, B. polyanthes*, and *Erythropodium caribaeorum* during 1998 and also during the 2005 and 2010 high thermal anomalies in the Florida Keys, Puerto Rico, Grenada, Curacao, and other Caribbean localities (Harvell et al. 2001; Weil and Hooten 2008; Weil et al. 2009; Prada et al. 2009; Weil unpublished data).

Two catastrophic octocoral mass mortalities occurred in the Ligurean Sea, in the northwestern Mediterranean during the summers of 1999 and 2003, respectively (Fig. 3, Table 1). Populations of species belonging to five phyla (Cnidaria, Bryozoa, Mollusca, Chordata, and Porifera) suffered extensive damage apparently produced by a fungal–protozoan coinfection in 1999 and a *Vibrio* bacterial infection in 2003. Both events were associated with high water temperatures (Cerrano et al. 2000; Coma et al. 2006; Bally and Garrabou 2007). Similar disease signs were reported for

Table 2 Octocoral species affected by different diseases in different geographic locations

Location-species	ASP	RBD	GAN	MFPS	LAB	BBD	GWS	BWS	BBN	EWS	FPS	VOS	BLE	BNS	ENS	PWS	OTH	TOT
Caribbean-Atlantic																		
Gorgonia ventalina	*	*	*	*	*	*	*						*				*	**9**
G. flabellum	*	*	*	*	*	*							*				*	**8**
G. mariae	*	*		*			*						*				*	**6**
Pseudoterogorgia americana	*		*			*											*	**4**
P. acerosa	*					*							*				*	**4**
P. keryii																	*	**1**
Pseudoterogorgia sp.	*		*										*				*	**4**
Plexaura flexuosa	*		*			*							*				*	**5**
P. homomalla			*			*							*				*	**4**
P. kuna	*		*														*	**3**
Pseudoplexaura porosa	*		*										*				*	**4**
Pseudoplexaura sp.			*										*					**2**
Plexaurella nutans	*	*					*						*				*	**4**
P. anceps			*															**1**
Plexaurella sp.	*												*				*	**3**
Briareum asbestinum								*	*				*				*	**4**
B. polyanthes								*	*				*				*	**4**
Erythropodium caribaeorum						*	*			*			*				*	**5**
Pterogorgia citrina													*				*	**2**
Muricea muricata													*				*	**2**

Muricea sp.													*				*	**2**
Eunicea laxispica													*				*	**2**
E. flexuosa													*				*	**2**
E. succinea													*				*	**2**
E. lascinata													*					**1**
Muriceopsis flavida													*					**1**
Phyllogorgia dilatata[1]																*		**1**
Eunicella verrucosa											*							**1**
Mediterranean																		
Corallium rubrum											*							**1**
Eunicella cavolinii											*				*			**1**
Eunicella singularis											*	*			*			**2**
Eunicella verrucosa											*	*			*			**2**
Leptogorgia sarmentosa[3]											*							**1**
Paramuricea clavata											*	*						**2**
Eastern Pacific																		
Pacifigorgia eximia	*																	**1**
P. rubicunda	*																	**1**
P. adamsi	*																	**1**
P. irene	*																	**1**
Western Pacific																		
Isis hippuris													*	*				**2**
Pacific Soft Corals																		
Lobophyton spp													*				*	**2**

(*continued*)

Table 2 (continued)

Location-species	ASP	RBD	GAN	MFPS	LAB	BBD	GWS	BWS	BBN	EWS	FPS	VOS	BLE	BNS	ENS	PWS	OTH	TOT
Sarcophyton spp.													*				*	**2**
Sinularia spp.													*				*	**2**
Total affected species	**15**	**4**	**10**	**3**	**2**	**7**	**4**	**2**	**2**	**1**	**7**	**3**	**28**	**1**	**3**	**1**	**23**	

ASP = aspergillosis; RBD = red band disease; GAN = growth anomalies; MFPS = Gorgonian multifocal purple spots; LAB = labyrinthulomycosis; BBD = black band disease; GWS = *Gorgonia* wasting syndrome; BWS = *Briareum* wasting syndrome; BBN = *Briareum*-bleaching necrosis; EWS = *Erythropodium* wasting syndrome; FPS = Fungal-protozoan syndrome; OVS = octocoral *Vibrio* syndrome; BLE = bleaching; BNS = black necrosis syndrome; ENS = *Eunicella* necrosis syndrome; PWS = *Phyllogorgia* wasting syndrome; OTH = other unidentified diseases; TOT = total diseases. Blue acronyms = pathogen identified the first time in northern latitudes where the condition affected populations of the cold water gorgonian *Eunicella verrucosa* (also present in the Mediterranean) at Lundy's Lane, a marine protected area in southwest England (Hall-Spencer et al. 2007). This species was one of the most affected during the 1999 outbreak in the Mediterranean (Cerrano et al. 2000).

The endemic octocoral fauna of the Colombian tropical Eastern Pacific (Fig. 3) was severely impacted by a disease-induced mass mortality event from 2008 to 2010 associated with a high thermal anomaly. Up to 70% of the colonies of at least three very abundant species (*Pacifigorgia adamsi*, *P. rubicunda*, and *P. eximia*) were killed between 12 and 20 m depth, with many others suffering partial mortalities. The pathogen was the fungus *A. sydowii* which was found in disease tissues collected in the area (Sánchez et al. 2011; Sánchez et al. 2014; Barrero-Canosa et al. 2013).

More recently, mass mortalities of the endemic Brazilian gorgonian octocoral *Phyllogorgia dilatata* were reported for the first time after community surveys in several subtropical locations off the southern coast of Brazil in 2013 and 2014, followed by reports of similar mortalities from other northern and oceanic locations (Cassola et al. 2016) (Fig. 3). The causative agent was not identified, but the multifocal lesions with purpling edges, the patterns of tissue loss, and other disease characteristics observed were similar to Caribbean ASP. Lack of microbiological and histopathological analyses prevents any conclusive statement of the agent, and no environmental or pollution correlates were identified.

The earliest report of a gorgonian disease in the Great Barrier Reef (GBR) indicated that 10% of the branching *Isis hippuris* colonies on Davies Island showed black necrotic areas associated with an apparent fungal infection that produced loss of both tissues and endoskeleton (Morrison-Gardiner 2001). Furthermore, results from the GBR disease surveys in 2003 indicated that up to 5% of soft octocorals at Lizard and Heron Islands showed signs similar to those in *I. hippuris* at Davies Island, with gorgonian octocorals being most affected on reefs around Lizard Island (Wei et al. 2004).

Octocorals seem to be one of the most disease-impacted cnidarian groups together with the scleractinians (Weil and Rogers 2011). By the early 2010s, more than 25 disease conditions affecting scleractinians, octocorals, sponges, CCA, and other important reef organisms had been described for the wider Caribbean (Sutherland et al. 2004; Rosenberg and Loya 2004; Raymundo et al. 2008; Weil and Rogers 2011), with new diseases being described and characterized almost every year. Up to 2016, at least 19 different disease conditions have been observed to affect high numbers of colonies of many common and widespread octocorals (around 42 species) across the Atlantic–Caribbean, Mediterranean, and the Pacific (Table 2). The sea fan *Gorgonia ventalina* is the best-studied octocoral in the context of disease ecology, etiology, and host immunity responses, mostly related to *Aspergillus sydowii* infections (see Kim and Harvell 2004; Kim et al. 2000a, b; Mydlarz et al. 2008; Burge et al. 2013; Kim and Rypien 2016).

3 Major Octocoral Diseases

3.1 Temperature-Induced Bleaching (BLE)

Most cnidarians living in shallow habitats harbor different strains of dinoflagellates called zooxanthellae. These symbionts are in the genus *Symbiodinium* and provide the host with protection from UV radiation, energy and other resources in exchange for protection, nutrients, and CO_2 from the host. The loss of the dinoflagellates, the reduction in pigment concentration, or a combination produces a discoloration known as bleaching.

Unlike in the Indo-Pacific, almost all Caribbean and Atlantic gorgonians harbor symbiotic zooxanthellae. In a typical southern Caribbean coral reef, only about 11% of octocoral species lacked symbionts (e.g., *Lophogorgia* spp. and *Leptogorgia* spp.) (Sánchez and Wirshing 2005). Few reports have documented bleaching in gorgonians (McClanahan et al. 2009; Prada et al. 2010), and Caribbean gorgonians seem to be more resistant to temperature-induced bleaching and less likely to expel their symbionts compared to other cnidarians such as scleractinians, hydrocorals, and sea anemones (Lasker 2003). Nevertheless, many colonies of different octocoral species have been observed to lose pigmentation (paling) and even bleach completely (turning white) during extreme thermal anomalies. Associated tissue mortality was observed mostly in *Briaerum asbestinum, B. polyanthes*, and *Erythropodium caribaeorum* during major bleaching events at several localities (Harvell et al. 2001; Weil and Hooten 2008; Weil et al. 2009; Weil unpublished data) (see below).

In many Caribbean locations, almost 90% (60 spp.) of the scleractinians, all five species (100%) of hydrocorals, a lower percentage of other cnidarians (four zoanthids, four actinarians), and a few sponges bleached during the high temperature anomalies of 2005 and 2010. Only between 20 and 30 species of gorgonian octocorals (±20% of 150 wider-Caribbean spp. reported) exhibited bleaching (Prada et al. 2010; McClanahan et al. 2009) (Table 2; Fig. 4). In La Parguera, Puerto Rico, for example, 24 species (68%) of the approximately 44 octocorals (Weil 2005) showed extensive bleaching in 2005–2006, with a mean bleaching prevalence of 18% ($n = 1823$ colonies surveyed) (Prada et al. 2010; Weil unpublished data). Overall, over 50% of the colonies were bleached, which is consistent with previous bleaching reports for octocorals under high thermal stress (Harvell et al. 2001). Average prevalence of bleached colonies ranged from 0% for *Pseudopterogorgia* and *Eunicea* to >90% for *Muricea*. Other genera exhibiting bleaching included *Gorgonia* (<5%), *Pseudoplexaura* (22%), *Muriceopsis* (37%), *Briareum* (46%), *Plexaurella* (70%), and *Pterogorgia* (85%) (Prada et al. 2010; Weil unpublished data) (Fig. 4C, D). Bleaching-associated mortality, however, was observed in *Briareum polyanthes*, *Erythropodium caribaeorum*, *B. asbestinum*, and *Muricea* spp. This last species complex suffered up to 90% mortality (Prada et al. 2010). These results suggest that the relatively high resistance to expulsion of their symbionts is overcome when thermal anomalies are extremely high, with several weeks of heat accumulation (degree heating weeks; Liu et al. 2003).

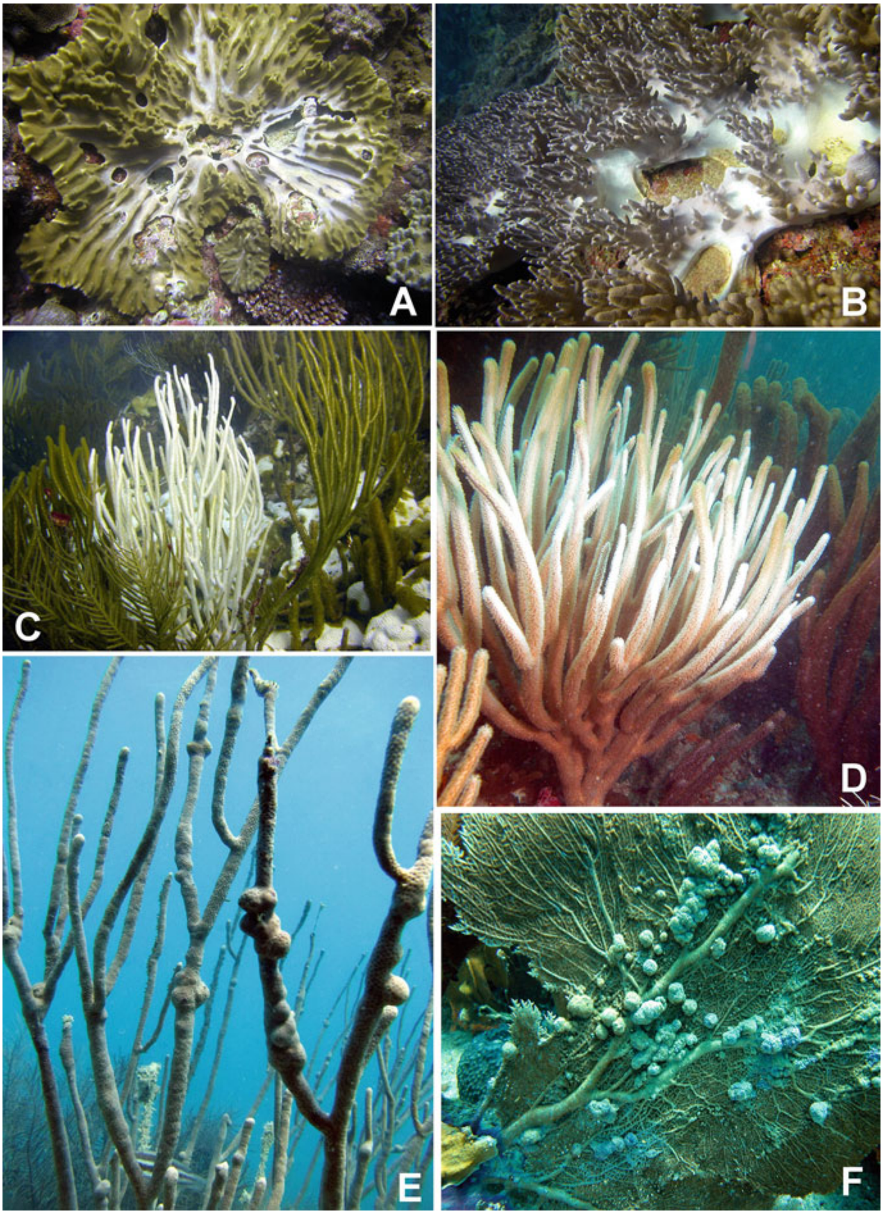

Fig. 4 Bleached colonies of soft octocorals in Okinawa, Japan, showing tissue necrosis and mortality (holes in the colonies) (**A**–**B**). Bleached colonies of the gorgonians *Pseudoplexaura porosa* (**C**) and *Plexaurella nutans* (**D**) during the 2005 bleaching/mortality event in Puerto Rico. Growth anomalies on *Pseudoplexaura porosa* and *G. ventalina* in Puerto Rico (**E**–**F**) (Photos EW)

Loss of *Symbiodinium* reduces availability of energy and other resources affecting essential physiological functions such as growth, feeding, reproduction, elimination of metabolic wastes, and immunity which could render octocorals more susceptible to diseases (Couch et al. 2008; McClanahan et al. 2009; Rypien 2016). Most disease outbreaks with significant mortalities have been associated with high thermal anomalies, which stress the organisms facilitating infection by fungi (*Aspergillus* spp.), protozoans, and pathogenic bacteria (Harvell et al. 2009; Burge et al. 2014). Although not well studied, Indo-Pacific soft octocorals seem to be susceptible to high water temperatures with bleaching reported during El Niño events (Strychar et al. 2005). During the mass-bleaching episode in 1998–1999 in the Great Barrier Reef, many colonies belonging to at least three abundant genera, *Sinularia, Lobophyton*, and *Sarcophyton,* bleached and then showed "tissue wasting"-like signs with extensive tissue mortality, colony constriction, and finally death (Willis et al. 2004) (Tables 1 and 2). More recently, during disease surveys conducted in Spring of 2011 at two reefs off Okinawa, Japan, several colonies of *Lobophyton* sp. were observed with extensive bleaching, signs of necrotic tissue, loss of structure, and partial mortality (Weil et al. 2012) (Fig. 4A–B).

Relative resistance or susceptibility to high temperatures and temperature-induced diseases could result in changes in octocoral community structure and composition, similar to what has happened with scleractinians. The increasing frequency of thermal anomalies and overall increase in average water temperature linked to climate change could potentially increase the frequency, intensity, and spatial extent of bleaching events and disease outbreaks and high colony mortalities resulting in shifts from scleractinian-dominated reefs to octocoral/algae-dominated reefs (if mortality is higher in scleractinians) in the near future (Ruzicka et al. 2013).

3.2 Aspergillosis (ASP)

The fungal disease ASP seems to have been responsible for the highest octocoral tissue and colony losses over time in the wider Caribbean and a few locations in the Eastern Pacific (Guzman and Cortes 1984; Smith et al. 1996; Kim and Rypien 2016; Sánchez et al. 2014) (Tables 1 and 2). Aspergillosis presumably affected thousands of sea fans on Caribbean reefs in Central America and other areas in the early 1980s and again, in 1995, when between 12% and 90% of colonies on reefs in 13 Caribbean countries were infected (Smith et al. 1996; Nagelkerken et al. 1997a, b). During this last outbreak, samples were collected from necrotic lesions surrounded by purple halos in the sea fan *G. ventalina* (Fig. 5A–D), the putative pathogen was identified as the terrestrial fungus *Aspergillus sydowii,* and the condition was described as aspergillosis (ASP). The isolated fungus was tested with Koch's postulates in controlled laboratory conditions and field reinfection tests (Geiser et al. 1998; Smith et al. 1996; and Weil 2004). More recently, a variety of other *Aspergillus* species have been shown to produce similar disease signs (Toledo-Hernandez et al. 2008). The octocoral coenenchyme tissue seems to be the main nutrient source for the fungi (Rivest et al. 2010). Therefore, ASP signs could be produced by a diverse

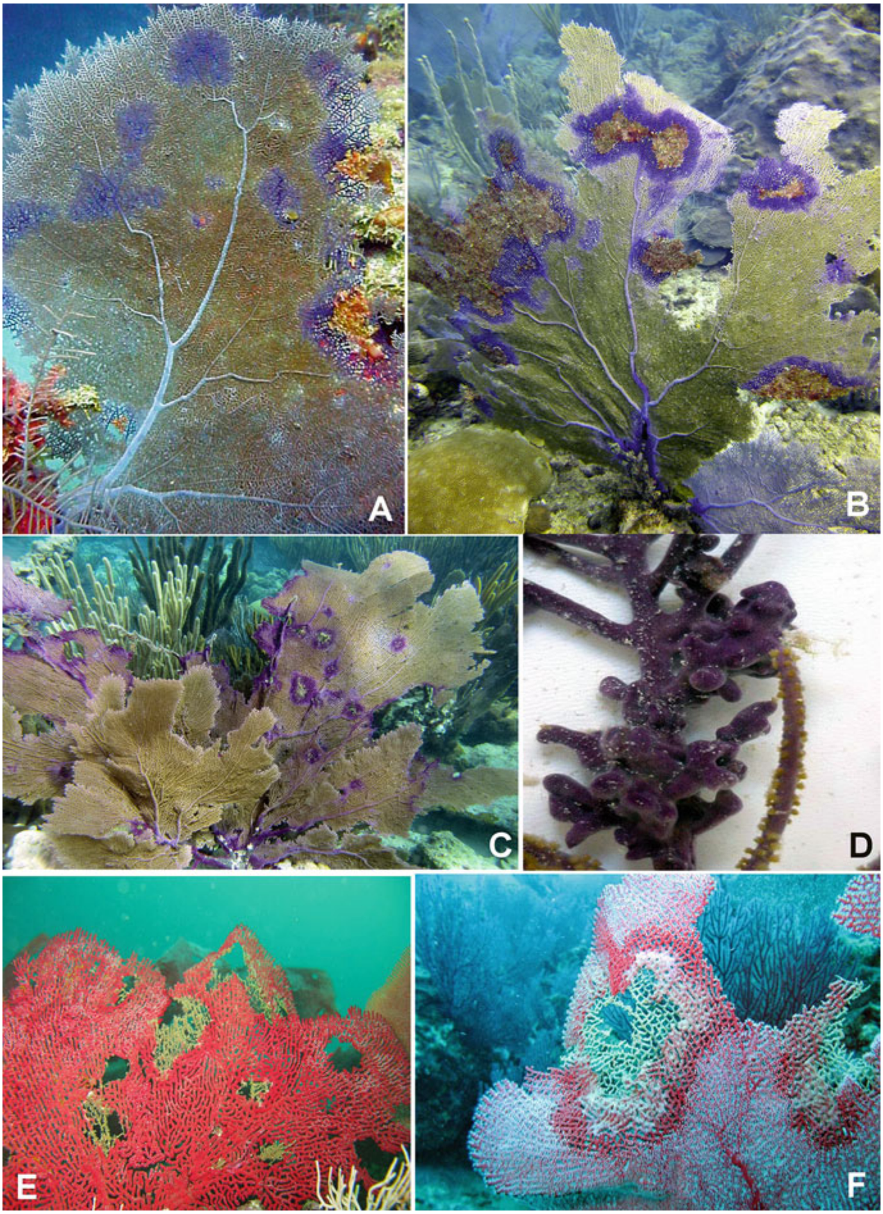

Fig. 5 Early stages and advanced lesions of Aspergillosis (ASP) showing tissue mortality at the edges of a colony (**A**) and the center fan area of *G. ventalina* with algae and cyanobacteria colonizing the denuded skeleton (**B**). Large sea fan colony with several ASP lesions (**C**). Purple galls encapsulating fungal hyphae in *Pseudoterogorgia americana* (**D**). Two species of Eastern Pacific gorgonian octocorals, *Pacifigorgia eximia* (E) and *P. rubicunda* (F) showing ASP signs during the disease outbreak in Choco and Gorgona Islands off the Colombian western coast (Photos **A**–**D** by EW and **E**–**F** by JA Sanchez)

group of *Aspergillus* taxa, and testing for the particular agent causing the disease is recommended when doing prevalence surveys.

Infection signs are characterized by initial degradation and recession of the coenenchyme (the outer rind tissue containing the living polyps of the octocoral), which then exposes the dark axial skeleton (central protein core) (see Kim and Rypien 2016). The exposed skeleton often becomes colonized by a variety of cyanobacteria, algae, sponges, hydrocorals, and other organisms, which can continue to kill the octocoral tissues. A change in color follows soon after the initial infection with a purpling of the adjacent tissues surrounding the injury and sometimes even before the coenenchyme retraction revealing the skeleton (Alker et al. 2004). Sea fans possess a range of disease resistance mechanisms which most likely act in concert and are modulated by environmental conditions (e.g., temperature, see below). The purpling around the injuries results from accumulation of sclerites and melanization as a barrier to the advance of the fungal hyphae in the infected tissues (Alker et al. 2004; Mydlarz et al. 2008). These responses together with production of secondary metabolites, enzymes (i.e., chitinase), and other cellular responses seem to comprise the repertoire of rapid, innate immune responses of the host to the fungal infection (Kim et al. 2000a, b; Alker et al. 2004; Mydlarz and Harvell 2007; Mydlarz et al. 2008; Douglas et al. 2007). Some, but not all, affected sea fans and other species seem to be able to restrain the advance of the fungal hyphae by encapsulating them in hard, calcified dark purple structures termed galls that are formed by accumulation of gorgonin and sclerites (Fig. 5D). Microscopic comparisons of gall-affected and unaffected tissues revealed the presence of fungal hyphae in all samples (Alker et al. 2004; Smith and Weil 2004).

Recent studies on population genetic patterns suggest that a single origin of *A. sydowii* in marine systems is unlikely and that the fungus is an opportunistic pathogen with ongoing gene flow between widely dispersed geographic regions (Rypien et al. 2008). Therefore, there could be multiple terrestrial sources that could explain the rapid geographic distribution of ASP. Continental dust storms (i.e., African dust) have been widely recognized as an important source of nutrients to the marine environment and as a vehicle for transporting fungal spores and bacterial pathogens. Fungal spores and bacteria have been found in African dust collectors in the Caribbean, but no *A. sydowii* (Rypien et al. 2008). Furthermore, a molecular study comparing the genetic structure of isolates of *A. sydowii* from many different sources (diseased corals, diseased humans, and environmental sources) indicated that this fungal saprophyte species is a single global population with sufficient gene flow to detect genetic structures (differentiation) across geographic locations (Rypien et al. 2008). Therefore, any coastal terrestrial environment is a potential source of the fungus to marine populations, rather than long-distance dispersal via stratospheric dust movement. This makes it difficult to control or manage the disease because new spores may be constantly getting into the coastal areas infecting new colonies.

The initial mass mortalities in the early 1980s in Central America primarily affected *G. flabellum* (Table 1), but subsequent field observations indicated that *G. ventalina* was more susceptible to ASP than *G. flabellum*, and laboratory experimentation showed that *G. mariae* had stronger antifungal compounds. The disappearance of *G. ventalina* from one reef off the Bahamas resulted in a shift of community dominance from *G. ventalina* to *G. flabellum* in a 3-year period (Smith et al. 1998). By 1999, observations (by the CARICOMP network and others) revealed that ASP had dispersed throughout the wider Caribbean, prevalence levels were increasing throughout the region, and at least ten octocoral species were affected by ASP (Smith and Weil 2004). In the Florida Keys alone, it was estimated that 50% of sea fan colonies and extensive amounts of live tissues were killed by ASP in just 6 years (1995–2001) (Kim and Harvell 2004). Aspergillosis became a Caribbean-wide, chronic disease by the early to mid-2000s (Smith and Weil 2004). The wide fan-like structure, an adaptation to filter and capture food, is also efficient in trapping parasites and pathogens. Overall, the genus is susceptible to at least nine disease conditions with *G. ventalina* being affected by the highest number (Table 2), as well as overgrowth by algae, sponges, hydrocorals, zoanthids, other octocorals, and cyanobacteria.

A regional study of Caribbean coral diseases indicated that by the early 2000s, ASP affected a high proportion of colonies (5.0–30.6%) of *G. ventalina* with averages between 8.8% and 18.7% across geographically distant localities. In 2001, the average prevalence of ASP in individual reefs varied between 2.5% and 22.5% in Grenada, 9.4% and 18.1% in Puerto Rico, and 4.2% and 21.3% in Bermuda (Weil et al. 2002; Weil 2004). Preliminary results from another long-term study (>10 years) in six reefs off La Parguera, Puerto Rico, showed similar increases in ASP prevalence and incidence, with high rates of tissue mortality initially correlated with increases in seawater temperature. Prevalence and incidence across populations and habitats varied. Prevalence of ASP increased from 8.8% (±3.5%) in 1999 to 13.4% (±3.5%) in 2001 and 15.3% (±5.2%) in 2002–2003. Then, the prevalence increased to 35% (25–42%) during and after the thermal anomalies of 2004–2005 (bleaching event of 2005), 7 years after the first observations of ASP in the area. The mean ASP prevalence slowly declined over the next 7 years reaching 10% in 2013 (Fig. 6). The average percentage of colonies of *G. ventalina* with diseases in La Parguera increased to 50% in 2009, peaking at around 65% during the thermal event in 2010, and declining afterwards (Fig. 6) (Flynn and Weil 2010; Weil et al. 2014; Weil personal observation). No extensive loss of entire colonies was seen, but significant amounts of tissue were lost from the colonies, which represent loss of photosynthetic, feeding, and reproductive area, reducing availability of energy for growth, resistance to pathogens, competitive ability, and reproductive output, essentially reducing fitness of the species. Furthermore, a systemic effect and significant reduction in fecundity was found in ASP-infected colonies compared to healthy-looking colonies in Florida and Puerto Rico (Petes et al. 2003; Flynn and Weil 2008, 2010). Reduction of reproductive output affects dispersion, recruitment, and potential recovery of local populations.

Few studies are long enough to characterize the temporal dynamics of ASP or many other diseases. Aspergillosis increased in prevalence and virulence (number of lesions per colony, percent tissue loss per unit time per diseased colony) in the Bahamas (from 1995 through 1998), Bermuda (from 1999 to 2001), Florida (from 1997 to 2000), and Puerto Rico (from 1999 to 2010) (Smith et al. 1998; Kim and

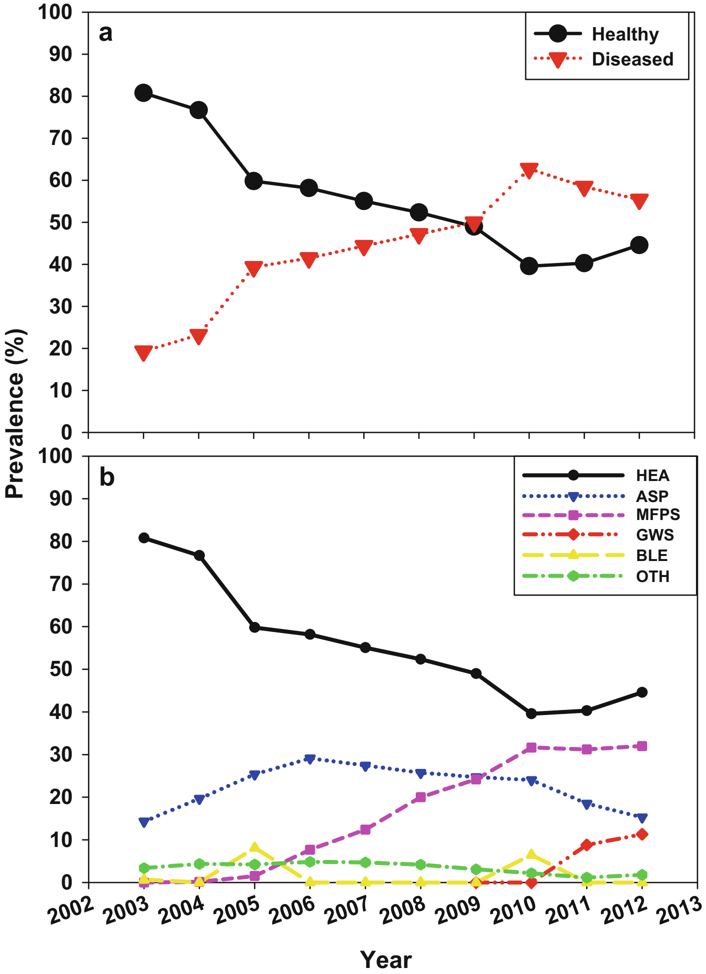

Fig. 6 Temporal variability in mean prevalence of diseased (total diseases) and healthy-looking colonies of the sea fan *Gorgonia ventalina* in La Parguera, Puerto Rico from 2003 to 2012 (**a**). Temporal variability in mean prevalence of the major diseases affecting *G. ventalina* (**b**). HEA = healthy; ASP = aspergillosis; BLE = bleaching; GWS = *Gorgonia* wasting syndrome, MFPS = multifocal purple spots; OTH = other undescribed diseases (Weil unpblished data)

Harvell 2004; Smith and Weil 2004; Flynn and Weil 2008, 2010; Weil et al. 2014). Furthermore, prevalence and the number of lesions per colony were positively correlated with water depth in some locations (Nagelkerken et al. 1997b). In the Florida Keys, the ASP outbreak reached its peak prevalence 3–4 years after the initial infections in 1999 and then, incidence and prevalence stabilized for some time before declining (Harvell et al. 2001). This was the first long-term (6 years) epidemiological study on an anthozoan disease, and it showed a significant decline in sea fan colonies and colony tissues, with drastic changes in the size structure of sea fan populations and reduction in fecundity and recruitment (Petes et al. 2003; Bruno et al. 2011).

The endemic octocoral fauna of the Tropical Eastern Pacific includes highly diverse genera such as *Pacifigorgia*, which comprises 35 species. Between 2007 and 2010, an outbreak of a condition with signs similar to ASP produced extensive octocoral mass mortalities in reefs of Gorgona and Malpelo islands off the western coast of Colombia (Fig. 5E–F). Up to 70% of the colonies of at least three abundant species (*Pacifigorgia adamsi*, *P. rubicunda* and *P. eximia*) were killed between 12 and 20 m depth, with many others suffering partial mortalities (Sánchez et al. 2011, 2014; Barrero-Canosa et al. 2013). The disease signs were similar to those produced by ASP in Caribbean sea fans but with reduced purpling at the edges of the injuries in some species (Fig. 5E–F). Microbiological and molecular analyses of samples identified *A. sydowii* as the potential causative agent (Barrero-Canosa et al. 2013). This is the first report of an ASP-related octocoral mass mortality for the Pacific region. Similarly to the previous mass mortality events in the Caribbean and Mediterranean, this outbreak was associated with a high thermal anomaly.

Overall, the available information indicates that ASP temporal dynamics vary across reefs and geographic locations and that variability in disease prevalence is most likely due to site-dependent factors such as host density, temperature, nutrient levels, water movement, as well as variability in the hosts' resistance to infection (Kim and Harvell 2004; Kim and Rypien 2016 and references therein). Differential species-specific mortalities associated with diseases have resulted in changes in the structure and function of octocoral communities (Scharer and Nemeth 2010; Ruzicka et al. 2013) affecting the ecological services they provide.

Overall, field observations, surveys, and laboratory experimentation indicate a consistent positive association between ASP outbreaks and thermal anomalies, as well as significant covariation between increasing prevalence and virulence levels with increasing seawater temperatures, depletion of antifungal activity, and accelerated infection rates (Weil et al. 2002; Ward et al. 2006; Mydlarz et al. 2008; Kim and Harvell 2002; Weil and Croquer 2009; Croquer and Weil 2009). These results add to the cumulative evidence of the link between marine disease outbreaks and increasing seawater temperatures associated with changing climate (Weil and Rogers 2011; Burge et al. 2013; Weil et al. 2014; Lafferty and Hoffman 2016).

3.3 Growth Anomalies (GAN)

Growth anomalies (i.e., tumors, hyper- and hypoplasias) in octocorals may be a generalized response to parasites, algal infiltration, fungal hyphae, competition, abrasion, or just sealing off injured areas as a prevention to bacterial infections (Morse et al. 1977, 1981; Goldberg et al. 1984; Botero 1990; Kim 2016). These abnormal growths have different shapes and sizes and can be found in any part of the colony but are usually present in the middle or tips of branches, or along the main axes and fan structure in sea fans (Fig. 4E–F). Growth anomalies are conspicuous in sea fans because they are usually heavily pigmented (purple), like the galls resulting from the encapsulation of ASP hyphae in *G. ventalina* (Petes et al. 2003; Smith and Weil 2004).

The presence of "tumor-like" growths on Caribbean octocorals was first noted by Morse et al. (1977, 1981) in Bonaire on colonies of *G. ventalina*. The solid nodules they saw were thought to result from the response to an "infection" by filamentous algae. Subsequently, these GAN on *G. ventalina* and other species have been observed all over the Caribbean. However, whether they have a common etiology with the originally described nodules is unknown. In other gorgonians, GAN form small-to-medium sized nodules that appear to have the usual polyp components and no change in color, which indicates an immune response to some agent inducing the tumorous growth. The filamentous Chlorophyte *Entocladia endozoica* sp. nov. was identified infecting *G. ventalina* in the Florida Keys (Goldberg and Makemson 1981) and subsequently in Santa Marta, Colombia (Botero 1990).

Sea fans react similarly to the presence of filamentous algae and to parasites as well as organisms with which they compete for space (and also to physical injuries). They use several innate immune responses (see below), such as secondary metabolites, melanization, relocation of scleroblasts, aggregation of purple sclerites, and increases in the number and volume of mesogleal cells, as in an inflammatory response (Mydlarz et al. 2008). An infiltration of granular amoebocytes into the mesoglea surrounding the algal-infected gorgonin with subsequent production of abnormal gorgonin and aggregation of sclerites ends up encapsulating the algal filaments, which is similar to the encapsulation of the ASP fungal hyphae in *G. ventalina* (Alker et al. 2004; Kim and Rypien 2016). The amoebocytes play a key role in isolating parasites and often kill them, although no major effect on the algae has been described. The resulting "tumor-like" structure was described as "hyperplasia"(Peters 1997; Mullen et al. 2006).

Tumor-like structures have been observed on other gorgonian species (i.e., *Pseudoplexaura flagellosa*, *Eunicea flexuosa*, and *Plexaura homomalla*). Although nodules in these species were also associated with filamentous algae, they differed histologically and histochemically from those in *G. ventalina*. Moreover, in these hosts the algae appeared not to have been encapsulated in gorgonin, instead forming mats, loosely packed in between the axis and the coenenchyme (Morse et al. 1981; Kim 2016). Nodules can grow and, in some instances, appear to coalesce (Fig. 4F). No information on rates of mortality associated with GAN or histopathology is available, but observations of the same colonies over time in several Caribbean locations indicate that most of these tumor-like structures seldom kill octocoral tissue (Weil personal communication).

3.4 Black Band Disease (BBD) and Red Band Disease (RBD)

Black band disease (BBD) affects >40 scleractinian species on reefs worldwide (Miller and Richardson 2014; Richardson 1998; Willis et al. 2004). The disease also affects soft octocorals in the Indo-Pacific (Antonius 1973, 1981) and several gorgonian species in the Caribbean (Weil 2004). It has been observed most commonly on *Pseudopterogorgia acerosa*, *P. americana*, *Gorgonia flabellum*, and *G. ventalina* (Tables 1 and 2) (Feingold 1988). Mean prevalence in *P. acerosa* populations in the Florida Keys was 3.5% in 1987 and varied seasonally, with higher values during the warmer months and overall low colony mortality. BBD appeared to spread through colony–colony contact of the diseased area and healthy areas, as has been observed in hard corals. Rate of tissue mortality in octocorals was estimated at 5 mm per day (Feingold 1988). The primary pathogens identified in scleractinian BBD were one species of cyanobacteria *Oscillatoria submembranaceae* (later renamed *Phormidium corallyticum*) and a marine fungus. Additionally, a sulfate-reducing bacterium (*Desulfovibrio*) and a sulfide-oxidizing bacterium (*Beggiatoa* spp.) were identified as key members of the consortium (Garrett and Ducklow 1975). No pathological, histological, and/or ecological work to identify the agent (s) and characterize the etiology of this disease in octocorals has been done.

Red band disease is another disease that emerged during the warm years of the early 1980s. It is characterized by a reddish, thick cyanobacteria mat (Fig. 7A–D) and was first observed in the Florida Keys affecting scleractinians (Rützler et al. 1983). It resembles BBD but the band is generally wider, reddish, and “thicker” with long cyanobacterial filaments clearly visible (Fig. 7D). The main component in the cyanobacteria mat is *Oscillatoria* spp., a different cyanobacterium from the one in BBD. The disease was redescribed after a second outbreak in the Florida Keys in the early 1990s, but the composition of the bacterial mat has not been completely characterized (Santavy and Peters 1997; Richardson 1998). In Puerto Rico and other Caribbean localities, RBD is mostly seen affecting the sea fan *G. ventalina,* with occasional infections observed on *G. flabellum*, *G. mariae*, and *Plexaurella nutans* (Weil personal communication). The etiology of this condition is similar to that of BBD, a red band advancing and killing octocoral tissues rapidly (1.0–3.0 cm/month) during the warm season (July – October), leaving bare endoskeleton behind that is rapidly colonized by algae, sponges, hydrozoans, and other invertebrates. RBD spreads through the water (detached cyanobacteria pieces during surge conditions) and by direct contact with neighboring colonies. It can kill small- and medium-sized colonies in a few months and arrests or disappears entirely during the cold winter months. Prevalence is generally low and no outbreaks have been observed in Puerto Rico or any of the other Caribbean locations surveyed in the last 12 years (Weil personal communication).

3.5 Fungal-Protozoan Syndrome (FPS) and Octocoral *Vibrio* Syndrome (OVS)

During the summers of 1999 and 2003, diseases killed large numbers of gorgonian octocorals in the Ligurean Sea in the northwestern Mediterranean, from Provence (France) and Linguri (Italy) to the island of Menorca, 700 km away (Cerrano et al. 2000; Coma et al. 2006; Bally and Garrabou 2007). Populations of at least six

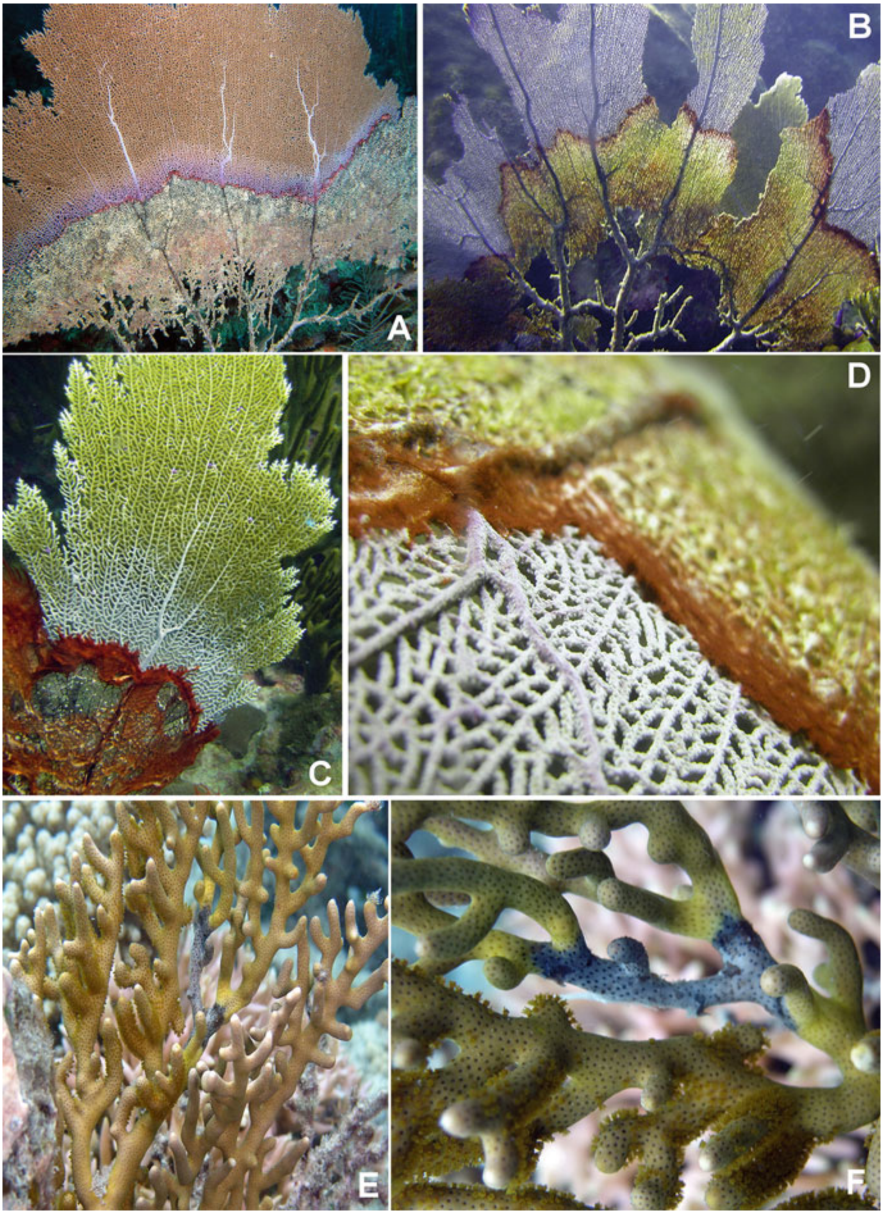

Fig. 7 Large colonies of the sea fan *G. ventalina* with advancing Red Band Disease (RBD) in Puerto Rico. Note the large dead areas already colonized by filamentous algae and other organisms (**A**–**B**). Thick mat of RBD eliciting a host response (color-change at edges) (**C**). Front edge of the RBD mat with visible cyanobacterial filaments over the healthy tissue (**D**). A gorgonian with dark areas of Black Necrotic Syndrome (BNS) in the Great Barrier Reef (**E**–**F**) (Photos **A**–**D** by EW and **E**–**F** by R. Baden)

common gorgonian octocorals were affected along with one scleractinian (*Cladocora caespitosa*), one zoanthid (*Parazoanthus axinellae*), Porifera, Mollusca, Ascidia, Bryozoans, and encrusting coralline algae. A fungal–protozoan coinfection linked to increasing water temperatures was preliminarily identified as the agent based on laboratory analyses of samples. This condition was later termed fungal–protozoan syndrome (FPS) (Sutherland et al. 2004). The disease etiology was characterized by an increase in mucus production, loss of tissue pigmentation, and loss of coenenchyme with exposure of the skeletal axis. Spicules in the coenenchyme lost their thin outer layer of epidermal cells and became disorganized. Morphological analyses showed fungal hyphae penetrated the coenenchyme tissues and then octocoral polyps were colonized and consumed by protozoan ciliates. The most abundant fungi associated with FPS were identified as belonging to the genus *Trichoderma*, but *Clodosporium, Penicillum*, and *Humicola* were also found (Cerrano et al. 2000).

In 1999, mean disease prevalence levels ranged from 60% to 100% in populations of the five most important and abundant gorgonians, which had initial densities of up to 27 colonies/m^2 in Provence and Liguria. The gorgonian *Paramuricea clavata* was the most affected in Menorca, and 4 years later, 59% of the colonies still exhibited some damage (Cerrano et al. 2000; Coma et al. 2006). During a second outbreak in 2003, *Eunicella singularis* and *P. clavata* were the most affected over their entire depth range (15–40 m). The bacterium *Vibrio coralliilyticus* was isolated from diseased tissues of *P. clavata* and tested with Koch’s postulates demonstrating that it was the agent infecting populations of this octocoral in 2003 (Bally and Garrabou 2007). This disease is therefore termed octocoral *Vibrio* syndrome (OVS) to differentiate it from the 1999 FPS outbreak. This was the first time that a pathogen mostly found in diseased scleractinian corals in the tropical Indo-Pacific had been involved in a disease of temperate octocorals, which may be linked to the high thermal anomalies experienced in this region in both years. Fungi and protozoa associated with the 1999 FPS outbreak may have been secondary opportunistic parasites, colonizing already stressed/infected colonies with *V. coralliilyticus* that were more susceptible and/or had compromised immune responses.

Overall, densities of octocorals were significantly reduced along several locations between Provence and Menorca, and population size class frequency distribution of surviving species indicated a lack of recruitment after the outbreaks probably as a result of the decline in fecundity and reproductive output due to loss of tissue and colonies. Modular organisms that suffer partial mortality usually redirect energy and resources to growth rather than sexual reproduction. At the community level, the 1999 and 2003 octocoral mortality events significantly changed the seascape of shallow water benthic communities along the impacted region and represented one of the strongest disturbances ever recorded for any temperate gorgonian species over such a large area (Coma et al. 2006), similar in some ways to events observed in tropical gorgonians in the Caribbean and Eastern Pacific (Smith et al. 1996; Nagelkerken et al. 1997a, b; Sanchez et al. 2011).

A few years later, disease signs similar to those reported for the FPS mass mortality in colonies of the gorgonian octocoral *E. verrucosa* in the Mediterranean were observed for the first time on many colonies of the same species in colder water environments at Lundy's Lane, a marine protected area in southwest England (Hall-Spencer et al. 2007). As in many other cnidarian disease outbreaks, these octocoral epizootics were associated with unusually elevated seawater temperatures linked to GCC which most likely stressed the octocorals and/or the associated microorganisms as in other reports of ciliate, fungal and bacterial infections in stressed scleractinian corals (Morrison-Gardiner 2001; Rosenberg et al. 2004; Kim and Harvell 2004; Page et al. 2016).

3.6 Black Necrotic Syndrome (BNS)

Concurrently with the Mediterranean FPS outbreak in 1999 (Cerrano et al. 2000), a similar disease was reported in the Great Barrier Reef right after the strongest El Niño event in recorded history in 1998–1999, which produced massive bleaching across the Pacific. Ten percent of the colonies of the gorgonian *Isis hyppuris* in Davies Reef had conspicuous black necrotic areas along the branches with rapid loss of tissues and endoskeleton, eventually leading to colony fragmentation and mortality. The disease was named Black Necrotic Syndrome (BNS) (Morrison-Gardiner 2001) (Fig. 7E–F).

Abundant fungal hyphae were found in the affected tissues and two species of *Penicillium* were isolated but Koch's postulates were not confirmed. The fungal cultures were used to infect healthy colonies of two other gorgonian species, *I. hippuris* and *Pinnigorgia* sp., and then, the fungi were reisolated but failed to produce the typical disease signs of BNS (Morrison-Gardiner 2001). No other microorganisms were isolated and/or identified from the samples. Furthermore, BNS signs were observed on moderate numbers of colonies of other gorgonian species at Lizard Island during the annual regional disease surveys conducted along the GBR, but no more information on BNS etiology and pathology is available (Willis et al. 2004).

3.7 Gorgonian Labyrinthulomycosis (LAB) and Multifocal Purple Spots (MFPS)

During field surveys in Mexico, Florida, and Puerto Rico in 2005, a new type of disease was observed on *Gorgonia ventalina*. The condition was characterized by small (1–3 mm in diameter), circular to oblong multifocal purple nodules that were initially called purple spots (Weil and Hooten 2008; Harvell et al. 2007; Weil and Rogers 2011) (Fig. 8). More recently, after some laboratory work and field observations in Grand Cayman, Curacao, and Grenada, the condition was renamed as *Gorgonia* multifocal purple spots (MFPS) (Burge et al 2012; Weil unpublished data).

A preliminary study revealed that a Labyrinthulomycota-like ovoid protozoan parasite was in or around MFPS lesions in light micrographs (Burge et al. 2012). In the same study, using DNA-based techniques, cultured Labyrinthulomycetes from

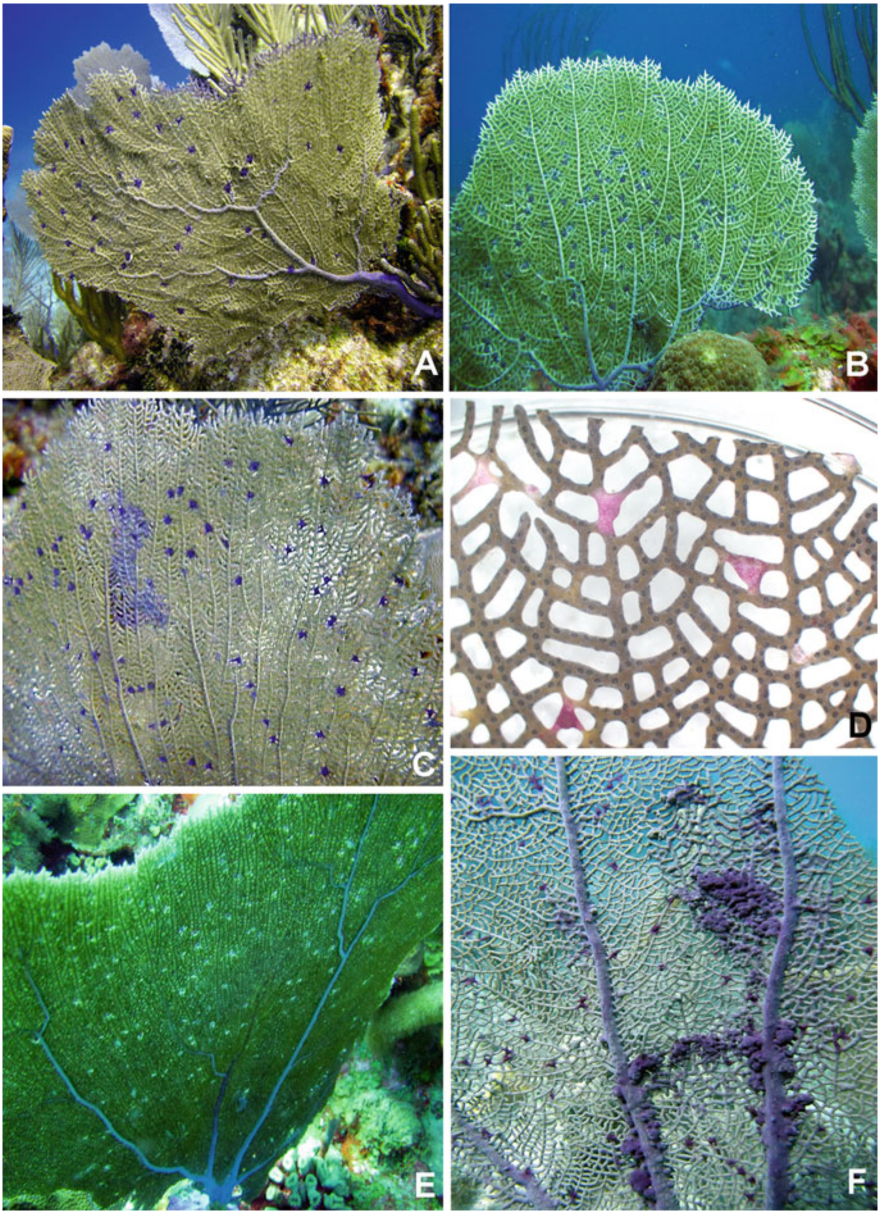

Fig. 8 Sea fan colonies in Mexico (**A**), Grenada (**B**), and Puerto Rico (**C**) with the characteristic purple dots of Multi Focal Purple Spots disease (MFPS). A microscopic photograph (10x) of an infected area showing pale (*top right*), pink (*middle*), and purple (lower) encapsulating nodules around the lesion in the fan area (**D**). Pale depressions with Labyrinthulomycetes without any pigmentation (melanization/encapsulation) in *G. ventalina* (**E**). Co-infection of MFPS and ASP with gall formations (**F**) (Photos EW)

apparently healthy and diseased sea fan samples from Florida and Puerto Rico were found to be in the genus *Aplanochytrium*, which was also isolated and cultured from MPFS collected in Florida. Histology and transcriptome analyses confirmed presence of protozoans within apparently healthy and MFPS-affected sea fans from Puerto Rico, and specific staining indicated a host melanization response only in colonies containing the *Aplanochytrium* and fungal infections (but not necessarily associated with the outward purpling) (Burge et al. 2013). Further field and laboratory observations indicated that otherwise normal-looking colonies had multiple, small, pale depressions that can be easily overlooked during surveys and that seem to be produced by the protozoan (Weil personal communication) (Fig. 8D–E). This could be an early stage of the infection, which after being recognized by the host immune system becomes encapsulated and purple. Continuous monitoring of individual infected colonies, dissection of the purple galls, and more laboratory tests are needed to better characterize the etiology of this disease.

More recently, large (4 mm) MFPS were observed on *G. ventalina* colonies in eight of 40 reefs in St. Eustatius (Netherlands). Microscope observations and dissection of the purple outgrowths revealed typical chambers enclosing one or two adult copepods (female, or female and male) that were identified as *Sphaerippe* sp. (Ivanenko et al. 2015). The only known species of the genus, *S. caligicola* Grygier 1980, was found in galls of the sea fan *Callogorgia* sp. at a depth of 355 m near Grand Bahama Island. Copepods that are morphologically highly modified endoparasites such as the Lamippidae have been found in galls or other cavities of various species of octocorals (Buhl-Mortensen and Mortensen 2004).

Disease surveys conducted from 2003 to 2012 at six reefs in La Parguera, Puerto Rico, showed increases in mean prevalence of MFPS in sea fans over time, from zero in 2003 to 34% in 2011, indicating an epizootic problem (Weil et al. 2014) (Fig. 6). Preliminary analyses showed aggregated patterns in the spatial distribution of diseased sea fans, which suggests the possibility of colony-to-colony transmission in spatially close colonies (direct contact or short-distance water-borne dispersion). This needs to be checked, however. Mean prevalence of MFPS and total octocoral disease increased with increasing water temperatures. The trend suggests that this parasitic infection could continue to spread in populations of *G. ventalina* and other sea fans as water temperatures continue to rise. No information is available on how the increasing MFPS density in the colony could affect physiological functions such as growth and reproduction. Work is continuing to characterize the etiology and the pathology of these two disease conditions, coinfection dynamics, and the overall effect on the physiological functioning of sea fans.

3.8 Octocoral Wasting Syndromes

Several conditions affecting octocorals have similar etiologies involving disorganization of tissues, discoloration (typically to black or grey), and decomposition of tissues following loss of pigments and sclerites in the outer surface layer leading to further sloughing off of the coenenchyme and the exposure of the axial skeleton. Affected tissues look necrotic and disorganized under the microscope and in histopathological slides. Colony surfaces appear with single or multifocal areas of missing tissue that can enlarge rapidly and coalesce with neighboring injuries until the colony is dead. This sequence was observed in *Briareum polyanthes* and *E. caribaeorum* in the Florida Keys and Puerto Rico after the 1998 and 2005 high thermal anomalies, respectively (Harvell et al. 2001; Weil et al. 2009). No putative pathogens have been identified for most of these diseases. Transmissibility experiments with some confirm agent transmission. Limited information prevents the characterization of the particular etiologies and their spatial and temporal dynamics and the agents causing these diseases. Five such disease conditions are described below.

3.8.1 *Briareum* Bleaching Necrosis (BBN) and *Briareum* Wasting Syndrome (BWS)

Colonies of *Briareum* spp. were observed losing large areas of tissue on three reefs in the Florida Keys during the thermal anomaly and bleaching event of 1998–1999 (Harvell et al. 2001). The study described rapid mortality of bleached colonies with multifocal, necrotic-tissue areas devoid of coenenchyme and the spicular axes (Fig. 9A–B), indicating a possible "infectious" agent as the cause. The disease probably developed as a consequence of increased susceptibility in the thermally stressed colonies. Experiments indicated that transmissibility was limited to bleached colonies and colonies that were bleached and diseased. It did not spread to healthy looking, unbleached colonies, even if they were in contact with infected tissues. Overall, 68% of the bleached and diseased colonies died, and by January 1999, 4 months after it started, bleached colonies had regained their pigmentation and lesions had healed (Harvell et al. 2001). This condition is here termed *Briareum* bleaching necrosis (BBN) to differentiate it from *Briareum* wasting syndrome (BWS), a disease with similar signs but in colonies that were not recently thermally stressed and had normal coloration (see below).

During and after the high thermal anomaly and extensive bleaching event of 2005, large numbers of bleached colonies of both species of *Briareum* in reefs off La Parguera, Puerto Rico, showed signs similar to the Florida BBN condition (Weil et al. 2009) (Fig. 9A–B). After the event was over, surviving colonies recovered their normal pigmentation. Annual surveys in Puerto Rico, Grand Cayman, Grenada, Curacao, and Bermuda between 2006 and 2015 showed many colonies of *B. polyanthes* and the other crustose octocoral *E. caribaeorum* (see below), with similar multifocal, necrotic areas and tissue mortality (Weil et al. 2009; Weil and Rogers 2011; Weil unpublished data) (Fig. 9C–D). This disease was named *Briareum* wasting syndrome (BWS) to differentiate it from the bleached condition (BBN) in case the pathologies turn out to be different. Prevalence has been increasing and the disease has produced significant mortalities mostly in the crustose *B. polyanthes*. The disease also affects the erect *B. asbestinum* but prevalence and mortality rates seem to be much lower than in the crustose species (Weil et al. 2014; Weil unpublished data).

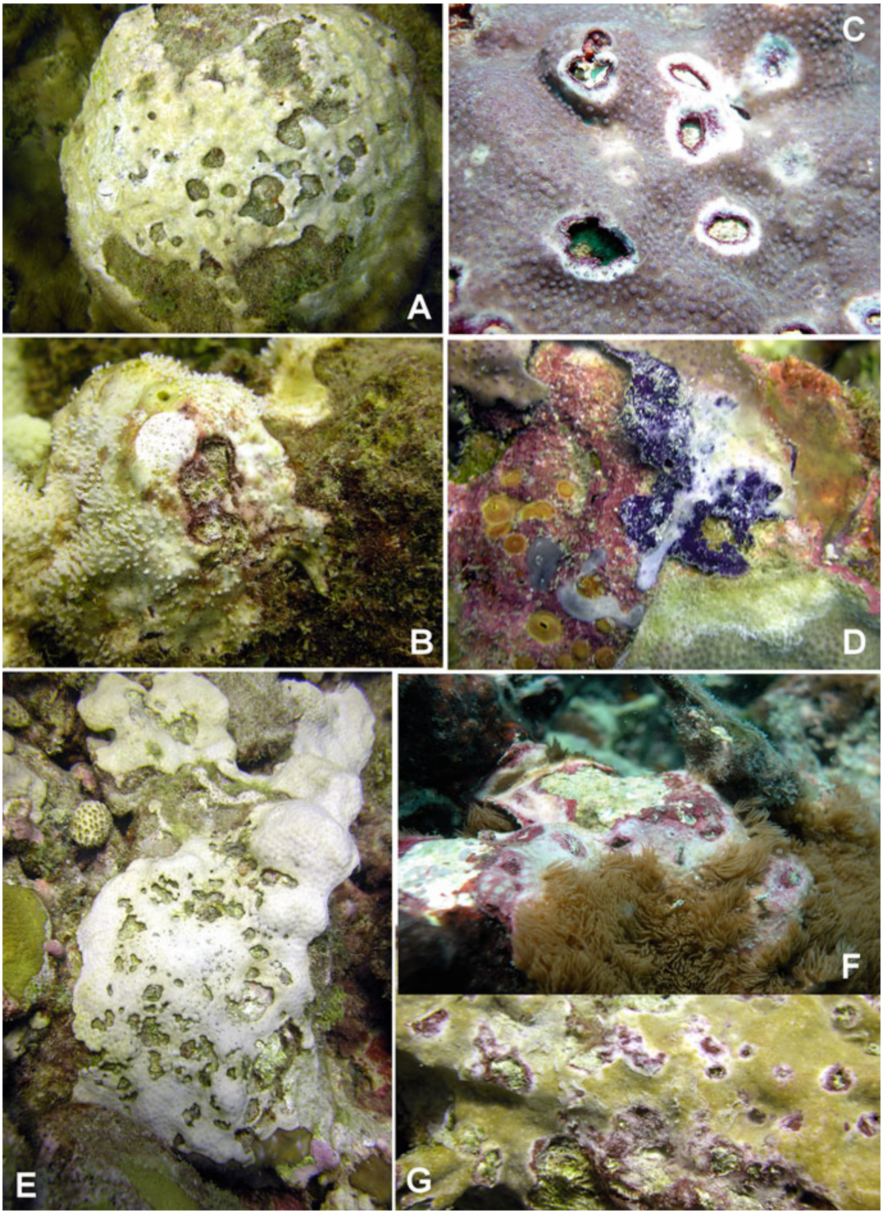

Fig. 9 Bleached colony of *Briareum polyanthes* with signs of *Briareum* Necrosis Syndrome (BNS) showing coenenchyme retraction and tissue loss (**A**–**B**). Diseased colonies with normal coloration but with *Briareum* Wasting Syndrome (BWS) lesions and necrotic areas (**C**–**D**). Bleached colony of *E. caribaeorum* with signs of *Erythropodium* Wasting Syndrome (EWS) (**E**), and colonies with normal pigmentation but with multifocal lesions and necrotic areas with tissue loss in Curacao (**F**–**G**) (Photos EW)

3.8.2 *Erythropodium* Wasting Syndrome (EWS)

Signs similar to those of BBN and BWS were observed in many colonies of the common, crustose octocoral *Erythropodium caribaeorum* during the high temperature anomalies of 2005 and 2010 in Puerto Rico and the other Caribbean locations (Weil. unpublished data) (Fig. 9E–F). The disease affecting healthy-looking (normal coloration) colonies is named *Erythropodium* wasting syndrome (EWS) (Tables 1 and 2). This octocoral is one of the first species to show signs of temperature stress (McClanahan et al. 2009) and large numbers of colonies bleached during the high thermal anomalies of 2005 and 2010. Colonies developed single and/or multifocal lesions bordered by dark-purple rims of necrotic tissue. The coenenchyme tissue was exposed and retracted, and died quickly, leaving multiple empty holes (Fig. 9E–F). Colonies were killed over the entire depth distribution of the species leaving open substratum that was quickly colonized by turf algae and other sessile invertebrates.

After the bleaching event was over and colonies had recovered their normal, tan coloration, they started to develop similar lesions and disease signs under normal temperature conditions. Our annual disease surveys and observations indicated that many colonies had signs of EWS and died from 2006 to 2013. EWS prevalence increased during the thermal anomaly of 2010 in Puerto Rico, Curacao, and Grenada, with significant tissue and colony losses (Weil unpublished data). The causative agent has not been identified, and transmissibility experiments and further observations are needed to better characterize the etiology, pathology, and epizootiology of this disease.

3.8.3 *Gorgonia* Wasting Syndrome (GWS)

A new disease affecting *G. ventalina* was first observed at intermediate to deep areas (10–25 m) of the mid-shelf and offshore reefs off La Parguera, Puerto Rico, during the high thermal anomaly of 2010. Signs included small individual or multifocal discolored (pale) areas, with necrotic tissues as the coenenchyme degraded, and peripheral tissue retraction that exposed the brown/black endoskeleton, which eventually disappeared leaving holes of different sizes over the fan's surface (Fig. 10A–E). Diseased focal areas expanded over time coalescing and forming larger tissue-devoid areas, which eventually disappeared leaving large holes and fragmented areas (Fig. 10F). Purpling of injured focal areas, an innate immune response in *G. ventalina* (Petes et al. 2003), does not occur in the early phases of the disease but occurs later, around many but not all of the advanced, larger lesions (Weil personal communication) (Fig. 10E).

Tagged colonies in Puerto Rico were monitored, and preliminary data indicated that the disease is highly virulent and can kill small colonies in a few months to a year. The disease was named *Gorgonia* wasting syndrome (GWS) (Weil et al. 2014) (Tables 1 and 2), and it has spread over reefs off La Parguera since 2010. Preliminary microbiological analyses showed hyphae of *A. sydowii* and a variety of bacterial species, but the putative pathogen was not completely identified and Koch's postulates were not tested. Field surveys, observations, and manipulations indicated an aggregated distribution of diseased colonies and transmissibility by direct contact, suggesting the pathogen might be waterborne. Mean GWS prevalence in

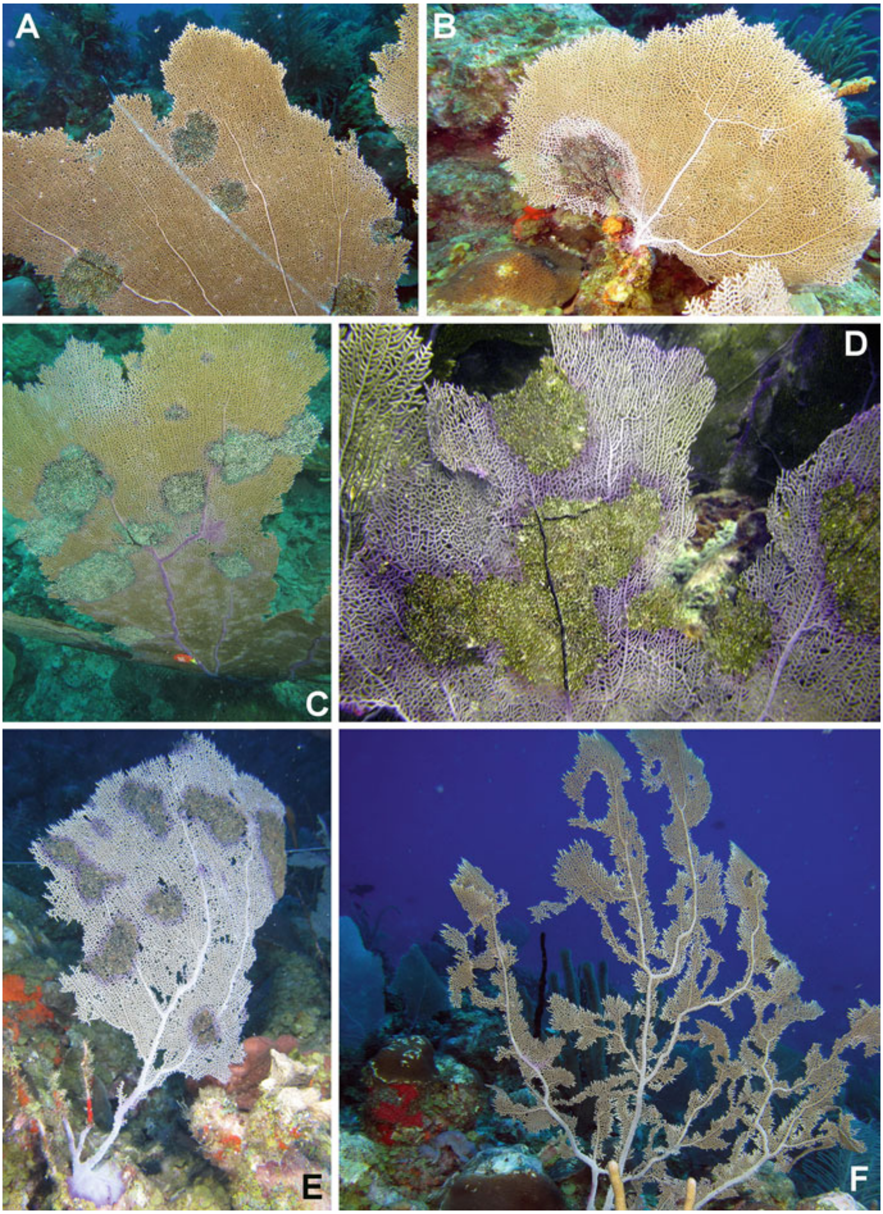

Fig. 10 Progressing stages of *Gorgonia* Wasting Syndrome (GWS) affecting sea fans in Puerto Rico. Small lesions develop first with tissues retracting and mortality leaving clear bare, dark endoskeleton (**A**). These small lesions expand as tissue continues to die (**B**) with some of them coalescing over time (**C**–**D**) forming large diseased areas with purpling edges indicating a host immune response (melanization) (**D**–**E**). Endoskeletons disappear and colonies are left with holes or most of the fan area gone (**F**). If disease arrests, colonies generally recover over time if environmental conditions are good (Photos EW)

G. ventalina populations increased slowly from 0% to 11% of all colonies surveyed ($N = 1876$) in 2 years (Fig. 6). We continue to monitor this condition to better characterize its etiology and pathology.

3.8.4 *Phyllogorgia* Wasting Syndrome (PWS)

Phyllogorgia wasting syndrome (PWS) is the first disease reported for a Brazilian gorgonian octocoral. This disease, with signs similar to GWS and ASP (Fig. 11), affected and killed large numbers of colonies of the endemic octocoral *Phyllogorgia dilatata* along the southern reefs and rocky areas off the coast of Brazil in the summer of 2013 (Fig. 2; Table 1) (Cassola et al. 2016). The disease was observed for the first time during benthic surveys along the coast of Arraial do Cabo. Results showed that by the time of the surveys, 48% of the colonies of *P. dilatata* were already dead, with only the denuded axes remaining attached to the substratum. Of the surviving colonies, 73% showed single or multifocal, necrotic or “wasted” lesions within the fan surface. Some of the lesions had purpling pigmentation around the edges and other areas of the colonies (Fig. 11). The injured areas coalesced forming large tissue gaps on the octocoral surface (Cassola et al. 2016). Close to half of the colonies at each sampled site lost at least 5% of their living surface over a period of 161 days, equivalent to an average rate of tissue loss of 0.07 mm d^{-1}, a slow rate compared to ASP in the Caribbean. No pathology was done, so the putative pathogen remains unidentified. *A. sydowii* was considered as a possible agent due to the similarity of the signs to Caribbean ASP, but microbial analyses revealed *Vibrio* spp. in diseased and healthy-looking tissue samples, which could be related to OVS in the Mediterranean. No environmental correlates were found, and high seawater temperatures and/or local pollution were not considered to be the potential drivers of the disease and the mass mortalities (Cassola et al. 2016).

3.9 Other Octocoral Disease Conditions (OTH)

Several other, unidentified, and uncharacterized health conditions continue affecting octocorals. Most of these have been observed in Caribbean reefs and coastal habitats. Large dark spots and/or bands have been observed in many colonies of *Eunicea spp.* in reefs off Curacao, Puerto Rico, and Grand Cayman (Fig. 12A). Signs similar to tissue wasting syndromes, with necrotic edges and continuous coenenchyme tissue loss from the base or the middle of the branches, or from the branch tip down, have been observed most commonly on *Plexaurella nutans*, *Pseudoplexaura porosa*, *Pseudoterogorgia americana*, *P. acerosa*, and *Muricea* spp. (Weil personal observations) (Fig. 12B–C and F–G). The sea fan *G. ventalina* has a suite of unidentified conditions ranging from tissue sloughing, conspicuous small to large, dark purple, irregular, amorphous areas, localized tissue discolorations and spots that may reflect immune responses to distinct parasites or other stressors (Fig. 12D–E). These are a just a few examples of abnormal conditions lacking enough information. Obviously, additional field and laboratory work needs to be done with the common and better known diseases and even more with all the uncharacterized and new syndromes we

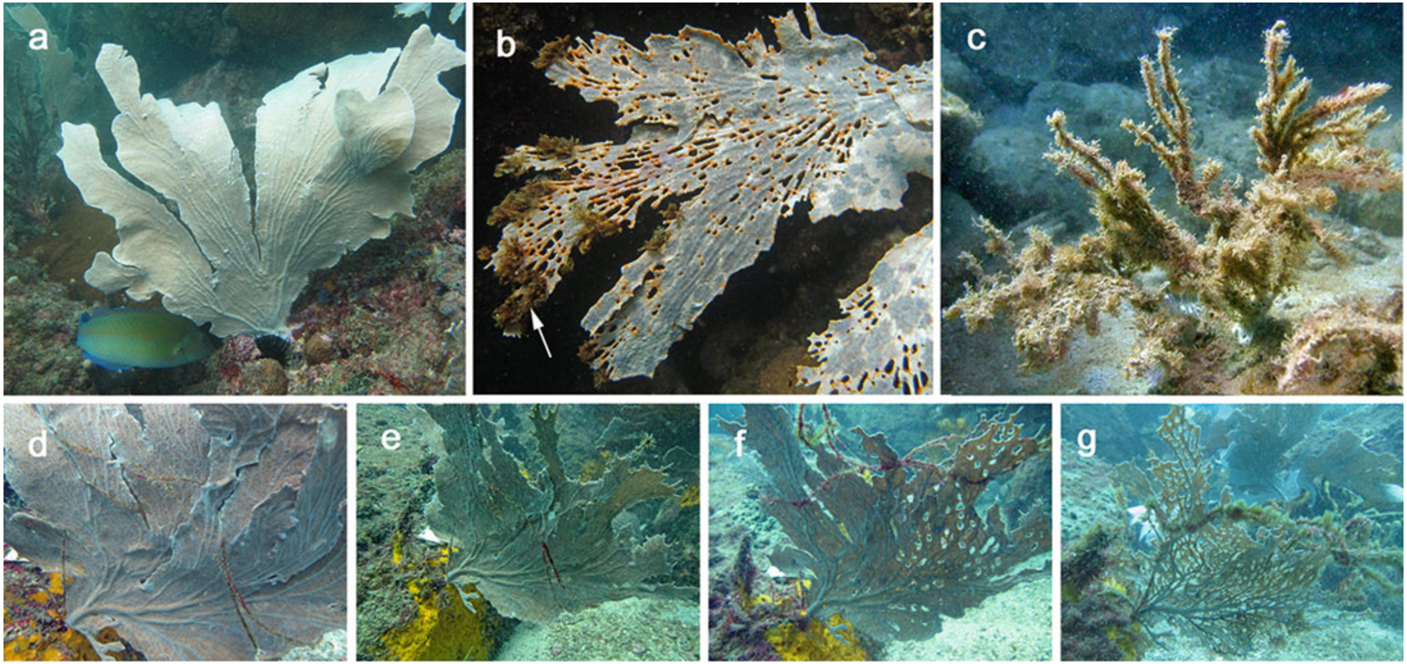

Fig. 11 Colonies of *Phyllogorgia dilatata* showing normal and disease signs in different stages of *Phyllogorgia* Wasting Syndrome (PWS) in Brazil. Healthy-looking fan area with intact laminae (**a**). Diseased colony with multifocal lesions and holes in the fan area, and partial secondary colonization of skeletal axes (**b**). Dead colony with heavily colonized endoskeleton (**c**). Different levels of tissue purpling and lesion development over fan area (**d**–**f**). Disease progression over 30 weeks in the same tagged colony (**g**) (Photos courtesy of Dr. Gabriel Cassola and Carlos E. Leite Ferreira)

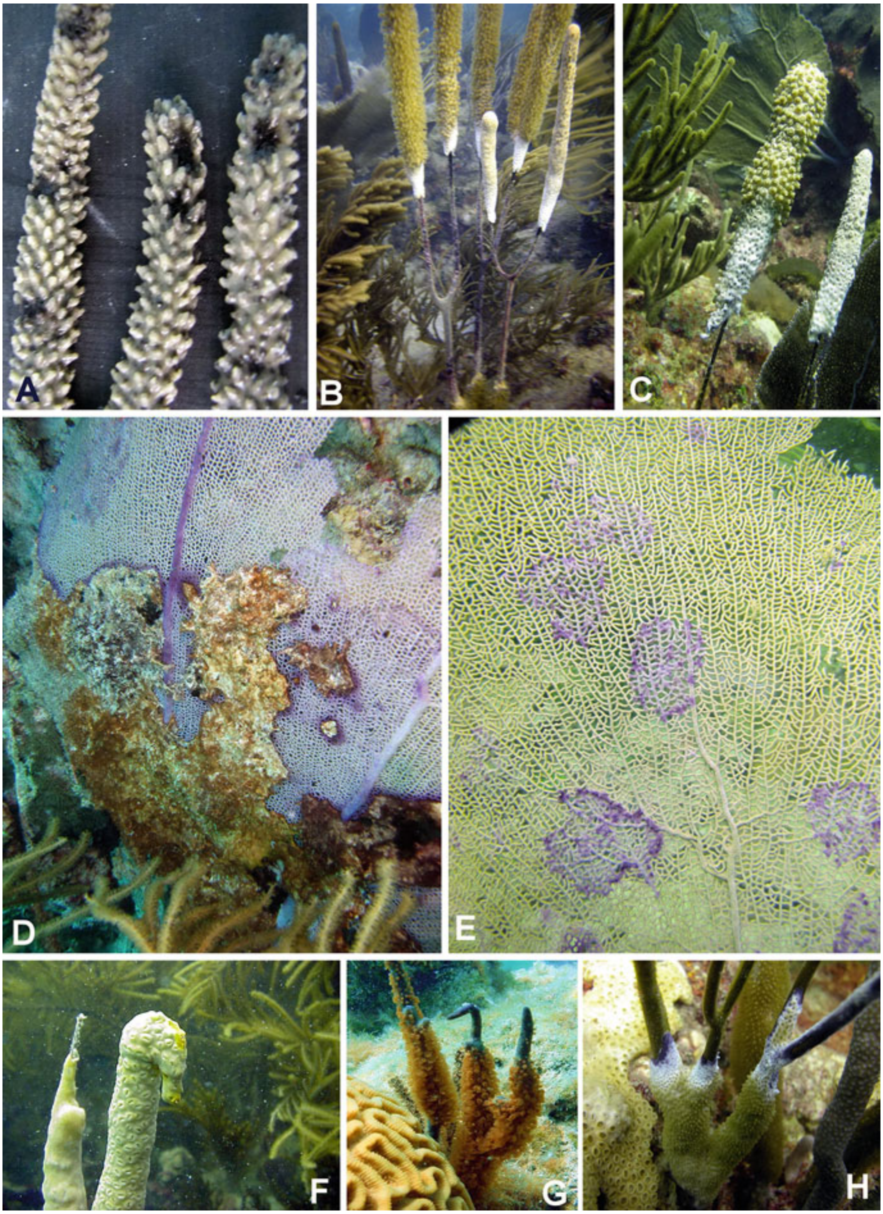

Fig. 12 Other disease conditions in octocorals observed in many locations around the Caribbean. Dark spots on *Eunicea* spp. in reefs off Curacao (**A**). A tissue wasting condition that affects colonies of *P. porosa* and *P. nutans* (**B**–**C**) in Puerto Rico. Two uncharacterized syndromes in *G. ventalina* (**D**–**E**). Sloughing tissues at the tips of branches of *P. nutans* in Bermuda and Puerto Rico (**F**–**G**) and decaying tissues at the base of *P. porosa* in Puerto Rico (**H**). Predation by fireworms and snails could have triggered the conditions in **F**–**G** (Photos EW)

are finding every year if we want to understand the full range of disease conditions affecting octocorals, their dynamics, and impact.

4 Biological Stressors: Predation and Competition

Predation and competition are common biological interactions and evolutionary drivers, especially in crowded substrates in coral reef and other benthic communities. These interactions usually produce injuries, physiological stress, and tissue and/or organismal mortalities that facilitate disease infections in soft-bodied invertebrates, including octocorals (Fig. 13). As a consequence, octocorals have evolved physical, chemical, and behavioral deterrents to protect themselves. They produce many biologically active toxins and other active compounds, which play a defensive role against predators, competitors (Harvell et al. 1996), and opportunistic parasites and pathogens (Kim et al. 2000a, b; Mydlarz et al. 2008).

There are only a few known octocoral predators in the wider-Caribbean, the flamingo tongue snail *Cyphoma gibbosum,* the fingerprint flamingo tongue snail *C. signatum*, the fireworm *Hermodice carunculata*, and a highly specialized nudibranch *Tritonia hamnerorum* (Reijnen et al. 2010; Lucas et al. 2014). Other occasional predators include butterflyfishes, surgeonfishes, and parrotfishes, and a blennid that leaves round, regular, pale marks on the fan area, similar to those reported in some scleractinian corals (i.e., *Siderastrea siderea*) (Fig. 13). *Cyphoma gibbosum* is probably the most damaging predator of Caribbean octocorals. It is a trophic generalist known to graze on numerous species in at least eight genera in four octocoral families in spite of the toxic chemical defenses (allelochemicals) they produce (Lasker et al. 1988). Prey preference and high abundances of three-dimensional octocorals providing refuge and microhabitats used for mating and/or egg deposition could be driving the spatial distribution of *C. gibbosum.* This snail preys on different octocorals in proportion to their abundances in the different habitats. *C. signatum*, on the other hand, feeds exclusively on *Plexaurella* spp (Lucas et al. 2014).

Snails leave distinct open lesions as they remove the coenenchyme tissue with their radulae along the axes and branchlets (Fig. 13A). These injuries are susceptible to colonization by opportunistic pathogens/parasites and other sessile organisms (Raymundo et al. 2016) (Fig. 13A–C). Intensive predation by high densities of snails (>100 snails per colony) caused tissue and partial and whole colony mortalities in *G. ventalina* and other octocoral species in Mona Island, Puerto Rico, in 2009 (Scharer and Nemeth 2010). High snail densities apparently resulted from a population explosion in the area. A few years later, some of the colonies had signs of recovery with new growth along the main axes, but most dead skeletons were overgrown by algae, sponges, hydrozoans, and other invertebrates (Weil personal communication).

A similar situation with a different predator occurred in 2005, when a population explosion of the nudibranch *Tritonia hamnerorum* (Fig. 13F) led to significant tissue losses in populations of *G. ventalina* in Bermuda (Murdoch 2006). *T. hamnerorum* is a

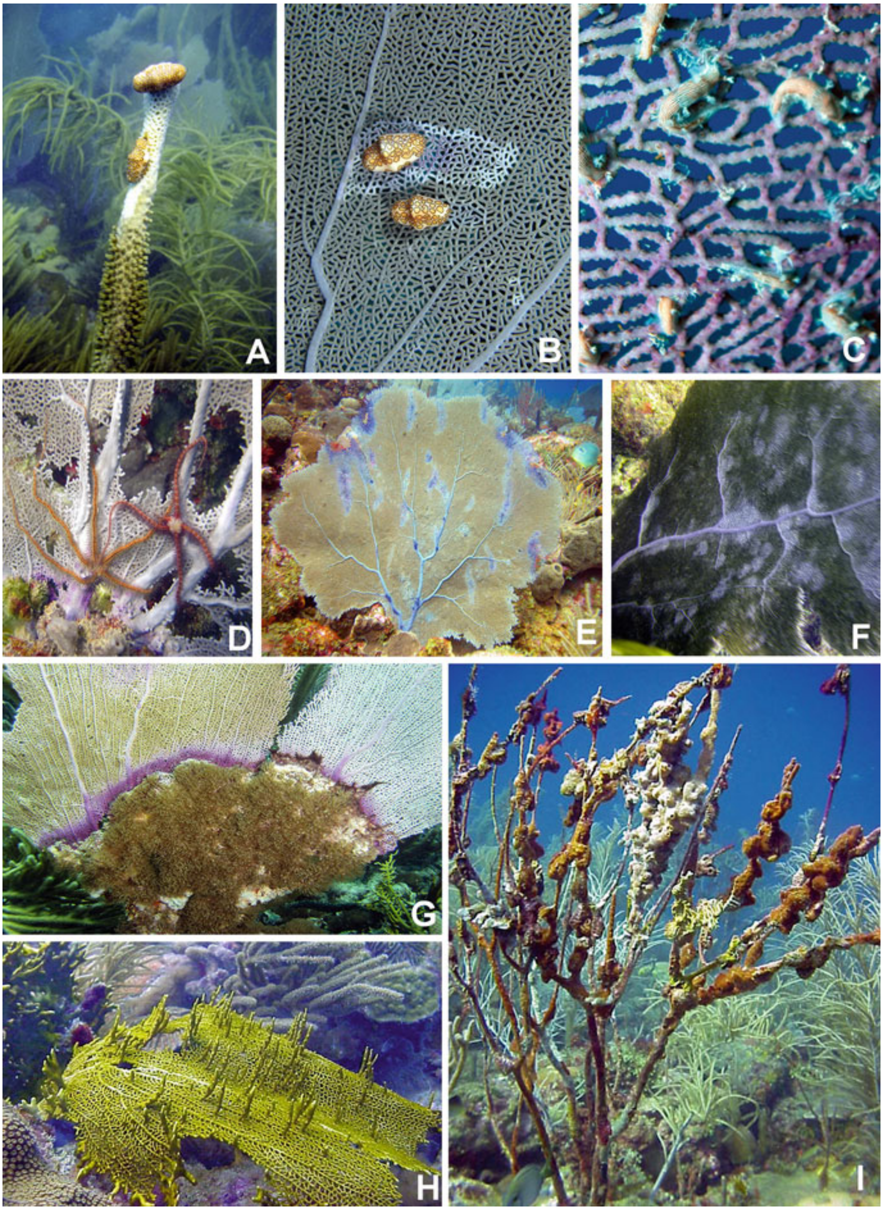

Fig. 13 Predation by the snail C. gibbosum on P. porosa (A) and G. ventalina (B). Abundant nudibranchs T. hamnerorum on G. ventalina after a population outbreak in Bermuda in 2006 (C). Ophiuroids and other echinoderms may graze on some octocoral species (D). Recent and old snail and fireworm predation scars and round "decolored" scars from blennid predation are visible on the fan of G. ventalina colonies (E – F). Competition and tissue mortality between G. ventalina and the crustose octocoral E. caribaeorum with signs of immune reaction at the advancing edge (G). Sea fan colony overwhelmed by the hydrocoral Millepora alcicornis (H), and algae and sponges growing on the endoskeleton of a dead colony in Grenada (I) (Photos EW)

small nudibranch that feeds exclusively on this sea fan. It has been observed across the northern Caribbean, in Honduras, the Cayman Islands, the Bahamas, and the Florida Keys. Densities in Florida reached 1700 nudibranchs per colony and rapidly caused partial and whole colony mortality (Cronin et al. 1995). Some of these predators may be vectors/reservoirs for some of the diseases through their feeding habits. Feeding on diseased tissues and then moving to other noninfected colonies might increase transmissibility of particular octocoral diseases as was shown for the fireworm *H. carunculata* in the Mediterranean coral *Oculina patagonica* (Sussman et al. 2003).

Extensive loss of tissues in individual colonies reduces the area available for photosynthesis and feeding, limiting energy available for reproduction (low fecundity) and therefore could impact recruitment, population recovery, and fitness. Energy resources are then usually diverted to growth since size is an important trait in modular organisms (the larger the colony, the higher the feeding area, fecundity, and survivorship). Redirecting available energy and resources to other physiological functions could also temporarily weaken immune responses and render colonies more susceptible to diseases (Petes et al. 2003; Kim and Harvell 2004).

Open injuries and large denuded axes with exposed endoskeleton are often rapidly colonized by filamentous algae, followed by sponges, hydrocorals, zoanthids, and other crustose octocorals that eventually will compete with the “host” for space and even kill the colony (Fig. 13). The crustose octocorals *B. asbestinum* and *E. caribaeorum* and the hydrocoral *Millepora* spp. are aggressive competitors that overgrow entire colonies starting at the base or at lesions on the branches using it as substratum and maybe as a source of nutrients.

5 Immunity in Octocorals

Immunity is an important biological property that promotes survivorship, fitness, and adaptability in organisms. Invertebrates, including cnidarians, possess innate, variable, and adaptive immune responses, which help them to defend against environmental stress and opportunistic infections and disease. Like all physiological functions, maintenance of the immune system and function requires energy and resources, which in stressful conditions involve trade-offs against energetic investment in other important functions such as growth, feeding, reproduction, etc. Several innate immunity mechanisms, including the ability to discriminate allogenic from xenogenic tissues, have been described for corals and octocorals (Mydlarz et al. 2008, 2010; Burge et al. 2013). This section summarizes information on the immune responses documented for octocorals with special emphasis on responses associated with some diseases. Descriptions of immune responses to pathogen exposure or disease in octocorals are relatively new. *Gorgonia ventalina* is the best-studied octocoral in terms of immunity responses.

Innate immune responses include production and movement of effector enzymes, small molecules that selectively bind to a protein regulating its biological activity. In naturally infected sea fans with dense amoebocytes, for example, a concurrent increase in prophenoloxidase (PPO) activity occurred. This is linked to the production of melanin that is deposited along the axial skeleton to prevent the fungal hyphae from entering the surrounding tissue (Petes et al. 2003; Mullen et al. 2006; Mylardz et al. 2008). Chitinases are enzymes that modify and degrade chitin, a major component of fungal cell walls. The release by stressed octocorals of exochitinases into the water column seems to be an effective defense against *A. sydowii* infections (Douglas et al 2007; Couch et al. 2008). Melanization is an important immune response in octocorals that helps octocorals to cope with pathogen infections by functioning as a physical barrier that prevents fungal hyphae from entering the surrounding tissue. Several histological studies have also illustrated a series of inflammatory responses of amoebocytes to infections in *G. ventalina* (Mydlarz et al. 2008). This includes the production of prophenoloxidase enzymes that enable the formation of a melanin barrier within the sea fan skeleton, the primary observed pathological response of sea fans to both fungal and Labyrinthulomycete protozoan infections (Burge et al. 2012).

Octocorals also produce a series of chemicals and structural defenses for predator deterrence (Harvell and Fenical 1989). However, the discovery of antimicrobial properties of octocorals occurred only a few decades ago. The antimicrobial activity of polar and nonpolar extracts against five marine bacteria was compared in eight octocoral species. Nonpolar fractions were more effective in inhibiting bacterial growth, but inhibition strongly depended on specific interactions among octocorals and bacteria species (Kim et al. 1994). Extracts from 39 species of Caribbean gorgonians were tested for antimicrobial activity against 15 strains of marine bacteria including three opportunistic pathogens, *Vibrio parahaemolyticus, Leucothrix mucor*, and *Aerococcus viridans* and 12 strains isolated from either healthy or diseased gorgonians (Jensen et al. 1996). These authors concluded that organic extracts of most Caribbean gorgonians lack potent, broad-spectrum anti-bacterial activity inhibiting growth, suggesting that the inhibition of bacterial growth is not the primary function of gorgonian secondary metabolites. Therefore, they argued that bacteria were not important selective agents in the evolution of gorgonian secondary chemistry. Kim et al. (2000a) concluded, after studying inhibitory activity of extracts from another 20 gorgonian species, that to be effective under natural conditions, antifungal compounds must be potent and occur in high concentrations inside living tissues. Octocoral species that are highly resistant to fungal infections contain potent inhibitory compounds. Furthermore, inhibitory potential against different pathogens varied spatially within and across several species of shallow water Caribbean octocorals (Kim et al. 2000a). Moreover, healthy colonies showed higher concentrations of these compounds and higher inhibitory capacity compared to diseased octocorals, suggesting a potential role in mediating disease susceptibility (Kim et al. 2000b). Couch et al. (2008) found that colony size did not have an effect on antifungal and antibacterial activity and only antifungal activity differed across sites in the Florida Keys.

Lesions of ASP in sea fans include tissue thickened with gorgonin (galls), small purpled spots, and necrotic areas surrounded by purple halos (Smith et al. 1996; Kim and Harvell 2002). Petes et al. (2003) investigated the structure and nature of these “purpling” signs and determined that they had dense deposits of melanin encapsulating *A. sydowii* hyphae and other organisms (i.e., filamentous algae). Melanosomes were also detected in amoebocytes adjacent to protective melanin bands in infected but not in uninfected sea fans. Sea fans sampled during the 2005 Caribbean high thermal anomaly event responded to heat stress with a systemic increase in numbers and densities of amoebocytes, consistent with responses to elevated temperature stress in laboratory experiments (Mydlarz et al. 2008).

Many key pathways and cellular responses help octocorals defend against natural microbial invaders, predators, and competing organisms. However, until very recently the functional and regulatory pathways remained obscure. Using RNA-Seq analysis, Burge et al. (2013) identified about 210 differentially expressed genes in sea fans exposed to the *Aplanochytrium* sp. parasite. They found expressed genes involved in immunity including pattern recognition molecules, antimicrobial peptides, genes involved in wound repair, and reactive oxygen species formation. Expression analysis revealed genes important in invertebrate innate immune pathways, as well as those whose roles were previously undescribed in cnidarians.

6 Management Perspectives

Seawater temperatures are predicted to continue increasing over the coming decades, and it is expected that the number and frequency of bleaching and disease outbreaks and their geographical distribution will also increase. Furthermore, the continuing deterioration of local environments (notably water quality) and overfishing will continue to compound this problem. The detrimental consequences of mass mortalities of foundation and keystone species, other important community members, and the associated cascading effects will likely result in major changes in community composition, structure, and function, with the consequent loss of biodiversity and essential ecological and economic services. It is therefore important that we improve and expand our knowledge and understanding of the complex marine disease problem we are facing today (Raymundo et al. 2008; Harvell et al. 2009; Weil and Rogers 2011; Burge et al. 2014; Groner et al. 2016).

In tropical regions, scleractinian corals create the physical architecture of coral reefs, the foundation for the ecosystem services that reefs provide. Octocorals, particularly gorgonians, are often abundant in coral reefs and hard bottom "pavement" areas surrounding reef zones dominated by scleractinian corals. In many locations, these hard bottom areas are more extensive than those characterized by the reef-framework building coral species (e.g., Wolff et al. 1999), and octocorals dominate some of these tropical and most temperate hard bottoms. A few animals feed on octocorals, but their importance derives primarily from the habitat and shelter they provide to fishes and many other invertebrates such as crinoids, mollusks, echinoderms, crustaceans, etc. Many fish species migrate between coral habitats, seagrass, mangrove areas, and gorgonian habitats. More information on all these relationships and dynamics as well as on the basic taxonomy, biology, and ecology of octocorals is needed to develop well-founded management approaches to ameliorate the potential impacts and loss of ecological and economic services as a response to an increase in disease-associated and/or pollution-associated mass mortalities in the near future.

Integration of disease surveys into time series and large spatial monitoring programs of marine coastal communities, complemented with extensive photographic and/or video records, can be used after the outbreak-associated mortalities for characterizations and/or comparison of the impact of different diseases in different organisms. Monitoring programs linked to a tissue/data base storage program allow tissue samples of diseased organisms (and healthy-looking individuals) to be collected and stored for future microbiological analyses when an outbreak occurs. Furthermore, disease outbreaks also occur in remote areas, within MPAs, or areas where disease researchers are not immediately available for proper identification of the agents. It will be valuable, therefore, if managers and stakeholders have access to training and means to properly collect and store/archive tissue samples of the affected organisms together with a good photographic record over time. These samples and information can then be shipped to a regional tissue/data base storage facility where microbiologists have access to do the analyses and identification. This would help to tighten the link between signs of disease and known pathogens. If there are not known pathogens, then appropriate protocols could be implemented to identify the agent/cause of the disease, including experimental work to test Koch's postulates (Raymundo et al. 2008). More scientific and financial support would provide for comprehensive epidemiological approaches to meet the stringent standards of human disease work and the US Center for Disease Control and Prevention (CDC), and involvement of health agencies in other countries affected by marine diseases will benefit this effort.

Community management efforts focused on coral reef communities have concentrated more specifically on the protection of scleractinian corals and reef fishes, with little attention to other important members of the community such as octocorals and sponges (but see Goffredo and Lasker 2008). Controlling local stressors like land-based pollution, effective enforcement of existing fishing and habitat use regulations, and establishment of marine protected areas are promising tools for protecting the habitats and species that make up the overall coral reef ecosystem, the processes that link them and their ecological services. It is not possible to prevent, or manage, disease outbreaks or bleaching events at this time. Management of disease outbreaks would require identification of hosts, the cause (agent or pathogen) of the disease as in any other epidemic, and the environmental drivers that facilitated their emergence. Far more research is needed on diseases affecting particularly the primary foundation species associated with coral reefs and other coastal communities, including the octocorals.

Natural populations of foundation and keystone reef species have already been affected at catastrophic levels, such as the acroporid and *Diadema* mass die-offs of the early 1980s in the Caribbean, and the gorgonian mass mortalities in the Caribbean, the Mediterranean, and the Eastern Pacific. Recovery from these extensive mortalities is dependent on successful sexual and asexual (for modular species) reproduction, recruitment, and survivorship, which in most cases depend on stable/

predictable and good environmental conditions including good water quality. Disease outbreaks and other selective pressures (pollution, thermal anomalies, predation, etc.) usually eliminate the susceptible genotypes from the populations. Surviving genotypes will then reproduce and repopulate impacted habitats with genotypes "resistant" to the particular agent or driver. Therefore, protecting benthic communities with high genetic diversity could improve the survivorship of important and particularly susceptible species when resistant genotypes are present.

Effective management of octocoral-dominated hard bottoms requires recognition that a fully functioning coral reef ecosystem depends on a mosaic of interconnected habitats that create the environmental conditions that support the ecosystem's rich biodiversity. Successful management plans for octocoral communities would include knowledge of the genetic variability of the foundation species that need to be protected, ensuring that those with the higher genetic variability would be included in the managed areas. Mortality from diseases, thermal stress, and other stressors will continue until GCC and direct human impacts are reversed, and species with high genetic variability have higher probabilities of surviving in particular areas. For modular, long-lived organisms such as octocorals, scleractinians, hydrocorals, and sponges, a few survivors could be enough to start population recovery if they have high genetic variability and favorable conditions for reproduction, recruitment, and growth.

Sound management of coastal watersheds and other areas adjacent to MPAs could enhance population recoveries, and additional research on the links among local stressors such as sediment, sewage, and nutrient runoff, and octocoral and scleractinian diseases will help to identify the actions that can be taken to protect these important marine communities.

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Conservation and Management of Vulnerable Marine Benthic Ecosystems

41

Ricardo Aguilar, Allison L. Perry, and Javier López

Abstract

Apart from natural factors such as climatic variation, which can drive species and habitats to extinction over the long term, and devastating sporadic episodes, like volcanic eruptions, animal forests (e.g., coral reefs, gorgonian gardens, and sponge fields, among others) are mainly threatened by human activities. Coastal destruction, dredging, mining, offshore infrastructure, oil and gas production, pollution, and climate change are among the main anthropogenic threats faced by marine ecosystems, but fisheries have become the human activity with the greatest and most widespread impact upon reefs and other benthic ecosystems. During recent decades, some international conventions have aimed to reduce these impacts, trying also to bring together governments in order to stop the loss of biodiversity in the oceans. However, marine conservation still lags far behind the advances that have been made in the protection of terrestrial ecosystems. Most marine species and habitats are generally not well known or valued by decision-makers or the general public, and many efforts to introduce conservation measures have been blocked as a result of intensive lobbying by the bottom trawling sector. As a result, advances in management, including conservation, have been slow. There is a general consensus about the need to protect different marine habitats, ecosystems, and communities that are very productive and useful for humankind in many different ways. These are ecosystems which support the life cycles of commercial species, are essential for the global economy, form biodiversity hotspots, or are part of spectacular seascapes that constitute part of natural heritage. Yet the way forward for the conservation of animal forests worldwide is uncertain; there is still a broad and interesting debate on what should be done to protect them, and how this protection should be developed and implemented, both within national waters and in areas beyond national

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jurisdiction. Advances in international and national policies related to conservation and fisheries management have provided the first steps. However, these developments only address the tip of the iceberg of what should be done, based on the available scientific knowledge.

Seamounts, submarine canyons, hydrothermal vents, cold seeps, and other topographic features are known in many cases to be important biodiversity hotspots. Coral reefs, sponge aggregations, gorgonian and black coral gardens, sea pen fields, mollusk beds, and other animal forests have been recognized as key habitats which occur in many cases in association with topographic features such as the ones mentioned above. Most of these ecosystems are gradually becoming part of the international list of vulnerable marine ecosystems (VMEs), and in some regions, measures are being developed to protect them, particularly within Regional Fisheries Management Organizations (RFMOs).

Marine science continuously provides data on new species, habitats, and communities, improving our understanding of their interspecific relationships, and the roles they play within marine ecosystems, and in the biosphere as a whole. In turn, marine management, including conservation, should also progress in light of this increasing knowledge. Human impacts must be necessarily included in the final equation, as we will continue to use marine resources. Ultimately, we are responsible for ensuring the long-term sustainability and health of the ocean realm.

Keywords

Vulnerable Marine Ecosystems (VMEs) • Fisheries impacts • Marine conservation • Regional Fisheries Management Organizations (RFMOs) • Corals • Sponges • Biogenic habitats • Animal forests

Contents

1 Introduction: Animal Forests Under Threat

Many animal forests are ecosystems which include communities with low resilience and are at the same time hotspots of biodiversity. Coral reefs and gardens, sponge aggregations, oyster concretions, mussel beds, polychaete reefs, etc., are among the most widespread animal forests, from shallow to deep waters worldwide (see Rossi et al. this volume). Some species that form animal forests, such as sea pens, require soft sediment to burrow; others, such as many hard coral species, need a hard natural substrate in order to settle. In some cases, the animals that create forests can provide a secondary hard substrate upon which other organisms (or they themselves) develop, as sometimes occurs with mussels. Biogenic reefs and other animal forests play an important role for physical and biological marine processes, including stabilizing sediments, serving as substrate for other species, and providing essential habitats (e.g., spawning, breeding, nursery, or feeding areas) for other organisms (Holt et al. 1998; see Henry and Roberts, Orejas and Jiménez, and Rossi et al., among others in this volume). Animal forests are also key players that contribute to the so-called good environmental status (GES) of the oceans, as the conservation of these ecosystems (including their full functionality) is considered an important aspect of GES. Their conservation is required under some international legislation, such as the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC) which applies to all countries that are part of the European Union. The concept of GES has also been adopted by regional seas conventions such as the Baltic Marine Environment Protection Commission (Helsinki Commission, or HELCOM) and the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR).

Across the world's oceans, animal forests face a wide array of anthropogenic threats. The most direct and obvious such threat is fishing. Various studies have examined animal forests around the globe and evaluated the impacts of fisheries on their communities, including loss of biodiversity, decreased productivity, and shifts in ecosystem function (e.g., Pansini and Musso 1991; McConnaughey et al. 2000; Moran and Stephenson 2000; Ilan et al. 2003; Kenchington et al. 2011; Buhl-Mortensen and Buhl-Mortensen 2014; Gonzalez-Mirelis and Buhl-Mortensen 2015).

The most damaging fishing activities are the ones using gears that come into direct contact with the seafloor, such as bottom trawls or dredges (see Hinz, this volume). The impacts of these activities on marine ecosystems are well known. A clear example regarding the effects of trawling is the dramatic decline of populations of the bamboo coral *Isidella elongata* in the Mediterranean (Maynou and Cartes 2011), leading this species to be considered Critically Endangered in the Mediterranean by the International Union for Conservation of Nature (IUCN) (IUCN 2016). These fishing methods are also responsible for high levels of bycatch and damage to other invertebrates, such as sponges and corals (Freese et al. 1999; Freese 2001; Hall-Spencer et al. 2002; Murillo et al. 2008). Oyster dredging also has a severe impact on other animal forests, such as those formed by bryozoans (Cranfield et al. 2003) and other benthic species, like other mollusks, polychaetes, and amphipods (Mercaldo-Allen and Goldberg 2011).

Although fishing is the most widespread human activity that threatens the marine environment (Halpern et al. 2008), with the most direct impacts on animal forests, many other anthropogenic activities – including mining, pollution, sedimentation, introduction of invasive species, and coastal destruction, among others – also threaten marine biodiversity (Fig. 1). The impacts of specific threats on marine ecosystems have been extensively studied during the last two decades, such as the effects of oil and gas activities in the oceans (NRC 2003; OSPAR 2009), plastic debris and lost fishing gears (Derraik 2002; Gregory 2010), and eutrophication (Smith et al. 1999). Considerable efforts have also been made to assess and predict the pervasive impacts of climate change on marine ecosystems (Hoegh-Guldberg and Bruno 2010; Poloczanska et al. 2013), with particular concerns raised about the immediate threat that rising temperatures and ocean acidification pose to tropical coral reefs (Hoegh-Guldberg et al. 2007; Burke et al. 2011; Bianchi et al., this volume). Nevertheless, we are still far from understanding the full nature and extent of human impacts on animal forests, and how their cumulative effects combine.

Animal forests that occur on hard substrates have traditionally been more studied and have represented the focus of many conservation efforts. Nevertheless, the species that face the most serious threats are those that live on muddy and sandy bottoms. All kinds of fishing gear, including damaging bottom-contact gear, can be used on soft bottoms; the dumping of waste, extraction of sand and gravel, anchoring, oil exploitation, mining, and many other activities also occur on soft substrates (as well as on hard substrates). Impacts on soft bottoms have been unfortunately disregarded in many cases, due partly to the widespread misperception that the resulting damage to soft substrates is not as important as that which occurs to hard substrates. As a result of the extensive exploitation of soft bottoms, and the scale and severity of the impacts upon them, many populations of typical soft bottom species that form animal forests on muddy or sandy substrates have suffered serious declines. These include, for example, some species of bamboo corals (Isidiidae) and other gorgonians (i.e., Chrysogorgiidae), sea pens (Pennatulacea), tube anemones (Ceriantharia), birds' nest sponges (*Pheronema* spp.), other Hexactinellids, several species of carnivorous sponges (Cladorhizidae) and other demospongiae (of the genera *Thenea, Rhizaxinella, Tentoria, Geodia*, etc.), and even Calcaronea (Fig. 2). In some cases, even in relatively well-studied areas, the recognition of such declines is likely to have been hindered by the effects of the "shifting baselines syndrome" (Pauly 1995), because scientists are unlikely to realize the extent of damage that may have already occurred as a result of previous impacts (e.g., Thurstan et al. 2010; Cook et al. 2013).

2 Protection of Key Habitat-Forming Species and Areas

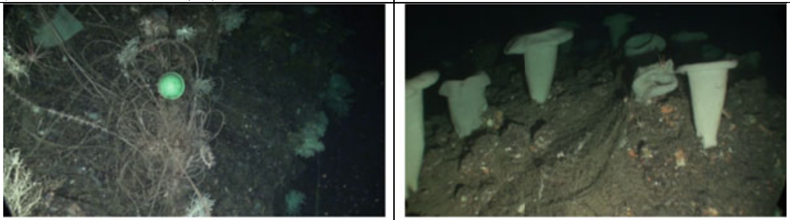
In response to the diverse and increasing threats, and thanks to increasing knowledge about benthic ecosystems, the protection of animal forests has gradually advanced, especially in recent decades. At the species level, measures have been applied at different geographical levels (e.g., local, regional, and international) to strictly

Net damaging coral garden. Chella Bank (Western Mediterranean, 190 m depth).

Fishing lines in sponge aggregation. Southwest Portugal (Atlantic Ocean, 440 m depth).

Fish (*Phycis blennoides* and *Helicolenus dactylopterus*) among accumulated garbage. Emile Baudot escarpment (Balearic Islands, 620 m depth).

Trawl net in gorgonian garden. South Portugal (Gulf of Cadiz, 110 m depth).

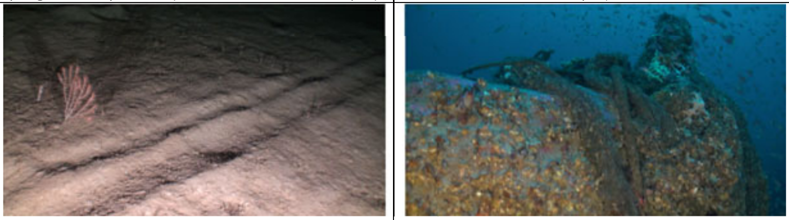


Long-line entangled in cold water corals. Alboran Sea (Western Mediterranean, 450 m depth).

Net damaging *Asconema setubalense* ground. Chella Bank (Western Mediterranean, 400 m depth).

Garbage damaging primnoid corals and hexactinellid sponges. Canary Islands (Atlantic Ocean, 820 m depth).

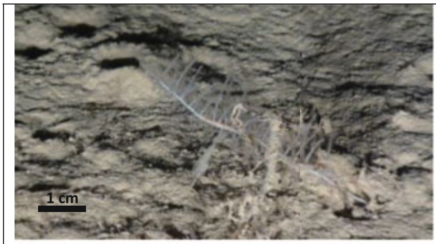
Sea bed destroyed by trawling. Alboran Sea (Western Mediterranean, 330 m depth).



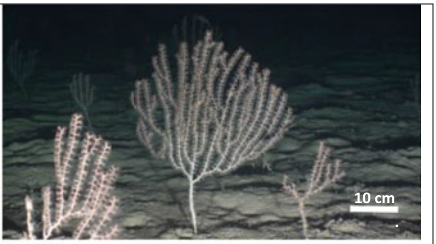
Bamboo coral (*Isidella elongata*) and sea pen (*Kophobelemnon stelliferum*) beside a trawling mark. Western Mediterranean Sea (510 m depth).

Trawl net covering sponge and oyster aggregations. Balearic Islands (Western Mediterranean, 80 m depth).

Fig. 1 Threats to animal forests



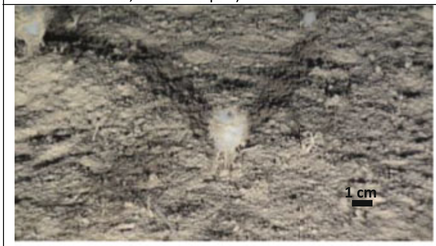
Cladorhiza abyssicola. Balearic Islands (Western Mediterranean, 450 m depth).



Bamboo coral (*Isidella elongata*).Western Mediterranean (460 m depth).

Funiculina quadrangularis. South Sicily (Central Mediterranean, 170 m depth).

Pennatula spp. Alboran Sea (Western Mediterranean, 125 m depth).



Thenea muricata. Western Mediterranean (440 m depth).

Kinetoskias sp. Balearic Sea (Western Mediterranean, 470 m depth).

Flabellum chunii. Gorringe Bank (Atlantic Ocean, 320 m depth).

Caryophyllia smitthi var *clavus*. Alboran Sea (Western Mediterranean, 280 m depth).

Fig. 2 Animal forests living on soft bottoms

protect some highly threatened species – particularly corals – through prohibitions on their exploitation and/or trade (see Annex). For example, the New Zealand Wildlife Act (1953) protects all species in the orders Anthipatharia (black corals), Gorgonacea (gorgonians), Scleractinia (stony corals), and the family Stylasteridae (lace corals) in New Zealand waters, while the United States currently lists 22 coral species under its Endangered Species Act (1973). At the international level, some regional seas conventions also offer strict protection, such as the Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (Barcelona Convention), which includes corals and sponges on its Annex II list of threatened or endangered species in the Mediterranean Sea. The Specially Protected Areas and Wildlife (SPAW) protocol of the Cartagena Convention for the Caribbean Sea also includes a long list of hydrozoans and corals that are protected under its Annex II of threatened or endangered animal species.

Although species-specific protection is important, the conservation of animal forests depends on habitat-level approaches, and most critically, upon spatial management of human activities, including the creation of marine protected areas (MPAs). MPA coverage has increased steadily during the last decades. According to the World Database on Protected Areas, run by IUCN and the United Nations Environment Programme (UNEP), marine protected areas now cover approximately 4% of the global ocean (UNEP-WCMC, IUCN 2016). However, marine protection still lags behind the protection of terrestrial ecosystems. This is partly due to the fact that there are still many oceanic areas which have been unexplored by science. Also, the fact that scientific study tends to lag behind commercial exploitation means that there remains the risk that scientists arrive too late to explore areas that have already been discovered – and damaged – by wide-ranging international fishing fleets. The slow pace at which MPAs are declared makes Aichi Target 11 under the United Nations Convention on Biological Diversity (CBD), of 10% of the world's oceans protected by 2020 (UNEP 2010), still a difficult goal to achieve. Even further off is the IUCN recommendation to protect 20–30% of the marine surface worldwide to stop the loss of biodiversity (IUCN 2003). This recommendation, which set a 2012 deadline for the creation of this global network of MPAs, was further developed at the World Parks Congress in 2014, with the added stipulation that at least 30% of the surface of those MPAs must be under "no-take zones" (IUCN 2014).

Unfortunately, fully protected no-take zones are still scarce. An assessment by Wood et al. (2008) estimated that only 0.08% of the world's oceans were included under fully protected areas or no-take zones, which corresponds to only 5% of the entire MPAs coverage worldwide. Another frequent problem regarding protection of MPAs is the lack of real protection measures. Many MPAs are just "paper parks" that lack sufficient management measures or enforcement, and as a result these areas fail to achieve their intended aims (White and Courtney 2005; Rife et al. 2013). Even in areas where management plans exist and are enforced, these plans are often far from comprehensive, still permitting activities that continue to damage epibenthic habitats, and thus animal forests. For instance, the regulation of bottom fishing activities has been weak or delayed in some European MPAs that were established specifically due to the presence of reefs formed by corals, mussels, polychaetes, etc., or fragile bubbling reefs (a type of cold seep). For example, fewer than 70% of Baltic MPAs have approved management plans, and when approved there are neither specific measures for protecting and recovering fragile habitats, nor almost any limitations on human activities (Paulomäki et al. 2014).

Improving the effectiveness of MPAs for animal forests will also require the protection of new, larger areas in deeper, offshore waters. Most MPAs are small, with a median size of just 2.7 km^2 (Costello and Ballantine 2015), which limits their potential to protect the species and habitats within their boundaries (Edgar et al. 2014). Even in areas where large MPAs have been established, their potential for protecting animal forests (and other species and habitats) from anthropogenic threats depends heavily on where they are placed. Many of the world's largest MPAs appear to be "residual" to extractive uses (Devillers et al. 2015) because they are located in remote areas, where such threats are relatively low (Burke et al. 2011; Spalding et al. 2013). A similar bias can be seen at the national level in Australia, where the most highly protected MPAs added to the National Representative System of Marine Protected Areas in 2012 were generally established in areas that did not overlap with the most intense extractive activities (Devillers et al. 2015).

Globally, there is a general bias toward protecting coastal and shallow waters, as these are typically the best studied areas, and also because of the legal and technical complexities associated with protecting areas in the high seas (Ardron et al. 2008; O'Leary et al. 2012). However, the creation of high seas MPAs may be made easier in the coming years, by the development of a new legally binding instrument on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (ABNJ), under the United Nations Convention on the Law of the Sea (UNCLOS). This instrument, which is currently in the early stages of preparation, is expected to include area-based management measures (including the creation of MPAs) as one of the main elements of the agreement (Wright et al. 2016).

3 International Legislation to Protect Animal Forests

3.1 Environmental Legislation

Various types of animal forests have gradually begun to be listed under categories such as "vulnerable marine ecosystems" (VMEs) and/or habitats, "sensitive habitats" (SH), and "essential fish habitats" (EFH). These faunal formations are listed alongside other species and habitats from other biological kingdoms (e.g., algae forests, seagrass meadows), as well as oceanic features that play important roles in the marine world (e.g., seamounts, submarine canyons).

For example, in 2008, OSPAR created a "List of Threatened and/or Declining Species & Habitats" that includes coral gardens, deep-sea sponge aggregations, intertidal *Mytilus edulis* beds, *Lophelia pertusa* reefs, *Modiolus modiolus* beds, *Ostrea edulis* beds, *Sabellaria spinulosa* reefs, sea pens and burrowing megafauna communities, and other (mainly topographic) marine features. This list is intended to guide OSPAR in setting priorities for its marine conservation work. Within OSPAR, there is a list of recommendations as well as agreed actions that should be applied to improve the status of listed species and habitats. However, it is worth noting that OSPAR has no competence concerning fisheries management, and so the potential benefits of these recommendations are limited for animal forests where the most significant threat is fishing activities.

In addition to listing and protecting some highly threatened species that form animal forests, the Barcelona Convention has approved two protocols to protect biogenic reefs and deep-sea habitats. These protocols contain specific references to bioconcretions, assemblages of engineering benthic invertebrates, underwater canyons, seamounts, and deep-sea chemosynthetic features.

At the global scale, the United Nations Convention on Biological Diversity (CBD) has taken into account the marine realm since the beginning of its establishment in 1992, but it has been proven difficult to develop clear guidelines or actions required to address the challenges, damages, and losses that marine ecosystems face. Under Article 6 of the CBD, on General Measures for Conservation and Sustainable Use, each Contracting Party committed to develop National Biodiversity Strategies and Action Plans. Unfortunately, the marine environment has not been treated equally by each country, and generally represents a marginal part of many strategies and plans.

Subsequent meetings and processes have provided further content to the CBD, including the 2008 adoption, during the ninth Conference of the Parties, of scientific criteria for identifying Ecologically or Biologically Significant Marine Areas (EBSAs) in need of protection in open-ocean waters and deep-sea habitats (CBD 2008). Seven criteria were approved as the basis for identifying EBSAs, many of which are relevant for animal forests: (1) uniqueness or rarity; (2) special importance for life history stages of species; (3) importance for threatened, endangered, or declining species and/or habitats; (4) vulnerability, fragility, sensitivity, or slow recovery; (5) biological productivity; (6) biological diversity; and (7) naturalness.

Although the identification of EBSAs is a scientific process, it was formally recognized in 2010 that areas meeting the criteria may require enhanced measures for management, including conservation. Since then, a series of regional workshops have been held worldwide to improve the identification and protection of EBSAs. However, scientific recommendations have not been always endorsed by politicians. EBSAs have not yet been declared for the Antarctic Ocean or the North-East Atlantic Ocean, and some of the most important EBSAs proposed by scientists for the Mediterranean Sea have been stopped due to political differences between governments.

To date, 204 EBSAs have been approved: 11 in the Arctic, 21 in the Eastern Tropical and Temperate Pacific, 15 in the Mediterranean Sea, 20 in the North Pacific, 7 in the North-west Atlantic, 44 in the South-Eastern Atlantic, 39 in the Southern Indian Ocean, 26 in the Western South Pacific, and 21 in the Wider Caribbean and Western Mid-Atlantic (CBD 2016). Many of these EBSAs include animal forests within their boundaries, such as aggregations of sponges, bryozoans, and red hydrocorals found near Moneron Island in the Sea of Okhotsk, and cold-water coral (CWC) reefs and gardens on the Coral Seamount, in sub-Antarctic waters of the south-west Indian Ocean (CBD 2014).

Unfortunately, despite these good intentions, many of the declared EBSAs are still pending the adoption of detailed plans and management measures to stop the decline of the ecosystems for which they were designated. The CBD, like other international conventions, depends on the political will of contracting parties to approve and implement the necessary measures to avoid further damage to these habitats, and to reach ambitious agreements that will apply to both national and international waters.

3.2 Fisheries Legislation and Vulnerable Marine Ecosystems

Fisheries management regulations and plans also include important conservation measures to protect animal forests. Many of these measures have been established at the international level, regarding the concept of vulnerable marine ecosystems (VMEs). VMEs are groups of species, communities, or habitats that may be vulnerable to impacts from fishing activities (FAO 2016). Within the VME framework, vulnerability reflects both the likelihood that short-term or chronic disturbance will cause substantial alteration, and the likelihood of recovery (FAO 2009). The protection of VMEs has been a legal obligation for states and regional fisheries management organizations (RFMOs) since 2008, with specific requirements laid out under United Nations General Assembly (UNGA) Resolutions 59/25, 61/105, and 64/72.

In order to assist states and RFMOs in fulfilling these obligations, particularly in relation to UNGA Resolution 61/105, the FAO published its *International Guidelines for the Management of Deep-Sea Fisheries in the High Seas* (FAO 2009). This document provides guidance on criteria for identifying VMEs, assessing potential impacts, developing management frameworks, improving data collection, and developing conservation and management plans and measures, in order to prevent significant adverse impacts from fishing activities on deep-sea VMEs, and to protect the biodiversity that they contain.

While specific lists of VMEs must be developed on a regional basis, the FAO guidelines (2009) provide examples of species groups, communities, and habitats that are considered sensitive to deep-sea fishing and may contribute to forming VMEs:

- Certain CWC and hydroids, e.g., reef builders and coral forest including: stony corals (Scleractinia), alcyonaceans and gorgonians (Octocorallia), black corals (Antipatharia), and hydrocorals (Stylasteridae)
- Some types of sponge-dominated communities
- Communities composed of dense emergent fauna where large sessile protozoans (xenophyophores) and invertebrates (e.g., hydroids and bryozoans) form an important structural component of habitat
- Seep and vent communities comprise invertebrate and microbial species found nowhere else (i.e., endemic)

The guidelines also highlight certain types of topographic features that may support the above-mentioned species groups and communities:

- Submerged edges and slopes (e.g., corals and sponges)
- Summits and flanks of seamounts, guyots, banks, knolls, and hills (e.g., corals, sponges, xenophyophores)
- Canyons and trenches (e.g., burrowed clay outcrops, corals)
- Hydrothermal vents (e.g., microbial communities and endemic invertebrates)
- Cold seeps (e.g., mud volcanoes for microbes, hard substrates for sessile invertebrates)

To date, most of the progress in establishing fisheries measures to protect VMEs has occurred at the regional scale, within the framework of RFMOs, and animal forests comprise an essential part of the regional VME lists that have been developed (FAO 2016). These lists are variable in their scope, which in turn directly affects which animal forest taxa are covered by VME management measures. For example, most RFMOs include CWC and sponges, but not all emergent faunal communities such as hydroids, bryozoans and sessile protozoans, and endemic seep and vent communities.

Across RFMOs, specific VME measures also vary widely (Table 1). For example, many (but not all) RFMOs have developed protocols to apply for vessels that encounter VMEs during the course of fishing operations, while spatial closures and restrictions on destructive gear types have been less consistently applied across regions, as it is outlined below.

In the Antarctic Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has implemented several conservation measures that are relevant to the protection of animal forests. Notably, in 2008, CCAMLR banned bottom trawling in the high seas area under its jurisdiction, with the exception of areas where conservation measures were already in place for bottom trawling (CCAMLR 2008). Several additional areas where VMEs have been documented have recently been closed to all bottom fishing (CCAMLR 2012).

The North-East Atlantic Fisheries Commission (NEAFC) has forbidden bottom fishing activities in specific areas to protect VMEs and has published a list of habitat types (including different types of animal forests) and physical features that are considered VME indicators (NEAFC 2014). NEAFC has also established an impact assessment protocol for proposed fishing activities outside the area that is currently fished, and no new areas may be opened to fishing without having sufficient information to assess its impacts.

In the Western Atlantic, the Northwest Atlantic Fisheries Organization (NAFO) has also developed a list of topographic VME indicator elements and benthic invertebrate VME indicator species, together with various maps of their distribution. Moreover, NAFO has established a process for assessing, managing, and evaluating proposed "exploratory bottom fisheries" beyond the current fishing footprint before allowing them to go ahead. Some areas have also been designated as closed to bottom fishing activities, in order to protect seamounts, corals, sponges, and sea pens (NAFO 2016).

In the southern hemisphere, the South East Atlantic Fisheries Organization (SEAFO) has implemented a series of measures for VME protection. SEAFO has

Table 1 Overview of current RFMO protection measures and protocols for VMEs

RFMO	VME indicator list	VME encounter protocol	Direct closure of fishing areas following encounters	Banning of bottom contact gears	Specific areas closed to protect VMEs	Onboard observers	Exploratory fishery protocol that includes potential impacts on VMEs	Requirements to collect information pertaining to bycatch of VMEs
CCAMLR (2008, 2010, 2012, 2013, 2015)	Yes	Yes	Yes	Bottom trawling and gillnets are prohibited	Yes	Yes	Yes	Yes
GFCM (2005, 2006, 2016)	No	No	No	Towed dredges and trawl nets prohibited below 1000 m	Yes	No	No	No
NAFO (2016)	Yes	Yes	No	No	Yes	Yes	Yes	Yes
NEAFC (2006, 2014)	Yes	Yes	Yes	Gillnets, entangling nets, and trammel nets are prohibited below 200 m	Yes	Yes, but only during exploratory fishing	Yes	Yes

NPFC – NW (2016a) – NE (2016b)	Yes (NW) Yes (NE)	Yes (NW) Yes (NE)	No (NW) No (NE)	Below 1500 m in some areas, and bottom fisheries closure from Nov-Dec (NW) No (NE)	Only very small areas (NW) No (NE)	Yes, for all vessels authorized for bottom fishing (NW) Yes (NE)	Yes (NW) Yes (NE)	Yes (NW) Yes, but only when observers on board (NE)
SEAFO (2009, 2015)	Yes	Yes	Yes	Gillnets are recommended to be banned	Yes	Yes, but only during exploratory fishing	Yes	Yes
SPRFMO (2013, 2016)	No	Yes but there are no agreed thresholds	No	Deep water gillnets are prohibited	Only very small areas	Observers on 100% of trawlers, and 10% of other vessels	Yes	No

defined the fishing footprint, established protocols for exploratory fishing, and prohibited the use of bottom contact fishing gears in 11 areas, most of which include seamounts, to prevent damage to VMEs (SEAFO 2015).

In other regions, progress to protect VMEs has been slower. For example, in the Mediterranean, the General Fisheries Commission for the Mediterranean (GFCM) has banned the use of towed dredges and bottom trawls in three specific areas (Santa Maria di Leuca, the Eratosthenes seamount, and the Nile delta cold hydrocarbon seeps), to protect deep-sea coral reefs and other sensitive habitats (GFCM 2006). The use of these same gear types is also prohibited below 1000 m depth across the Mediterranean (GFCM 2005), although it should be emphasized that most VMEs occur in waters above this depth. GFCM is currently beginning the process of preparing a list of Mediterranean VME indicator species and developing new measures for VME protection.

In the Pacific Ocean, the North Pacific Fisheries Commission (NPFC) – for the Northeastern and Northwestern basins – has adopted a series of conservation and management measures related to the protection of VMEs, in particular seamounts, hydrothermal vents, and CWC. These measures include standards for identifying potential VMEs and assessing the impacts of bottom fisheries on those VMEs, a protocol for exploratory fisheries, and a prohibition on engaging in directed fishing on Alcyonacea, Antipatharia, Gorgonacea, and Scleractinia (NPFC 2016a, b). The South Pacific Regional Marine Fisheries Organization (SPRMFO) has also adopted standards for impact assessments and exploratory fisheries (SPRFMO 2016).

In addition to measures within the framework of RFMOs, the EU has also recently agreed on a regulation (Regulation (EU) 2016/2336) establishing new conditions for deep-sea fisheries in EU waters of the North-East Atlantic, and for the EU fleet in certain areas in international waters of the area under the jurisdiction of the Fishery Committee for the Eastern Central Atlantic (CECAF). This regulation contains specific requirements for the protection of VMEs, including: the prohibition of bottom trawling below 800 m; a protocol for identifying and closing VME areas below 400 m to bottom fishing; and the freezing of the deep-sea bottom-fishing footprint, such that impact assessments will be required before any fishing can be authorized beyond existing fishing areas.

In the high seas, beyond the waters under the jurisdiction of nations or RFMOs, VME protection is limited. The European Union requires its bottom fishing fleets in the high seas to apply measures in accordance with the UNGA requirements for VME protection, including an encounter protocol, prior impact assessment, and the closure of VME areas to bottom fishing (Council Regulation (EC) 734/2008). Further developments of such measures for high seas VMEs are likely to remain one of the topics of discussion within the ongoing process to create a new international legally binding instrument on the conservation and sustainable use of marine biodiversity in ABNJ, under the umbrella of UNCLOS.

As VME protocols and measures continue to evolve and be developed, there are a number of weaknesses that should be taken into account and addressed, if they are to confer effective protection to marine animal forests. A clear example to illustrate this point concerns VME encounter protocols, which require vessels to report VMEs encountered during fishing operations, and to cease fishing in the area where an encounter occurs (i.e., to follow "move-on" rules). Across RFMOs, many of the below weaknesses limit the effectiveness of these protocols:

(a) Encounter thresholds. "Encounters" are defined with respect to quantitative thresholds (e.g., kg of indicator species retained in fishing gear) that have been arbitrarily defined, with no scientific basis. The thresholds currently defined are generally too high to have any conservation value. For instance, SEAFO and NEAFC do not consider a sponge encounter to have occurred unless the quantity caught exceeds 400 kg of live sponge. Studies have recommended either adopting a simple presence/absence approach or much lower thresholds (Auster et al. 2011; Rogers and Gianni 2010), as well as taking into account details of the species biomass and density, habitat type and complexity, size of the area fished, and catch efficiency of gear.

(b) Retention of VME indicator species in fishing gear. Quantities of VME indicator species retained depend heavily on the retention efficiency of fishing gear. For most sessile benthic organisms, what is retained by trawl nets is a very poor indicator of actual species composition and density on the seabed. Retention rates of vulnerable species are generally low, for example: $<1\%$ for asteroids, echinoids, and mollusks; $<5\%$ for holothurians; and $<10\%$ for most coral and sponge species (see Auster et al. 2011). Therefore, actual quantities of VMEs affected can be ten to 100 times higher than what is retained by nets, while potential VME indicator species that are not retained by fishing gears in detectable quantities remain effectively unprotected by these protocols.

(c) Live vs. dead VME indicator species. Nearly all encounter protocols define thresholds based on captured quantities of live indicator species, which can be problematic (Rogers and Gianni 2010; Auster et al. 2011). For example, deep-sea coral reefs are complex patchworks of actively growing areas and dead areas where the coral structure remains intact; the vast majority of other species associated with complex reef ecosystems are often also abundant in the patches of dead coral (Weaver et al. 2011). Focusing only on live coral retained in trawls is inconsistent with the intentions of the UNGA resolutions to protect these ecosystems.

(d) Fished vs. unfished areas. General concerns have been raised about differing levels of VME protection existing fishing areas versus areas that have not previously been fished, including how encounter protocols are applied (Rogers and Gianni 2010). The density of VMEs is likely to be lower in fished areas than in unfished areas, and lower captures of VME indicator species are therefore expected in fished areas, making it even less likely that vessels will exceed the defined encounter thresholds in those areas. Nonetheless, such remnant VME areas also require protection, to allow them to regenerate and recover. Thresholds set for areas that are already fished should therefore be lower than for areas where fishing has not previously been carried out.

(e) Identifying encounter locations. It is not usually possible to determine the specific location along a trawl track where a VME encounter occurred. While many RFMOs require vessels to move a set distance (e.g., 2 nm) away from an encounter, it is not possible to identify the exact location of an encounter (or encounters). Trawl tows also vary greatly in length. Rather than assuming a particular location for the encounter, the move-on rule and associated fisheries closure should apply to a buffer area around the entire trawl track.

(f) Area closures. Many current protocols establish that only the vessel which exceeds the VME threshold is required to leave the encounter area, when this provision should trigger the closure of the area to all fishing vessels using similar gears (Kenchington 2011; Hansen et al. 2013). Following encounters, areas should be closed until there is clear scientific evidence that bottom fishing will not have significant adverse impacts on VMEs.

(g) Compliance. In most RFMOs, very few or no VME encounters have been officially reported. This may indicate a lack of compliance with the protocols (Gianni et al. 2011), the fact that thresholds have been set too high, or, on the positive side, that as a result of the protocols, fishing vessels actively avoid areas where VMEs might be encountered. To effectively implement encounter protocols and improve compliance, 100% observer coverage is necessary (see Large et al. (2013) for an overview of observer coverage across RFMOs).

It is clear that there are still many aspects to improve regarding the protection of VMEs. Such measures must be precautionary and should be adapted in accordance with assessments of their effectiveness and improved scientific knowledge about VMEs.

4 Broader Legal Tools for the Protection of Animal Forests

In contrast to VMEs, Sensitive Habitats (SH) and Essential Fish Habitats (EFH) are less developed concepts. At the national level, only the USA has included one of these terms (EFH) within its legislation, specifically in the Magnuson-Stevens Fishery Conservation and Management Act. It describes EFHs as: “all waters and substrate necessary for fish for spawning, breeding, feeding, or growth to maturity.” These habitats have been identified and mapped by NOAA Fisheries and the regional fishery management councils in the USA, for nearly 1000 species, and they include animal forests such as coral reefs and oyster reefs (NOAA 2016). The term EFH has also been used in other areas, such as in UK waters (MMO 2016) and in relation to the Mediterranean Sea (STECF 2006; Valavanis 2008). However, the connections between animal forests, SH, and EFH have been less well developed.

A closely related concept that was included in the 2013 EU Common Fisheries Policy (Regulation (EU) 1380/2013) is that of “fish stock recovery areas.” These are defined as “biologically sensitive areas in which there is clear evidence of spawning grounds, or large concentrations of fish below minimum conservation reference size (i.e., juveniles)”. Where animal forests represent important fish spawning or nursery areas, this provision could allow for their protection, because the law allows for the restriction or prohibition of fishing activities in these areas, in order to conserve marine ecosystems.

One additional European instrument is also potentially beneficial for animal forests. The Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC) requires the achievement or maintenance of “good environmental status” (GES) for marine waters. The MSFD lays out eleven qualitative elements, or “descriptors” related to GES; one important such descriptor is “sea-floor integrity” (Descriptor 6) which should be “at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems, in particular, are not adversely affected” (see Berg et al. 2015 for further discussion). EU Member States that have identified sea-floor integrity as a priority descriptor for their waters are legally required to implement measures that will contribute to achieving or maintaining GES of benthic ecosystems. The legal recognition of the importance of protecting benthic ecosystems as a specific element of the MSFD carries an important message for the wider protection of marine animal forests.

5 Vulnerable Habitats and Animal Forests

As noted above, a variety of denominations are used to refer to habitat-forming species and related topographic features across different scientific, legal, and management frameworks and fora. Many related terms, such as Vulnerable Habitats, VMEs, SH, and in some cases, EFH, refer to habitats that are either formed by animal forests, or in which animal forests play an important role.

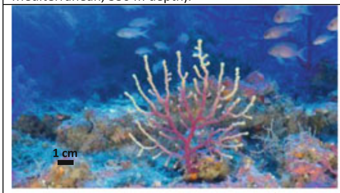
Corals and sponges are among the most common species reflected in these different habitat/ecosystem categorizations; this is due to their role in forming large, three-dimensional structures and their relative dominance in the epifauna of deep seas and in the majority of the world’s oceans (Cathalot et al. 2015; Orejas and Jiménez, this volume). The high value of both shallow and deep coral reefs for biodiversity is very well known (Bellwood et al. 2003; Buhl-Mortensen and Mortensen 2005; Mortensen and Fossa 2006; Jackson et al. 2014; Buhl-Mortensen et al., this volume), while studies of sponge aggregations are also unveiling their role as hotspots for biodiversity, providing refuge and habitats for fish and invertebrates, and serving as a source of basic nutrients (Klitgaard 1995; Klitgaard and Tendal 2004; Maldonado et al. 2011, 2012, and this volume) (Fig. 3).

Other animal forest phyla (such as polychaetes, mollusks, crustaceans, echinoderms, bryozoans, etc.) can play similar functional roles to corals and sponges, in both shallow and deep areas (Buhl-Mortensen et al. 2010). Despite this fact, conservation measures to protect these other benthic communities are scarce, and a few well-protected areas are in place to safeguard them.

Colonial animals are commonly considered to be the main components of animal forests, but high densities of solitary individuals can also occur and are important for characterizing marine benthic communities. Such habitats dominated by solitary animals must also be considered within the category of animal forests. For example,

Lophelia pertusa reef. Cabliers Bank (Western Mediterranean, 330 m depth).

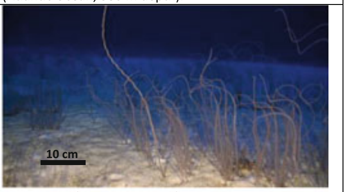
Asconema setubalense aggregation. Chella Bank (Western Mediterranean, 400 m depth).



Gorgonian garden. Western Mediterranean (100 m depth).

Lithistids and other deep-sea sponges. Gorringe Bank (Atlantic Ocean, 380 m depth).

Soft coral (*Nidalia studeri*). Western Mediterranean (200 m depth).



Black corals (*Stichopathes* sp.). Dacia seamount (Atlantic Ocean, 130 m depth).

Viminella flagellum garden. Chella Bank (Western Mediterranean, 160 m depth).

Morid among glass sponge garden. Bimbache seamount (Atlantic Ocean, 880m depth).

Black corals (*Leiopathes glaberrima*). Alboran Sea (Western Mediterranean, 440 m depth).

Narella sp. Gorringe Bank (Atlantic Ocean, 390 m depth).

Large sponges (*Geodia atlantica* & *Phakellia ventilabrum*). North Sea (Atlantic Ocean, 180 m depth).

Fig. 3 Coral forests and sponge fields solitary scleractinian corals (such as *Desmophyllum dianthus*) can be highly abundant in well-preserved areas (Althaus et al. 2009), while organisms such as *Flabellum* spp. (Buhl-Mortensen et al. 2007), *Caryophyllia smithii* var. *clavus* (Oceana, IEO 2014), *Deltocyathus* spp. (Arantes et al. 2009), and others can form large communities in detritic beds (Fig. 2).

Knowledge of these communities and the importance accorded to them in international fora is also biased toward hard-bottom habitats. This bias is understandable due to the fact that hard bottoms act like reefs, as substrate that allow many species to settle which are much scarcer in areas dominated by sedimentary bottoms. This, together with the fact that soft bottom areas are for various commercial and other human activities (e.g., fisheries, dredging, waste dumping, mining, and hydrocarbon exploration), has relegated these habitats to a much lower priority level for protection among governments.

5.1 Not only Corals and Sponges

Apart from corals and sponges, other habitat-forming animals play important roles in the benthic realm but are, as mentioned previously, usually ignored in international lists and laws. For example, bryozoans, polychaetes, mollusks, crustaceans, and brachiopods can also create key animal forests (Fig. 4, see for instance chapters by Montiel and Cárdenas, ▶ Chap. 9, “Coexistence in Cold Waters: Animal Forests in Seaweed-Dominated Habitats in Southern High-Latitudes,” Försterra et al., ▶ Chap. 10, “Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters,” Gutt et al., ▶ Chap. 11, “Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems,” Milazzo et al., ▶ Chap. 12, “Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean,” and Orejas and Jiménez, ▶ Chap. 23, “The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep,” this volume).

Bryozoans like *Celleporaria agglutinans* and *Hippomenella vellicata* can form reef-like structures in the Southern Pacific (Bradstock and Gordon 1983), as do *Pentapora fascialis* and *Myriapora truncata* in the Atlantic and Mediterranean (Cocito 2009). On soft bottoms, they may even be abundant, such as *Kinetoskias* sp. and some species of the Candidae family (Harmelin and d’Hondt 1993; Aguilar et al. 2013).

Mollusks such as mussels, oysters, and quahogs have suffered severe declines in distribution (AquaSense 2001; Beck et al. 2009; Nehls et al. 2009), and in the faunal assemblages associated with them (Rodney and Paynter 2006). We are now beginning to understand the role of these and other species recently discovered in deep-sea areas (Wisshak et al. 2009), which build key animal forests in these great depths (López-Correa et al. 2005; Johnson et al. 2013).

Tube-dwelling crustaceans like Ampeliscidae are practically unknown to the general public and are almost nonexistent in international legislation, despite their importance as animal forests and their wide distribution (Dauvin and Bellan-Santini

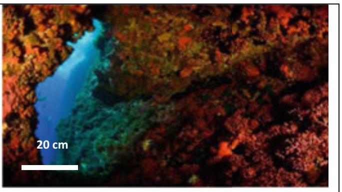
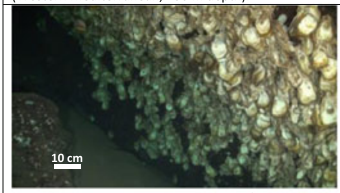
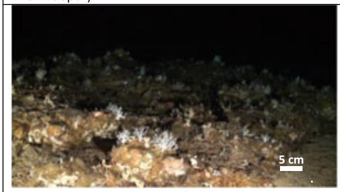
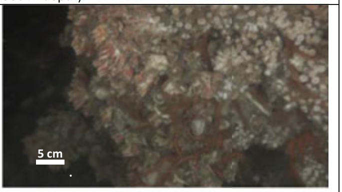
 *Cyclopterus lumpus* in *Mytilus* reef. Baltic Sea (20 m depth).	 *Myriapora truncata* aggregation in front of a cave. Malta (Central Mediterranean, 25 m depth).
 Ray among Ampeliscidae. Ausias March seamount (Western Mediterranean, 230 m depth).	 *Polydora tubicola*. Kattegat (20 m depth).
 *Neopycnodonte zibrowii*. Canary Islands (Atlantic Ocean, 770 m depth).	 *Neopycnodonte cochlear*. Gorringe Bank (Atlantic Ocean, 190 m depth).
 Stylasteridae. Gorringe Bank (Atlantic Ocean, 660 m depth).	 *Filograna implexa*. Southern Portugal (Atlantic Ocean, 580 m depth).
 Hydroid gardens. Mediterranean Sea (120 m depth).	 Reef formed by barnacles, corals and oysters. Alboran Sea (Western Mediterranean, 240 m depth).
 Sea squirt aggregation. North Sea (Atlantic Ocean, 165 m depth).	

Fig. 4 Animal forests formed by groups other than corals and sponges

1996), including in hydrothermal vents (Vinogradov 1995; Esposito et al. 2015). They serve as key habitats and feeding grounds for commercial fish species (Göransson et al. 2010; Bowman 1979; Edwards 1976), and for protected species like the gray whale (Demchenko et al. 2016).

Other important tube-dwelling animal forests are those formed by annelids. Some that form reefs in shallow waters, like the Sabellarid worms, are better known and are even included under regional conservation legislation (e.g., OSPAR 2008) due to their importance for biodiversity (Dias and Paula 2001; Dubois et al. 2002; Chen and Dai 2009). However, many worm constructions have been and are still largely ignored. For example, reef-like structures of the polychaete *Filograna implexa* are found in both the western and eastern Atlantic, from Norway to the Gulf of Maine (ICES 2009) (Fig. 4). The *Lanice conchilega* reefs in the North Sea (Degraer et al. 2008) also represent an important habitat. Other worms can also form reefs or large aggregations, such as *Alvinella pompejana* (Van Dover 2000), *Riftia pachyptila* (Jones 1981; Ramirez-Llodra et al. 2007), and *Serpula vermicularis* (Moore et al. 1998) on hydrothermal vents.

Similarly, fire corals (Milleporidae) are well known animal forests in shallow tropical reefs (Lewis 1989; Nagelkerken and Nagelkerken 2004; Andréfouët et al. 2014), while their lesser known deep and/or cold-water counterparts (Stylasteridae) are also among the most important habitat-forming organisms (Lindner 2007), from deep to shallow waters and from polar to temperate oceans and seas (Häussermann 2007; Lindner 2007; Salvati et al. 2010; Häussermann and Försterra 2014) (Fig. 4).

Other hydroids, sea squirts, anemones, cirripeds, etc., and even organisms from other biological kingdoms (i.e., Xenophiophora, Foraminifera) can also create important forests (see, for example, Yakovis et al. 2005; Voultsiadou et al. 2007; Buhl-Mortensen et al. 2010; Thresher et al. 2011).

6 Biodiversity, Animal Forests, and Fisheries

Animal forests are recognized biodiversity hotspots, and well-preserved animal forests are important for maintaining marine biodiversity on both hard and soft bottoms (Krieger and Wing 2002; Buhl-Mortensen and Buhl-Mortensen 2014). However, the benefits of their conservation are not only a matter of compliance with international laws to halt biodiversity loss and ensure the good environmental status of the oceans; the protection of animal forests is also important for supporting and enhancing the recovery of commercial stocks.

Worldwide, studies of the role of habitat-forming animals have proven their importance for fisheries, and revealed the close associations between commercial species and the presence of animal forests in all kind of substrata and geological features, from hard to soft bottoms, and from seamounts to canyons, slopes, etc. (Freese and Wing 2003; Auster 2007; Bianchi 2011; Miller et al. 2012; Kenchington et al. 2013; Biber et al. 2014; Pham et al. 2015). Some studies have also compared areas where animal forests were present, with other areas where these species do not occur, or where they have been damaged or reduced (Nouar and Maurin 2001; Krieger and Wing 2002; Edinger et al. 2007; Hixon and Tissot 2007; Maynou and Cartes 2011; Cartes et al. 2013). These investigations have clearly shown a higher biomass of species of commercial interest in animal forest ecosystems with a healthy conservation status.

Animal forests serve as spawning areas for a variety of commercial species (Fig. 5). Tree-like sponges and corals provide the perfect substrata to which some species attach their eggs. This has been observed with cephalopods using erect sponges (Cuenot 1936; Larcombe and Russell 1971; Okutani and Sasaki 2007), and sharks laying their eggs on black corals (Henry et al. 2013; Cau et al. 2014). It is also well known that many commercial species aggregate to spawn on coral reefs and in other animal forests (e.g., Sadovy de Mitcheson and Colin 2012). Following reproduction, animal forests can also play an important role in juvenile survivorship, providing refuge and "biological corridors" linking primary habitats (Lindholm et al. 1999; Auster et al. 2003; Fuller et al. 2008; ICES 2009).

The damage and destruction of animal forests can trigger cascade effects affecting the entire ecosystem, producing changes in the diversity and abundance of not only benthic flora and fauna, but also pelagic species (Lindley et al. 1995). Pelagic and benthic ecosystems are strongly interlinked, and benthic bioturbation – both natural and anthropogenic – can drive changes in both habitat types. Three main mechanisms have been identified that underlie this coupling between pelagic and benthic habitats: organism movements (including dial vertical migrations, species with bentho-pelagic lifecycles, etc.), trophic interactions, and biogeochemical processes (Baustian et al. 2014; Rossi et al., this volume).

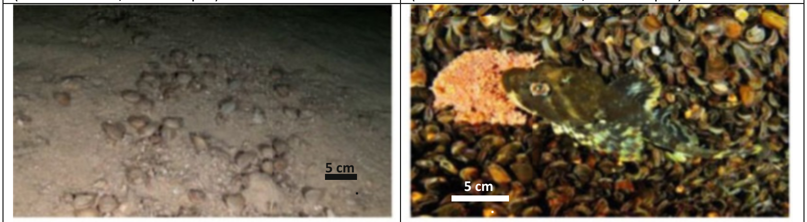
Even dead animal forests, such as old coral reefs and fossil sponge aggregations, may still serve as refuges for many fishes and other species (e.g., Wilson et al. 2010; Takada et al. 2012).

7 Other Animal Forests: Dynamic and Mobile Habitats, not only Sessile Species

While the term "animal forest" mainly refers to sessile taxa acting as structural engineers, dense aggregations of mobile species have been shown to form temporary habitats. Such "mobile" or "ephemeral" animal forests are built up, for example, by species of echinoderms, one of the most widely distributed phyla in deep marine ecosystems (Fig. 6). Crinoids, holothurians, ophiuroids, echinoids, and asteroids can concentrate in high-density groups, forming feeding aggregations (Scheibling 1980; Ball 1991; Gutt and Piepenburg 1991; Lauzon-Guay and Scheibling 2007; Jamieson et al. 2011). These large concentrations of mobile benthic species are used as seasonal or temporary habitats by different fauna, and some aggregations are considered sensitive and essential habitats. For example, the crinoid *Leptometra* sp. can be found covering extensive areas with densities over 10 individuals/m^2

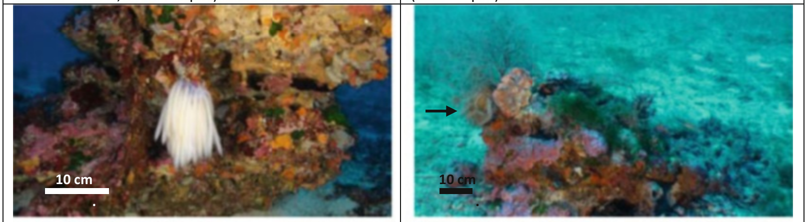
Crinoids (*Leptometra celtica*). Southern Portugal (Atlantic Ocean, 600 m depth).

Crinoids (*Leptometra phalangium*). Alboran Sea (Western Mediterranean, 340 m depth).



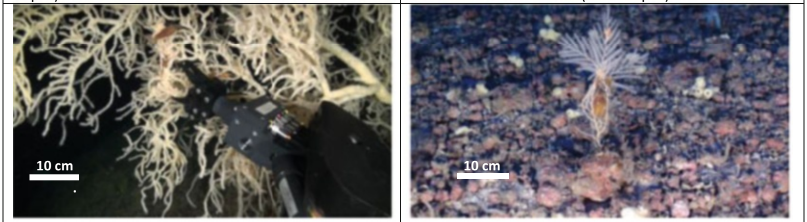
Gryphus vitreus. Balearic Islands (Western Mediterranean, 230 m depth).

Myoxocephalus scorpius eggs in mussel bed. Baltic Sea (30 m depth).



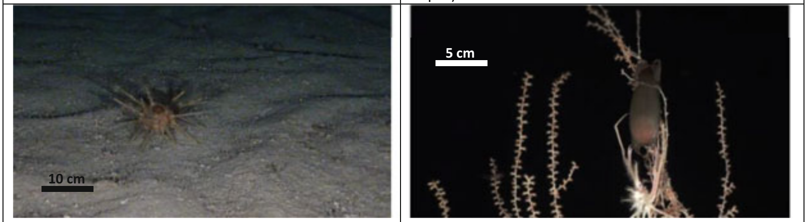
Squid eggs among sponges. Mediterranean Sea (25 m depth).

Squid eggs (indicated by arrow) below hydrozoans. Western Mediterranean (75 m depth).



Shark eggcase on black coral (*Leiopathes glaberrima*). Cabliers Bank (Western Mediterranean, 410 m depth).

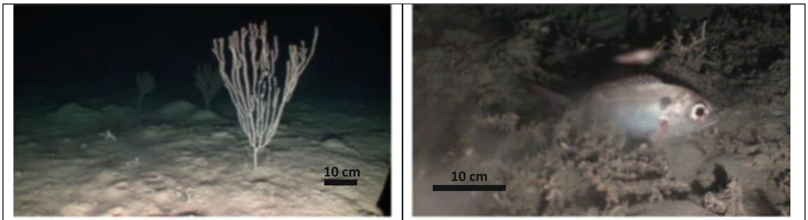
Shark eggcase on gorgonian (*Callogorgia verticillata*). Emile Baudot seamount (Western Mediterranean, 125 m depth).



Shark eggcase on sea urchin (*Stylocidaris affinis*). Emile Baudot escarpment (Western Mediterranean, 210 m depth).

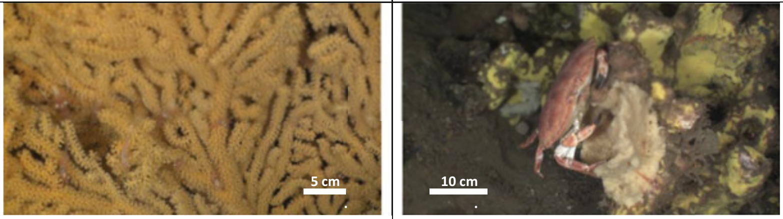
Shark eggcase in bamboo coral (*Isidella elongata*). Ausias March seamount (Western Mediterranean, 450 m depth).

Fig. 5 (continued)



Nephrops norvegicus among bamboo corals. Balearic Islands (Western Mediterranean, 460 m depth).

Pagellus bogaraveo among dead corals. Alboran Sea (Western Mediterranean, 600 m depth).



Northern shrimp (*Pandalus borealis*) on gorgonian (*Paramuricea placomus*). North Sea (150m depth).

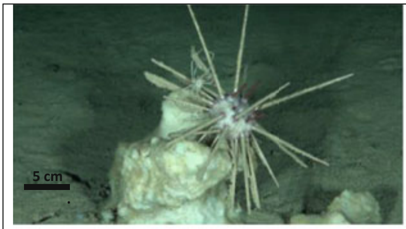
Edible crab (*Cancer pagurus*) in sponge garden. North Sea (165 m depth).

Fig. 5 Animal forests as essential fish habitats for spawning and breeding

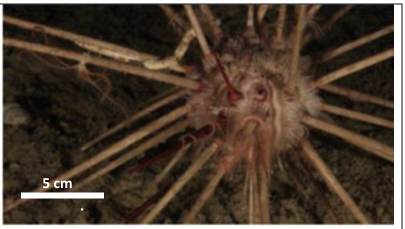
(Angeletti et al. 2010; Fonseca et al. 2014), creating what is considered an EFH (Colloca et al. 2004; Mangano et al. 2010) in the Mediterranean Sea. Also in the Mediterranean, the presence of important commercial species has been associated with the brachiopod *Gryphus vitreus*. For example, the pink spiny lobster (*Palinurus mauritanicus*) feeds upon this species (Delance and Emig 2004). The aggregations it forms have also been proposed as sensitive/essential fish habitats or VMEs (STECF 2006; Rogers and Gianni 2010).

Sea urchins can also form large aggregations that are crucial to marine environments, sometimes as mobile habitats, and sometimes as feeding areas for other animals. As with crinoids, urchins' three-dimensional shape allows them to provide "substrata" for other species. For example, hydroids, sponges, barnacles, and many other organisms settle upon them; crustaceans, such as crabs, climb onto urchin spines to gain access to food; fish even lay their eggs on them; and predators such as lobsters feed on sea urchin grounds (Fig. 6). Echinoids themselves play a strong role in marine ecosystems, with effects that can be devastating both as a result of their population increases or decreases. Very well-known are the overgrazing barrens due to the high abundance of *Diadema africana* in the Eastern Atlantic, *Strongylocentrotus* spp. in North America or northern Europe, and *Centrostephanus rodgersii* in Tasmania (Filbee-Dexter and Scheibling 2014). In contrast, the die-off of *Diadema antillarum* in the Caribbean was a key driver of algal overgrowth on coral reefs (Lessios 1988; Knowlton 2001).

In deeper areas, other echinoderms, the sea cucumbers (holothurians), are the most ubiquitous animals; their role in those environments has not yet been fully explained.



Anamathia rissoana on *Cidaris cidaris.* Triton seamount (Atlantic Ocean, 320 m depth).



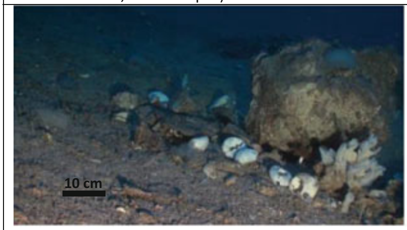
Crinoids and ophiuroids on *Cidaris cidaris.* Western Mediterranean (400 m depth).

Hydrozoans and lepadomorphs on *Cidaris cidaris.* Alboran Sea (Western Mediterranean, 250 m depth).

Rochinia carpenteri on *Cidaris cidaris*. Triton seamount (Atlantic Ocean, 310 m depth).

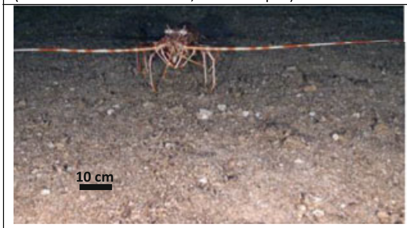
Palinurus elephas feeding area. Alboran Sea (Western Mediterranean, 180 m depth).

Palinurus mauritanicus feeding area. Avempace Bank (Western Mediterranean, 360 m depth).

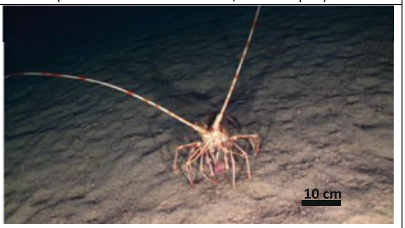


Palinurus mauritanicus feeding area. Alboran Sea (Western Mediterranean, 300 m depth).

Spatangus purpureus. Crayfish hunting grounds. Balearic Islands (Western Mediterranean, 80 m depth).

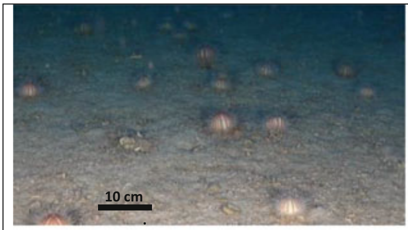


Palinurus elephas hunting sand sea urchins. Balearic Islands (Western Mediterranean, 135 m depth).

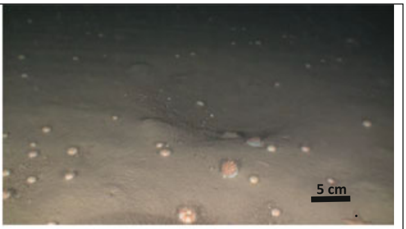


Palinurus elephas hunting sand sea urchins. Alboran Sea (Western Mediterranean, 85 m depth).

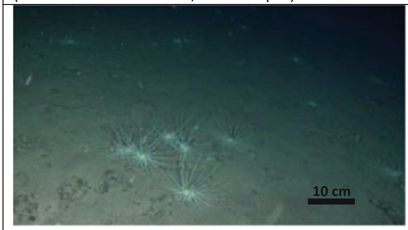
Fig. 6 (continued)



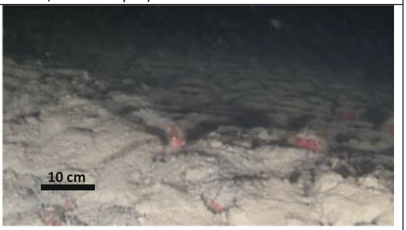
Gracilechinus acutus aggregations. Balearic Islands (Western Mediterranean, 220 m depth).



Gracilechinus acutus aggregations. North Sea (Atlantic Ocean, 110 m depth).



Coelopleurus cf. *floridanus* aggregations. Triton seamount (Atlantic Ocean, 280 m depth).



Brissopsis lyrifera aggregations. Kattegat (90 m depth).

Cidaris cidaris aggregations. Chella Bank (Western Mediterranean, 340m depth).

Fig. 6 Mobile animal forests

8 Habitat Mapping and Management

A fundamental requirement for being able to protect, conserve, and restore animal forests is to know where they occur. The value of mapping marine habitats is clear. It has yielded key information for identifying potential new protected areas and improving fisheries management (Le Pape et al. 2014), as well as for locating EFH for commercial species (Brown et al. 2000). Some studies that have combined information on fisheries effort and habitat status have even provided data about illegal activities and trends in VMEs (e.g., Reed et al. 2005).

However, despite decades of survey effort at sea, much of the ocean floor remains unexplored, let alone mapped (Hu et al. 2014). In many large areas, the available bathymetric data contain gaps, with too coarse a resolution to permit the identification of some topographic features where animal forests may occur, such as small seamounts (Wessel et al. 2010). As a consequence, conservation efforts to identify priority areas for protection often depend on surrogate physical variables (e.g., bathymetry, temperature, depth, substrate type) and/or modeling to identify the potential distribution of benthic habitats (Roff et al. 2003; Althaus et al. 2012). Habitat mapping based on these pragmatic approaches is a very useful tool for helping to fill information gaps for marine conservation planning (Dunstan et al. 2012), although it is not a replacement for finer-scale mapping based on detailed field surveys.

Various international conventions have urged their contracting parties to develop and present maps of the distribution of benthic marine habitats. Such mapping is a basic requirement for informing marine conservation and management. However, in many cases, a combination of ignorance and lack of political will have resulted in delayed or no progress. Many countries still do not provide data on the existence of animal forests in their waters to international conventions, and even in cases where they have done so, a few countries take the necessary follow-on actions to preserve them.

Managers and policy makers need to understand marine complexity in order to be able to tackle the challenges of marine conservation. For example, when the protection of a specific benthic ecosystem is under discussion, it must be taken into account that these ecosystems typically comprise different habitats and communities which form a mosaic. Given the complexity of their interactions, management cannot succeed if it is monospecific or “monohabitat,” thus excluding these crucial interrelationships.

It is very well known that effective habitat mapping should include not only biological information but also geological and oceanographic data (Kenny et al. 2002; Brown et al. 2011). In order to identify and assess the threats facing animal forests, and to improve their management, it is critical that such habitat maps be combined with additional spatial data regarding the location and intensity of human activities such as fishing, maritime traffic, marine dumping, offshore oil and gas production, etc. Unfortunately, many countries have so far been very reluctant to provide such crucial information, or to allow researchers to have access to it. The situation is beginning to improve as increased emphasis is being placed on data-sharing under international conventions, and under recent regulations such as the European Union MSFD, and as formal mechanisms and platforms are being developed to support those efforts.

9 Economics and Conservation

Over the last two decades, economic considerations have entered more strongly into the marine realm, not only in the context of fisheries or mineral extraction but also in relation to assessing the “value” of ecosystems (Costanza et al. 1997; TEEB 2010). The ecosystem services provided by marine habitats have become an important factor in marine conservation (Millenium Ecosystem Assessment 2005), and some efforts have been made to assess and map the ecosystem services associated with benthic habitats (e.g., Galparsoro et al. 2014). Ultimately, the protection and conservation of ecosystems are far less costly than later restoration efforts, and over the long-term, yield many more benefits than short-term economic gains from activities that damage or destroy ecosystems (Balmford et al. 2002).

Estimates of global ecosystem services have increased from USD 33 trillion/yr in 1995 to some USD 125–145 trillion/yr. in 2011 (Costanza et al. 1997, 2014). While there are no such estimates available across marine animal forests, it is known that they play many different roles that are economically important for humans (see Paoli et al., this volume). The lengthy list of ecosystem services they provide includes food provisioning, CO_2 sequestration, biomass and organic compound production, coastal protection, cultural values, tourism, marine chemical balance, food chain maintenance, and contribution to nutrient cycles. For coral reefs alone (the type of animal forest for which ecosystem service values have been most studied), de Groot et al. (2012) estimated the total annual value of ecosystem services to be international $ 352,915 for an “average” hectare of reefs, but with a potential maximum of up to 2,129,122 international $/ha/yr.

It has been estimated that protecting 20–30% of the world’s marine surface, as demanded by the World Parks Congress, would cost between USD 5–19 billion per year (Balmford et al. 2004). The investment is clearly worthwhile, considering the estimated USD 14.9–22.4 trillion annually in ecosystem services that these MPAs can provide (i.e., estimated following Balmford et al. 2004, as 20–30% of the USD 74.5 trillion per year in renewable ecosystem services provided by marine ecosystems, from Costanza et al. 2014).

The estimated values of ecosystem services are almost certain to increase as we continue to improve our knowledge about the role of different species aggregations and animal forests. For example, further research on the importance of marine biodiversity to the chemical balance of the oceans will provide new valuable information on natural chemical and nutrient cycles, as we are already learning from deep-sea holothurians that regenerate and recycle nutrients in marine benthic ecosystems (Moriarty 1982; Amon and Herndel 1991a, b; Uthicke 2001), carbonate accumulation by CWC (Titschack et al. 2015), and interactions between sponges and silicon (Maldonado et al. 2011).

10 Looking to the Future

There is a general agreement that protecting and restoring the most productive marine habitats, together with a more sustainable approach to managing marine resources, will allow stocks to recover, will maintain biodiversity, and will help marine ecosystems to regain their healthy status.

In recent decades, the importance of such habitat protection has been recognized within international conventions, and under many national and regional laws and agreements. Formal processes have also been established and developed through which protection may be achieved. In practice, however, the rate at which measures are being adopted and implemented is extremely slow.

So far, efforts are still mostly focused at the level of “macro” animal forests, habitats, and ecosystems (i.e., larger, more visible animal forests), and primarily only on those ones that appear to be more productive or important for fisheries and other economic activities. Yet “micro” habitats (i.e., those animal forests that are smaller and less visible, such as brachiopods or Foraminifera) are also part of the bigger puzzle of life and interact with all of the other ecosystem components. As such, the need for their protection should also be taken into account.

A future challenge for animal forest conservation will be to extend protection efforts to include other ecosystems and communities that are currently ignored, because they are small, unattractive, largely unstudied, or unappealing to the general public. Once again, the conservation of those systems must not be carried out in isolation, but should be part of a broader, holistic approach to ecosystem protection.

An ongoing challenge is the fact that many governments and international conventions still address fisheries and environmental issues separately, in an inexplicable attempt to convey the impression that fishing activities are entirely unconnected from the marine environments where they are carried out. This fragmented, sectoral approach can no longer be justified. The need for an integrated approach to marine governance has been increasingly recognized, particularly given the scale of human pressures on the marine environment and the increased emphasis on implementing ecosystem approaches to marine management (e.g., European Commission 2008; van Hoof et al. 2012; Salomon and Dross 2013; Rice and Smith, this volume). Ideally, regional conventions aimed at managing and conserving the oceans should be merged into real oceanic bodies with the responsibility for managing entire ecosystems and the activities that occur within them. At the very least, a much stronger basis of understanding and collaboration is needed among relevant authorities, and among regional conventions.

Conservation of what remains is not enough. The aim of marine management must also be to focus on identifying areas where lost animal forests can potentially be recovered and to implement the necessary measures to make it happen.

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11 Cross-References

- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests in the Chilean Fjords: Discoveries, Perspectives, and Threats in Shallow and Deep Waters
- ▶ Animal Forests of the World: an overview
- ▶ Antarctic Marine Animal Forests: Three-Dimensional Communities in Southern Ocean Ecosystems
- ▶ Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- ▶ Caribbean Coral Reefs: Past, Present, and Insights into the Future

- ▶ Drawing the Line at Neglected Marine Ecosystems: Ecology of Vermetid Reefs in a Changing Ocean
- ▶ Ecosystem Functions and Services of the Marine Animal Forests
- ▶ Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest
- ▶ Genetic Connectivity and Conservation of Temperate and Cold-Water Habitat-Forming Corals
- ▶ Global Biodiversity in Cold-Water Coral Reef Ecosystems
- ▶ Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests
- ▶ Impact of Bottom Fishing on Animal Forests: Science, Conservation, and Fisheries Management
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998
- ▶ Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral Transplantation
- ▶ Sponge Grounds as Key Marine Habitats: A Synthetic Review of Types, Structure, Functional Roles, and Conservation Concerns
- ▶ The Animal Forest and Its Socio-ecological Connections to Land and Coastal Ecosystems
- ▶ The Builders of the Oceans – Part I: Coral Architecture from the Tropics to the Poles, from the Shallow to the Deep
- ▶ The Impact of Anthropogenic Activity on Cold-Water Corals

Annex

Examples of national and international laws and frameworks for the protection of animal forests, as referred to in the text

Name	Geographic area	Webpage
Baltic Marine Environment Protection Commission – Helsinki Commission (HELCOM)	Baltic Sea	http://www.helcom.fi/
Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (Barcelona Convention)	Mediterranean Sea	http://web.unep.org/unepmap/
Cartagena Convention	Caribbean Sea	http://www.cep.unep.org/cartagena-convention
Commission for the Conservation of Antarctic Marine Living Resources (CCMLAR)	Area south of the Antarctic Convergence	https://www.ccamlr.org/

(*continued*)

Name	Geographic area	Webpage
Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR)	North-east Atlantic Ocean	http://www.ospar.org/
EU Council Regulation (EC) 734/2008 on the protection of vulnerable marine ecosystems in the high seas from adverse impacts of bottom fishing gears	High seas beyond national and RFMO jurisdiction	http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32008R0734&from=EN
EU Marine Strategy Framework Directive 2008/56/EC	European Union waters	http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32008L0056&from=EN
EU Regulation 2016/2336 establishing specific conditions for fishing for deep-sea stocks in the north-east Atlantic and provisions for fishing in international waters of the north-east Atlantic	North-east Atlantic and certain international waters of the Eastern Central Atlantic	https://ec.europa.eu/fisheries/better-future-eu-deep-sea_en http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32016R2336&from=EN
FAO International Guidelines for the Management of Deep-sea fisheries in the High Seas	Worldwide	ftp://ftp.fao.org/docrep/fao/011/i0816t/i0816t.pdf
General Fisheries Commission for the Mediterranean (GFCM)	Mediterranean Sea	http://www.fao.org/gfcm/en/
New Zealand Wildlife Act	New Zealand waters	http://www.legislation.govt.nz/act/public/1953/0031/latest/whole.html
North Pacific Fisheries Commission (NPFC)	International waters of the North Pacific Ocean	http://npfc.r-cms.jp/
Northwest Atlantic Fisheries Organization (NAFO)	International waters of the North-west Atlantic Ocean	https://www.nafo.int/
North East Atlantic Fisheries Commission (NEAFC)	International waters of the North-east Atlantic Ocean	https://www.neafc.org/
South East Atlantic Fisheries Organization (SEAFO)	International waters of the South-east Atlantic Ocean	http://www.seafo.org/
South Pacific Regional Fisheries Management Organization (SPRFMO)	International waters of the South Pacific	https://www.sprfmo.int/
United Nations Convention on Biological Diversity (CBD)	Worldwide	https://www.cbd.int/
United Nations Convention on the Law of the Sea (UNCLOS)	Worldwide	http://www.un.org/depts/los/convention_agreements/convention_overview_convention.htm
United Nations General Assembly (UNGA) Resolution 59/25	Worldwide	https://documents-dds-ny.un.org/doc/UNDOC/GEN/N04/477/64/PDF/N0447764.pdf?OpenElement

(*continued*)

Name	Geographic area	Webpage
UNGA Resolution 61/105	Worldwide	https://documents-dds-ny.un.org/doc/UNDOC/GEN/N06/500/73/PDF/N0650073.pdf?OpenElement
UNGA Resolution 64/72	Worldwide	https://documents-dds-ny.un.org/doc/UNDOC/GEN/N09/466/15/PDF/N0946615.pdf?OpenElement
U.S. Endangered Species Act	USA waters	https://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf
U.S. Magnuson-Stevens Fishery Conservation and Management Act	USA waters	http://www.nmfs.noaa.gov/sfa/management/catch_shares/legislation_history/documents/msa_amended_2007.pdf

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The Animal Forest and Its Socio-Ecological Connections to Land and Coastal Ecosystems

42

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Abstract

Tropical landscape and seascape systems are intimately linked by complex ecological relationships that provide environmental services to human societies located in coastal areas and beyond. Paradoxically, nonsustainable activities from these human societies are threatening the functions and benefits of these systems. Anthropogenic processes that damage tropical seascapes are rapidly increasing as a result of coastal and tourism development, increasing human population, unsustainable economic growth, and extensive transformations of natural landscapes. In addition to this overwhelming trend, tropical coastal seascapes are threatened by global climate change. Thus, to address this problem, it is essential to understand the complex ecological relationships between the components of coastal seascape systems and their links to land ecosystems, including the positive and negative effects of humans. The physical and ecological relationships between tropical landscapes and seascapes often define the energy and matter fluxes through which human activities exert their influence on coastal ecosystems. We illustrate these relationships by presenting a case study and conceptual model of coastal and tourism development in the Yucatan Peninsula, Mexico.

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Scientific knowledge and proposals for better governance practices are available to guide management actions and to protect the connectivity of seascape systems. Nonetheless, political will, coupled with the implementation of local and regional integrated management schemes of coastal zones, is urgent. More examples are needed of inland and coastal human societies that successfully integrate scientific knowledge of the links among ecosystems and their decision-making processes in order to achieve sustainable development based on the services provided by their surrounding seascapes.

Keywords
Tropical seascapes • Connectivity • Mangroves • Seagrass • Coral reefs • Yucatán Peninsula

Contents

1 Introduction

In tropical waters, seascapes, or interlinked patches of marine ecosystems ranging from mangroves to seagrass beds to coral reefs constitute a major feature of the coastal zone and are often located adjacent to each other (Ogden 1997). The tropical seascape is a spatially heterogeneous area of coastal environment that can be perceived as a mosaic of patches, a spatial gradient, or some other kind of geometric pattern found in either benthic or pelagic environments (Böstrom et al. 2011). A seascape encompasses meta-ecosystems, i.e., sets of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries (Loreau et al. 2003). This concept represents an expansion of the notion of meta-communities through the integration of mass and energy transfers among these ecosystems. It provides a theoretical framework for the understanding of interlinked processes among different ecosystems, such as dissolved and particulate matter fluxes, the exchange of living material, the export and import of matter and energy, and diversity-production patterns, among others (Loreau et al. 2003).

The capacity for the development of each particular ecosystem within a tropical seascape can be enhanced by its interaction with other ecosystems. This may be one of the reasons why tropical seascapes are major providers of natural resources and ecosystem services for millions of human beings (Moberg and Rönnbäk 2003). The structural and functional values of the different mosaics of ecosystems that constitute these tropical seascapes and their interactions with humans are highly relevant. Interactions between seascape components (including the human societies living in these areas) can largely be subdivided into chemical, biological, and physical fluxes (Ogden 1997). Examples of some of the interactions among ecosystems include exchanges of larvae, juvenile and adult fauna, plankton and nutrients (Lowe and Falter 2015), detritus, water, sediments (Nagelkerken 2009a), and sewage pollution from terrestrial runoff (Wear and Vega-Thurber 2015).

1.1 Connectivity in Tropical Seascapes

The coastal tropical seascape is a continuum that spans inland ecosystems, coastal ecosystems, and the ocean. Although rivers represent only a quarter of the coastal area of the world, the vast majority of water and sediment is discharged through this land-sea connection, so the flow and exchange of dissolved and particulate materials from land to sea are substantial. Also, groundwater is an important source of nutrients such as dissolved inorganic nitrogen (DIN) for coastal ecosystems and coral reefs, particularly in areas with high coastal development. Submarine groundwater discharge (SGD) brings an estimated range of 3–800 mmol h^{1} of nitrogen per meter of shoreline (Paytan et al. 2005). In areas with permeable and porous carbonate karst geology, such as Yucatan, Mexico, the water quality is regulated by groundwater discharges and may be similar in magnitude to that of rivers; these inputs are linked to agro-industries, atmospheric deposition, urban-public activities, and industrial activities, with an estimated nitrogen to phosphorus (N:P) discharge ratio of 194.9:1 (Aranda-Cirerol et al. 2006).

Bouillon and Connolly (2009) consider that tropical rivers in coastal margins deliver most of the carbon and nutrients supplied from land to sea. According to Alongi et al. (2014), global water discharge from tropical rivers is higher in America than in other continents, while the highest global sediment discharge is in Asia. Tropical rivers channel up to 55–64% of the total global flux of riverine dissolved inorganic carbon (DIC), with the highest yields taking place in Asia, where carbonate rock is most abundant. Approximately 30% of the global particulate inorganic carbon (PIC) flux is discharged from the tropics. Equatorial rivers have lower DIC but higher dissolved organic carbon (DOC) concentrations than those at other latitudes. This can be attributed to the carbon-rich African soils, and the prevalence of peat and black-water rivers in tropical Asia and the Americas. The total DOC discharge accounts for 63–66% of the total global flux. Moreover, most of the tropical particulate organic carbon (POC) discharge occurs in the Americas and Asia, with the total POC discharge from the tropics estimated at 64–70% of the global flux.

Oceans also shape the structure and function of tropical seascapes. For example, currents carry out an enormous amount of larvae to tropical seascapes, where they can further develop. Oceans are the main regional connection drivers among meta-ecosystems, through waves, streams, coastal upwelling, and cyclones (Lowe and Falter 2015). These physical processes transport key materials, nutrients, and plankton, supporting life in the tropical seascapes. As Lowe and Falter (2015) mention, although oceans play a fundamental role in shaping the distribution of species, a modern understanding of the complex interactions between oceans and coral reefs is emerging. Nevertheless, oceans play a critical role within the patterns of biodiversity distribution through the dynamics of currents at different scales and the interaction of nutrients among ecosystems. Oceans not only have an enormous influence on the growth, metabolism, and community structure (Hammer and Wolansky 1988) of the different assemblages and ecosystems that compose a tropical seascape but also on the hydrodynamic processes related to heat dissipation, transport and mass transfers (nutrients and carbon), heat, temperature, and momentum (drag and dissipation) (Lowe and Falter 2015).

Several tropical seascape features can contribute to the stability of local ecosystems. These features include tropical forests, mangroves, seagrass, fringing reefs, barrier reefs, the generation of continental margins, reef lagoons, and the control of coastal erosion through the mitigation of energy from waves. Different aspects of the tropical seascape structure and functioning depend on the geomorphology of the coastal zone and continental shelf, which are connected through the movement of inorganic matter, detritus, and living material (Loreau et al. 2003). In these seascapes, mangroves and seagrass beds promote the development of offshore coral reefs by interfering with discharges of freshwater and acting as sinks for pollutants and organic materials, filtering the runoff water that may eventually reach coral reefs (Harborne et al. 2006; Berkström et al. 2012; Gillis et al. 2014). These coastal vegetation systems control the concentration of nutrients such as nitrogen and phosphorus as well as suspended sediment in the water column. Nevertheless, these ecosystems can also naturally be net exporters of nutrients to coral reefs (Bouillon and Connolly 2009). In turn, coral reefs create a protective environment for seagrass beds and mangroves by buffering the energy from oceanic waves and currents (Harborne et al. 2006; Berkström et al. 2012) and by protecting the coast from pounding waves, storms, and hurricanes (Gillis et al. 2014).

There are also movements of floating living material, such as macroalgae (for instance, the brown alga *Sargassum*) and seagrass, which can strongly influence populations, consumer-resources, food availability, and community structure (Polis et al. 1997). Biological interactions through the biological transfer of material among different ecosystems due to ontogenetic migration or trophic relay (Bouillon and Connolly 2009), as well as the transport of larvae from one ecosystem to another may influence the shape of the coral reef community, as in the case of fish assemblages (Mumby et al. 2004). It is known, for example, that both mangroves and

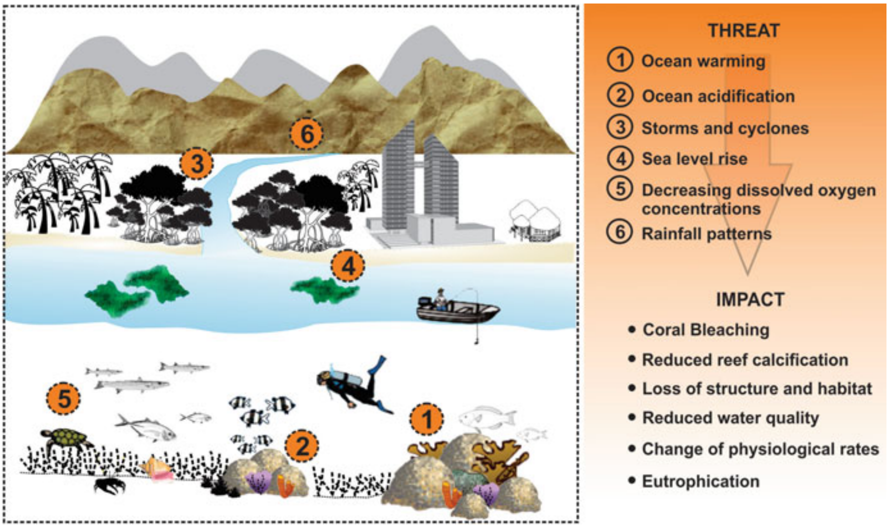

Fig. 1 The main climate change threats and impacts on the tropical seascape include: (1) ocean warming, (2) ocean acidification, (3) increase in the frequency of tropical storms and hurricanes, (4) sea-level rise, (5) decreasing dissolved oxygen concentrations (hypoxia), and (6) change in rainfall patterns

seagrasses act as nursery grounds for fish recruits, decapods, and many other organisms (Nagelkerken 2009a) or fish, which subsequently integrate into or interact with coral reef communities (Nagelkerken 2009b; Mumby et al. 2004)

1.2 Global Climate Change Impacts on Animal Forests

The coastal tropical seascape is crucial for global climate change, particularly for the circulation of heat, salinity, and water vapor (Alongi et al. 2013). While some ecosystems are likely to benefit from climate variations, coral reefs are extremely vulnerable. For instance, coral bleaching can be caused by a gradual increase in water temperature (1–2 °C above the maximum temperature recorded), causing stress and the expulsion of the endosymbiotic zooxanthellae that provide its main energy source, as this bleaching causes their death (Munday et al. 2008). It is estimated that over 16% of coral reefs worldwide have suffered serious damage from massive bleaching events (Wilson et al. 2006). Projections of temperature models indicate that bleaching may become a recurring phenomenon worldwide in the course of this century, threatening the ecological balance of seascape systems (Buddemeier et al. 2011) (Fig. 1). In addition, 33–50% of coral reefs have been largely or completely degraded by a combination of local factors and global climate change (Wilkinson 2008).

The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) provides high certainty that anthropogenic emissions have caused measurable changes in the physico-chymical aspects of ocean environments, including warming and associated phenomena such as sea-level rise, hypoxia, and acidification (Howes et al. 2015). These changes imply direct effects on ocean biological processes. In the ocean, key biological processes such as the dispersal and replenishment of larvae may undergo changes in association with the high sea surface temperatures of the sea (Ayre and Hughes 2004). Increased ocean temperatures are expected to affect larval development in corals, which, in turn, may lead to declines in adult stocks and change temporary patterns of dispersal and gene flow. This may eventually cause spatial and latitudinal constrictions or expansions (Ayre and Hughes 2004) in populations. In fact, it has recently been suggested that high temperature may lead to increases in the local retention of coral reef larvae (Figueiredo et al. 2014).

Species population and their connectivity could also be compromised by the increased fragmentation of reef habitats resulting from ocean acidification and bleaching of coral reefs (Munday et al. 2008). Ocean acidification will cause deficiencies in calcification rates and a reduction of recruitment by disrupting coral larval settlement and algal interactions, among other effects (Doropoulos et al. 2012). It is estimated that drops in pH values by the formation of bicarbonate ions (HCO_3) in seawater due to surplus atmospheric carbon dioxide (CO_2) may reduce the availability of carbonate ions in seawater by up to 50% by the year 2065 (Cao and Caldeira 2008). Carbonate ions are essential for organisms that produce shells or exoskeletons based on calcium carbonate ($CaCO_3$), such as corals, mollusks, echinoderms, foraminifera, and crustaceans (Doropoulos et al. 2012).

Another impact associated with temperature is the concentration of dissolved oxygen: water warming causes a decrease in the availability of oxygen (O_2) in the ocean (hypoxia) (Vaquer-Sunyer and Duarte 2008). Future scenarios of the concentration of dissolved oxygen are not encouraging, as it has been predicted to decline by 1–7% worldwide in the next 100 years (Keeling et al. 2010). Most affected are aquatic fish and invertebrates because their physiological mechanisms are determined by the concentration of dissolved oxygen in the water. The sensitivity and susceptibility to hypoxia vary considerably among taxa (Vaquer-Sunyer and Duarte 2008). Thus, the biological and ecological impacts of hypoxia are extremely complex and difficult to estimate (Pörtner and Knust 2007).

Sea-level rise is perhaps the most pervasive threat to the integrity of seascapes that encompass coastal lagoons, mangroves, and coral reefs. Higher sea levels may result in a larger influence of seawater in coastal systems where the balance between salt and fresh water is critical to many ecological processes. Among these systems are coastal lagoons, seagrass communities, and mangrove forests whose suitability as nurseries for pelagic and reef species may be compromised by imbalances in salinity (Harborne 2013). Indeed, Gilman et al. (2008) suggest that sea-level rise may cause large-scale loss of mangrove habitat, coastal dunes, and lagoon ecosystems. Sea-level rises may also result in increased wave energy and modifications of wave regimes that can fundamentally alter the morphodynamics of coasts. In the case of reefs, the loss of coral crests due to bleaching and other processes may be exacerbated by projected increases in annual mean wave heights and changes in wave direction (Hemer et al. 2013). The loss of this wave mitigation effect may, in turn, affect other physical and biological elements of reefs themselves and, in the case of barrier reefs, even those of ecosystems located on the adjacent coast. However, it has also been suggested that under sea-level rise scenarios, coral cover, and reef growth may significantly increase (Hopley 2011).

Coastal cities and small island nations are the most vulnerable to sea-level rise. Social-ecological ecosystems are currently under threat and will further face severe challenges due to global climate change. This may have unprecedented effects on local communities that live on the coast and depend on fishing and marine resource extraction. It can impact nearly all fisheries, coastal societies, and economies worldwide because it may affect the biodiversity of seascapes as a whole.

2 Linkages and Complexities of Social and Ecological Systems

Coastal ecosystems are transformed by humans and are facing a great variety of local and global stressors that produce important changes for marine animal forests (Burke et al. 2011). Within seascapes, coral reefs are among the world's most diverse ecosystems. A recent estimation establishes that coral reefs offer food and shelter to 830,000 species (95% confidence interval: 550,000–1,330,000 species) (Fisher et al. 2015). Associated with this high diversity, coral reefs provide many valuable services for humans, including shoreline protection, livelihoods from ecotourism, fishery production, and a living factory of compounds for biomedical use with a global value of over US$ 31 billion (estimated for 2014) for all reefs combined (Wear and Vega- Thurber 2015). Nevertheless, 75% of coral reefs are currently at risk from local stressors and thermal stress. It is envisaged that by 2030, over 90% of reefs might be at risk, along with the benefits they provide (Jackson et al. 2014).

The great majority of global coral reefs are close to coastal zones. Globally, human influences are producing dramatic shifts from coral to algae cover and are disrupting biodiversity (Acosta-González et al. 2013) and ecosystem functioning and services (Morberg and Folke 1999). A small disruption in biodiversity can cause the collapse of key services that coral reefs provide, such as habitat for the recruitment of commercial species. In turn, the loss of coral reef services may negatively affect the resilience of the socio-ecological system as an imbalance develops between human demand for such services and the actual capacity of ecosystems to supply them.

Linking social and ecological systems is necessary to better understand the complex interactions between humans and coral reefs. There is growing interest in the dynamics and sustainability of the natural environment and human interactions (Diaz et al. 2011) and the conceptualization of social-ecological systems (Biggs et al. 2015). The socio-economic system can be characterized by the human activities that have been developed, such as tourism, urban development, or fishing. These drivers can impact tropical seascapes (seagrass, mangroves, and dunes) and therefore lead to negative feedback loops in the ecosystems services. Nevertheless,

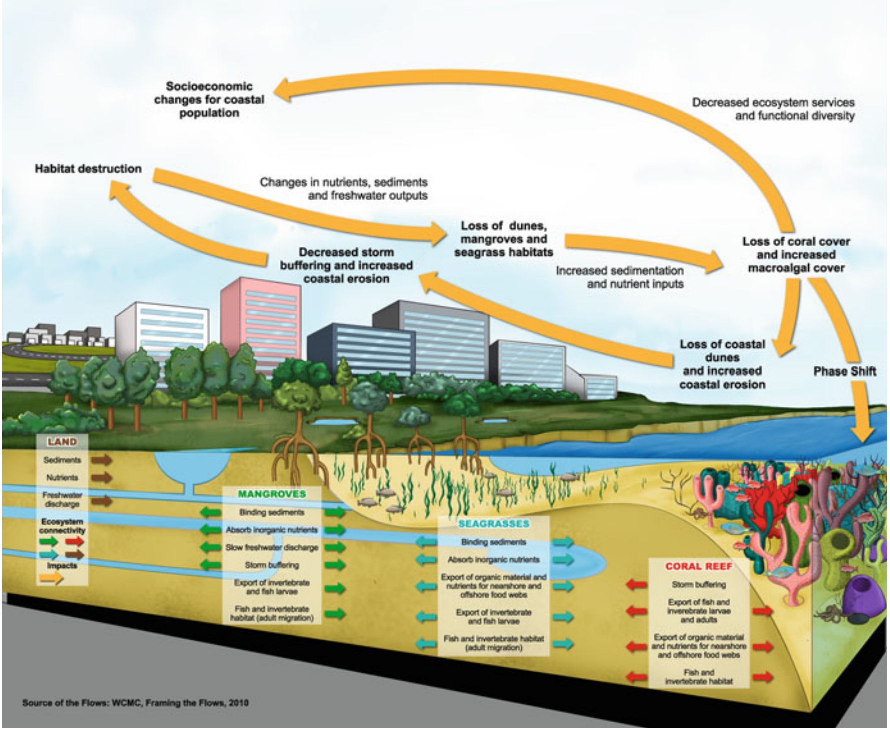

Fig. 2 A conceptual model demonstrating key processes, impacts, and negative feedbacks (*yellow arrows*) within tropical coastal seascapes and the connectivity of land (*brown arrows*), mangroves (*green arrows*), seagrass (*blue arrows*), and coral reefs (*red arrows*) in the Yucatan Peninsula, Mexico (*arrows*/flows adapted from Silvestri and Kershaw 2010)

the management of seascape connectivity –for instance, through the establishment of marine protected areas or the protection of habitats – may involve direct actions and solutions to environmental problems and may include economic, political, and cultural decisions that create positive feedback loops between the ecological and socio-economic systems. Overall, the ecological system may be characterized by the state of ecosystem services, such as herbivorous fish biomass that can control macroalgae, the condition and architecture of coral reefs, commercial fish stocks, fish biodiversity, and fish feeders that can control lionfish.

2.1 Transformations of the Yucatan Peninsula

2.1.1 Conceptual Model of the Yucatán Peninsula

In this section, we define a conceptual model of the cross-interactions and connectivity within seascapes, with a focus on the Yucatán Peninsula as a case study (Fig. 2). In the model, the orange arrows show the negative feedbacks and the impacts of the destruction of habitats such as mangrove vegetation, dunes, beaches, and seagrass ecosystems and their influences on the loss of coral cover and increased macroalgae, leading to phase shifts in coral reefs due to increased nutrient inputs and sedimentation. All these feedbacks result in a decrease of ecosystem services and functional diversity, which may entail socio-economic changes for coastal populations.

The main ecosystem functions provided by the connectivity of ecosystems are also represented by colored arrows and are further described. The land (brown arrows) influences other habitats through sediments, nutrients, and freshwater discharge, but also through pollutants carried through groundwater. Mangrove ecosystems are the first buffers to receive land inputs, which then help slow down the freshwater flow; and along with sea grasses, both assist in the binding of sediment loads and in the absorption of inorganic nutrients.

These nutrients catalyze primary production within the system and result in an export of organic material for near shore and offshore webs. It is important to note that the state of these interactions is related to the amount of nutrients in the system, biogeochemical cycles, the balance/unbalance of the food web in each of the ecosystems, and the overall functional diversity of species in the tropical seascape. Overall, the seascape shares key services, such as storm buffering and the net export of fish invertebrates in all life cycles (larval, juvenile, adults), areas of reproduction, and habitat zones.

One example is the rapid transformation of the Caribbean coastal zone of the northern Yucatán Peninsula (State of Quintana Roo, Mexico). The development of Cancún and the Mayan Riviera from the 1970s to 1990s has caused profound changes in the coastal seascape and the socio-ecological system (Torres and Monsen 2005) (Fig. 3). Cancún is by far one of the most dramatic cases of coastal transformation from a natural habitat to an urbanized tourism destination and is a picture-perfect case for demonstrating how the alterations of a coastal ecosystem have occurred over a short timescale (20 years) and continue to progress.

Cancún is the main beach tourism in Mexico, with visitors from all over the world (4,013,032/year) and significant revenues of $4,135 million dollars (USD) per year (as of November 2014) (McCoy 2015). Despite the substantial economic benefits (jobs, income generation, international tourism destination) of this activity, Cancún is far from being sustainable and is considered to have reached its environmental capacity, with complex deteriorations in its social and cultural capital (McCoy 2015).

Moreover, multiple stressors act on the transformation of coastal seascapes on the Caribbean coast of the Peninsula, including direct clearing of tropical forests and mangroves, and the construction of housing developments for low-income families, and the construction of hotels and other infrastructure on coastal dunes. Due to this development, this area suffers severe problems with coastal erosion (González-Leija et al. 2013). Moreover, thousands of hotel rooms have been built, and many of the low-income housing developments dispose of their sewage through septic tanks that are connected to absorption wells (Torres and Monsen 2005). Even when sewage is treated, only a fraction of it goes through water treatment plants. Hence, wastewater

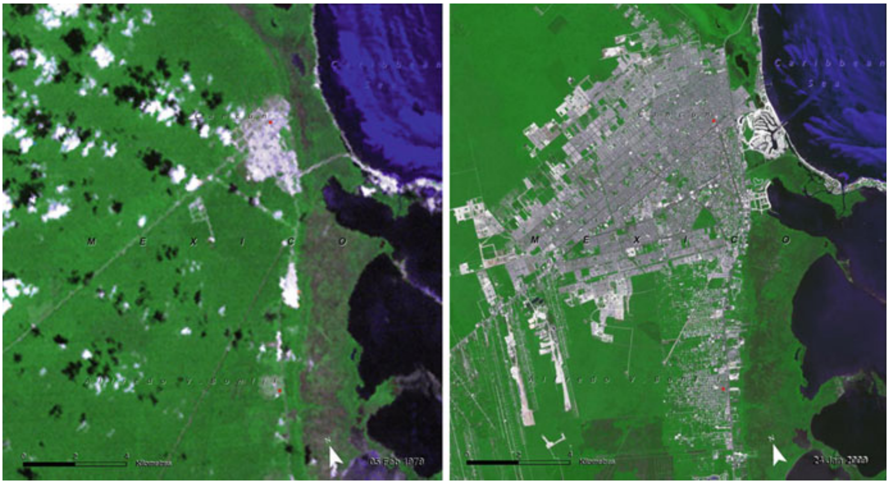

Fig. 3 Urban transformation and growth in Cancún, northern Yucatan Peninsula, Mexico, due to tourism expansion promoted by the Mexican Government, along with national and foreign investors. Satellite images taken on February 5, 1979(left) and January 24, 2009 (right). (Image source: United Nations Environment Programme (UNEP), from Latin America and the Caribbean Atlas of our Changing Environment, 2010)

and its pollutants eventually reach the groundwater and make their way into coastal lagoons and reef areas (Hernández-Terrones et al. 2015).

2.1.2 Geological Formations Influence the Tropical Seascape

The vulnerability of tropical seascapes in the Yucatán Peninsula is intimately related to the geological dynamics of the region. The peninsula is a partially emergent calcium carbonate platform extending to the north and northwest into a massive continental shelf (Perry et al. 2003). There is almost no surface runoff on most of the peninsula, and the aquifer system has developed within a nearly horizontal permeable limestone and dolostone karst whose oldest rocks are from the Tertiary period (Perry et al. 2003). Thus, a fresh groundwater lens flows through this karstic plain above a saline intrusion layer. The depth of the nearly flat water table (gradient = 2 cm/km) is determined by elevation above mean sea level, the depth of the interface between fresh and seawater, and, to a lesser extent, by the recharge of the aquifer from annual precipitation, which increases from 500 to 1,500 mm along a northwest-southeast axis. The water table is frequently exposed in places where the ceiling of underground cavities has collapsed, forming sinkholes, or *cenotes* (from *dzonot*, the Mayan word for well) as they are locally known, while in coastal areas, groundwater usually forms springs (especially on the West and North coasts of the peninsula). Other interactions include the flows of fresh ground water from karstic cave systems into the sea, which are more often on the Caribbean coast. Overall, the balance of fresh and seawater has been a major determinant of coastal geomorphology, influencing the formation of coastal lagoons and even coral reefs.

Another element that shapes coasts on the Yucatán Peninsula is the transport, removal, and deposition of fine biogenic sand by currents and winds. This is the predominant geomorphological process along the Northeast, North, and West coasts of the peninsula. This constant transport of sand makes for a more turbid water column than on the Caribbean coast of the Peninsula, and its clearest effect is the formation of sand barrier islands on the Northeast, North, and West coasts, as currents and waves coming inshore from the northeast transport and deposit sands in an east-to-west direction. Thus, "cul-de-sac" lagoon systems eventually form, in which the windward edge of the barrier island joins the continent by sand deposition, while the leeward edge remains open. As a result, areas near the mouth of these lagoons are under direct influence of the sea, while conditions at the closed end are more influenced by evaporation, rainfall, and groundwater sources. This creates salinity and nutrient gradients that result in a wide variety of terrestrial and aquatic habitats. As the geomorphological development of these lagoons progresses, the leeward mouth is finally blocked by sand, and they turn into enclosed lagoons and wetland systems, where the balance among evaporation, rainfall, and groundwater input becomes critical in defining ecological conditions.

The Caribbean coast of the Peninsula is substantially different from the others in that karstic rock often reaches the sea, creating long extensions of rocky coast interspersed with stretches of sandy beaches. Another major difference is the absence of a vast continental shelf and the presence of the Mesoamerican Reef (MAR), the world's second-largest barrier coral reef, running parallel to the coast. The absence of an extended continental shelf and the fact that sands are usually confined to certain areas of the coast result in much clearer waters than on the North and West coasts of the Peninsula. Groundwater usually reaches the coast and the sea more directly than on the other coasts through karstic cave systems that were above sea level during the last glacial period but have been flooded by seawater to different degrees ever since that period ended.

3 Human-Derived Fluxes and Animal Forest Habitat Change

In addition to the complex impacts of global stressors, coastal ecosystems are exposed to a number of problems associated with changes in the local environments. Overall, these changes derive from alterations of chemical, biological, or physical fluxes, which are caused by the growth of human settlements and infrastructure, habitat loss, resource overexploitation, and land reclamation activities that can completely destroy whole components of tropical seascapes (Fabricius 2005).

As a complement to the conceptual model of a socio-economic and ecological system, Figure 4 shows real case images of the complex direct and indirect interactions. It also demonstrates the linkages of human-derived fluxes (drivers, impacts, and ecosystem state) that result in the loss of ecosystem services. The main drivers of the socio-economic system (red) are related to tourism and urban development, increases in migration and low-income housing, and overfishing. The loss of key habitats in the tropical seascape is shown in light brown. Such losses may cause

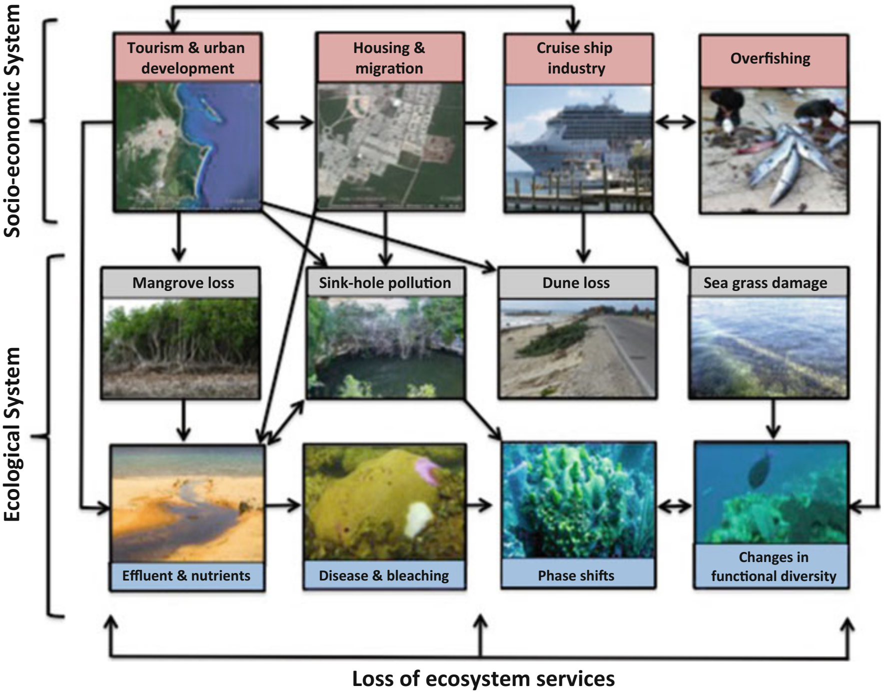

Fig. 4 Interactions of complex drivers of change, impacts and ecosystem state within the socio-ecological system of a tropical seascape (Image sources: INEGI, 2015; DigitalGlobe, Google Earth. Elaboration: CINVESTAV-LEEAC, Mexico, and all other images: Andrea Rivera-Sosa)

coastal transformations to the ecological system (light blue). As mentioned before, the ecosystem state (light blue) may be in distress due to phase shifts and decreased resilience, whereas coral reefs may be exposed and prone to further impacts of bleaching and disease outbreaks.

3.1 Chemical Fluxes

3.1.1 Water Quality and Nutrient Inputs

Locally, one of the most pressing issues is the decline in water quality in coastal areas, which is associated with land transformations in order make way for agricultural expansion and urban development. These changes alter watershed runoff and chemical fluxes from land to sea. Water quality parameters such as dissolved inorganic nutrients (nitrogen and phosphorus) and suspended particulate organic matter concentrations may increase due to these land use conversions and affect coastal ecosystems by increasing turbidity, sedimentation, and pollution (Fabricius 2005).

Each of these parameters is associated with a medium to moderate negative impact on calcification, tissue thickness, zooxanthellae density, photosynthesis, and survival of adult colonies in reefs. In contrast, it has been documented that particulate organic matter in the water column may have positive effects on the ecological processes of coral reefs (Fabricius 2005). Corals can adapt to reduced light caused by high turbidity in the water column by increasing lipid reserves in polyps, thus ensuring energy levels necessary to survive low light conditions (Maynard et al. 2010; Fabricius 2005). However, despite their ability to adapt to high turbidity or sedimentation, corals are highly vulnerable to chemical toxins (heavy metals, insecticides, and fungicides) that can be deleterious at different life history stages, ranging from fertilization to larval development processes (Markey et al. 2007).

Sewage pollution is often identified as a problem for coral reefs, but it has not received the serious attention that is needed. As Wear and Vega-Thurber (2015) recently noted, even treated sewage can introduce a variety of substressors to coral reefs. These individual stressors chemically interact with one another, thus having more intense negative effects on corals (e.g., nutrient-enhanced pathogen growth). These synergistic interactions are poorly understood, and it is suspected that they may potentiate the impacts of other nonrelated stressors, such as bleaching or overfishing leading to phase shifts. Redding et al. (2013) also showed an important correlation between an increase in derived nitrogen from sewage pollution and disease severity in the coral genus of *Porites* in Guam. Similarly, Mora (2008) and Bozec et al. (2008) showed that in the Caribbean, the abundance of macroalgae and coral mortality was correlated with human density in areas neighboring coral reefs.

Studies in the Pacific and Atlantic oceans are showing that phase shifts involve not only transitions from coral to algal dominance but also from coral to sponge dominance (McMurray et al. 2015). In particular, Knapp et al. (2013) suggested that sponge dominance in the lagoon of the Palmyra Atoll, in the Central Pacific Ocean, was a result of a decrease in environmental quality: sponges thrived as sediments, turbidity, and food availability increased in an environment that was originally dominated by *Acropora* species, crustose coralline algae, turf algae, and the giant clam *Tridacna maxima* (Knapp et al. 2013). In another example, surveys conducted in Florida between 2000 and 2012 showed that the population and recruitment of the barrel sponge *Xestospongia muta* has been increasing over time, while scleractinian coral cover has been decreasing (McMurray et al. 2015). In the Caribbean, major phase shifts are causing changes in reef structure, as larger more structurally complex species, such as those in the *Orbicella* complex, are being replaced by less complex species, such as those in the genus *Porites* (Alvarez-Filip et al. 2013).

Excessive nutrient inputs not only cause phase shifts in coral reef ecosystems but may also affect seagrass ecosystems (Fig. 5). The nitrogen and phosphorus derived from filtration of septic tanks from coastal housing may cause the proliferation of algae and cause direct competition for light, space, and nutrients in seagrass. This problem may be exacerbated in lagoon systems where less nutrient dispersion occurs due to high resident times of seawater due to the protection of barrier reef systems.

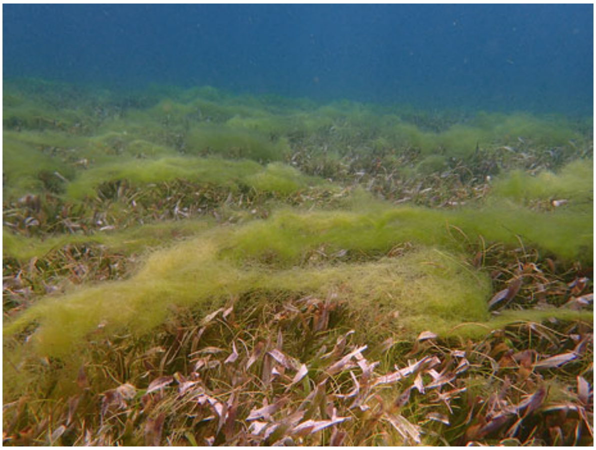

Fig. 5 Seagrass ecosystem dominated by *Thalassia testudinum and Syringodium filiforme,* covered by filamentous green macroalgae (*Chaetomorphalinum*) in Big Corn Island, Nicaragua (Image source: Andrea Rivera-Sosa, Date: 09/3/2016)

3.2 Biological Fluxes

3.2.1 Phase Shifts

Stressors such as nutrients from sewage and groundwater pollution may be the main precursors of phase shifts from coral-dominated to algae-dominated reefs although they may act in conjunction with fishing pressures, bleaching, and hurricane events (Bozec et al. 2008). Contrary to what is generally proposed in the coral reef literature (Burke et al. 2011), groundwater pollution on the Caribbean coast seems to have resulted in a benthic phase-shift scenario that is thought to be independent of the distribution of herbivorous fish (Bozec et al. 2008). The nutrient-rich wastewater may itself cause the proliferation of macroalgae over a threshold where herbivores may not be able to control them, even if herbivore populations are not affected (Williams and Polunin 2001). This bottom-up process of the benthic phase shift has seldom been documented, but it constitutes an interesting explanatory alternative to the paradigm of fishing reducing the abundance of herbivorous fish (mainly parrot fish species) and allowing macroalgae to overgrow and outcompete corals (Russ et al. 2015).

Recent work (e.g., Bozec et al. 2008; Kramer et al. 2015; Russ et al. 2015; Wear and Vega-Thurber 2015) suggests that such a bottom-up control is relatively simpler that the top-down control, as it only implies a change in habitat consisting of increased nutrient availability (Russ et al. 2015). Thus, the underlying cause of habitat change could also be from different sources of local or regional coastal impacts and global climate change, such as dredging, sedimentation, sewage pollution, hurricanes, or coral bleaching. In contrast, top-down control may imply more processes (Russ et al. 2015): (1) fishing to reduce herbivore (i.e., parrot fish) abundance, (2) reducing grazing pressure, (3) increasing cover of macroalgae, and (4) decreasing coral cover (algae outcompetes adult corals for space or inhibits coral recruitment).

Fig. 6 Phase shifts from a coral- to an algal-dominated coral reef in Mahahual reef, Mexico (Image source: Roberto Hernández-Landa, Date: 2010)

Particularly in the Mesoamerican reef region (MAR), different bottom-up processes may produce benthic phase shifts, both at the local (Bozec et al. 2008) and regional scales, even within marine protected areas where there has been an evident increase of herbivorous fish (Kramer et al. 2015). This pattern is consistent with those observed in coral reefs in the Philippines (Russ et al. 2015) and New Caledonia (Carassou et al. 2013).

Moreover, although there are no quantifications of the loss of species produced by changes at a large scale, there has been a recent phase shift from coral to algae in the Mahahual reef system, Quintana Roo, Mexico (Fig. 6). This area has shown that the establishment of a cruise ship pier and the loss of vegetation cover linked to tourism and housing expansion may have produced the loss of 40 fish species and 43 ha (~10 km^2) of coral cover (Acosta-González et al. 2013; Martínez-Rendis et al. 2015). This type of massive tourism development is seen in many locations in the Mesoamerican Region and may be another precursor of phase shifts.

3.2.2 Loss of Tropical Wetlands

Humans vastly benefit from the ecology of mangrove ecosystems via provisioning services (food and natural resources), regulating services (ecosystem processes), and cultural (nonmaterial) services. Mangroves play a critical ecological role in providing breeding and nursery habitats for valuable commercial species and fisheries (Davidson 2014). Mangrove wetlands and seagrass habitats make crucial contributions in terms of biogeochemical processes, serving as sinks for inorganic nutrients and sediments and as exporters of organic matter (Childers et al. 1999). However, changes in temperature, salinity, and extensive development are also leading to major decreases in seagrass ecosystems, which through ecological connections can negatively affect other components of the seascape.

Despite their vast ecological services, tropical wetlands are among the most vulnerable ecosystems and are disappearing at an alarming rate. An estimated 54–57% of mangrove ecosystems have been lost over the last century (Davidson 2014). Wetland cover losses are linked to the overexploitation of natural resources, modification and/or reclamation of land for urban development, and aquaculture operations (Davidson 2014).

In Mexico, it is estimated that in the last 25 years, at least 10% of the mangrove ecosystems and cover have been lost or severely altered (Valderrama et al. 2014). Many of the tropical wetland ecosystems in the Cancún area and Riviera Maya have been vulnerable since the tourism expansion of the 1970s. Due to increased pressure to preserve important habitats, a series of Protected Areas were designated. Even though wetlands are under current protection, those located adjacent to or near the areas of the urban expansion of Cancún continue to be affected.

The government, through the National Fund for Tourism Development (Spanish acronym FONATUR) and other federal sectors, actively promotes tourism development through the purchasing of land with tourism potential and the reselling of it to interested investors (Saldivar 2016). In the years 2005, 2009, and 2011, the Mexican Secretariat of Natural Resources (Spanish acronym SEMARNAT) provided legal permission for the construction and expansion of new tourism developments for the Tajamar Esplanade (74.24 ha) (SEMARNAT 2016). However, The General Wildlife Law (Article 60-TER-1/02/2007) states, “no removal, filling, transplanting, pruning or any work or activity shall intervene in the integrity of the hydrologic flow of a mangrove ecosystem” (SEMARNAT 2016). Despite this, the federal government gave permission for the destruction of 49.10 ha (total area varies depending on the information source) of wetland ecosystem to expand the Tajamar Esplanade in Cancún, causing a major national and international uproar from the civil society and nonprofit organizations (Fig. 7).

Overall, there are many issues with the interpretation of laws for the formal protection of the wetlands and natural resources, yet political or economic interests may influence the decision-making processes. For instance, the FONATUR donated to SEMARNAT a total of 3,533 ha to be designated a Natural Protected area, namely, the Mangroves of Nichupté and Ecopark Cancún (107 ha-2013) (SEMARNAT 2016), but this donation may be used in strategic political decisions to allow the development of certain areas. Moreover, in response to the environmental destruction, the federal government issued a public statement that mentioned: “If permission had not been given to clear cut the area, the lawsuits of the investors who acquired the land with the permission of SERMANAT and FONATUR would have resulted in a potential financial loss to the Mexican government of more than three billion Mexican pesos, which is equivalent to more than half the budget of the Mexican Ministry of Tourism for 2016”. Currently, the project has been “temporally suspended” (SEMARNAT 2016; Saldivar 2016).

The destruction of wetland and mangrove ecosystems is an eminent threat to coastal areas with high tourism demand. However, concerns and misconceptions

Fig. 7 Destruction of mangrove and wetland ecosystems of the controversial project Tajamar Esplanade, Mexico, due to tourism development and expansion (Image source: Christian Alva-Basurto, Date: 14/03/2016)

have arisen regarding the recovery and restoration of these ecosystems. Once the ecosystems have been lost, the trajectories of recovery are extremely costly, and their success can only be measured in the long term. The urgent need to recover essential wetland ecosystems has led to an emerging field of restoration, which includes the de-canalization of wetlands and rivers, rehabilitation of degraded floodplains, decommissioning of dams, replanting of vegetation and wildlife, and the implementation of conservation and management plans to protect wetland ecosystems. This has been partly due to the economic valuation of wetlands and the fact that more than half of the world's diverse wetlands have disappeared (Davidson 2014).

The field of economic valuation of wetlands offers an opportunity to place a monetary value on a wetland that reflects its ecological and social importance in order to ensure its protection. For this reason, scientists are increasing their understanding of the major carbon stocks and fluxes in mangrove ecosystems as well as how they vary across species and zones to determine how much organic carbon can be stored (aboveground or at various layers underground). According to Herrera et al. (2016), many regions in Mexico, particularly those in the Gulf of Mexico, along with riverine type mangroves, contain species that can be considered high carbon sink facilitators. Also, mangroves in the Yucatan Peninsula were found to have the highest content of organic carbon (218.98 Mg C ha^{-1}) in the first layer of underground substrate (0–30 cm), followed by mangroves of the Gulf of Mexico Herrera et al. (2016). This important information allows for the estimation of total captured carbon, providing data to quantify the total value of an ecosystem and its loss when converted. This would enable the establishment of negotiating mechanisms for the conservation of wetland habitats to prevent and discourage the conversion of natural lands to filled lands for construction. In addition, this conversion of land releases the carbon stored in the soil, increasing the carbon dioxide and methane concentrations that contribute to climate change (Herrera et al. 2016).

Fig. 8 Interaction of the constructed coastline and dunes in Cancún, Mexico (Image source: Andrea Rivera-Sosa, Date: 30/06/2009)

3.3 Physical Fluxes

3.3.1 Coastline Modifications

Tourism development continually demands a larger area of coastline, increasing the interface where natural processes interact with built-up areas and coastal dunes (Fig. 8). In general, there are certain natural and anthropogenic factors that influence coastal erosion on different timescales. The most important coastal processes affecting sediment transport and the building up of coastal dunes are hydrodynamic factors such as waves, currents, and tides, and wind (Masselink and Hughes 2003). Other short-term events such as storms may also influence coastal erosion and dune formation.

Naturally, coastal dunes develop in areas where there is sufficient wind to transport sediment (i.e., fine sand), after which vegetation growth stabilizes the sand. Thus, vegetation plays a very important role in securing the sand dunes and preventing wind erosion. Also, vegetation increases the fertility of the sand and favors the accumulation of debris, which then helps moisture to be retained. Over time, the dune increases in size, offering natural protection against beach erosion and serving as a sediment storage system (Masselink and Hughes 2003).

These dynamic processes vary in different areas, but it is indisputable that human settlements have a huge impact on beach recovery. Alteration of dune formation and vegetation for the construction of roads and other urban infrastructure considerably impacts the geomorphology of a coastal area (Fig. 9).

For instance, the roads not only have a direct impact on coastal dunes, but they also allow a continual flow of traffic and people, which continues to alter dunes. Sediment transport can also become unbalanced by modifications of the coastline, such as those caused by piers, groins, sea walls, boardwalks, and other human-made structures (Masselink and Hughes 2003). Moreover, the direct removal of sensitive components of ecosystems is widespread. As a result of coastal development, many hotels and resorts remove seagrass to make the beach more suitable for swimming.

Fig. 9 Coastal roads built on dunes primarily for tourism transit on the island of Cozumel, Mexico (Image source: Moritz Kuch, Date: 24/11/2015)

Fig. 10 Coastal and marine attractions for cruise ship visitors concentrated at the tropical seascape in Cozumel, Mexico (Image source: Andrea Rivera-Sosa, Date: 23/11/2015)

Excessive and intensive tourism-related aquatic activities and attractions are concentrated for cruise ship visitors, further altering seagrass and coastal dunes (Fig. 10). Other impacts involve mechanical damage to corals or subaquatic vegetation due to recreational diving, anchoring, fishing (nets), and marine transportation.

There are even more extreme cases of coastal changes. This is the case of the Spratly Islands, south of China, where biodiverse atoll and seagrass ecosystems have been completely dredged and built over to create functional islands so that the government can gain control over territorial seas (Larson 2015). In addition, to complete habitat destruction, land reclamation, and dredging can produce sediment plumes and can reduce the availability of sediment, affecting the coastal morphology and processes in distant parts of the seascape (Masselink and Hughes 2003). In this process, the connectivity between populations of key species is also hampered (Larson 2015).

4 Management and Conservation of the Animal Forest and Tropical Seascapes

Worldwide, the main mechanism for the conservation and management of the tropical seascape is known as the Marine Protected Area (MPA). It is estimated that 27% of all coral reefs worldwide are currently within MPA schemes, but only 6% of these areas are considered effectively managed (Côté and Reynolds 2006; Burke et al. 2011). In Caribbean countries, there are more than 630 MPAs, encompassing 30% of the region's coral reefs, and many locations still have to increase their areas of protection (Burke et al. 2011). For instance, Mexico, one of the largest countries in Latin America, has MPAs on 22.7% of its territorial sea, on 12% of its continental platform, and on 1.5% of its Exclusive Economic Zone (EEZ) (Bezaury-Creel et al. 2009).

MPAs are specifically delimited geographical areas that cover extensions of the continental platform and the seascape. MPAs can be internationally or nationally declared for the conservation of biodiversity, resources, environmental services, and cultural heritage (Kelleher 1999). Their main objective is the protection of habitats from destructive activities, the recovery, and productivity of fisheries, and the implementation of actions to increase resilience to impacts and maintain ecological processes across the seascape (Moberg and Folke 1999; Pandolfi et al. 2005; Mumby 2013). These areas may be established under a wide variety of criteria, standards, and levels of protection, which may include marine spatial planning, no-take reserves, regulation of fisheries, and accepted levels of resource exploitation (Aswani et al. 2015). Their design and operation might be federal and/or state-based, comanaged (NGO and state-based or private entities and the state), top-down (the most common), or bottom-up (community-based), run by indigenous organizations and/or include a mixture of involvement. The increasing number of different comanagement schemes is a result of the lack of direct funding from state and a lack of adequate management and implementation.

Efforts to preserve key marine ecosystems face major challenges due to a lack of funding, low capacity, and the absence of political will to enforce the environmental laws and regulations at the core of MPAs. This can effectively turn MPAs into "paper parks" (Mora et al. 2006), where conflicts with political interests (such as industrial fishing or tourism development), and problems with communities whose livelihoods depend directly on scarce natural resources cannot be managed. Moreover, when the capacities for management and effective intervention are lacking, scientific knowledge may actually become irrelevant as technical documents and recommendations are put forward but not implemented (Bearzi 2007).

Indeed, it is estimated that two-thirds of conservation assessments published in peer-reviewed scientific literature are not followed by conservation actions (Bearzi 2007). Another common problem between conservation science and the real world (Knight et al. 2008) is that few policy makers are willing to face the great challenge of inspiring people to protect the environment. Marine conservation requires a long-term commitment to pursue direct actions and a multidisciplinary approach to benefit marine ecosystems. In addition to solid science and well-conceived action plans, what is desperately needed to promote MPAs is public pressure (Bearzi 2007). An effective MPA plan is one that links knowing and doing (Knight et al. 2008).

4.1 Social Inclusion in the Management of Marine Protected Areas

A complex issue in social-ecological systems is when people and/or indigenous communities have been part of a seascape and have depended on its productivity long before it is declared an ecologically sensitive area to be protected. Also, many settlements within MPAs continue to live in poverty under precarious and marginal conditions (Bezaury-Creel et al. 2009).

The establishment of MPAs and the inclusion of indigenous and local populations to ensure effective and rights-based access to resources has been a growing field of study, with controversial cases throughout the world that need to be constantly revisited. Case studies conducted globally have all argued the importance of the inclusion of local people in the establishment, management, and enforcement of MPAs (Christie et al. 2009). In many cases, livelihood alternatives are sought. Eco-tourism and community-based tourism (CBT) also seem to be proposed often.

However, it is important to mention that the establishment of an MPA and its management plan from a top-down approach may include programs for economic alternatives for the community that may not always be welcomed and perceived as a good initiative by local populations. Tensions, conflicts, and nonapproval can result from an improper process. Community-based tourism does not always work, and the mechanisms of its employment (or the politics of the MPA) may entail a variety of complex sociological and ecological factors that need to be taken into account.

For example, in Honduras, the first MPA in the country (the Natural Marine Archipelago Monument in Cayos Cochinos-1993) was promoted by national investors and a philanthropist, along with technical assistance from the Smithsonian Institution and financial support from international organizations. This area comprises 2 main islands and 13 cays with important seascape ecosystems, and it has a long history of resistance from indigenous fishing communities that benefit from the area (Brondo and Woods 2007). To foster acceptance among communities, the Honduran Coral Reef Foundation (HCRF) (a comanaging authority), local NGOs, and international organizations have promoted community-based tourism programs (in their management plans since 2004) as an alternative to fishing through training and confidence-building (Brondo and Woods 2007).

However, recent changes in the comanagement structure have provided a 10-year concession to the Mexican Azteca Foundation, which has resulted in other priorities related to tourism development (Kuch 2015). There are resource-based restrictions, and the majorities of the cays are privatized and have limited local communities use to one island and two cays. Moreover, the new concession actively promotes the filming of international reality shows (which are seeing increasing revenues abroad) in the sensitive habitats of the MPA (in cays designated for bird and turtle nesting habitats within the management plan) that have closed access to local indigenous people. This type of tourism confers very little benefits upon the locals (750$ each per 4 communities/per filming), and the management is further creating social inequalities (Kuch 2015). This highlights the negative impacts of a nonsustainable type of tourism on the socio-ecological system. This case is interesting because it shows how neoliberalism can overrule the goals of sustainability included in the management plans of an MPA, which ends up further disrupting indigenous groups by creating double standards in favor of groups with higher capital (Brondo and Woods 2007; Kuch 2015).

4.2 Current and Future Management Tools

Optimistic scenarios have resulted from the implementation of MPAs, particularly fishery management tools, which have restored overharvested stocks and helped protect fish and invertebrate populations (MacNeil et al. 2015). Historically, the exploitation of fisheries (large vertebrates and shellfish) may have been the first large human disturbance of coastal ecosystems (Jackson et al. 2014). There is also adequate evidence that fishing affects food webs, population structures, and the distribution of species and that it contributes to the loss of biodiversity and ecosystem services. There is also evidence that the alteration of specific functional groups, such as herbivores, leads to the cascading deterioration of reef communities (Jackson et al. 2014).

For this reason, MPAs need a mixture of adaptive management schemes to work alongside land use planning across all sectors (tourism, urban development) and the implementation of marine spatial planning to enforce fishing areas and recreational areas (Fig. 11). Enforced zones that target no-take zones, closed seasons, and size and species restrictions have demonstrated proven results in the restoration of food webs from previously overfished conditions (Bellwood et al. 2004). Other actions in MPAs involve sustainable tourism practices and the establishment of educational centers to increase awareness.

In addition, a watershed- and ecosystem-based management approach is often needed for the employment of measures such as reducing fertilizer inputs, increasing forest cover, and installing sewage treatment plants to reduce sedimentation and nutrient pollution (Burke et al. 2011). The understanding that bottom-up processes may be just as important as top-down processes in bringing about phase shifts in coral reefs is extremely important for the management of seascape ecosystems. Preserving coral-dominated reefs may require regulating not only the fishing of herbivorous fish but also the growth of human settlements on the coast, in addition to requiring the treatment and disposal of wastewaters. Even if eutrophication and pollution threaten coral reefs as much as overfishing (Burke et al. 2011; Wear and Vega-Thurber 2015), eutrophication has received considerably more attention from conservation organizations, possibly because of the practical challenges of dealing with a large-scale threat. For instance, pollution sources are often multiple, geographically widespread or far from the reefs they affect. These factors, combined with the diversity of pollutants involved, the high cost of water treatment systems,

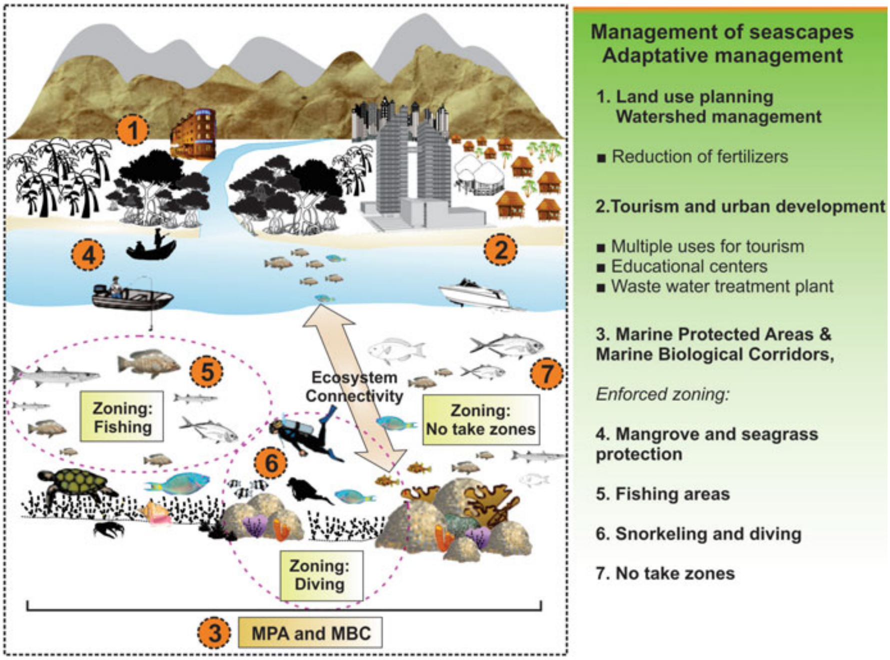

Fig. 11 Management of tropical coastal seascape connectivity demonstrating the importance of adaptive management schemes in Marine Protected Areas located adjacent to areas of high tourism development

and the need to coordinate different government levels and jurisdictions, make management actions difficult to implement.

Conservation initiatives in the MAR region have recently focused on empowering MPA managers to understand elements of resilience and successfully ameliorate the impact of local and global stressors on the region's reefs (Maynard et al. 2010). A new review by Aswani et al. (2015) provides an excellent summary and recommendations on how to move forward with emerging areas of science that may offer tools for the development and improvement of management actions regarding coral reefs. Overall, the main findings show that new technologies in molecular biology and marine biogeochemistry (stable isotopes) can be applied to isolate cause-and-effect relationships between stressors and biotic responses. They can also be used to determine the genotypic diversity within a population to further understand the levels of connectivity among tropical seascape populations. In addition, as global climate change continues to further impact ecosystems, scientists are studying genetic intervention strategies in the field of restoration by focusing on thermo-tolerant and disease-resistant corals from local source colonies and the translocation of these species to other areas. These actions must be followed to enable the effectiveness of mitigation and management efforts to be evaluated in order to provide insight into the potential resilience of particular coral reef species and genotypes to both local and global stressors (Aswani et al. 2015). In addition, the study promotes the shift in MPA designation and approach from the sole protection of "pristine locations" to areas under continual stress, where species with built resilience have been adapting over time and may offer genes tolerant to the tropical seascape.

4.3 Governance to Improve the Management of Seascape Connectivity

The creation of marine biological corridors (MBCs) has been widely encouraged as a response to the vulnerable condition of seascapes (McCook et al. 2010). The concept of MBCs was adapted from the Biological Corridor Program, a strategy to provide connectivity between protected areas that was implemented in the Mesoamerican region to enhance transcontinental biotic exchange, ensure gene flow, protect the migration routes, and widen the protection of habitats (Ankersen 1994). The same goals apply to MBCs, which consist of protected stretches of marine and coastal ecosystems linking national and international MPAs. In its simplest form, a protected corridor would be established to bridge a gap between two identical ecosystems encompassed by two neighboring MPAs. For instance, two MPAs covering two nonadjoining parts of a barrier reef could be linked by protecting the barrier reef areas between them. However, a more integrated view of corridors could protect areas linking landscapes and seascapes through places where crucial geochemical fluxes occur, currents flow, or migrations take place. The management of corridors would thus focus on protecting key links between MPAs, sometimes regulating and monitoring human activities that do not obviously or directly affect the MPAs. Although the effectiveness of implementing MBCs has faced criticism, the concept seems promising. Overall, the purposes of establishing conservation and management programs for marine and coastal corridors are to protect key ecosystem processes and strengthen the resilience of these ecosystems to disturbances and fluctuations (Maynard et al. 2010).

To holistically manage the complex interactions of the tropical seascape, governments, key actors, and stakeholders require the implementation of Integrated Coastal Zone Management (ICZM) approaches. ICZM, together with watershed approaches, aims at creating sustainable coastal development initiatives in which policy makers can jointly protect resources while enhancing economic development. The ultimate goal is to devise development strategies based on local protection and management plans in order to reduce anthropogenic threats and propose overarching solutions. To achieve integrated management, the following minimum criteria need to be met: (1) a comprehensive vision of land use and planning policies; (2) implementation of water and sanitation regulations; (3) MPAS and zoning of areas for public use (including tourism); and, of course, (4) agreements and synergies among key actors and stakeholders to move forward. In addition, adapted approaches such as marine ecosystem-based management (EBM) in tropical regions accentuate the need to include social systems and governance at their core (Christie et al. 2009). Moreover, the level of success of ICZM or EBM schemes will depend on how policy is implemented and adopted by all involved sectors and key actors. When smaller-scale management has been complex, management over large geographic scales such as the Caribbean region has proven to be extremely difficult.

In the Caribbean, the main industrial fisheries have targeted ecologically important species such as queen conch (*Lobatus gigas*), lobster, shrimp, groupers, and snappers, all of which are in decline (WECAFC 2011). More recently, commercial harvesting of sea cucumbers and historical catches of sharks, rays, and chimeras have been recorded (WECAFC 2011). Moreover, fishing pressures are simultaneously placed on coastal mangrove forests and coral reef systems, which enhance negative feedback loops between these components of the seascape. It has been observed that in many developing countries such as Honduras in Central America, the lack of regulations or the means to enforce them can result in the use of undersized nets that target juveniles in coastal lagoons and in large-scale fishing operations targeting spawning aggregation sites, further threatening sensitive and endangered species such as groupers and snappers.

Despite this complexity, there are several success stories in the MAR region. For example, the seven Central American countries enforced regional regulations for the Caribbean spiny lobster (*Panulirus argus*). These regulations include size limits, closed seasons, and export regulations (AECID/OSPESCA/SICA 2009).

Also, regional agreements and national and international environmental legislation have increased across all countries in the MAR. In particular, political interests in the conservation of trans-boundary tropical seascapes (such as the declaration of Tulum in 1997) (Kramer et al. 2015) have set an important path for the establishment of The Convention for the Protection and Development of the Marine Environment in the Wider Caribbean Region (WCR). The WCR includes very important technical agreements such as the Protocols on Oil Spills, Specially Protected Areas and Wildlife (SPAW), and Land-Based Sources of Marine Pollution (LBS). These agreements have served as governmental and international platforms to implement local strategies (Caribbean Environment Program 2015).

Leadership in organizations such as the Healthy Reefs Initiative, which coordinates and gathers information with over 60 key actors in Mexico, Belize, Guatemala, and Honduras, has been successful in promoting management actions based on science in the MAR region (Kramer et al. 2015). In particular, actions in Belize to establish moratoria on fisheries targeting herbivores, as well as banned petroleum exploration in MPAs and nearby zones, are a recent achievement of many institutions working together. The first shark sanctuary in the Americas has been established in Honduras, representing the implementation of key political decisions to preserve marine ecosystems. Moreover, in Quintana Roo, Mexico, there have been initiatives to manage one of its largest protected areas, known as the Sian Ka'an Biosphere Reserve (6,510 km^2), using an ecological conceptual model that is driven by local and national societal needs and is implemented as an integrated resource management plan (Mazzotti et al. 2005).

For these reasons, new cross-sector political agendas and creative solutions need to be developed in order to ensure governance for the true management and sustainability of the tropical coastal seascape. Aswani et al. (2015) recommend the establishment of five principles to ensure effective governance:

1. Develop leadership and raise awareness
2. Develop hybrid institutions or novel institutional collaborations (sustainable funding mechanisms)
3. Establish clear and fair rules with conflict resolution mechanisms
4. Experiment and adapt
5. Develop evaluation programs that monitor both social and ecological systems

Finally, Finkbeiner and Basurto (2015) recommend that societies rapidly adjust from regular comanagement schemes to seeking "multilevel" comanagement and peer-to-peer/governance networks. Doing so may require democratic participation in the creation of hybrid comanagement systems that can be tailored to historical, cultural, and ecological contexts.

5 Conclusions

Undoubtedly, achieving the much sought-after development of coastal human societies without compromising the animal forests and tropical seascapes of which they are a key component will require a deep understanding of the complex socio-ecological networks connecting the physical, chemical, biological, and human components of such seascapes. Accepting that human activities and the transformations they entail are an intrinsic aspect of most modern ecosystems is fundamental to establishing governance mechanisms and achieving sustainable interactions within socio-ecological systems.

It is also critical to realize that human settlements located inland, away from coastal areas, can have profound effects on the ecology of seascapes and the services they provide to other human populations. These complex inter-relations need to be documented, measured, and incorporated into models and management programs over considerably larger geographical scales than those considered so far. If we are to successfully tackle the challenge of sensibly using the resources and services that coastal seascapes offer, we will need creative solutions based on sound scientific and technical knowledge.

Scientists and coral reef managers now have the tools to understand the natural resources, ecological processes, and value of ecosystem services that allow better management decisions (Burke et al. 2011). Nevertheless, many of the actions needed are highly dependent on the power of political will and commitment. It is important to be aware that from a management point of view, knowledge alone can be of little use without the involvement of all those stakeholders whose actions most directly affect natural resources and services. The integrated management of social systems, seascapes, and animal forests will inevitably require changing some of our practices so that our negative impact on these natural systems is reduced and resilience mechanisms can absorb it. Perhaps among the most difficult practices to modify will be those derived from political and economic inertia among some of the most powerful stakeholders. Again, an adequate regulatory framework, availability of resources to enforce it, and political will are crucial. Both top-down (e.g., institutional support, enforcement, and legislation) and bottom-up (proactive inclusion of community governance systems) approaches need to be integrated (Aswani et al. 2015). Overall, the management of the connectivity of the tropical seascape needs to be adaptive, holistic, and efficient in order to decrease negative feedback loops.

The full protection of remnant sensitive areas will never be achievable if governments continue to overlook their own environmental legislation and actively promote the destruction of natural habitats to fulfill neoliberal agendas. Civil society has an important duty to hold governments accountable. This is not an easy task, and there still are many transnational obstacles to overcome, such as implementing political decisions to reduce carbon emissions worldwide. There are also more complex social factors that are likely to further influence coastal seascapes in the MAR region. For instance, in addition to traditional landscape transformations, large-scale forest destruction and land conversion to pasture, cattle ranching, and agriculture (oil palm) are now being financially propelled by organized crime (McSweeney et al. 2014). How such an increase in land use conversion will further impact tropical seascapes needs to be explored in the near future. As mentioned before, the overarching problems hindering the effective implementation of management, such as corruption, lack of governmental will, and economic interests that hinder conservation, need to be tackled.

Finally, the understanding of socio-ecological systems needs to be coupled with widespread involvement and commitment from society to realize a rapid increase in success stories, showing that sustainable development based on the wealth of animal forests is, in fact, possible.

6 Cross-References

- ▶ Caribbean Coral Reefs: Past, Present, and Insights into the Future
- ▶ Conservation and Management of Vulnerable Marine Benthic Ecosystems
- ▶ Ecosystem-Based Management: Opportunities and Challenges for Application in the Ocean Forest
- ▶ Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998

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Resilience of the Marine Animal Forest: Lessons from Maldivian Coral Reefs After the Mass Mortality of 1998

43

Carlo Nike Bianchi, Carla Morri, Roberta Lasagna, Monica Montefalcone, Giulia Gatti, Valeriano Parravicini, and Alessio Rovere

Abstract

Resilience is the ability of the ecosystem to recover after a perturbation. Assessing the resilience of marine ecosystems in the face of the increasing disturbance regime has become a major concern for their conservation. Among marine ecosystems, animal forests are expectedly little resilient. Their recovery may take long, increasing the risk of hysteresis and phase shift. Historical data series for most animal forests are virtually inexistent due to the challenging difficulty of the study of deep- and cold-water habitats. Tropical coral reefs, thriving in warm shallow waters, have undoubtedly been the best studied example of animal forest for a long time and may therefore provide ideas and concepts to be applied to the study of other animal forests. In this chapter, a historical data series on the coral reefs of the Maldives, which suffered mass mortality following the bleaching caused by the extreme El Niño – Southern Oscillation (ENSO) episode of 1998, is analyzed using an array of different descriptors to measure

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resilience. According to the specific descriptor considered, resilience varied between 4 and 16+ years, but full recovery may even be considered unachieved, as there are species that have not come back yet. The main take-home message from this Maldivian example is the need of adopting several distinct descriptors to assess the resilience of animal forests. Concentrating on the demography of the dominant species is not sufficient to get a reliable measure of whole ecosystem resilience.

Keywords

Animal forests • Resilience • Coral reefs • Bleaching • Hard coral cover • Recruitment • Trophic structure • Long-term monitoring • Maldives

Contents

1 Introduction

Resilience (from Latin *resilire*, to leap back) is the ability of the ecosystem to recuperate its structure and functions after a perturbation. In the ecological literature, the term resilience has been used inconsistently over the years (Standish et al. 2014), perhaps depending on how ecosystem dynamics and the role of natural and anthropogenic disturbances are interpreted (Nyström et al. 2000). For example, it has been equated to recovery or extended to embrace the sister concept of resistance (Côté and Darling 2010). The latter term (from Latin *resistere*, to stand back) should rather refer to the opposition that the ecosystem offers to a perturbation. Clearly, resilience and resistance are the two sides of the same coin: the stability of the ecosystem in the face of environmental change (Montefalcone et al. 2011). This chapter focuses on resilience, measured as the time needed to recovering the preexisting conditions after a perturbation. Resilient ecosystems recover fast; non-resilient ecosystems recover slowly and may be prone to hysteresis (from Greek *husterein*, to be behind), i.e., the lagging of the effect when the cause has ceased, or even to phase shift (from Greek *phasis*, appearance, and Old English *sciftan*, to arrange), i.e., a substantial modification of the structural state of the ecosystem.

Marine ecosystems are globally exposed to a number of pressures, such as increased nutrient and sediment load from land, littering and pollution, overfishing or other direct human impacts, extreme weather episodes and thermal anomalies, pathogen diseases, and alien species invasion (Rossi 2011). These pressures are producing biodiversity loss and may lead to dramatic change in ecosystem functioning and in the provision of services. Assessing resilience of marine ecosystems has therefore become a prime concern for ecology and conservation (Hughes et al. 2005; Lotze et al. 2011) and research in the field has grown tremendously in the last few decades (Duarte et al. 2015).

Among marine ecosystems, animal forests are normally shaped by long-lived organisms (mostly anthozoans and sponges), which can subsist for centuries or even millennia (Schuhmacher et al. 2002; McMurray et al. 2008; Parrish and Roark 2009; Bo et al. 2015). In the sessile benthos, longevity typically correlates with scarce reproductive potential and poor dispersal capacity, and the resilience of animal forests after episodes of mass mortality of these K-selected species is therefore expectedly low. Recovery may take long, increasing the risk of hysteresis and phase shift (Rossi 2013). While information about mass mortality episodes has accumulated in the last decades, our knowledge about patterns and timing of recovery is still inadequate. Recovery (from Old French *recovree*, past participle stem of *recovrer*, in turn from Medieval Latin *recuperare*, to regain health or strength) may be defined as a return to a normal state, but such a “normal state” is often not known for the marine animal forests. Estimating magnitude, patterns, and trajectories of change is indeed necessary to evaluate the possibility of recovery of animal forests but requires information on their previous conditions. Unfortunately, this kind of historical data on marine animal forests are extremely rare for most regions of the world ocean due to the challenging difficulty of the study of deep- and cold-water habitats, such as seamounts, cold-water coral reefs, the Mediterranean coralligenous, etc. (Schlacher et al. 2010; Gatti et al. 2015a). The nature, tempo, and trajectories of ecological changes that follow a major disturbance are therefore virtually unknown for this kind of animal forests (Williams et al. 2010).

Tropical coral reefs, thriving in warm and comparatively shallow waters, are easily studied and undoubtedly the best known example of animal forest (Rossi 2013). They may therefore provide ideas and concepts to be applied to the study of other animal forests. Based on literature analysis, coral reef recovery after major disturbances (bleaching, hurricanes, crown-of-thorn attacks, diseases, etc.) may require several years to decades (Nyström and Folke 2001; Bianchi et al. 2003; and references therein). Such different estimates could depend on geographic location, reef type, exposure, and depth but also on how resilience is actually measured. Most useful descriptors and metrics include either demographic or community parameters: recruitment, mean colony size, species diversity, similarity with the premortality condition, percent coral cover, and reef structure complexity (Bianchi et al. 2006). In addition, the threshold of the specific disturbance considered is central to measuring resilience (Standish et al. 2014), as the same animal forest may be highly resilient to minor disturbances but not resilient at all to major ones.

A major example of a global disturbance that hit a paradigmatic animal forest has been the mass bleaching event that followed the extreme El Niño – Southern Oscillation (ENSO) episode of 1998 (West and Salm 2003; Obura 2005). The Maldives have been among the most affected countries, with 60–100% coral mortality reported (Bianchi et al. 2003). This chapter uses historical data series on Maldivian coral reefs (Morri et al. 2015), aiming at illustrating their recovery trajectory and taking into account multiple descriptors: (1) recruitment, (2) colony density and size, (3) colony health, (4) cover, (5) diversity, (6) community composition, (7) trophic organization, (8) structural complexity, (9) constructional capacity, and (10) seascape. The Maldivian example will be discussed in order to draw attention to the implications of the choice and use of a specific descriptor to measure the resilience of animal forests.

2 Recruitment

Together with regrowth and asexual reproduction of the survivors, the main step toward recovery of an animal forest following a mass mortality event is obviously recruitment. Recruits may come from local survivors or from distant parents, which may be either brooders or broadcasters. Brooders incubate embryos on their own body, and larvae are released when already competent for settling. This normally implies short pelagic life and hence limited larval dispersal capacity. In broadcasters, fertilization normally occurs in the water, and larvae can live free for a comparatively long time and thus disperse over longer distances. Early phases of recovery may therefore be characterized by the recruits of the same species that previously constituted the forest if the local survivors are brooders, otherwise may be more prone to the colonization by different species. However, this somewhat simplistic schematization may be complicated by differential dispersal capacities and patterns of connectivity within and among reefs. Larvae from brooders may travel long distance when attached to floating object (Jokiel 1992), while long-lived larvae from broadcast spawners may stay around their natal reef if local currents prevent their large-scale dispersal (Sammarco and Andrews 1988; Black et al. 1991).

In the Maldives, hard coral recruitment was quantified from 1999 to 2014 by counting colonies smaller than 5 cm in diameter within replicated quadrats of 1 m^2, randomly placed in the reef flat and upper slope. Recruits were divided into three categories: *Acropora*, *Pocillopora*, and "others" (Cardini et al. 2012); especially in the case of "others", which included massive and encrusting species, particular care was taken in the field to avoid counting surviving patches of preexisting adult colonies. Despite high spatial variability, a general temporal trend was recognizable (Morri et al. 2015), and four distinct phases could be described: (i) 1999, (ii) 2000–2003, (iii) 2004–2008, and (iv) 2009–2014 (Fig. 1).

In 1999, many recruits were found on dead coral colonies, especially in shallow reefs. The most abundant among these recruits were encrusting Agariciidae, followed by massive Faviidae and Poritidae, all belonging to the category "others". Both encrusting and massive corals suffered comparatively lower mortality rates,

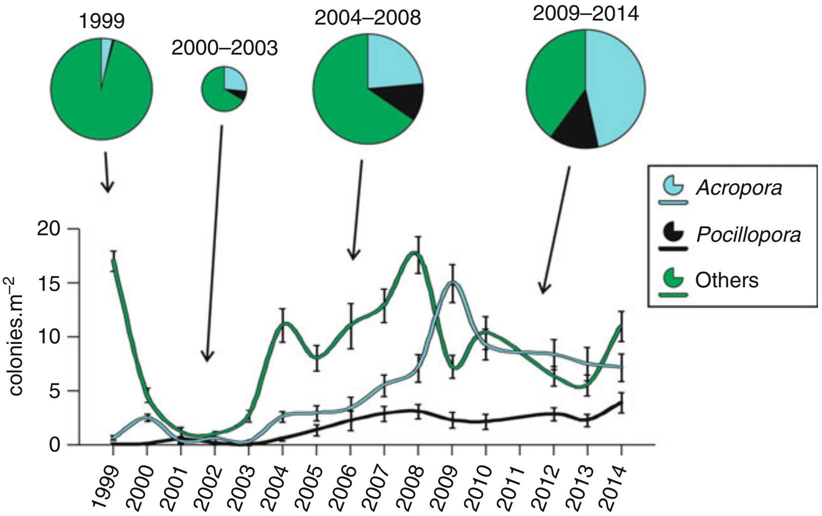

Fig. 1 Time trends between 1999 and 2014 of the number of coral recruits (mean ± standard error) belonging to three categories (*Acropora*, *Pocillopora*, and others) in the coral reefs of the Maldives (Data from Morri et al. 2015)

and the high recruitment observed nearly one year after the bleaching has been interpreted as the result of an "emergency spawning" following the thermal stress. Emergency spawning could be a paradoxical strategy to face environmental change and can be compared to hormesis, the phenomenon for which a stress factor produces positive effects at a sublethal level (Bianchi et al. 2003). Recruitment by *Acropora*, which suffered the highest mortality in 1998 (Bianchi et al. 2006), was extremely low in 1999. Although scarce, some *Acropora* colonies reached 14 cm in height. This size is compatible with the yearly growth rate reported for several species in the genus, and it can therefore be inferred that the first recruitment waves for this coral arrived soon after the mortality event, possibly from colonies surviving in deep refuges. No recruits of *Pocillopora*, which also suffered high mortality in 1998, were recorded in 1999. Between 2000 and 2003, recruitment of all corals was extremely low, possibly due to the scarcity of living adult colonies. From 2004 to 2008, recruitment rate increased, especially for the category "others", which resulted dominant. Adult colonies of *Acropora* and *Pocillopora* had been nearly extirpated in 1998, and the recruitment of these corals could start only after the newly settled colonies matured. Finally, in the period 2009–2014, recruitment rate by the others slowed down while that of *Acropora* increased. *Acropora* became codominant with the "others"; *Pocillopora* recruits, always scarce in the previous phases, became comparatively abundant, especially on shallow ocean reefs.

Differential success of the three coral categories was due to a combination of recruitment and post-settlement survival, while regrowth and asexual reproduction (such as fragmentation) of older colonies appeared unimportant (Morri et al. 2015).

Recruit community composition in 2014 roughly mirrored adult community composition: acroporids, massive and encrusting corals (i.e., the “others” in the recruitment counts), and branching corals (mostly pocilloporids) characterized Maldivian coral reefs as in 1997–1998.

3 Colony Density and Size

The canopy of animal forests is defined and shaped by colonial invertebrates (e.g., cnidarians; in the case of sponges the term colony may be inappropriate). Measuring colony density and size after a major disturbance is therefore of prime importance to evaluate the recovery potential of animal forests.

In tropical coral reefs, the canopy is often formed by tall arborescent species, such as many *Acropora* corals. In the Maldives, large tabular *Acropora* corals used to dominate at shallow depths before 1998 (Morri et al. 1995; Bianchi et al. 1997) but nearly disappeared following bleaching. In 2004, Maldivian reefs appeared rich in tabular *Acropora* colonies again, especially at some sites (Fig. 2). *Acropora* tables were counted, and their diameter measured, in replicated belt transects (20 m × 2 m) randomly laid in reef flats and slopes. Only colonies with diameter equal or greater

Fig. 2 Examples of Maldivian shallow reef coral communities dominated by large tabular *Acropora* before (1997) and after (2004) the mass bleaching and mortality of 1998 (Modified from Lasagna et al. 2010a)

than 15 cm were taken into account, as tables bigger than this size are known to stabilize their radial extension at a nearly constant rate of 10 cm · a^{-1} (Lasagna et al. 2010a).

A total of 192 colonies of *Acropora* tables was counted in 2160 m^2, averaging 4.8 colonies per transect (40 m^{-2}) but reaching 8–10 colonies per transect in quiet lagoon reefs. Most colonies had diameters smaller than 40 cm, but some were larger, up to 105 cm. Assuming a radial extension rate of 10 cm · a^{-1}, colonies larger than 65 cm can be interpreted as the survivors of the mass mortality of 1998; conversely, they may represent the result of enhanced growth rates in uncrowded situations as those characterizing the coral reefs of the Maldives in 2004. Tabular *Acropora* colonies are known to grow rapidly and to be able to outcompete the neighboring corals – two features that facilitate their recovery after a disturbance.

4 Colony Health

The mortality caused by a disturbance may be total or partial. The former involves the death of the whole colony, and recovery would therefore require recruitment of new organisms coming from outside in the form of larvae issued from sexual reproduction. The latter produces more or less wide necrotic areas in the colony, which remains anyway alive. Recovery, therefore, might in theory take place – at least in part – thanks to the regrowth of living tissue from the borders of necrotic areas. In coral reefs, for example, branching coral colonies, such as *Acropora* and *Pocillopora*, typically undergo total mortality, while massive coral colonies (e.g., Faviidae) often exhibit partial mortality (Bianchi et al. 2003).

Quantifying the proportion of colonies totally or partially dead and the amount of damage on the latter ones may therefore be useful to assess the state of the animal forest after a disturbance. Similarly, the repetition of this quantification over time may help evaluating recovery: the persistence of damaged colonies may suggest hysteresis, while a proportional increase of healthy corals will be an unequivocal indication of recovery.

Lasagna et al. (2014) devised a Coral Condition Index (CCI) based on the proportional abundance of coral colonies belonging to six ordinal categories that represent their condition: (i) recently dead, (ii) bleached, (iii) smothered, (iv) upturned, (v) broken, and (vi) healthy. These categories were assigned a different degree of health, according to the following scale: Degree 0 – recently dead corals, whose colonies evidently had no possibility of recovery; Degree 1 – bleached coral colonies, which could survive bleaching if intensity and duration of the causal agent (i.e., high temperature) do not exceed certain limits, beyond which corals die; Degree 2 – smothered coral colonies, which can survive provided that the loose sediment deposited on the branches is removed by physical agents or shed along with coral mucus; Degree 3 – upturned coral colonies, which could express potential for reattachment and growth, especially if landed on solid substrates; Degree 4 – broken coral colonies, which could show signs of growth of new tips and had no evidence of disease; Degree 5 – healthy coral colonies.

The Coral Condition Index (CCI) was computed on the basis on the above hierarchical scale and the abundance of coral colonies, according to the formula:

$$\mathrm{CCI} = [(\mathrm{H}/\mathrm{T} \times 5) + (\mathrm{B}/\mathrm{T} \times 4) + (\mathrm{U}/\mathrm{T} \times 3) + (\mathrm{S}/\mathrm{T} \times 2) + (\mathrm{W}/\mathrm{T})] \times 5^{-1}$$

where H is the number of healthy coral colonies, B is the number of broken coral colonies, U is the number of upturned coral colonies, S is the number of smothered coral colonies, W is the number of bleached coral colonies, and T is the total number of coral colonies. CCI ranges from 0 (100% dead corals) to 1 (100% healthy corals).

The CCI was applied in the Maldives from 2005 to 2010 to tabular *Acropora* and *Pocillopora* colonies, using replicated belt transects (20 m × 1 m) at several depths and across different habitats (Lasagna et al. 2014). The majority of coral colonies were found in healthy conditions, and damaged corals represented on average only 20% of the total: consistently, CCI ranged from 0.23 to 1.00, with an overall average of 0.84. In general, bleached and recently dead colonies represented the highest proportion of damaged corals. Smothered corals were never abundant and so were upturned corals. Broken corals were most represented in 2005, but their proportion decreased afterward; it should be recalled that the Maldives were hit by the Sumatra-Andaman tsunami of 26 December 2004.

The CCI condenses, integrates, and summarizes information on the status of individual colonies, providing an instrument for the early detection of environmental alteration. It did not show correlated to the number of total coral colonies, which means that it could be successfully employed independently of the coral abundance in the specific site under study. Further, it has the advantage of being of simple use and then applicable in long-term and large-scale monitoring plans.

A high proportion of corals with damage of the highest degree of severity (i.e., bleached and recently dead colonies) leads to a low value of CCI and suggests large-scale disturbances (e.g., climate anomalies). In contrast, moderate values of CCI suggest specific disturbances acting on a small scale, therefore predicting change that can be averted by local management actions.

Co-occurrence of different damage types, resulting from multiple pressures, could produce an increase of instability and fragility of the entire community. The abundance of severely damaged corals (low value of CCI) is indicative of bad reef conditions and may represent a point beyond which, in the worst hypothesis, resilience is eroded, and the consequent hysteresis may lead to phase shift, which will require huge and perhaps hopeless efforts for restoration (Montefalcone et al. 2011). CCI may be proposed as a complementary tool to measure ecosystem health and as such may serve to evaluate the feasibility of restoration plans. As CCI asks for detailing the kind of damage, it could be employed not only for the evaluation of present condition but may also be used as a predictive approach to assess community resilience and to help well targeted restoration programs. The experience in the Maldives by Lasagna et al. (2014) can be exported with no or little change to other Indo-West Pacific localities (Ferrigno et al. 2016), where species of *Acropora* and/or *Pocillopora* are normally abundant. Damage due to a specific disease can be added in the formula in regions or situations where diseases are important (e.g., the wide Caribbean). Appropriate taxa, belonging not only to scleractinians but also to gorgonians, antipatharians, sponges, or other canopy organisms, should be individuated in other areas and/or in other kinds of animal forest. Gatti et al. (2012) used the percentage of epibiosis and/or necrosis to assess the health state of the canopy-forming organisms in the Mediterranean coralligenous. The selection of few representative organisms able to show specific responses as a consequence of environmental stresses is a major concern for any index of biotic integrity.

5 Cover

Cover is one of the most universally used metrics to quantify sessile benthic organisms and communities on hard substrate, and is usually expressed as percentage (Bianchi et al. 2004). The mortality induced by natural or anthropogenic disturbances always implies a more or less severe reduction of biotic cover, which is therefore a useful tool for monitoring and assessing both algal and animal forests. In coral reefs, in particular, it is customary to measure the percentage of hard coral cover.

In the Maldives, Morri et al. (2015) collated historical data on hard coral cover obtained from published sources, including grey literature, and their own field surveys. An overall yearly mean of hard coral cover was computed irrespective of reef type, site, and depth zone (flat and upper slope) to describe the general trend of coral cover on Maldivian reefs during the last decades (Fig. 3).

The earliest data on coral cover in the Maldives come from the pioneer work done during the celebrated *Xarifa* expedition in the late 1950s (Wallace and Zahir 2007). Maldivian coral reefs at that time might be considered near pristine conditions, and coral cover averaged 65–75%. Early development, from coastal works at the British military base of Addu in the 1960s to increased extraction of coral rock as building material and growing tourism through the 1980s, was accompanied by a fall of coral cover to about 50%. The pressure regime changed in the 1990s. Maldivian coral reefs experienced not only increased human pressure, implying sediment loading and eutrophication, but also “minor” bleaching events and attacks by the crown-of-thorn starfish *Acanthaster planci* (Morri et al. 2010, 2015). Local reductions of coral cover down to 10–30% were nevertheless followed by rapid recovery to values >50%, suggesting an intrinsic high scope for resilience of Maldivian coral reefs. Things showed completely different after the mass bleaching of 1998, which caused living coral cover to fall to 2–8% (Bianchi et al. 2003). Although recovery started soon (Bianchi et al. 2006), coral cover has been increasing at an extremely low pace (Lasagna et al. 2008) and returned to values >50% only in 2014 (Morri et al. 2015). This contrasts with the comparatively fast coral recovery observed in the 1990s after minor disturbances. However, the Maldives of those years were still little impacted by human pressures, while today they are experiencing a tumultuous increase of tourism, urbanization, and coastal development (Nepote et al. 2016).

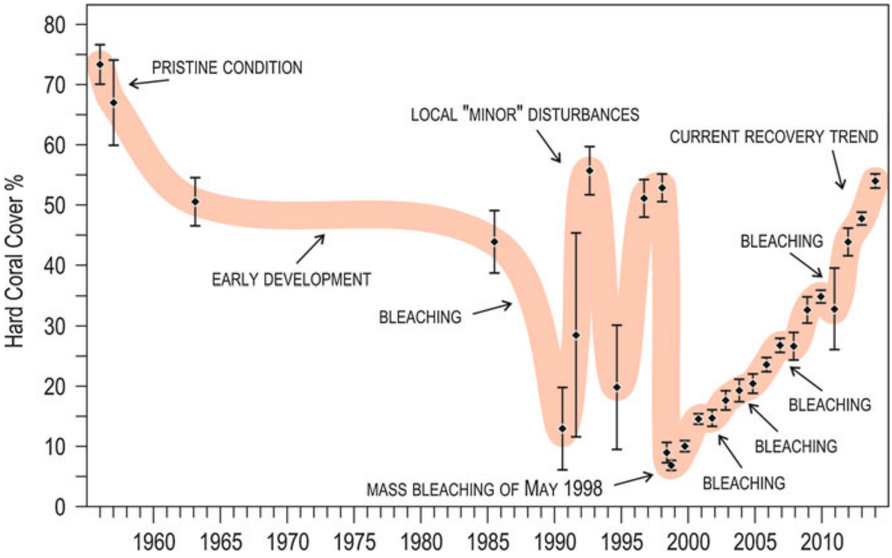

Fig. 3 Time trend (mean ± standard error) of hard coral cover in the Maldives, 1956–2014 (Redrawn and modified from Morri et al. 2015)

6 Diversity

The importance of biodiversity for ecosystem functioning has been underlined in thousands of articles and books, and the measure of diversity is often taken as a proxy for the appraisal of ecosystem complexity. The high number of taxa living associated to animal forests make them biodiversity hot spots in the sea, and species richness is one of the recommended parameters to estimate ecosystem recovery after major disturbances (Bianchi et al. 2006).

The first attempt to dress a complete list of the coral species living in the Maldives was done by Pillai and Scheer (1976), largely based on the results of the *Xarifa* expedition (Wallace and Zahir 2007). Other earlier inventories included the works of Wells and Spencer-Davies (1966) for Addu, of Pillai (1971) for Minicoy (administratively attached to the Laccadives), and of Ciarapica and Passeri (1993) for Felidu and North Malé. Amending previous coral inventories, both Pillai (1972) and Sheppard (1987) recorded 166 species for the Maldives. Unfortunately, no inventory was undertaken in the Maldives immediately after the mass bleaching of May 1998, which might have caused the local extinction of the most vulnerable species. In 2002, Bianchi et al. (2003) recorded 147 species. On the basis of a species-effort curve, they extrapolated a total number of coral species equal to 168, extraordinarily close to Pillai's and Sheppard's estimates before the bleaching. Thus, 4 years had

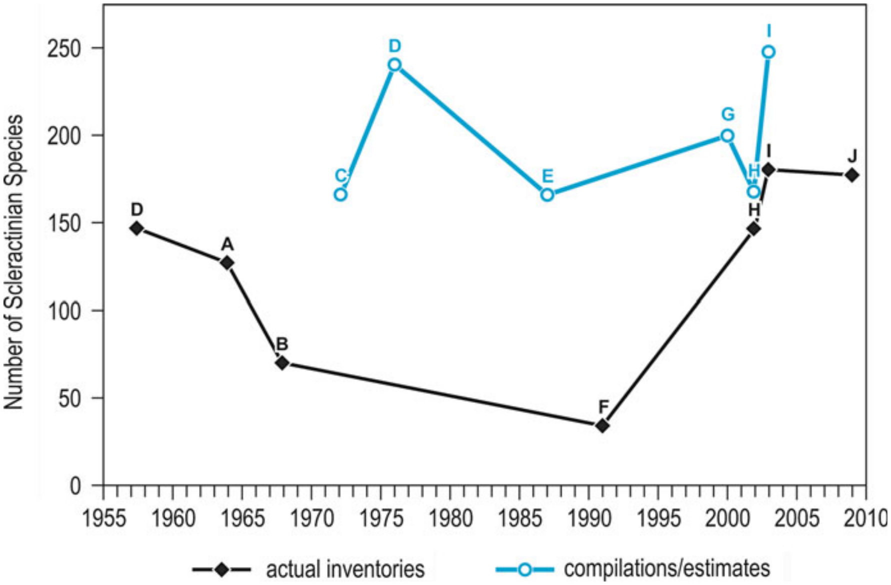

Fig. 4 Time trend of coral species richness in the Maldives (Data from: **A**, Wells and Spencer-Davies 1966; **B**, Pillai 1971; **C**, Pillai 1972; **D**, Pillai and Scheer 1976; **E**, Sheppard 1987; **F**, Ciarapica and Passeri 1993; **G**, Veron 2000; **H**, Bianchi et al. 2003; **I**, Pichon and Benzoni 2007; and **J**, Bigot and Amir 2012)

been enough to reestablish the preexisting species richness of Maldivian coral communities. Later thorough inventories recorded 180 species from South Malé, Felidhu, Wataru, and Ari (Pichon and Benzoni 2007) and 177 species from Baa (Bigot and Amir 2012) – i.e., figures higher than before the bleaching (Fig. 4). According to various compilations and estimates, including Veron (2000), the coral species richness in the Maldives might well exceed 200.

Notwithstanding present coral species richness is apparently higher than in the past, there are examples of taxa that have virtually disappeared from the Maldives, such as the scleractinians *Stylophora* and *Seriatopora* (Bigot and Amir 2012) and the hydrocoral *Millepora* (Gravier-Bonnet and Bourmaud 2012). A severe reduction in zooxanthellate soft corals has also occurred after the mass mortality of 1998 (Fig. 5), but no information is available about the species concerned by this reduction.

In general, knowledge of most marine phyla in the Maldives remains poor and with little background information (Andréfouët 2012), hampering comparison with the pre-disturbance situation. This is equally true for most animal forests, and especially for the deepwater ones, which only recently have been studied with some detail (Schlacher et al. 2010), thanks to the development of emerging technologies such as technical diving and remotely operated vehicles (ROV).

7 Community Composition

The quali-quantitative composition of the communities inhabiting the animal forests may be expected to change after the occurrence of a perturbation. Different species exhibit different sensitivity to a particular disturbance, and the resulting mortality rates can vary greatly among individual species. Early phases of community recovery may experience an increased proportion of r-selected species, which take advantage from the newly available space; on the contrary, recruitment of K-selected species may be delayed. According to the level of hysteresis (Montefalcone et al. 2011), the change in community composition may persist for some time or even result in a phase shift, with a stable community completely different from the one existing before the disturbance. Monitoring the quali-quantitative composition (e.g., the cover of the individual component species) is therefore important to evaluate the stability of the whole animal forest community.

While research on community composition is deemed necessary to understand the disturbance history of coral reefs (Graham et al. 2014), the knowledge of the taxonomic composition of coral reef communities in the Maldives is inhomogeneous and therefore not sufficient for many major groups (Jimenez et al. 2012). However, earlier studies evaluated the cover of non-taxonomic benthic categories, i.e., lumped levels of classification of sessile organisms, combining higher taxa with growth forms (Morri et al. 2010). Using 20 such non-taxonomic categories (*Acropora* branching, *Acropora* digitate, *Acropora* tabular, coral branching, coral foliose, coral massive, coral encrusting, *Tubastrea micranthus*, *Heliopora coerulea*, *Millepora*, corallimorpharians, *Palythoa*, soft corals zooxanthellate, soft corals azooxanthellate, whip- and wire corals, seafans, algae, sponges, *Tridacna*, tunicates) plus three non-biotic attributes (sand, rubble, rock), the coral reef communities have been monitored between 1997 and 2014, i.e., before, during, and after the mass bleaching and mortality of 1998 (Morri et al. 2015). This time series offers a unique opportunity to estimate the magnitude of change and the patterns and trajectories of recovery of an animal forest community after a major disturbance.

Each year between 1997 and 2014 (but in 2011), the percent substratum cover of the abovementioned benthic categories was estimated by replicated point intercept transects 20 m long laid parallel to the reef edge in the outer flat and upper slope. Correspondence analysis of the data provided an ordination plot in which the trajectory connecting year centroids illustrates a more or less conspicuous change between 1997–1998 and 1999–2000 and then a slow and irregular trend of return toward the initial situation of 1997–1998 (Fig. 6). Combining this trajectory with the time trend in the cover of the individual category (Fig. 5), five main phases can be recognized: (i) 1997–1998, (ii) 1999–2002, (iii) 2003–2004, (iv) 2005–2010, and (v) 2012–2014.

In 1997–1998, before the mass bleaching event, Maldivian reefs were dominated by hard and soft corals, followed by algae and sponges; many other organism groups were also present, while non-biotic attributes exhibited comparatively low cover values. In 1999–2002, following the bleaching, hard and soft corals virtually

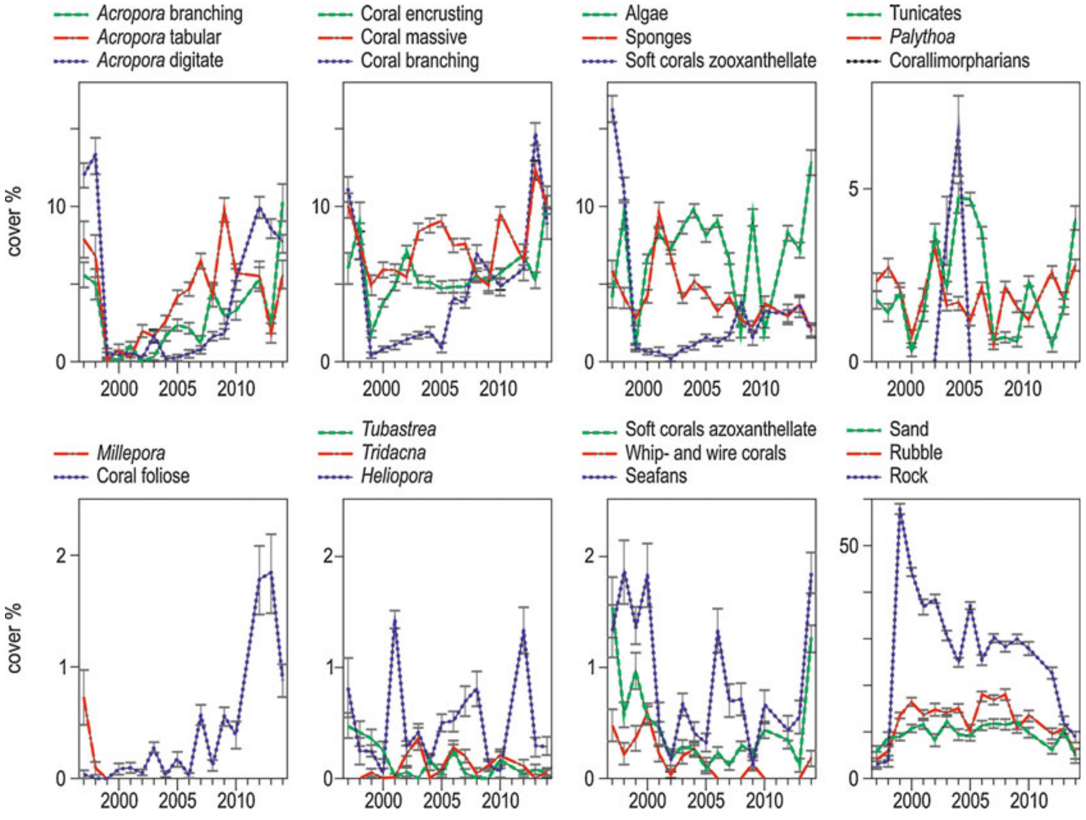

Fig. 5 Time trend of percent cover (mean ± standard error) of different benthic organism categories and non-biotic attributes in the coral reefs of the Maldives. Note different scales on Y axis (Data from Morri et al. 2015)

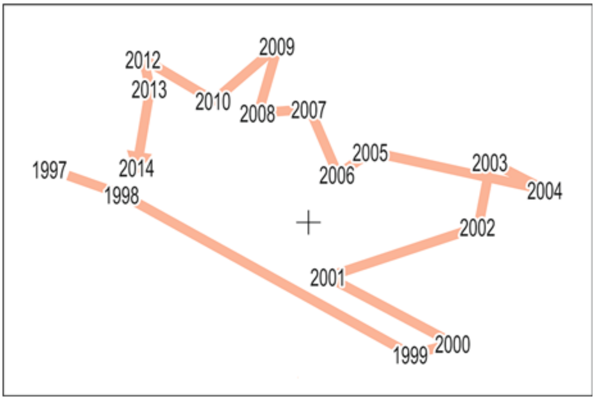

Fig. 6 Ordination plot on the first two axes from the correspondence analysis of a matrix containing percent cover data of 23 benthic categories in 1224 transects in Maldivian coral reefs: first axis (horizontal) explains 15.4% of the total variance; second axis (vertical) explains 14.0% of the total variance; the cross depicts the center of the axes. For the sake of simplicity, only year centroids are indicated, together with the average time trajectory between years (Data from Morri et al. 2015)

disappeared, with the exception of massive and encrusting corals, which had been less affected by mass mortality (Bianchi et al. 2003). The cover of other organisms did not change significantly, while that of non-biotic attributes, and especially of rock, increased tremendously. In 2003–2004, the cover of all categories of hard corals started to re-increase and that of rock to decrease; corallimorpharians showed abundant for the first time. In 2005–2010 corals, and especially tabular and branching *Acropora* and branching corals, continued increasing, corallimorpharians disappeared, and non-biotic attributes remained similarly abundant as in the previous period, suggesting that Maldivian reefs were still in a recolonization phase (Lasagna et al. 2008). Finally, in 2012–2014, although non-biotic attributes showed still comparatively abundant, the cover of hard coral categories returned to the pre-bleaching value. *Millepora*, however, was never found again, and zooxanthellate soft corals remained scarcer than before the bleaching. All the remaining categories changed little through the whole period of study (Fig. 5).

Throughout this time series, the shift from a coral-dominated state to an algal-dominated state, which often characterizes the global degradation of coral reefs (Cheal et al. 2010), has never been observed. Other studies in the Indo-Pacific demonstrated that grazing by herbivorous fish plays a fundamental role in hampering algal dominance (Hughes et al. 2007a, b). Data on fish assemblages in the Maldives for the study period are not available, but between 2003 and 2005 we noticed unusually large schools of Scaridae and Acanthuridae grazing during our field work; in 2003, we observed abundant *Bulbometopon muricatum*, an otherwise rare sight in the Maldives.

8 Trophic Organization

The foundation species of animal forests are by definition heterotrophic; virtually all of them are passive suspension feeders or active filter feeders, taking particulate matter (plankton and/or detritus) from the surrounding water. However, in well-lit and even in mesophotic animal forests, autotrophy is still possible. Macroalgae, even if usually not dominant, may thrive more or less copiously amidst gorgonians and sponges, while many coral species, obviously dominant in coral reefs but also present in other habitats, harbor endosymbiotic microalgae belonging to the dinoflagellates and commonly called zooxanthellae. Zooxanthellae are not restricted to cnidarians but also occur in clionaid sponges, tridacnid bivalves, and other animals. Many sponges and some didemnid ascidians harbor zoocyanellae (cyanobacteria), and some sea anemones harbor zoochlorellae (chlorophytes).

These animals hosting photosynthetic endosymbionts challenge the distinction between autotrophy and heterotrophy and well deserve the epithet "zoophytes" that nineteenth-century naturalists granted them with. They get part of their energetic needs thanks to the translocation of photosynthates from their symbiotic algae and complete their nutritional needs in terms of proteins and lipids capturing zooplankton. The relative importance of the two sources vary according to the individual species: within the corals of the genus *Porites*, for instance, *P. astreoides* is known to primarily use zooplankton for nutrition, whereas *P. porites* is capable of being fully autotrophic, zooplankton ingestion representing an insignificant component of its energy intake (Morri and Bianchi 1995). There is no universally accepted term for organisms that functionally lie between autotrophs and heterotrophs. The word mixotrophs seems etymologically adequate but is commonly employed for certain microorganisms that have the property of assimilating organic compounds as carbon sources but not as energy sources. A term recently crept into the coral reef literature is holobiont, coined to indicate the intimate symbiosis between the coral and its zooxanthellae (Yap 2007); there are examples, however, in which this symbiosis is not obligate, and the same species can live with or without zooxanthellae (Schuhmacher and Zibrowius 1984). Zooxanthellate corals have often been called polytrophs, but the term is both vague and ambiguous. It refers to the capacity to feed on multiple types of food, or to obtain nutrients in more than one way, and most so-called filter feeders are actually polytrophs in that they can incorporate both particulate and dissolved organic matter. As zooxanthellate (zoocyanellate, zoochlorellate) animals combine autotrophy and heterotrophy, they will be named "combo" organisms in this chapter.

Global disturbances such as seawater warming affect differently autotrophs, heterotrophs, and combos, which is expected to cause shift in the trophic organization of the foundation species assemblages of animal forests. Change may propagate through the food web of the associate mobile consumers, upsetting both the detritus pathway and the benthic-pelagic coupling.

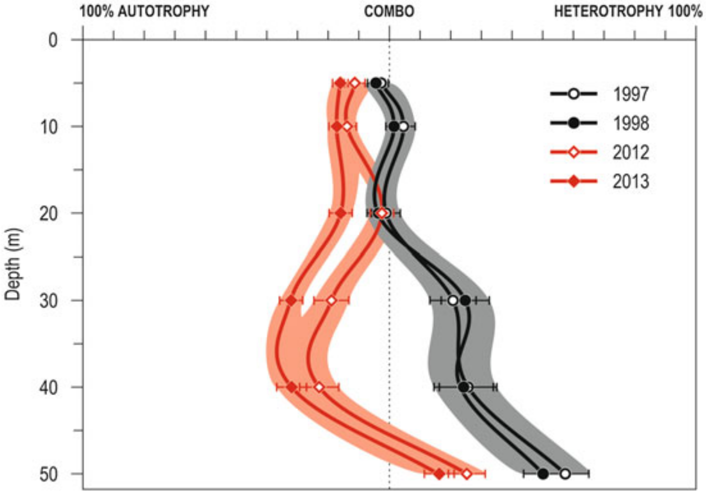

Fig. 7 Change in trophic organization with depth in Maldivian coral reefs in years before (1997 and 1998) and after (2012 and 2013) the mass mortality of 1998. Trophic organization is synthesized in an index ranging from −1 (100% autotrophy) to +1 (100% heterotrophy), with 0 indicating absolute dominance of combos or equal proportion of autotrophs and heterotrophs (see text). Horizontal bars and shadowed areas represent standard errors around mean values (Data from Morri et al. 2015)

The bleaching event of 1998 caused the mass mortality of combo species (zooxanthellate scleractinians, alcyonarians, hydrocorals, *Tridacna*) in many tropical areas. In the Maldives, the relative proportion of the three aforementioned trophic strategies (autotrophy, heterotrophy, and combo) was visually assessed in the field with the plan view technique in replicated spots of about 25 m^2 at 5, 10, 20, 30, 40, and 50 m depth along the reef profile (Morri et al. 2015). Surveys were carried out twice before the mass bleaching (in 1997 and 1998) and twice after (in 2012 and 2013). Trophic organization was synthesized in an index ranging from −1 (100% autotrophy) to +1 (100% heterotrophy), with 0 indicating absolute dominance of combos or equal proportion of autotrophs and heterotrophs. Results showed heterotrophy increasing with depth in both periods (Fig. 7), as expected from the gradual dimming of ambient light. In 2012–2013, combos returned dominant down to about 20 m depth, as they were before the bleaching. However, in 2012–2013 the proportion of combos was reduced in favor of autotrophs at all depths, and especially at 30 and 40 m, with respect to 1997–1998. Thus, although a phase shift from coral-dominated to algal-dominated reefs has not been evidenced in terms of community composition, the analysis of the trophic organization suggests that the food web basis has changed significantly. Thus, ascertained structural and compositional resilience may not necessarily vouch for functional resilience of the animal forest ecosystem (Duarte et al. 2015).

9 Structural Complexity

Like their vegetal counterparts on lands, animal forests evolve following a successional path from early assemblages of pioneer species that settle directly on the bare rock to a dense canopy and high biotic coverage of the substratum. This process implies increasing structural complexity both in terms of species diversity and spatial entanglement. Major disturbances inducing mass mortality of foundation species inevitably lead to a decrease in the structural complexity of animal forests. Graham et al. (2015) calculated that structural complexity was one of the main factors favoring Indo-Pacific coral reef recovery after a major climate-induced bleaching event.

Structural complexity is the result of a long successional history of growth and stratification. The most mature animal forests consist of taller and more branched corals, more intricate and bigger sponges, etc., which can alter major current flows and particle retention. In contrast, immature animal forests have a smaller surface exposed to the major currents, and therefore their capacity for capturing carbon, nitrogen, phosphorus, and other elements is much lower: in synthesis, simplified animal forests can process less energy (Rossi 2013).

In coral reefs, three different stages of structural complexity have been recognized: (1) young or immature stage, (2) mature stage, and (3) regressive stage. In the young stage, reef communities are characterized by the dominance of reef builders (scleractinian corals and coralline algae); reef accretion and consolidation are encouraged and erosion is reduced. The mature stage represents a balance between coral growth and sediment deposition, with a comparatively lower abundance of scleractinian corals. Finally, the regressive stage has sparse living hard coral cover and high amounts of rubble and sand. Rowlands et al. (2016) used similar terms (juvenile, mature, and senile) to describe aggradation capacity, stating that high reef resilience is more common in mature reefs. Before the mass mortality of 1998, the coral reefs of the Maldives were mostly in young to mature stages. In 2006–2007, the state of Maldivian reefs was evaluated paying attention to the three ecological stages, assessing by the plan view technique the relative importance of three biogeomorphological descriptors: (1) living hard corals, (2) rubble and sand, and (3) coralline algae (Lasagna et al. 2010b). Surveys were done in the reef flat and in the slope in 16 replicated sites with different wave exposure.

A great number of the reefs studied in 2006–2007 were still in an ecological regressive stage, suggesting no recovery. Rubble and sand were widespread in all sites, whereas coralline algae, which contribute to their cementation, were comparatively infrequent. However, some of the reefs were in the young stage, and few in the mature one, thus suggesting some recovery (Fig. 8). The ecological stage depended on depth and exposure. The reef flat appeared in young stage in sheltered sites and in regressive stage in exposed to very exposed sites. Thus, wave energy in the flat acts essentially as a deterrent for coral growth. In the slope, the ecological stage appeared inversely related to wave energy: “young” in very exposed sites, “mature” in exposed sites, and “regressive” in sheltered sites. On the slope,

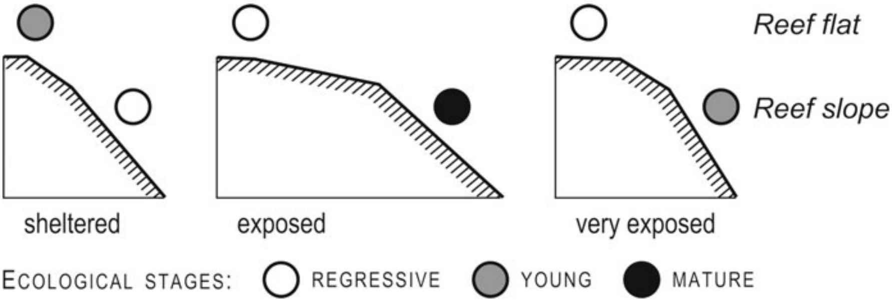

Fig. 8 A summarizing scheme of the ecological stages (young, mature, regressive) observed in the coral reefs of the Maldives in 2006–2007, according to depth zone (reef flat and reef slope) and exposure (see text) (Redrawn and modified from Lasagna et al. 2010b)

therefore, wave energy was favoring reef recovery. The environmental regime is thus likely to play a major role in the resilience of animal forests, as far as the structural complexity is considered.

10 Constructional Capacity

Animal forests are shaped by autogenic ecosystem engineers, i.e., organisms that modify the physical environment with their own mass. Arborescent anthozoans and sponges may build a canopy more than 1 m high, thus providing new habitat for other species, either epibionts or mobile associates. Such a new habitat is defined “biologically mediated habitat”, and the phenomenon is called “biological habitat provision” (Cocito et al. 2000). When the autogenic ecosystem engineers possess calcareous skeletons, the deposit of a carbonate structure persisting after their death is called “bioconstruction”, the term indicating either the process or the product (Bianchi 2001).

The best known bioconstructors are scleractinian corals, which are the main builders of both shallow-water tropical coral reefs and deep- or cold-water coral reefs. However, many other bioconstructors exist in the sea. Mediterranean coralligenous reefs, for example, are mostly built by calcified rhodophytes. Bryozoans, barnacles, serpulids, vermetid gastropods, oysters, mussels, and other invertebrates with calcareous skeletons and tests normally act as binders or secondary constructors but may even play the role of primary builders under certain circumstances (Bianchi 2001). Both coral reefs – at any depth – and coralligenous reefs result from the dynamic equilibrium between bioconstruction and destruction processes (by borers and physical abrasion), which create morphologically complex substrates where highly diverse benthic assemblages develop.

Mass mortality of bioconstructors following major disturbances may stop or hamper the process of bioconstruction, facilitate erosion, and leave place to soft-bodied organisms that frequently exhibit fast growth rates. Should this happen, the

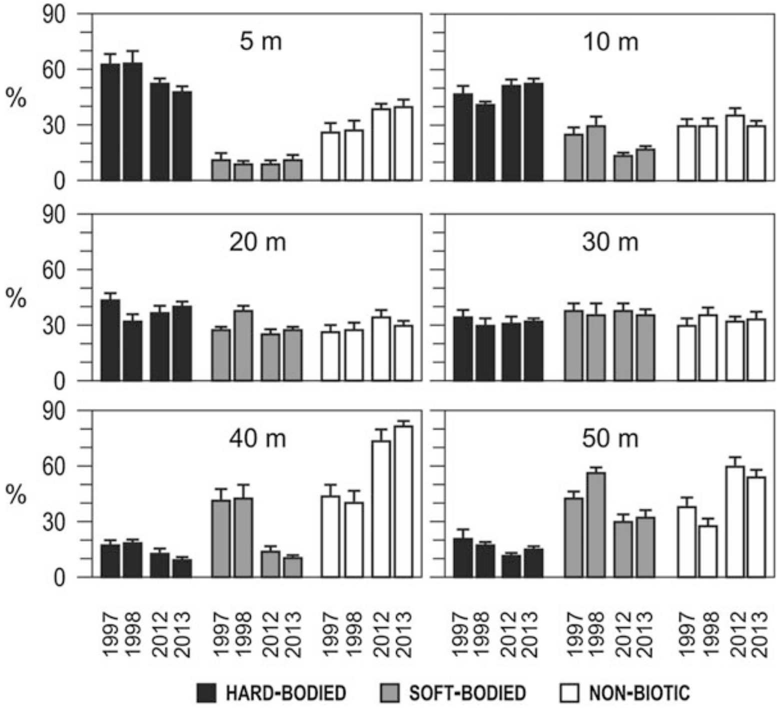

Fig. 9 Change in constructional capacity of Maldivian reefs at different depths in years before (1997 and 1998) and after (2012 and 2013) the mass mortality of 1998. Constructional capacity is expressed by the % proportion (mean ± standard error) of hard-bodied organisms, soft-bodied organisms, and non-biotic attributes (Data from Morri et al. 2015)

recovery of bioconstructors would be further delayed. The constructional capacity in Maldivian coral reefs following the mass bleaching and mortality of 1998 was evaluated in 2012 and 2013 at various depths down the reef profile and compared with the situation before the bleaching (1997 and 1998). Three categories were considered: hard-bodied organisms (mostly scleractinian corals, plus occasional large clams), which include all the primary and secondary bioconstructors; soft-bodied organisms (mostly soft corals, sponges and fleshy macroalgae), which have no construction potential per se but can act as bafflers, helping retain sediments within the reef; and non-biotic attributes (rock, sand, rubble), which evidently do not contribute to the bioconstruction. The substrate occupancy (in percentage) of these categories was visually assessed in the field with the plan view technique in replicate spots at 5, 10, 20, 30, 40, and 50 m depth (Morri et al. 2015).

The dominance of hard-bodied organisms at 5 m and 10 m depth appeared restored in 2012–2013, but the absolute values were lower than before the bleaching at 5 m (Fig. 9). In 2012–2013, the abundance of non-biotic attributes at 5 m was greater than in 1997–1998, whereas that of soft-bodied organisms at 10 m was lower.

Hard-bodied organisms, soft-bodied organisms, and non-biotic attributes were similarly represented at 20 m and 30 m depth in both 1997–1998 and 2012–2013. On the contrary, at 40 m and 50 m non-biotic attributes were more abundant in 2012–2013 than in 1997–1998, to the detriment of soft-bodied organisms. This may be interpreted as the result of increased sediment (rubble and sand) production after the mass coral mortality. Mostly generated in the flat and upper slope, this coral-derived sediment eventually deposited on the terraces that characterize Maldivian reefs at those depths (Bianchi et al. 1997).

Significant constructional capacity resulted therefore limited to the shallowest depths (<20 m). Change in cover of different bioconstructor guilds was therefore evaluated between 1997 and 2015 (but in 2011) at shallow depths (5–15 m) in both ocean reefs (ocean-facing sides of atoll rims) and lagoon reefs (lagoon patch reefs or lagoon-facing sides of atoll rims). In particular, four bioconstructional guilds and one group of non-biotic attributes were considered: (i) primary builders are those organisms that build the reef framework and therefore assure reef aggradation; (ii) secondary builders provide calcareous material to fill in the frame; (iii) binders are encrusters that consolidate the reef edifice; (iv) bafflers are soft-bodied algae and colonial invertebrates that, although not actively participating in the bioconstruction, help retaining sediment; and (v) non-biotic attributes (rock, rubble, sand) do not give any contribution to the bioconstruction. A bioconstruction potential index (BCP) was then devised using the following formula:

$$\mathrm{BCP} = \sum_{\mathrm{i}=1}^{\mathrm{n}} (s_{\mathrm{i}}\mathrm{C}_{\mathrm{i}}\%) \times 100^{-1}$$

where, n is the number of guilds (5, in this case), s_{i} is an importance score assigned to the i^{th} guild, and $\mathrm{C}_{\mathrm{i}}\%$ is the cover of the i^{th} guild. The value of s_i has been established at 3 for the primary builders, 2 for the secondary builders, 1 for the binders, 0 for the bafflers, and -1 for the non-biotic attributes. Therefore, BCP ranges theoretically from 3, in the unrealistic case of 100% cover by primary constructors, to -1, when only non-biotic attributes are present and no bioconstruction is possible, the reef thus being prone to erosion and drowning.

Applied to the Maldives data (Fig. 10), BCP resulted highly correlated ($\mathrm{R}^2 = 0.979$) to total hard coral cover (which is evidently desirable) but provided clear threshold values to evaluate constructional capacity. Negative values imply no bioconstruction, and they characterized Maldivian reefs between 1999 and 2003 (lagoon reefs) or 2007 (ocean reefs). Values between 0 and 1 depict reefs virtually deprived of primary builders and therefore capable of constratal growth only. Reefs might not be able to keep up with the ongoing sea level rise. These values characterized Maldivian reefs between 2004 and 2010 (lagoon reefs) or 2008 and 2013 (ocean reefs). Values of BCP greater than 1 (corresponding to a hard coral cover >50% in the Maldives) are indicative of superstratal growth, due to the relative abundance of primary builders, and characterized Maldivian reefs in 1997–1998 and again after 2012 (lagoon reefs) or 2014 (ocean reefs).

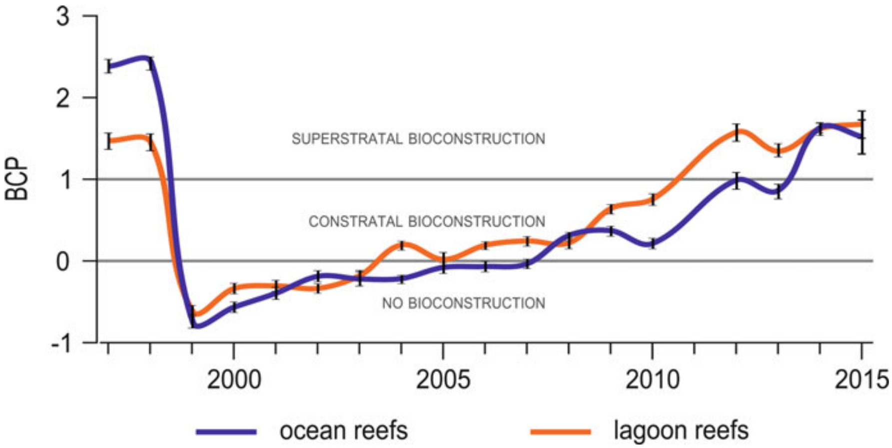

Fig. 10 Time trend of BCP, the bioconstruction potential index, on shallow (5–15 m) ocean and lagoon reefs in the Maldives, 1997–2015. Negative values of BCP imply no bioconstruction, values between 0 and 1 depict reefs capable of constratal growth only, values greater than 1 are indicative of superstratal growth (see text)

The coral reefs of the Maldives have therefore recovered most of their constructional capacity, even if hard coral cover on ocean reefs is still lower than pre-bleaching values. The other side of bioconstruction is obviously bioerosion (Hutchings 1986; Glynn 1997). The incidence of bioerosion in the destruction of Maldivian corals after the mass mortality of 1998 has not been studied; however, during our field work we had the opportunity to notice the abundance of clionaid sponges in dead massive corals, which might have contributed to the huge production of coral rubble recorded in 1999 (Lasagna et al. 2006).

11 Seascape

Forests on land are major landscaping elements, and the structure and dynamics of the mosaic of different vegetation (and hence habitat) patches are the core of landscape ecology. Animal forests in the sea are miniaturized mimics of vegetal forests on land but may nevertheless be considered as a prime example of submerged seascape. However, differences in biodiversity patterns between land and sea (Boudouresque et al. 2014) and, especially, lack of perception by common people of what thrives under the sea surface (Rovere et al. 2011) hampered the development of the discipline of seascape ecology until recently (Bianchi et al. 2005). Marine scientists are now aware that the application of landscape ecology concepts and techniques to the sea plays a central role in the study and monitoring of the multiscale processes that drive environmental change (Pittman et al. 2011). Terms such as benthoscape (relating to the seafloor) and reefscape (relating to coral reefs) were born, whereas no special terminology has been developed for the pelagic environment. Critical ecological thresholds are known to exist in the structural patterning of biogenic seascapes; exceeding these thresholds triggers abrupt phase shifts (Boström et al. 2011).

Seascape approaches integrate various levels of information from species identification to community structure and habitat characterization. They describe relationships between ecological processes and the spatial configuration of ecological mosaics. In the ecological literature, animal forests have been in turn defined as eco-ethological crossroads, biocoenoses, polybiocoenotic entities, assemblages, communities, community puzzles, and seascapes (Gatti et al. 2012; and references therein). Since animal forests are characterized by high heterogeneity, extreme patchiness, and coexistence of several ecological groups, a seascape approach seems to be the most reasonable solution for their characterization. Yet, few studies have applied landscape metrics to quantify coral reef resilience (Martínez-Rendis et al. 2016).

An important spatial pattern of animal forests is the increase of habitat three-dimensionality thanks to their stratified structure, which implies significant vertical elevation from the level bottom. At least three main distinct layers can be recognized: (1) upper layer, characterized by organisms with considerable (>10 cm) vertical growth, which forms the canopy; (2) intermediate layer, constituted by organisms with moderate (1–10 cm) vertical growth, which forms the understory of the forest; (3) basal layer, constituted by encrusting organisms, which protects and consolidates the substrate (Gatti et al. 2015b). Further layers can be recognized both at the highest and the lowest vertical extremes of the forest, namely, in the epibionts and the mobile biota associated to the canopy and in the borers and coenobites living in the interstices of the substrate, respectively.

Both natural and anthropogenic disturbances typically depress the 3D structure of marine forests (either algal or animal), thus causing seascape getting flatter (Bianchi et al. 2012). The destruction of the animal forests, in particular, would lead to an oversimplification of benthic ecosystems (Rossi 2013). The mass bleaching and coral mortality of 1998 did not change at first the reefscape of Maldivian coral reefs (Fig. 11). Notwithstanding the severe loss in living coral cover, the three-dimensional structure of the reef was preserved, dead coral colonies still being in place (Morri et al. 2015). By 2000, however, these dead coral colonies started to be destroyed by physical and biological erosion; by 2002, the three-dimensional structure of the reef was largely lost due to the breakage of dead colonies, which were reduced to rubble and sand (Lasagna et al. 2006). These loose detrital elements eventually deposited on reef slopes, smoothing the substrate and reducing reef rugosity. By 2004, a canopy of tabular *Acropora* was formed again, and the upper layer of the 3D structure was therefore reestablished (Lasagna et al. 2010a). However, both the intermediate and the basal layers remained severely underdeveloped (Fig. 2). In 2014, Maldivian reefscape looked yet very different (Morri et al. 2015) from what described before the bleaching (Morri et al. 1995; Bianchi et al. 1997). Morri et al. (2010) argued that the reconstruction of the structural framework is a prerequisite for complete reef recovery.

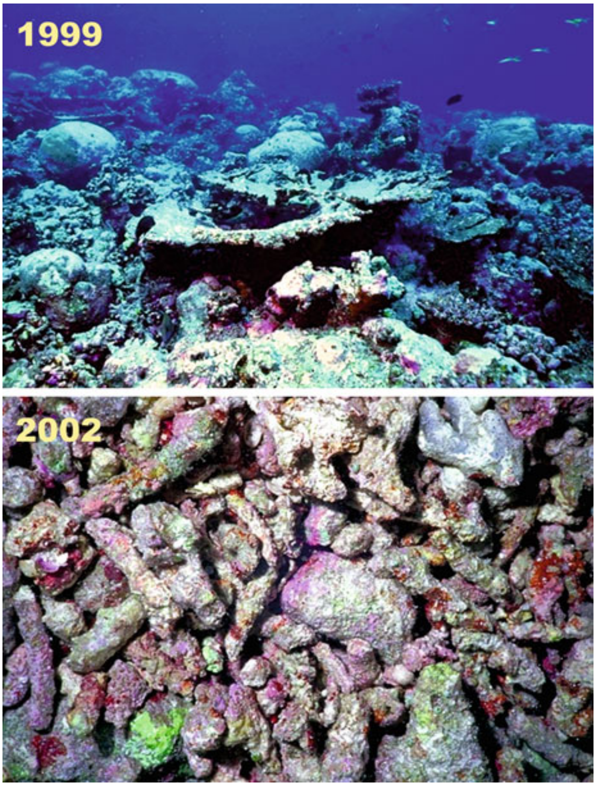

Fig. 11 Change in the Maldivian reefscape following the mass mortality of 1998. The dead coral colonies that remained initially in place, thus preserving temporarily the three-dimensional structure of the reef (1999), had been later reduced to rubble by physical and biological erosion (2002)

12 Final Remarks and Recommendations

This chapter used a data series on Maldivian coral reefs as a model study case of pattern and timing of animal forest recovery after a major disturbance: the bleaching of 1998 that killed nearly 95% of the foundation species of this particular animal forest (Bianchi et al. 2003). In this era of global change, coral reef resilience has been the object of many studies in different regions of the world ocean (Hughes et al. 2003, 2010; and references therein), but a major difficulty is finding the adequate empirical descriptors of resilience (Nyström et al. 2008). The Maldivian data set (Morri et al. 2015) is unique in that it considers an array of ten different descriptors, ranging from demographic parameters to ecosystem and seascape aspects. This provides the opportunity to compare different assessments of recovery and resilience (Table 1).

Sustained monitoring showed that Maldivian coral reefs reached complete or almost complete recovery when considering demography (recruitment, colony density and size, colony health) or synthetic descriptors like hard coral cover and diversity (in terms of species richness). Diversity, however, provided ambiguous

Table 1 Recovery and resilience of Maldivian coral reefs after the mass mortality of 1998, as estimated by yearly monitoring (till 2014) and ten different descriptors

	Descriptor	Recovery	Resilience
1	Recruitment	Probably complete; pre-disturbance information not available	11 years
2	Colony density and size	Complete for the main canopy species	6 years
3	Colony health	Almost complete	8 years
4	Cover	Almost complete	>16 years
5	Diversity	Complete for the total number of species; there are species missing	4 years
6	Community composition	Partial	14 years
7	Trophic organization	Incomplete	15 years
8	Structural complexity	Incomplete	9 years
9	Constructional capacity	Almost complete	14 years
10	Seascape	Partial	>16 years

results, as the total number of species was reestablished, but some previously common species has never been found again; recovery might therefore be considered unachieved. Diversity provided equivocal results also in one of the few studies that evaluated recovery of seamounts (Williams et al. 2010).

When considering descriptors at ecosystem level, recovery of Maldivian coral reefs was partial (community composition, seascape) or incomplete (trophic organization, structural complexity); only the constructional capacity appeared nearly reestablished. Consistently, resilience varied from 4 to more than 16 years (always remembering that recovery was rarely complete) according to the specific descriptor considered. Thus, although the risk of a structural phase shift seems avoided, Maldivian coral reefs are possibly suffering hysteresis. Marine animal populations and ecosystems are known to show some capacity of recovery but rarely to former levels of abundance (Lotze et al. 2011). Maldivian data series results are consistent with earlier studies estimating that the resilience of coral reefs after large mortalities is comprised between 5–6 years and more than 100 years (Bianchi et al. 2006). In the ample literature on coral reef recovery after disturbance, it has generally been assumed that recovery will eventually occur (Nyström and Folke 2001). On the other hand, it has also been observed that there may be critical thresholds beyond which resilience is lost (Mumby et al. 2007).

It is difficult to say to what extent the Maldivian lesson could apply to other animal forests. Resilience of ecosystems dominated by corals is low compared to most other marine systems (Williams et al. 2010). This chapter, however, showed that large differences in timing could, at least in part, depend on how resilience is actually measured. Notwithstanding the various attempts of rigorous definitions that followed one another in the last 40 years, the concept of resilience remains vague, varied, and difficult to quantify (Standish et al. 2014); similarly, there is no standard definition of recovery (Lotze et al. 2011). Resilience has even been defined as a nonconcept (Bianchi 1997), as there is no going back for species and ecosystems (Bianchi et al. 2012). After disturbance, animal forests are more prone to the invasion of alien species, which may replace the original components and further reduce the scope for returning to the original state (Gatti et al. 2015a). The highly species-rich animal forests in tropical shallow waters are supposedly less vulnerable to invasions, but this is not true. For instance, the Atlantic octocoral *Carijoa riisei* has invaded the Indo-Pacific (Calcinai et al. 2004), while the Indo-Pacific scleractinian coral *Tubastraea micranthus* has invaded the Atlantic (Sammarco et al. 2010). Little is known, for this respect, about deep- and cold-water animal forests.

Despite these conceptual difficulties, trying to estimate animal forest resilience remains of paramount importance for both science and management. The main take-home message from the Maldivian example analyzed in this chapter is the need of adopting several descriptors at various levels of integration. While tropical coral reefs are usually polytypic (Bianchi 2001), the animal forest canopies in temperate or cold waters are mono- or oligotypic, being shaped by just one or few species. This justifies that recovery and resilience are often estimated using only demographic descriptors (Teixidó et al. 2011; Santangelo et al. 2015). Population recovery is not necessarily indicative of ecosystem recovery (Lotze et al. 2011), as shown by the tabular *Acropora* example in the Maldives. Concentrating on the population structure and dynamics of a single or few dominant species may not be sufficient even in nontropical temperate forests, as change in community composition may persist after the apparent recovery of the canopy (Gatti et al. 2015a). Combining demography with several descriptors at the ecosystem level may be of help to get a reliable measure of animal forest resilience.

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13 Cross-References

- ▶ Animal Forests in Deep Coastal Bottoms and Continental Shelves of the Mediterranean Sea
- ▶ Animal Forests of the World: an overview
- ▶ Animal Forests Through Time: Historical Data to Understand Present Changes in Marine Ecosystems
- ▶ Caribbean Coral Reefs: Past, Present, and Insights into the Future
- ▶ Ecosystem Functions and Services of the Marine Animal Forests

- ▶ Global Biodiversity in Cold-Water Coral Reef Ecosystems
- ▶ Growth Patterns in Long-Lived Coral Species
- ▶ Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages
- ▶ Mesophotic Coral Ecosystems
- ▶ Where Seaweed Forests Meet Animal Forests: the Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem

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Ecosystem Functions and Services of the Marine Animal Forests

44

Chiara Paoli, Monica Montefalcone, Carla Morri, Paolo Vassallo, and Carlo Nike Bianchi

Abstract

Marine animal forests supply several services based on a multiplicity of ecological functions, thus generating a set of benefits to humans. Services have been studied in coral reefs, whereas less is known about the role of other animal forests. Actual estimates of economic value of the ecosystem services provided by reefs highlighted their ability to generate benefits for humankind, but these approaches cannot be considered complete. The fulfillment of sectorial valuations, adopting an anthropocentric approach, hindered an effective quantification, even economic, of total value and consequently of potential damages imposed to habitats. The adoption of a system view, based on the understanding of the entire habitat functioning generating services, is then required. Only from the assessment of functions, and then of natural capital disposition together with its present exploitation level, managers and scientists will be able to perform long-run plans for conservation. System methodologies, and in particular emergy analysis, can fulfill these needs by reversing the traditional approach to the valuation issue. System methodologies adopt a donor-side approach, which evaluates the ecosystem services as the amount of resources invested by nature independently from the presence of users and the value that humans assign to a service. The fulfillment of donor-side evaluations, free from subjective preferences, can be crucial for those ecosystem functions that are essential for the existence of marine animal forests but are not perceived by humans or scarcely evaluated by the market.

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Contents

1 Introduction

Making nature’s value visible to humans is becoming a key issue for the twenty-first century (MEA 2005; Sukhdev et al. 2010; de Groot et al. 2012). Awareness about the importance of conservation, protection, and valuation of the natural capital is continuously increasing, as a scientific, government, and management issue.

Over the past few decades, efforts addressed the topic of the link between ecosystems and human well-being. During the 1990s a “total lack of appreciation of societal dependence upon natural ecosystems” emerged (Daily 1997). Strains and damages generated by this attitude to natural environments became more and more evident, such as climate change, chemical risks, eutrophication, biodiversity reduction, and water crisis.

Gradually, humans began to perceive (and forcefully face) that changes imposed to nature by their activities provoke effects, direct or indirect, on all components of well-being. Negative outcomes appeared in many and different fields, from the fulfillment of basic needs (e.g., food, water, and shelter provision) to social relations, security, freedom of choice and action, spiritual, and aesthetic enjoyment. From these perceptions, the concept of ecosystem services (ES) arose, aiming at bringing to the light the relationships between people and nature embedded in the daily life and to mobilize environmental conservation and management. ES have been defined as the direct and indirect contributions of ecosystems to human well-being: in synthesis, ES are benefits people obtain from nature, directly enjoyed, consumed, or used (Sukhdev et al. 2010). From this original definition, the concept has been later applied and interpreted in multiple and often contested ways and raised a number of significant questions of scientific and ethical nature (Flint et al. 2013; Jax et al. 2013).

Costanza and Daly (1992) introduced the concepts of natural capital, associated with human capital and manufactured capital. Natural capital includes land, air, water, sea, and ecosystems themselves, human capital comprises all individuals' capacities for work, while manufactured capital encompasses all material goods generated through economic activity and technological change. Interactions between the three capital types generate well-being.

An intense debate aroused over the issue of substitutability of manufactured capital for natural capital in the production of goods and services. Turner (1993), on the basis of substitutability theory, defined four different kinds of sustainability, from very weak to very strong.

Very weak sustainability assumes the complete substitutability, while the very strong imposes the absolute non-substitutability and the consequent maintenance of natural capital untouched. If humans adopt the weak sustainability while the different types of capital are not perfectly substitutable, welfare will be irreparably decreased. On the contrary, if natural capital is kept distinct from other kinds of capital and preserved, its contribution to well-being can be examined, as well as the chance to partially replace it with the other types. Starting from the strong sustainability, it is possible to gradually shift toward the weak, while the vice versa is not possible. It is then important to identify and measure the natural capital, first from an ecological and then from an economic point of view, to make it comparable with other capital types.

How can we practically measure natural capital in ecological and economic terms? At this purpose scientifically sound methodologies, able to provide information that can be easily passed on to different stakeholders, from common people to managers and decision-makers, should be identified.

2 From Natural Capital to Well-Being: A Pathway From Nature to Humans

A correct evaluation of ES lays on the estimate of natural capital value. Human economy is supplied (and constrained) by the availability of natural capital stocks and ecosystem services flows (Sukhdev et al. 2010).

When dealing with natural capital and ES valuation, two main obstacles can be encountered: (1) the difficulty to measure something that sometimes we do not even perceive and (2) the necessity to translate ecological complexity in schematic and easily accessible information.

During the last decades, important steps forward have been made with the definition of some determining concepts: ecosystem functions, ecosystem services, and well-being. The clarification of the mutual links and relationships among these three components lead to the formulation of the so-called pathway from ecosystems to well-being. De Groot et al. (2002) defined an ecosystem function as “the result of the natural processes of the total ecological sub-system of which it is a part. Natural processes, in turn, are the result of complex interactions between biotic (living organisms) and abiotic (chemical and physical) components of ecosystems through the universal driving forces of matter and energy,” which is an economic metaphor for the limited stocks of physical and biological resources found on the Earth. Functions represent the potential to generate services that arise from these stocks; they originate directly from the natural capital, i.e., the ecological structures and processes of ecosystems and their mutual interactions (Sukhdev et al. 2010).

It can be said that, if services are what nature donates to humans for exploitation, functions are what nature keeps for itself and donates to species other than humans. Even if humans are mainly able to valuate only what they directly exploit and judge useful, their needs would not be satisfied in absence of the entire supporting ecosystems and their “hidden” functions. For example, an area hosting fish juveniles carries out a nursery function anyway, but generates a service only if commercial species are present among the juveniles hosted. Nonetheless, the service can be generated only if the trophic network supporting commercial species is maintained in healthy conditions.

According to the classification proposed by de Groot et al. (2002), functions can be split in four main categories: regulation functions, habitat functions, production functions, information functions.

1. Regulation functions govern fundamental ecological processes and are critical to all other functions and to the provision of ES. For instance, water, atmospheric gases, climate, soils, nutrients, and wastes move through ecosystems according to regulation functions.
2. Habitat functions provide space for animals and plants, used for refuge, foraging, or reproduction. This function category contributes to the conservation of biological and genetic diversity and to evolutionary processes.
3. Production functions originate the resources exploited by humans. Autotrophs convert solar energy, carbon dioxide, water, and nutrients into carbohydrates through photosynthesis and nutrient uptake. Carbohydrates are then exploited and transformed by secondary producers. These processes generate resources essential for human life, from food and raw materials to energy resources and genetic material.
4. Information functions are those originating from immaterial services such as reflection, spiritual enrichment, cognitive development, recreation, and aesthetic experience. They can be identified with the ability of ecosystems to maintain a variety of natural features that provide opportunities and choices for species.

A more detailed list of specific functions pertaining to each macrocategory, together with the originating natural processes, is reported in Fig. 1.

ES are actually conceptualizations of the useful things that ecosystems directly and indirectly generate for people. The importance, value, and perception of services change over time with cultural, social, and economic conditions. On the contrary, functions exist and remain together with their potential independently from humans’ behavior (Sukhdev et al. 2010).

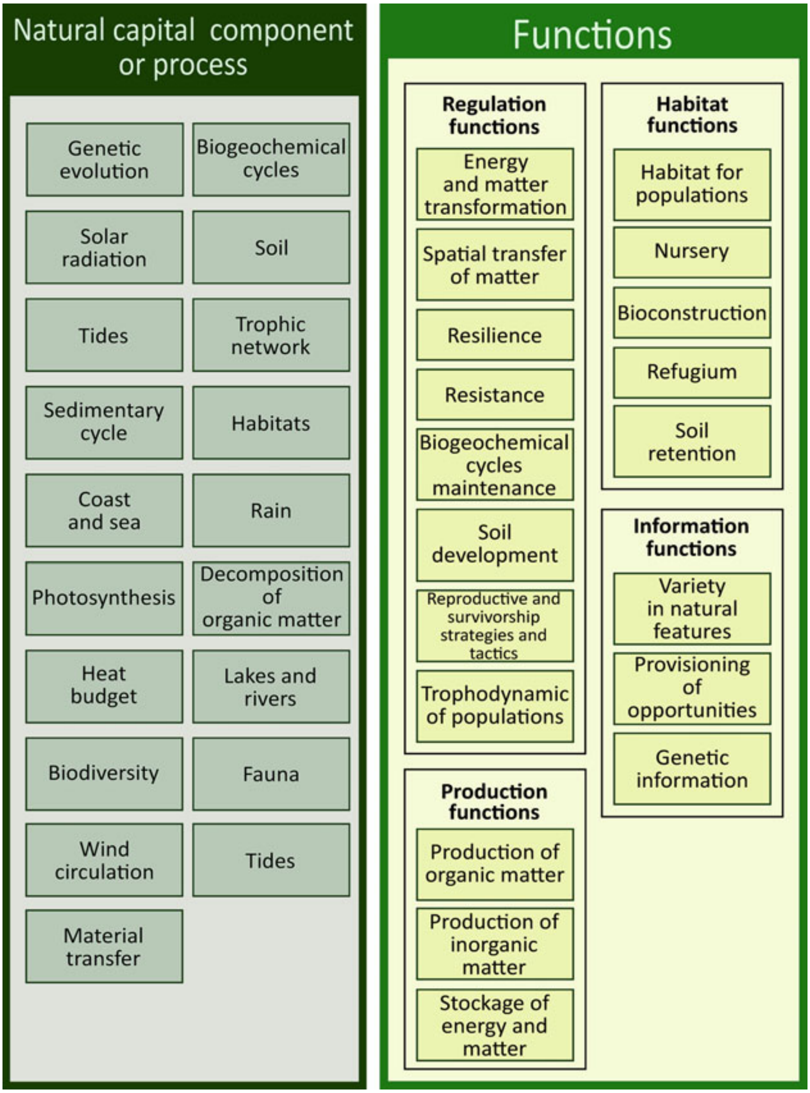

Fig. 1 Functions and originating natural processes

3 Functions of Animal Forests

Six main habitat groups have been considered: coral reefs (tropical, mesophotic, deep-sea, and cold-water reefs), coralligenous reefs (developing on shallow and deep circalittoral rocky bottoms), vermetid reefs, oyster reefs, serpulid reefs, and sponge grounds.

Coral reefs, once considered restricted to shallow, warm waters in tropical and subtropical regions, have also been found in dark, cold, and nutrient-rich deep waters. These cold/deep reefs have been found in fjords, on the continental slope, in canyons and seamounts in almost all the world oceans and seas at depths between 40 and 3000 m. Most of the studies addressing cold/deep-sea coral reefs have been conducted at high latitudes, even if these reefs have been increasingly found at lower latitudes and at greatest depths.

Coralligenous reefs are biogenic calcareous structures developing in Mediterranean benthic environments, mainly generated by the accumulation of encrusting algae in dim light conditions at depths between 20 and 120 m. Although coralline algae play a fundamental role in both coral reefs and coralligenous reefs, benthic animals may be dominant and may represent the main reef builders, especially in coral reefs, as well as the main component involved in structuring the complexity of a reef.

Vermetid reefs are bioconstructions created by the gastropod mollusks belonging to *Dendropoma* (and related genera) in association with coralline algae. Vermetid reefs are unique and highly diverse and play important functional roles. Oyster reefs were dominant in estuarine environments in the past. Oysters are ecosystem engineers able to construct reefs that have been supporting entire communities for millennia. Reefs are constructed by few species (Beck et al. 2011). About 85% of oyster reefs have been destroyed over the past 130 years; at present, restoration has been undertaken in different sites as, for example, 594 locations within Chesapeake Bay and the Maryland and Virginia coastal bays (Kellogg et al. 2013). Serpulid reefs play roles similar to those of oyster reefs (Bianchi and Morri 2001) in various habitats and world areas (Bianchi et al. 1995). Sponge grounds are aggregations of large sponges associated in beds, fields, or reefs. In the last decades, they received a growing interest aimed to fill the gap of knowledge about these structures (Hogg et al. 2010).

According to the previous classification, the main functions of animal forests will be here synthetically described and presented.

3.1 Regulation Functions

Energy and matter transformation. Coral reefs show higher rates of primary production in comparison with other marine ecosystems even if they live in oligotrophic environments. Production in shallow waters ranges from 1500 to 3700 $\mathrm{gC{\cdot}m^{-2}{\cdot}a^{-1}}$, equal to more than twofold the production of tropical rainforests (460–1600 $\mathrm{gC{\cdot}m^{-2}{\cdot}a^{-1}}$) and around tenfold that of central ocean gyres (4–40 $\mathrm{gC{\cdot}m^{-2}{\cdot}a^{-1}}$). Coralligenous reefs may present richness, biomass, and productivity in the range of tropical coral reefs (Bianchi 2001). Recent studies showed that vermetid reefs are highly diverse habitats structurally comparable to coralline reefs and showing a particular trophic flexibility (Vizzini et al. 2012; Colombo et al. 2013). The high degree of biodiversity found in animal forests allows the creation of complex trophic networks where diverse feeding and competitive relationships are displayed (filter-feeding, deposit-feeding, herbivore, carnivore strategies). Carbon is then transferred from autotrophs to top predators by means of different paths: photosynthesis, predation, remineralization, symbiosis (McMahon et al. 2015).

Shallow-water corals obtain nutrition from zooxanthellae, but can also capture food with tentacles and mucus or by absorbing dissolved nutrients directly from the water column. In mesophotic, cold, and deepwater reefs, organisms balance a decreased possibility to photosynthesize with an increased heterotrophy, depending on the supply of zooplankton and organic matter transported by currents for food (Slattery et al. 2011). Anyway, in healthy corals, heterotrophy accounts for 0–66% of the carbon fixed in the skeleton and contributes 15–35% of the metabolic needs.

The variety of foraging behaviors and nourishing strategies shown by many benthic sessile suspension feeders not only makes them efficient in transferring energy from different trophic levels but also allows them feeding on a wide range of preys and consequently surviving in the variable environments they occupy (Fig. 2a). Studies of energy transfer in Mediterranean coralligenous communities showed that hydroid species, even if they contribute less than 0.5% of community biomass, can capture approximately 10% of the yearly algal production. Sponges in reefs remove from the water column in 30 min the same amount of DOM that free-living bacteria take up in 30 days (de Goeij et al. 2013).

Kellogg et al. (2013) demonstrated the role played by oyster reefs in enhancing secondary and tertiary production: macrofaunal abundances have been found greater in a restored oyster reef than in a control site and, even if the 86% of the increase was due to oyster themselves, the remaining increased biomass was represented by organisms different from oysters. The most part of non-oyster biomass was composed by organisms living on oyster shells, but, anyway, the mobile fauna was two orders of magnitude greater than in the control site.

In sponge grounds, specific microbial associations can be found, as epibionts or endosymbionts. These microbes are bacteria and fungi playing a role in sponge's nutrition and carbon fixing and providing to sponges secondary metabolites they employ to protect from predation and competition (Hogg et al. 2010).

Spatial transfer of matter. Molecules are moved between sites through biogeochemical cycles and following paths of different media such as rain, rivers, wind, or organisms. It is recognized that benthic system controls water column biomass converting it into macrofauna biomass with lower respiration rates (Paoli et al. 2016). In such a way, materials shift from pelagic to benthic material pool and vice versa. Suspension feeders play a key role in this process uptaking dissolved inorganic nutrients and transforming them in organic matter. In such a way they connect the abiotic compartment with the biotic community and couple water column productivity with the secondary productivity of benthic communities.

Another example of this function can be represented by the transport of broken skeletons, for example, of corals, which move and accumulate as sediments, thus creating new habitats.

Resistance. Resistance of coral reefs has been studied, for example, with reference to bleaching caused by climate change, including ocean acidification. It has been shown

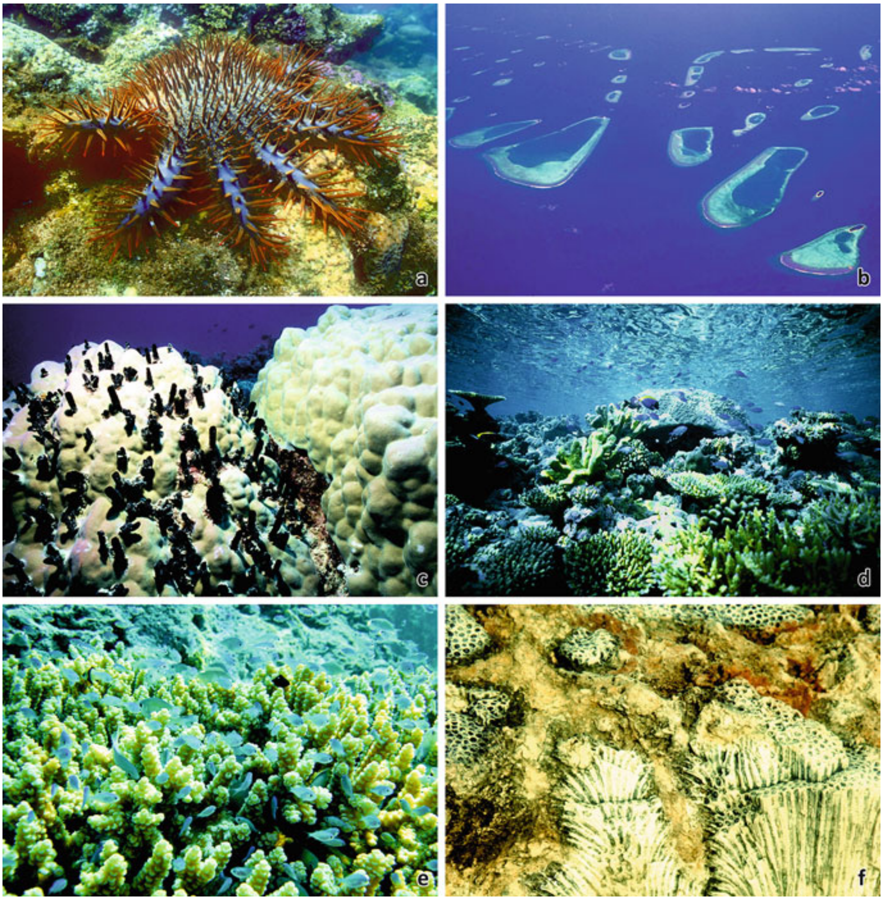

Fig. 2 Coral reef ecosystem functions. Regulation functions, energy and matter transformation: the crown-of-thorn starfish *Acanthaster planci*, a specialized coral feeder, exemplifies the complex trophic networks of coral reefs (Manado, Indonesia) (**a**). Regulation functions, soil development: many tropical island nations literally live on coral, as their "land" has no bedrock but just coral sand (Maldives) (**b**). Regulation functions, biodegradation: sponges of the family Clionaidae excavate a massive colony of the coral *Porites* (Maldives) (**c**). Habitat functions, living space: the three-dimensional structure imparted by coral growth to the submerged seascape increases the availability of living space for the associated marine organisms (Maldives) (**d**). Habitat functions, refugium: dozens of fishes find refuge in a single colony of the coral *Acropora* (Maldives) (**e**). Habitat functions, bioconstruction: fossil remnants of corals, the main primary bioconstructors, in a raised reef (the Havana, Cuba) (**f**)

that coral reef and coralligenous reef organisms are sometime able to show a certain degree of persistence through acclimatization, evolutionary adaptation, or other strategies. Vermetid reefs seem to be less sensible than coral reefs to temperature variations. Usually shallow-water reef corals reach their survival threshold at 18 °C, while vermetids can bear a 14–16 °C sea surface temperature (Vescogni et al. 2008).

Nonetheless, in general terms, animal forests are considered delicate and vulnerable environments needing protection from human disturbances.

Resilience. Coral reefs and coralligenous reefs faced a number of different disturbances, and in the past, they were considered as stable ecosystems and played a role helping other ecosystems to recover (Fig. 4a). For example, even if the topic needs to be further deepened, it seems that mesophotic reefs played a refuge role during past environmental disturbances, acting as a source for shallow-water reef regeneration. In the absence of severe human impacts, reefs are able to reassemble after disturbances such as tropical hurricanes. Nonetheless, today animal forests are exposed to a wider and different set of threats due to human impacts acting at local level, such as uncontrolled coastal development, increasing pollution, and heavy fishing practices. The delicate balance between bioconstruction and bioerosion that maintains these ecosystems can be easily disrupted in case of heavy pressures from humans or environment. The capacity of reefs and their composing organisms to "bounce back" when exposed to disturbances can depend on the frequency and magnitude of the events and interact with several factors (Nyström et al. 2000). These factors include genetic variability, diversity, and functional groups of species. Sequential, chronic, and multiple disturbance events can irreparably damage these delicate systems. Certainly it should be taken into account that even if bioconstructions are able to recover after a disturbance, this usually requires long periods (Morri et al. 2015). This is ascribable to the low rate of development that, for instance, for coralligenous constructions (mainly due to calcareous Corallinales algae), is equal to 0.006–0.83 $\text{mm}\cdot\text{a}^{-1}$ in the western Mediterranean Sea (Bellwood et al. 2004; Ballesteros 2006; Mora 2015; Weijerman et al. 2015; Doxa et al. 2016). The great diversity shown by animal forests would suggest the presence of functional redundancy, allowing greater resilience due to the ability to compensate the loss of a species with another. However, high diversity may also lead to a great degree of specialization, making every species essential and increasing the vulnerability level of these systems. McClanahan et al. (2012) carried out a survey where reef scientists and managers were asked about the importance, strength of scientific evidence, and feasibility of assessment/measurement of 31 resilience indicators. From this original set, only 11 resilience indicators were selected as most suitable to assess reef resilience. The main finding of the study was that while reefs are complex system, they are "frequently controlled by just a few strong variables operating at a given scale."

Biogeochemical cycles' maintenance. As previously described, exchange processes occur from water to the bottom sediment (termed as pelagic-benthic coupling) or vice versa (termed as benthic-pelagic) (Asmus and Asmus 2011). This allows the recycling of nutrients and represents a connection between abiotic and biotic pools. Benthic organisms can act either as sinks or sources of elements, such as inorganic nitrogen, phosphorus, and silicon. As far as coral reefs are concerned, the basis for nutrient and material exchanges among different environmental compartments resides in the symbiotic association between corals and zooxanthellae. Zooxanthellae contribute to the nutrition of heterotrophic organism; provide organic carbon, nitrogen, and phosphorous; and at the same time consume inorganic carbon, nitrogen, and phosphorous produced by corals. Organic and inorganic nutrients can be also obtained from the surrounding water but, in tropical coral reefs, nutrient concentration in the water column is too low, and thus fixation is mainly allowed by this symbiosis. In particular, shallow tropical reef crests have been identified as optimal environments for nitrogen fixation (Harborne et al. 2006).

Corals and coralline algae are also important in the carbon and carbonate cycles, being the major contributors to CO_2 fluxes. They represent a carbon sink for carbon dioxide in geological times and a carbon source on a human time scale. Carbon is taken from seawater where it is available as dissolved ions and fixed by reef organisms for the maintenance of organisms themselves and for the construction of skeletal structures. When these skeletal structures disaggregate, they become important pathways of inorganic carbon. Moreover, these bioconstructors have a significant role in the planetary calcium balance, since they precipitate calcium to construct biogenic structures (Salomidi et al. 2012).

Oysters and other organisms dwelling in their reefs modify biogeochemical cycles through filtering activity being key elements in the benthic-pelagic coupling (Rodney and Paynter 2006; Kellogg et al. 2013). Organic matter, e.g., phytoplankton, is taken from the water column. A part is employed for growth and maintenance, a part is remineralized as nutrients and available for reuse or deposited on the sediment surface as feces and/or pseudofeces, while a share is stocked as nutrients in bivalve shells or in animal biomass. In subtidal environments, suitable environments for oyster reef restoration, they are able to concentrate organic material in aerobic environments with low light levels contributing to nitrogen removal through microbial-mediated denitrification. Moreover the increased presence of deposit-feeding and bioturbating organisms increases nitrogen removal since the reworking of sediments by these organisms alters organic matter turnover and nutrient recycling and can enhance denitrification rates (Kellogg et al. 2013). Comparing a control site with a restored oyster reef site, Kellogg et al. (2013) estimated a flux of 556 kg N $ha^{-1}a^{-1}$ removed as a consequence of reef restoration. Analogously to other animal forests, oyster reefs and serpulid reefs sequester carbon as calcium carbonate accumulated in shells and tubes.

Soil development. Coral reefs build islands, as in the case of many island nations in the tropical belt (Figs. 2b and 4c). The sedimentary limestone creates atolls and reef platforms that represent the basis for eolian, fluvial, alluvial, or colluvial deposition and for the formation of soil. Coral reefs develop according to calcification, binding, sediment deposition, transportation, and destruction. These processes generate a semi-consolidated reef mass, which is later converted into reef limestone by diagenesis. Reef construction in a habitat is also influenced by different factors such as the net balance of light, wave, sediment, exposure stresses, antecedent topography, and sea-level changes. Fundamental is the role played by bioerosion: in St. Croix, it was estimated that nearly 55% of the carbonate production on a reef was reduced to sediment by bioerosion. Finally, broken skeletal structures can contribute to create sand and beaches (Harborne et al. 2006).

Biodegradation. Several organisms erode calcareous concretions of biogenic reefs, such as the excavating sponge of the family Clionaidae, the bivalve *Lithophaga*, and several annelids (Fig. 2c). Sea urchins are also important biological agents that substantially erode coral reefs and coralligenous concretions. Microborers, such as cyanobacteria, green algae, and fungi, have a role as well.

Reproductive and survivorship strategies and tactics. Corals and other anthozoans typical of mesophotic and coralligenous reefs have developed an array of behaviors and strategies to reproduce. They can be hermaphroditic or gonochoristic. Fertilization occurs through spawning or brooding. Often members of one species or multiple species reproduce in synchrony: on the Great Barrier Reef, up to 30 species on a single reef may spawn within a few hours from each other (Knowlton and Jackson 2013). This variability assures the efficacy of the process. Similarly, other organisms living around coral reefs or coralligenous reefs, for example, fishes, show highly developed reproductive strategies and a wide variety of spawning systems. Vermetid reefs represent exclusive settlement habitats for many invertebrates and algae, becoming an essential habitat for reproduction of other species.

Trophodynamics. In reefs, feeding and competitive relationships are extraordinarily complex and diverse. Primary production in shallow reefs is largely driven by symbiotic, turf-forming, frondose, and calcium carbonate skeletons depositing algae. Each group shows a delicate balance between organic and inorganic production on which the life of the community depends. Sunlight is then the main driver associated with waves and currents that transport nutrients and export waste products. Filter-feeding invertebrates can be found on the surface and in crevices; hence reefs have been defined as a “wall of mouths.” The reef hosts herbivores and carnivores cruising for food and deposit sifting. The role of each group is important. The activity of grazers assures a rapid removal of primary producers, thus keeping an early stage of succession and high photosynthetic rates (McClanahan et al. 2002). Secondary consumers can influence reef trophism by supplying nutrients to their prey. Microbes and multicellular parasites are involved in the food web. A study of Caribbean reef food web showed the presence of more than 3000 trophic linkages, and research about competitive relationships proved that competitive networks were not linear but contained loops. Specialized associations such as mutualism, commensalism, and parasitism are abundant even if still not completely known.

Rogers et al. (2015) modeled the food web of coral reefs characterized by 16 functional groups and their interactions; they identified different types of reefs according to four different combinations of habitat complexity and productivity. Finally, they identified changes in abundance of functional groups in response to stressors, reef types, and management.

The trophodynamics of coralligenous reefs has been analyzed by Paoli et al. (2016) in the context of a study about habitat complexity: coralligenous reefs showed the greatest complexity level due to the highly functional trophic network, based on suspension feeders, able to convey the particulate organic matter suspended in the water column to the benthic system.

Rodney and Paynter (2006) proved the ability of a restored oyster reef community in transferring energy at higher trophic level in comparison with a degraded environment. Oyster reefs create a special environment where energy exchanges are facilitated acting as “foraging ground” for higher trophic level.

3.2 Habitat Functions

In general terms animal forests play a key role in coastal-marine habitats forming, given their abilities to create microhabitats, included in the wider ones, to affect the local hydro-sedimentary patterns and to offer numerous spatial niches for diverse and often unique associated species.

Living space. Coral reefs support a high diversity of habitats: they provide a home for an estimated 25% of marine organisms (Fig. 2d). Many studies found a positive correlation between the substratum complexity and species richness and diversity. The presence of coral or vermetid reefs allows the maintenance of other habitats, such as mangroves and seagrasses, since reefs act as a barrier to currents and waves and thus create suitable conditions for their establishment and proliferation. Their ability to dissipate wave energy creates lagoons and new environments (Harborne et al. 2006). Coral reefs supply sand to beaches in different ways, for example, marine organisms (such as fish, snails, sponges, worms, and urchins) that feed into a reef can remove and/or excrete small calcium carbonate sediments. These sediments, suspended in the water, may be carried and deposited ashore by waves. Coralligenous reefs are very complex structures characterized by holes and cavities and hosting a variety of organisms such as fishes, mollusks, or crustaceans. In coralligenous reefs a range of microhabitats with a great heterogeneity can be found. A diversified fauna, either sessile or motile, excavating or buried in the sediment, live in coralligenous habitats. A study regarding the presence of sponges inside and outside a coralligenous formation in the Ligurian Sea (NW Mediterranean) showed that the number and biomass of sponges were greater inside than outside and that a certain number of species were exclusively present inside the blocks (Calcinai et al. 2015). Also vermetids, oyster reefs, serpulid reefs, and sponge grounds provide habitat for an abundant and diverse reef-associated macrofaunal community (Kellogg et al. 2013).

Vermetid reefs are structurally comparable with coral reefs and coralligenous being able to make the flat transitional area between the midlittoral and the infralittoral a three-dimensional zone (Colombo et al. 2013). Oyster reefs and serpulid reefs are often the only hard substrate in a predominately soft-sediment environment, creating a vertical biogenic structure that offers habitat for dense assemblages of other invertebrates and fish (Grabowski and Peterson 2007).

Sponge grounds create complex habitats in difficult environments: in Canada the reef known as “glass sponge reef” can reach up to 25 m high and provide topographically variable habitat. If the habitat is investigated at a lower scale, the diverse shapes created by living sponges and dead skeletons create a set of microscale habitats (Conway et al. 2007).

Sponges in Antarctic regions become a major biological structuring agent able to create habitat in deep environments providing food and shelter, and they are significant centers for invertebrate species associations (Hogg et al. 2010).

Specific associations between sponges and crustaceans have been documented. In North Atlantic the isopod *Caecognathia abyssorum* has been found living in sponges, where it found a preferential habitat, and young red king crabs *Paralithodes* *camtschaticus* were found associated with sponges: later studies demonstrated that the crab larvae prefer to settle on a complex substratum rather than on sand (Hogg et al. 2010 and references herein).

It is possible that deepwater sponges form a network of habitat "patches" in deep-sea settings around the world: future studies are expected to deepen this topic as well as the roles played by these habitats in sustaining deepwater biodiversity.

Several researches demonstrated that reefs create a complex habitat able to host a rich macro- and megafauna and that engineered structures modify current regime offering shelter to mobile organisms (Roberts and Ormond 1987). The idea of a link between habitat and species diversity was born in the 1940s. Later it has been proved that a greater habitat complexity induced by benthic constructors, able to make bidimensional habitats to three-dimensional ones, increases biological diversity (Bianchi 2001). In particular in deep waters, these accretions are often the only available three-dimensional structures and may serve as feeding grounds for fishes. Some species of deepwater corals are able to form mounds, analogous to the shallow tropical coral reefs, which can reach the thickness of 30 m such are, for example, the accretions of *Lophelia pertusa* in the Norwegian Sea (Freiwald et al. 2004; Biber et al. 2014; Linley et al. 2015).

Nursery. Tropical but also cold and deep-sea cold-water coral reefs are recognized as spawning and nursery areas for many species, offering a variety of microhabitats (Bongiorni et al. 2010). Baillon et al. (2012) demonstrated the presence of fish larvae in cold-water sea pen fields collected as bycatch from epibenthic surveys conducted along the eastern Canadian coast. The role of coralligenous reefs is still under study since the great complexity of this habitat makes finding juveniles in cavities difficult (Guidetti and Boero 2002). Anyway, it is probable that they act as nursery areas for the juvenile stages of fishes and other animals they host. Vermetids and coralline algae bioconstructions represent a shelter, nursery, and/or refuge for many invertebrates such as corals, zoanthids, ophiuroids, ascidians, sponges, polychaetes, and mollusks (Spotorno-Oliveira et al. 2015). Serpulid reefs and oyster reefs are employed by juvenile fishes and other invertebrates as recruitment, refuge, and foraging grounds (Bianchi and Morri 1996; Grabowski and Peterson 2007). The complex architecture of sponge grounds creates intricate habitats that act as nursery grounds for juvenile fish in their early stages of growth (Auster 2005).

Refugium. Coral reefs and coralligenous reefs, forming complex structures, offer protection against predators and then are supposed to be refuge areas (Fig. 2e). The various habitats they create offer interstices for a rich and diverse mobile endofauna, while other animals live, attached, and unattached to the surface, on the main structure, or on the sediment it retains. Structures created by bioconstructors, rich in cryptic microhabitats, offer protection from wave erosion, predation, and high light irradiance, and as a consequence they represent selective habitats for a range of organisms, which can be easier found in crypts than on open surfaces. Ballesteros (2006) made a census of 1241 invertebrates in the coralligenous habitat, being this information conservative due partly to the scarcity of studies but also to the difficulty to count such a rich fauna in a so complex and heterogeneous habitat. For example, Bertolino et al. (2013) verified that when cryptic sponges are considered, the number of species associated with the coralligenous concretions increased to 302 with respect to 142 listed by Ballesteros (2006). At present, while cryptic fauna of coral reefs is comparatively well known, the greatest part of studies about coralligenous takes into account only the visible epibenthic fauna, confirming the great importance played by this habitat that anyway is still far to be fully discovered (Calcinai et al. 2015). Also oyster reefs and serpulid reefs organizing shells or tubes in a complex arrangement, rich in interstitial refugia, can play a role as shelter. This is proven by the lowered predation mortality rate on new recruited oysters in oyster reefs (Rodney and Paynter 2006). Fishes exploit the complex habitat created in sponge grounds to obtain shelter for both food and reproduction (Hogg et al. 2010).

Bioconstruction. Accretions created by bioconstructional organisms are built by means of three main processes: growth or in situ piling up of rigid organisms, binding and cementing action of secondary builders, and filling of sediments trapped in the framework within the cavities. Marine cementation can contribute to strengthen the structure by occluding cavities and lithifying the trapped sediments (Fig. 2f).

Coral reefs are the world's largest biogenic structures, the only one visible from space. Coral reefs, both tropical and cold water, are renowned for their structural complexity. Corals are ecological engineers with their skeletons forming complex three-dimensional structures. In temperate areas, like the Mediterranean Sea, calcareous algae represent the major builders in shallow areas. Coralline algae, associated with a number of animal builders, mainly bryozoans and polychaetes, are the main builders of coralligenous reefs, Mediterranean bioconstructions that cannot be strictly considered as reefs, but fall within the "buildups," a kind of reliefs not implying wave resistance or any evidence of control over surrounding environments (Di Geronimo et al. 2002). *Dendropoma cristatum* (= *D. petraeum*) is one of the best studied reef-forming vermetids. Optimum environmental conditions for *D. cristatum* are the intertidal or immediate subtidal zone, where wave action ensures food supply, carries away wastes, and reduces competition. *Dendropoma* can develop borders parallel to the shore for several kilometers, with a maximum height of 70–100 cm and a width of 20–30 m and where the portion exposed to the wave action usually shows a more densely bioconstructed assemblage.

3.3 Production Functions

Animal forests are characterized by complex trophic networks and great diversity, while the complex architecture of their habitats creates a variety of substrates and refuges available for organisms of different types finding here the suitable conditions for nutrition or reproduction. Biomass of coralligenous formations has been estimated to be around 500 $g_{dw} \cdot m^{-2}$, a quantity comparable to that measured in tropical coral reefs. The production generated by these structures does not relate only with living organisms but also with the abiotic compartment. These accretions generate a multitude of shapes, materials, and chemicals offering diversity not only from the biological point of view. Cold/deep-sea reefs have a key role in the context of production functions since they act as hot spot and aggregating points for fishes and other animals being patches of high diversity in a low-diversity environment (Garcia and Ragnarsson 2007; Baillon et al. 2012, Fig. 4b). Vermetid reefs are place of nourishment for mollusks, sea urchins, and fishes (Cerrano et al. 2001; Salomidi et al. 2012; Spotorno-Oliveira et al. 2015).

3.4 Information Functions

The great variety of organisms and the complexity of habitats characterizing animal forests originate a range of opportunities and choices surely for humans but also for nature. For example, vermetid reefs have recently been recognized as natural archives able to record past sea surface temperature variations and sea-level changes (Vescogni et al. 2008; Chemello and Silenzi 2011). The coralligenous habitat hosts, within at least 1600 species (Ballesteros 2006), various organisms that are vulnerable, as, for example, diverse species of sharks, representing a cultural capital since they may reduce or disappear in the absence of the coralligenous habitat (Salomidi et al. 2012).

Hydrodynamically exposed coralligenous communities are commonly characterized by the presence of spectacular gorgonian facies.

Being high-diversity ecosystems, coral, coralligenous, and vermetid reefs maintain a vast genetic library and facilitate evolution with this complexity.

From function description, animal forests appear as extremely complex ecosystems with an uncertain future (Pandolfi et al. 2011). This complexity, as well as the vulnerability, requires to be correctly evaluated with the application of methods that allow obtaining a full understanding and a correct valuation and forecasting the consequences of potential disturbances.

4 From Functions to Ecosystem Services and Well-Being

If functions depend on natural capital, services arise from functions and similarly to functions, services can be split in categories. A well-known and widely adopted classification is the one proposed in the Millennium Ecosystem Assessment (MEA 2005, Fig. 3):

1. **Regulating services** are the benefits obtained from the regulation of ecosystem processes such as climate and water regulation or erosion control.
2. **Provisioning services** are the products useful for humans derived from ecosystems such as food, fiber, fuels, and natural medicines.
3. **Habitat services** are those necessary for the production of all other ES.
4. **Cultural services** are the nonmaterial benefits such as spiritual enrichment, cognitive development, meditation, recreation, and aesthetic experiences.

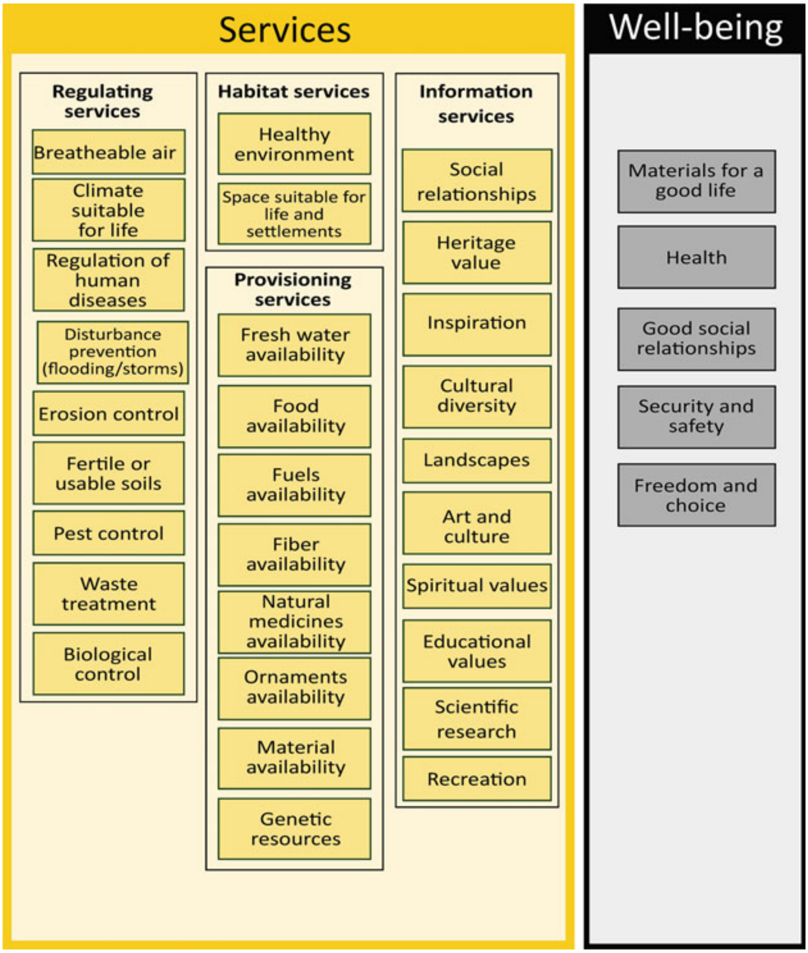

Fig. 3 Ecosystem services classification and well-being originated

In the pathway from ecosystem to well-being, ES provisioning is a keystone step for well-being achievement. The distinction between ES and well-being is often not intuitive. It can be stated that ES are the determinants of well-being (Dasgupta 2004).

In general terms, five components of well-being can be identified: materials for a good life, health, good social relations, security and safety, and freedom and choice (MEA 2005).

Well-being is clearly influenced by a range of human-driven components, first of all the economic status. Nonetheless, ecosystem condition is among the many factors affecting the quality of human life. It should be taken into account that if the ability of ecosystems to provide services is compromised, the access to well-being will be forbidden, since natural capital is the essential basis for the satisfaction of human needs. Obviously, even if an attempt of categorization is deserved in order to better conceptualize the theory, functions and services overlap as well as the five dimensions of well-being are strictly and mutually interconnected. It is quite impossible to find a single, unambiguous link between a natural capital component and a function or between a function and a service. Realistically, different natural capital components contribute to create one or more functions, and different functions interact to originate a service or a group of services, as well as a group of services participate to one or more components of well-being.

Probably, it should be more appropriate to speak about a network from natural capital to well-being rather than a pathway.

Changes in ecosystem status generate impacts on our well-being that are often subtle and complicated to be identified but may affect it deeply. This is why the ES valuation issue should be faced with a system perspective and why measuring natural capital is preferable than directly measuring well-being.

5 Services From Animal Forests

The importance of seas and oceans for human health and well-being is now fully recognized (Legat et al. 2016). Ecosystem services of animal forests have been analyzed in detail, with particular reference to coral reefs, by Moberg and Folke (1999). Nonetheless, studies can be increasingly found in relation with other environments such as coralligenous and vermetid reefs. According to the classification proposed in the previous paragraph, the main services identified for coral reefs and coralligenous reefs have been grouped and analyzed.

5.1 Regulating Services

Breathable air. Even if the role, as carbon source or sink, of coral reefs, vermetid reefs, and coralligenous reefs is still controversial, surely they have an active role in regulating gas balance, being carbon fixers and CO_2 releasers. Calcifying photosynthesizers represent at the same time a sink and a source of CO_2 since they act as sink with photosynthetic processes and as producers with respiration and $CaCO_3$ production. Carbon is stored by corals and coralline algae in deposits in all different types of structures. Studies performed during the 1990s report coral reefs as carbon sink, while more recent analyses, on the contrary, indicate them as CO_2 source (Kinsey and Hopley 1991; Suzuki 1998; Suzuki and Kawahata 2003).

Disturbance prevention. Coral and vermetid reefs create a barrier against storms acting as a physical protection that weakens and dissipates the energy of waves and currents. In such a way, these reefs prevent damages to other ecosystems and to human settlements and properties, providing thus services to humans. Coral reefs are able to absorb up to 90% of the energy from wind-generated waves: reef crests alone dissipate most of this energy (86%) (Ferrario et al. 2014). Although the protection role offered by reefs (coral and vermetid) is widely recognized, scientific data are rare and most of the evidence is observational and anecdotal. In southern India, local villagers equate a gulf, protected by the coral reef, as “male” and a bay not protected by a reef as a “female.” The gulf is hit by waves, but waves decrease their force before they reach the shore since they clash against the reef. The bay is recognized as female since it is generally characterized by calm water but suffering great damage when storms happen due to the lack of the reef. In Sri Lanka, at Hikkaduwa, where the reefs are in a better condition than in other sites of the country being located in a marine park, the 2004 tsunami caused damage to a distance of 50 m inland and waves were 2–3 m high. At Peraliya, where the reefs were affected by coral mining, waves were 10 m high, and damage and flooding occurred up to 1.5 km inland (Wells and Ravilious 2006).

Erosion control. As previously described, animal forests contribute to create new soil and to supply materials to other environments (e.g., sand from broken skeletal residues). Moreover coral reefs, vermetid reefs, and oyster reefs directly protect the coastline from currents and waves since they act as a barrier through wave reflection, dissipation, and shoaling (Peterson et al. 2003; Grabowski and Peterson 2007; Chemello and Silenzi 2011, Fig. 5d). In such a way, reefs protect the land and also offer protection and biological support for other ecosystems having an active role in coastal protection, such as seagrass beds or mangroves. There are not many studies quantifying the ability to protect shore of reefs; nonetheless, in Sri Lanka, it has been estimated that a kilometer of coral reef can prevent annually 2000 m^2 of material to be eroded (Wells and Ravilious 2006).

Waste treatment. Coral reefs are able to transform, detoxify, and sequester wastes released by humans since they are able to immobilize persistent pollutants. Moreover, corals, sponges, and other organisms in reefs, being filter feeders, consume particulate matter suspended in the water column, making nearshore waters clearer (Gili and Coma 1998). Through filtration activities, serpulid reefs and oyster reefs as well as suspension-feeding bivalves in general can help counteracting the impacts of estuarine eutrophication (Bianchi and Morri 1996; Jackson et al. 2001).

The employment of oyster reefs to reduce nitrogen load charge has been proposed in Chesapeake Bay by Kellogg et al. (2013), due to their ability to remove and stock nutrients as well as to the capacity of the associate community to facilitate the decomposition of organic matter. Moreover, oysters remove suspended inorganics, phytoplankton, and detrital particles, thereby reducing turbidity and improving water quality (Peterson et al. 2003).

5.2 Provisioning Services

Food availability. Reefs originate a variety of seafood products such as fishes, mollusks (clams, scallops, cephalopods, oysters), crustaceans (crabs, lobsters, shrimps), and others (Spalding et al. 2001). Coral reefs represent a nursery area for about a quarter of the ocean’s fish, including many commercial fishes. Fisheries associated to coral reefs constitute over 7% of global fisheries; six million tons of fish are caught annually in these ecosystems, which can provide up to 35 t of fish per squared kilometer and per year (Sale 1991; White and Vogt 2000; White et al. 2000, Fig. 5a). The economies of certain developing countries are greatly dependent on resources provided by coral reefs, and their presence is essential for the survival of these people: for instance, in the Philippines, more than one million small-scale fisheries depend directly on coral reefs for their livelihood (Wells and Ravilious 2006; Ahmed et al. 2007). It should be remarked that an uncontrolled exploitation can lead to the complete depletion of these resources: for example, the Bolinao coral reefs in Pangasinan, which directly support approximately 50,000 fishermen and an additional 20,000 people engaged in fishery-related occupations are, at present, seriously at risk due to irreversible damages. This condition can be ascribed to the combined effects of overexploitation, open access, and the absence of an active management addressed to coral reef protection (Ahmed et al. 2007). Cold and deepwater coral reefs are gaining more and more importance as biodiversity hot spots hosting resources for fisheries: they are essential habitat for fishes and crustaceans offering food, protection from currents and predators, and nursery or reproduction sites. It was hypothesized that deep reefs may represent centers of spreading for associated fauna, and they host diverse species of economic interest such as *Aristaeomorpha foliacea* and *Helicolenus dactylopterus* (Salomidi et al. 2012).

Peterson et al. (2003) synthesized the results from a set of studies about fish utilization from restored oyster reefs. They estimated that restoration of 10 m^2 of reef in the Southeast United States results in an additional 0.26 $kgm^{-2}\ a^{-1}$ of fish biomass. This was due to the ability of oyster reefs to create a suitable habitat and a foraging ground for fishes' preys. Moreover, a greater diversity and abundance of invertebrates in oyster reefs has been demonstrated (Rodney and Paynter 2006): many of these organisms are food items for several commercially and recreationally important finfish species. Several species of groundfish, including cod and ling, are often found in trawl catches along with sponges: this is a proof of the association of commercial species of fish with sponge-formed habitat. It has also been noted that the removal of the sponge grounds by trawling has influences on fish fauna composition confirming the crucial role of sponge grounds even if more data and studies are still required.

Natural medicine availability. Marine organisms possess the capacity to produce a variety of unique and biologically potent natural products for treating human diseases (Jaspars et al. 2016). Anticancer, anti-inflammatory, HIV treatments, painkillers, and other useful substances can be extracted from organisms thriving in animal forests, such as corals, mollusks, and sponges (Fig. 4d). For instance, the compound named discodermolide, able to inhibit cancer cell proliferation by interfering with the cell's microtubule network, can be isolated from the deepwater sponge *Discodermia* (Ter Haar et al. 1996).

Sponges have been well known since ancient times for their medicinal properties: texts by Homer and Aristotle refer to their use in medicine. In general terms, marine invertebrates are considered the most reliable sources of useful, for beauty of medical purposes, bioactive compounds, and, among these, sponges are the most prolific group (Hogg et al. 2010). Animal forests play, hosting an increased diversity

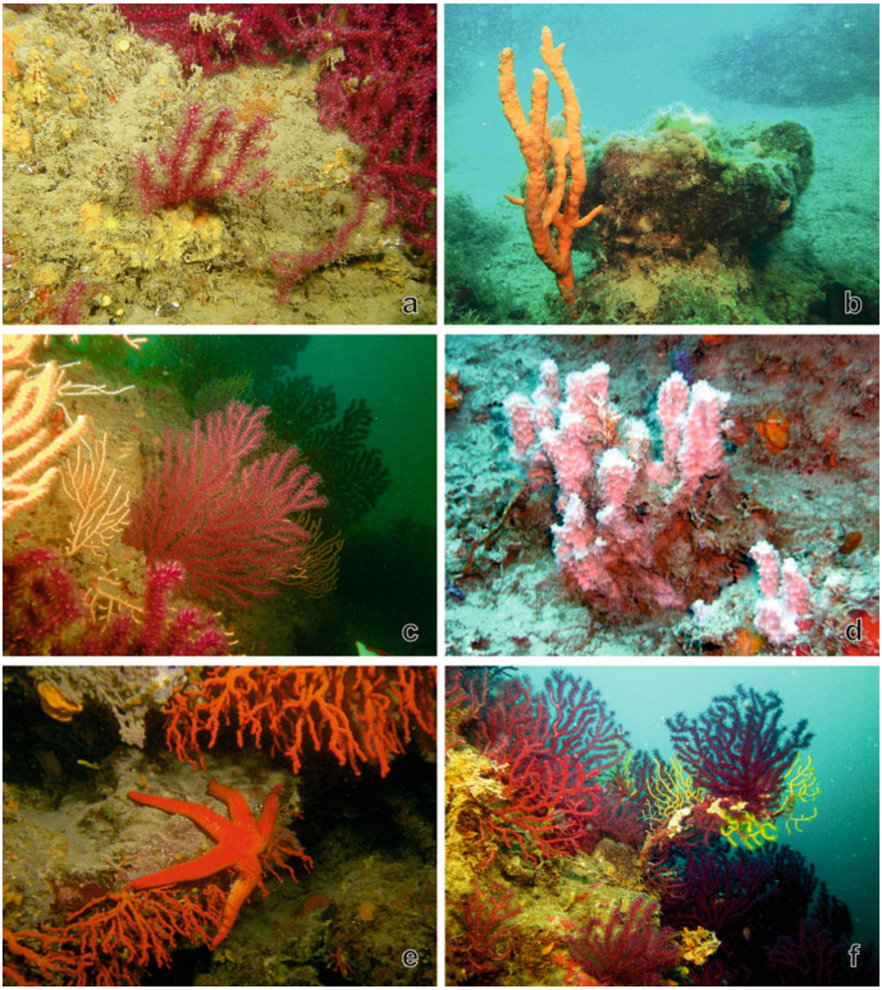

Fig. 4 Coralligenous reef ecosystem functions and services. Regulation functions, resilience: the ability of the ecosystem to recover after a perturbation may depend on recruitment, as for the gorgonian *Paramuricea clavata*, a long-lived species that suffered mass mortality events in recent years (Portofino, Italy) (**a**). Production functions, stockage of energy and matter: large filter feeders, such as the two sponges *Axinella polypoides* (bushy) and *Sarcotragus foetidus* (massive), convert the fluctuating planktonic production into stable benthic biomass (Punta Manara, Italy) (**b**). Habitat functions, soil retention: the planar structure of the gorgonians *Eunicella cavolini* and *Paramuricea clavata* acts as a baffler to retain suspended sediment and nutrients (Portofino, Italy) (**c**). Provisioning services, natural medicine availability: sponges, for instance, *Dysidea avara*, produce an array of different active compounds that have medical applications (Portofino, Italy) (**d**). Provisioning services, ornaments' availability: the red coral *Corallium rubrum* is harvested to create precious jewels, whereas *Hacelia attenuata* and other starfishes are collected and sold as souvenirs (Portofino, Italy) (**e**). Information services, landscapes: the three-dimensional structure provided by coralligenous species creates a complex submerged seascape highly appreciated by divers (Punta Manara, Italy) (**f**)

Fig. 5 Provisioning services, food availability: reef fish are the main protein source for many tropical oceanic islanders (Maldives) (**a**). Provisioning services, material availability: for centuries, houses on coral islands have been built using coral rock and massive coral colonies (Maldives) (**b**). Provisioning services, ornaments' availability: shells and starfish among other curios are sold as souvenirs to tourists in tropical regions (Maldives) (**c**). Regulating services, erosion control: fringing reefs protect island shores and coastal human settlements (Manado, Indonesia) (**d**)

in the complex habitats they create, a crucial role in providing this nature's service to humans.

Ornaments' availability. *Corallium rubrum* (in coralligenous reefs), *Heliopora coerulea* (in coral reefs), antipatharians (in mesophotic reefs), and many shells or shell parts (including mother-of-pearl) are exploited for jewelry (Spalding et al. 2001; Goldberg 2013); other reef-associated animals are collected and sold as curios or souvenirs (Figs. 4e and 5c). Many organisms are extracted from animal forests to feed aquarium industry: many coral reef fishes and invertebrates are shipped to Europe and North America for the aquarium trade. In 1997, 1200 t of corals were traded internationally, 56% directed to the USA and 15% to the European Union, and it was estimated that half of this quantity was addressed to aquaria (Spalding et al. 2001; Cesar et al. 2003). CITES and other international agreements, as well as national laws in most countries, have been designed also to ban or limit this exploitation.

Material availability. Building materials such as lime, mortar, or cement are mined from coral reefs (Fig. 5b); lime is also employed in agriculture. Corals are employed as stone buildings in Maldives and in general in nations where other natural building material is scarcely available. Also in this case, laws have been designed to avoid overexploitation. In some area, the reef flat is employed for land reclamation and this leads to the partial destruction of the reef. In Hurghada, the entire fringing reef has been destroyed being invaded by hotels, and now tourists must travel by boat to see the reef once located just a few meters from their accommodation (Spalding et al. 2001).

Fuel availability. Reefs can be a suitable environment for oil and gas formation that can be obtained from fossil reefs. Reef complexes are potential reservoirs due to their porosity and permeability and because they may function as potential traps if enclosed by impermeable sediments. Petroleum can be found in a varying way in reefs located in a certain area: some reefs can contain oil, some others gas, and some others water. The organic matter, from which petroleum is originated, is only for a small part formed in situ since the environment is oxidizing with high-energy water conditions not favorable for the conservation of organic matter. Petroleum is channeled to reef through migration paths. Even if part of these sources is not yet exploited, petroleum industry is periodically interested in their use (Moberg and Folke 1999). Fossil reefs have been exploited during the 1990s, for example, in West Texas, Canada, Iran, and Iraq. During the 1950s some oil companies invested in research into fossil and modern coral reefs in Canada, New Mexico, the USA, and Australasian regions (Chapman 2000; Hopley 2011; Jones 2012). As a consequence reef reservoirs were labeled as more difficult to find than traditional ones. Nowadays oil drilling is banned on and in the nearby of several coral zones such as the Great Barrier Reef, Belize Barrier Reef, and Lofoten Røst Reef.

Genetic resources availability. Due to the great biodiversity hosted in coral reefs and coralligenous reefs, these ecosystems stock genetic information for future generations that could be exploitable for different purposes. For example, this service is strictly linked to the provision of natural medicines since the genetic diversification allows the evolution of new substances to be potentially employed for pharmaceutical purposes (Spalding et al. 2001).

5.3 Habitat Services

Usually habitat services fall into the category of supporting services. Habitat services have been identified as a category as proposed by Sukhdev et al. (2010): supporting services are generally defined as those necessary for the production of all other ES; nonetheless, this kind of classification increases the risk of double counting when aggregating valuations across service categories (Sukhdev et al. 2010). Moreover, the difference between regulating and supporting services is often difficult to perceive, and even some services, like erosion control, can be considered as supporting and regulating service, depending on the time scale and immediacy of their impact on people. By creating space and habitat, bioconstructors generate conditions for the provision of the other services listed. Animal forests are spread at all latitudes: calcareous algae can be found from tropical to polar environments as well as corals (photosymbiontic and not), and vermetids colonize coasts located at subtropical and temperate latitudes. The habitats created are varied, from the Great Barrier Reef extending thousand kilometers off Australia, to the “cuvette” habitat, located in the central part of vermetid reefs and similar to tidal pools, to the microhabitats created in cavities of, for example, coralligenous structures. In shallow environments, diversity, also in habitat terms, is fostered by the variability of physical and chemical conditions created by waves and tides that, interacting with habitat-modifying species, increase habitat complexity, alter hydrodynamics, and increase overall habitat surface area (Bianchi 2001). It is recognized that, by means of their bioconstructional activity, vermetids and associated coralline algae increase complexity and biodiversity playing a pivotal role in modifying the shape and ecological characteristics of the transitional area between midlittoral and infralittoral flats, creating three-dimensional environments, and amplifying the available space for organisms (Vizzini et al. 2012; Spotorno-Oliveira et al. 2015). The distribution of bioconstructional coralline algae can influence that of marine invertebrates since they create physical and biological conditions allowing the settlement of many invertebrate larvae. This means that coralline algae, and the habitat they create, can have major impacts on the life cycles of many mollusks that can be directly exploited by humans or serve as food for commercial species (Spotorno-Oliveira et al. 2015).

5.4 Information Services

Recreation. Recreational services provided by reefs are various and mainly due to their aesthetic value attracting tourists; they include diving, snorkeling, and viewing (Brander et al. 2007). Many people move to tropical resorts only to visit coral reef seascapes, and many economies are completely based on this kind of tourism. Coral reefs generate the white sand of many tropical beaches, which represent a tourist attraction. Coralligenous creates spectacular seascapes built by gorgonians that are among the preferred diving sites in the Mediterranean Sea (Figs. 4f and 6a–c). Tourism represents undoubtedly an economic resource, and it has been considered for a long time a low-impact option, in particular for coral reef use, if compared with extractive practices such as fishing. Nonetheless, in recent years, studies began to demonstrate that reefs can be damaged and degraded as a result of uncontrolled tourism representing a considerable impact (Zakai and Furman 2002; Barker and Roberts 2004). Impacts related to tourism development include sedimentation, loss of habitat by land reclamation, dust, disposal of solid waste and sewage, anchoring, and direct damages (Cesar et al. 2003).

In particular mass tourism not only poses a threat to reefs' health but paradoxically even limits, in the long period, potential income from coral reefs and associated recreational activities to the local populations (Cesar et al. 2003).

For instance, scuba divers may even unintentionally damage reefs affecting their growing or reproductive capacity (Zakai et al. 2000). In the Philippines coral reefs for scuba diving and snorkeling represent major tourism attractions. Here the number of diving resorts is continuously increasing as well as the number of boats that drop their anchors on the reef. At present, the damage from these impacts seems to be relatively restrained but it begins to be perceived in some sites (White et al. 2000). For example, Apo Island, hosting 700 inhabitants in two little villages, accommodates approximately 1000 people as resident for at least one night each year and over 7300 visiting divers and snorkelers. Fin damage to coral colonies was estimated at 10.7% over a 10-month period (White et al. 2000; Raymundo 2002). Linares et al. (2010) found an association between diving pressure and survival rates during *Paramuricea clavata* mass mortality events: it seems that survival rate could vary from 0% (no control) to 7% (diving restriction).

These researches may manifest how tourism, to be a real resource, should be managed in a sustainable manner, able to protect the reefs themselves and to represent an alternative to destructive practices.

Scientific research. Reefs are able to monitor and record polluters since they act as recorders of chemicals' presence, such as metals. Coral reefs and coralligenous reefs are able to track recent and long-term changes in the marine environment due to human disturbances (Fig. 6d, e). Bioconstructors act as climate records since the chemical composition of skeletons can be used to obtain information about sea surface temperature and to track variations in salinity. Cold-water corals and vermetid reefs are increasingly studied as natural archives, in order to retrieve information about past water properties, sea-level variations, and circulation patterns (Salomidi et al. 2012). Sponges in recent years acquired importance due to their potential in providing new designs for fiber, optics, glass, civil engineering, and semiconductors (Hogg et al. 2010). The complex architecture of marine sponge skeleton can potentially inspire the development of new concepts in materials science and engineering.

Inspiration. Coral reefs and many organisms of coralligenous are an inspiration source for photos, films, and painting. In the Mediterranean, vermetids' remains were used to date the recent tectonic uplift of the coasts of Greece islands and also as biological indicators to date eight seismic events happened in the Holocene that provoked the shoreline shifts in the island of Rhodes (Antonioli et al. 1999).

Spiritual values. Religious rituals and cultural traditions have been developed around coral reefs in many tropical areas (Fig. 6f, g). Many coastal communities in the Pacific have traditional practices linked to reefs. The effect of these practices on reefs themselves has been rarely studied and quantified and then it remains ambiguous, even if some studies demonstrated a positive influence.

Fig. 6 Coral reef ecosystem services. Cultural and information services, recreation: millions of scuba diving tourists visit coral reefs each year (Isla de la Juventud, Cuba) (**a**). Cultural and information services, recreation: like tourists on safari in the savannah, divers appreciate the possibility to approach big and wild animals visiting coral reefs, such as many shark species or the manta ray *Manta alfredi* (Maldives) (**b**). Cultural and information services, recreation: a diver practicing fish watching observes *Ocyurus chrysurus* swimming over a colony of the coral *Dendrogyra cylindrus* (Isla de la Juventud, Cuba) (**c**). Cultural and information services, scientific research: warm water and good visibility typical of most coral reefs make them a favorite locale for field studies in marine biology and ecology (Maldives) (**d**). Cultural and information services, scientific research: education and training are another cultural activity that can be easily carried out in the field in coral reef areas (Maldives) (**e**). Cultural and information services, spiritual values: gorgonians, such as *Annella mollis*, contribute to the beauty of the underwater seascape (Maldives) (**f**). Cultural and information services, spiritual values: colorful reef organisms, such as the giant clam *Tridacna*, are a source of inspiration for photographers and nature enthusiasts (Hurghada, Egypt) (**g**)

Ahus Island has six reef areas that are restricted to fishing activities from at least 60 years. Up to three times per year, fishing is allowed without restriction for a brief period of time (2–3 h) to provide fish for ceremonial occasions that mark significant events in the village. The restriction regime is very complex, including different island clans that claim for exclusive rights on the reefs. Each family maintains a portion of the reef, and some also can harvest specific species or employ a specific technology. Cinner et al. (2005) proved that the presence of the traditional restrictions' regime can play a role in reef conservation. Fish biomass and sizes were more than 60% and 20% higher, respectively, within restricted areas compared with control areas proving that the management system promotes larger and more mature fish. Periodic harvesting appeared to have little effect on fish stocks. As a consequence, traditional practices can not only represent a cultural heritage to be conserved but moreover can play as a sort of training ground to test and to obtain information about management practices.

6 The Measure of Ecosystem Services

Two approaches can be adopted when dealing with the valuation of something: the instrumental and the intrinsic one. The instrumental (or utilitarian) approach identifies value with usefulness to someone or something. The intrinsic value of something exists independently from the benefits derived from its employment (Hawkins 2003).

The neoclassical economic approach to ecosystems is instrumental and anthropocentric, since it assumes that something owns a value only if it generates benefits for humankind, neglecting other species. In the neoclassical perspective, ecosystems, their functions, and their services can be valuable, most of all in economic terms, only if they are useful for humans, if they generate well-being, and if humans are aware about them (Hawkins 2003). Many authors recognize the existence of non-anthropocentric values and the inadequacy of many classical methods in ascribing a value to natural goods and services (National Research Council 2004). To date, the difficulty to identify alternative methods, as well as the need to employ approaches accessible to a general public and, at the same time, approved by the scientific community, hampered the introduction and the validation of more ecocentric valuation methods (Fisher and Brown 2015).

6.1 The Concept of Value

Once the main concepts and definitions about ES theory have been outlined and the main typology of functions and services encountered in animal forests have been sketched in summary, the concept of value needs to be better defined, since value is what we have to measure in practice. Different meanings of value have been proposed in the literature. For example, usually use and nonuse values are presented by economists as complementary. An instrumental or use value is identified with the benefit, real or potential, provided by a service to people in order to obtain a goal. Use values can be split in direct and indirect. A direct use value is linked with the immediate, physical fruition of the service, while an indirect use value is associated to positive externalities of the service and to what is able to support things that own a use value. Regulation and habitat functions own, then, an indirect use value. For instance, fish provides food for humans but also food for other species that in turn represent food for humans. Use values can be then consumptive (e.g., fishing) or nonconsumptive (e.g., recreation).

Intrinsic, nonuse values do not imply a physical interaction. It is the residual value that remains when the service loses benefits, e.g., the beauty of landscapes, and includes other value categories such as existence, bequest, and option (Hawkins 2003). In particular:

- Option value. It is linked with the wish of people to maintain the possibility to enjoy a service in the future.
- Existence value. It mirrors the will to safeguard the existence of certain goods or services, such as a particular species or habitat: usually it is included in nonuse values together with option values.
- Bequest value. It is linked to benefits people receive assuring future generations to enjoy the same environmental benefits they take advantage.

Another categorization is linked with the attitude employed to approach the issue of value and identify two types of value: anthropocentric and ecocentric.

- Anthropocentric value. It originates from the assumption that something has a value only if humans ascribe a value to it.
- Ecocentric value. It originates from the assumption that goods and services own objective values even if not recognized by humans.

A third classification is related to the sector involved and distinguishes ecologic from sociocultural and economic values.

- Ecologic value. It is the value associated with the general functioning of the ecosystem and derives from maintaining intact ecological functions. An ecologic value is connected with the valuation of system parameters such as complexity, diversity, or rarity. For example, a value can be ascribed to a resource analyzing the position it occupies in the hierarchy of transformations leading to its generation.
- Sociocultural value. It is associated with the ability of ecosystems to influence our well-being through intangible components such as psychic health or social identity.
- Economic value. It is determined by direct or indirect exchange value of a good or a service; it can be identified, for example, with economic costs necessary to replace an extinguished service.

Several other types of value can be identified, and it is clear that each of these categorizations and definitions cannot be isolated from the other: for example, in an anthropocentric perspective, only humans own an intrinsic value, and values pertain mainly to the socioeconomic domain.

As previously explained, to attain to a solid ES valuation, natural capital should be initially measured, because contemplating only instrumental and anthropogenic values would be hasty and risky. Traditionally the valuation of ES has been mainly intended in economic terms. This is logical since the money is a worldwide understood measure. Moreover, attaining a monetary valuation leads to a number of advantages, including the accessibility of information for policy decisions, the immediate assessment of damage or benefit estimates deriving from changes in natural resources, and the possibility to immediately include estimate in national account. In general terms it is accepted that the total economic value of a good or service is composed by both use and nonuse values. These valuations should be performed applying methods based on the evaluation of natural resources employed rather than on perception of the user.

7 Classical Methods for Ecosystem Services Valuation: A Brief Review

Researches about ES topic and their valuation proliferated within the last 40 years. Even if these approaches should be nowadays supported by more ecocentric valuation techniques, significant part of the present literature about ecosystem functions and services is based on traditional methods.

Neoclassical methods, as schematized in Table 1 (MEA 2005), for economic valuation of ES are based on the premise that people have personal preferences about both marketed and nonmarketed goods, which much depend on subjective tastes and attitudes. These preferences have a certain degree of substitutability since, if the quantity of one good diminishes, in some cases the quantity of a different good can be increased to fulfill demand. Important information about values can be obtained analyzing these substitutions and then this is the theoretic basis on which methods for economic valuation of goods and services are formulated.

Generally speaking, classical methods fall into two categories: revealed preference and stated preference. Revealed preference approaches estimate the value of a good or a service by means of observations of users' actual behavior. Stated preference measurements obtain a value through users' responses to hypothetical questions (Freeman 2003). Revealed preferences methods can be, in turn, split into direct market valuation methods and surrogate (indirect) market valuation methods. Direct market valuation can be applied to services traded in the market since they own a market price that coincides with their value. Clearly, these represent the minority of ES. This method can be generally applied mainly to provisioning services, such as raw materials (de Groot et al. 2002). As the largest part of ecosystem functions and services does not own a market price, the surrogate market valuation methods must be applied. This means that the price must be derived

Table 1 Synthesis of methods commonly employed for ecosystem services valuation

Methodology	Approach	Common applications	Limits
Revealed preferences			
Market price method	It estimates the economic value of ecosystem products or services that are bought and sold in commercial markets	Traded services	Available for a limited number of goods and services; it does not fully reflect the real value
Changes in productivity	Evaluations of effects on production due to modifications imposed to ecosystems	Provisioning services	Data relating directly to ecosystems and goods production are often lacking
Replacement cost (and variations)	Cost required to artificially generate the service	All services' categories	It can lead to very different estimates according to the replacement method chosen
Travel cost	It obtains the demand curve from data about travel expenses of users	Information services	Mainly applied to recreation services
Hedonic pricing	It infers the effect of environmental factors on the price of good influenced or depending by environmental variables	Information services	A great effort to collect necessary data is required
Stated preferences			
Contingent valuation	It consists in asking directly to users their willingness to pay for a certain service	All services' categories	Potential errors in replies
Contingent choice method	It asks people to make a choice valuing a range of options based on hypothetical scenarios	All services' categories	

indirectly by analyzing those factors, linked to the ES, which have a market price. Indirect market valuation techniques are, for example, avoided cost (the cost to incur in the absence of a function or a service, such as flood control), replacement cost (the cost to artificially generate and replace a function or a service), travel cost (the value is expressed as the money and the time people are willing to spend to join the place where the function or the service is located), and hedonic cost (the value associated with environmental quality, which is evaluated as embedded in housing prices) (de Groot et al. 2002; Freeman 2003).

The most applied stated preference method still remains the contingent valuation. By means of contingent valuation, the value is directly asked to individuals through a survey or questionnaire. Values can be expressed as willingness to pay (the maximum amount a person would be willing to pay for an increment of a good) or willingness to accept (the minimum amount a person would require as compensation for the loss). Contingent valuation has been as widely applied as criticized, but it holds the great quality of flexibility since it can be applied to whatever function or service. Nonetheless, this flexibility leads to criticisms about reliability (Bunse et al. 2015).

Usually, methods for ES evaluation are based on users' preferences and on a utilitarian approach. Traditionally, an entity owns an economic value only if people consider it desirable and are willing to pay for it; in this context, natural resources are regarded as instruments devoted to human satisfaction. Economy lays on consumer sovereignty principle, on the base of which welfare can be achieved if allocation of resources is chosen so as to satisfy to the maximum extent possible the wants of individuals (Vassallo et al. 2013). But preferences are mutable, particularly over longer time frames that are the temporal scale of ecosystems. Preferences vary under the influence of education, advertising, and variations in abundance and scarcity, changing cultural assumptions and specific social and environmental contexts.

A paradox lies in the fact that often and most of all in industrial and postindustrial societies, humans were only able to perceive the value of final man-made or natural products mainly generated with natural resources considered as free. According to these appraisals, classic economy principles cannot be applied to environmental goods and services, whose value should be retained as a precaution to assure the maintenance of a certain well-being level for us and for future generations. In this perspective, the overall investment made by nature to generate resources must be carefully evaluated by means of techniques based on ecological accounting principles (Niccolucci et al. 2007). In particular, in the last years, an alternative approach has been proposed: the emergy analysis. This method, belonging to the so-called system methodologies, is able to identify a common source originating any resource and to tackle the issue of ES valuation with a donor-side perspective.

8 System Methodologies for Ecological Valuation

System methodologies include a range of analyses widely applied in order to take information about the general behavior of what is analyzed (namely, the system). A system is an irreducible set of elements composing subsystems. Its parts interact and produce a unique behavior that can only be assigned to the total system as a whole, since "the whole is more than the sum of the parts" (Von Bertalanffy 1972). Complex systems are open systems that interact with their environment and evolve over time. They contain feedback loops and have a history; prior states have an influence on present states, which, in turn, will have an influence on future states. Complex systems are nested and encompass various organizational levels and have emergent properties. This means that at each system level some features, structures, or patterns, novel and coherent, which are not predictable from the composing subsystems if observed in isolation, arise due to the process of self-organization (Goldstein 1999) and this is why an overall perspective should be employed. Emergy analysis is able to meet these requirements. Current methods for economic valuation of ES internalize externalities by valuing nonmarket-traded goods and services. Odum and Odum (2000) suggest that internalities should be externalized by using solar energy as a common basis for valuing goods and services generated by natural and man-made ecosystems. Emergy accounting is a quantitative method capable of assessing the work of biosphere in terms of direct and indirect solar energy converging to support the production of products and services (Odum 1996). According to this method, the more work of biosphere is embodied in generating natural resources and ecosystem services, the greater is their value. As a consequence, the emergy method can provide an alternative measure of value of natural capital and ES by assessing their cost of production in terms of biophysical flows used to support their generation, extraction, and use (Franzese et al. 2015; Paoli et al. 2016).

9 Emergy and Ecosystem Services Valuation

Emergy is able to attribute a cost to resources that do not own a market value and to put them at the same level of items valued by economy. Moreover, emergy allows providing an objective valuation of resources, based on the effort made by nature to supply energy and material flows that allow the provisioning of services (Vassallo et al. 2009). Inputs having different units of measure are standardized to solar emergy Joules (seJ), so that different items can be compared and the total amount of resources required by the system can be reckoned.

Emergy is versatile, being developed to analyze natural and anthropogenic systems. Emergy theory is defined by two key concepts: solar emergy itself and solar transformity. Solar emergy is identified by the quantity of solar energy required, directly or not, to provide a given flow or storage of energy or matter (Odum 1996). Emergy, expressed in solar emergy Joules (seJ), is usually calculated on an annual scale. Transformity measures the input of emergy per unit output and is calculated as the ratio of the emergy necessary to produce a flow or a storage to the actual energy of that flow or storage. The transformity is expressed in solar emergy Joule per Joule of output flow ($seJ \cdot J^{-1}$). For certain products or flows easily quantifiable in units of mass or money, a conversion value expressed in $seJ \cdot g^{-1}$ or $seJ \cdot €^{-1}$ can be used (Paoli et al. 2008a, b). These coefficients are named specific emergy and emergy per unit money, respectively; transformity, specific emergy, and emergy per unit money can be gathered under the locution of Unit Emergy Value (UEV: Paoli et al. 2013).

The first step in the emergy analysis consists in drawing a system diagram as a box containing components and surrounded by all inputs on the left and upper boundaries. On the outside right boundary are located outputs, while heat losses are represented below. The diagram from Vassallo et al. (2013), referring to *Posidonia oceanica* habitat (i.e., a vegetal forest) and the services it provides, is here reported as example (Fig. 7).

From a system diagram, an emergy table is built, where all inputs to the system are listed, with the corresponding unit of measure, followed by the UEV and the final emergy values. Emergy values are obtained from the multiplication of input flows and UEV. The sum of emergy values provides an estimate of total resources amount required by the system to work.

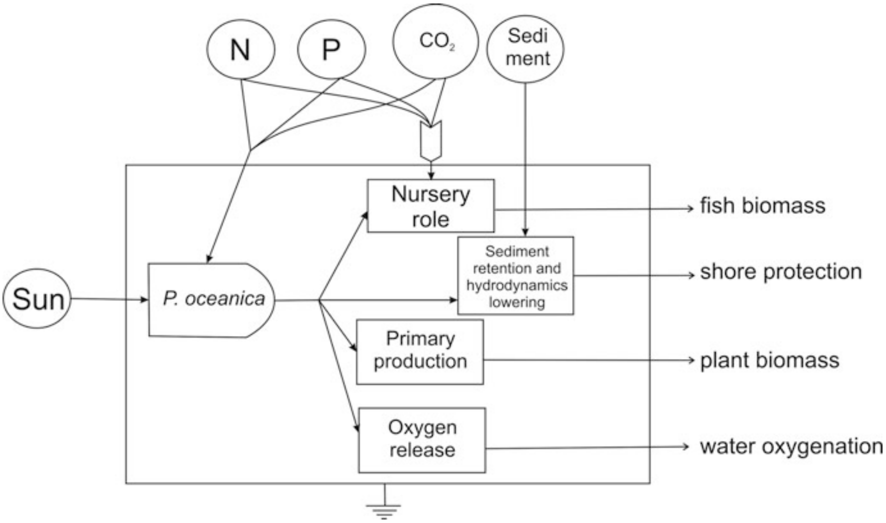

Fig. 7 Emergy diagram of *Posidonia oceanica* and associated services provided (from Vassallo et al. 2013). Sources keeping the system working are depicted as *circles* around the upper part of the main box. Producers within the systems are indicated as a *bullet*, while functions and ecosystem processes are depicted as *smaller boxes* within the limits of the main one

Emergy has been widely applied to ecosystems even if its employment to the valuation of ES and functions has been approached mainly in theory, while practical applications are rare and pioneering. Theory about how to associate emergy and ES evaluation has been recently deepened by Pulselli et al. (2011), with the aim of connecting the ecosystem approach with the neoclassical market valuation, creating a link between a donor-side approach and a user-side approach for ecological services.

Emergy is an ecological measure of wealth in the system, while economy quantifies wealth in monetary terms. Emergy values can be classified as donor-side values since they are calculated by quantifying the convergence of matter and energy (several inputs) to a system on a common basis. Market values are, on the other hand, receiver values since the receiver, the user, decides them. ES traditional approach is an anthropocentric, user-side approach, based on the users' preferences.

Emergy approach to ES is based on system science instead of economic science: ES are valued as the amount of resources invested by nature (and then as natural capital) to satisfy human needs and as the work done by nature to provide a flow or a service expressed as solar energy processed (and memorized) in space and time. This measure is thermodynamic and independent from the presence of users and from the value they ascribe to a service (Pulselli et al. 2011). Emergy flows depend on natural dynamics, while neoclassical evaluation of ES lays on the utility that humans take from nature: as a consequence, it results hasty to perform a direct quantitative relation between the two. However, an indirect use of the relation between emergy and ES evaluation can be done using the ratio between the two entities. Campbell

(2000) proposed a global emergy budget, required to maintain the entire biosphere, equal to 9.26E + 24 seJ·a^{-1}. Costanza et al. (1997) found that the global value of services provided by terrestrial ecosystems ranges between 1.82 and 6.15E + 13 €·a^{-1}. Dividing the world ES value by the emergy flow to the biosphere, we obtain the amount of money that is, on average, produced by one seJ of solar emergy, which can be considered as an estimate of the ability of the biosphere to provide a kind of economic wealth for humans.

This ratio has been named Environmental Emergy Money Ratio (EnEMR hereinafter), the Emergy Money Ratio (EMR) being a classic emergy index that links emergy to economy, calculated as the ratio of the emergy flow of a nation to its gross domestic product. EMR is expressed in seJ·currency^{-1} (seJ·€$^{-1}$ in our case) and represents emergy purchasing power since it values how much emergy corresponds, on average, to one unit of money produced by the national economy (Odum 1996).

EnEMR has a value between 5.09E + 11 seJ·€$^{-1}$ and 1.51E + 11 seJ·€$^{-1}$, depending on the minimum and the maximum values calculated by Costanza et al. (1997): as a precautionary attitude, the lowest value should be adopted.

If the total amount of resources feeding a system is quantified and then expressed in emergy terms, a monetary value based on an ecological, donor-side, intrinsic value can be obtained by multiplying the emergy amount and the EnEMR. Practical applications and case studies have been recently developed (Paoli et al. 2013; Vassallo et al. 2013; Turcato et al. 2015). Turcato et al. (2015) evaluated the loss of ecosystem services associated to bast scale (*Matsucoccus feytaudi*) invasion of forests in the Mediterranean area. A pinewood without visible damages from bast scale was compared to a damaged pinewood by means of emergy analysis to estimate a loss equal to 2250 Em€·ha^{-1}·a^{-1} that, if extended to the entire surface of the National Park where forests are located, leads to a total loss of one million Euro per year. Paoli et al. (2013) analyzed a beach restoration project with the aim to assess the environmental cost associated with the project fulfillment. The analysis allowed evaluating whether costs imposed to the environment to restore a service corrupted by human employment are correctly estimated by economy. Results proved that environmental costs (and then the use of ecosystem services) are two orders of magnitude greater than economic costs, demonstrating that humans are imposing a double pressure on the environment: first, by worsening, with their activities, littoral erosion, which implies the loss of natural habitat and the decay of beach ecosystem, and, second, when, to manage negative outcomes caused by erosion to nature and human settlements, humans draw natural materials subtracting them to other possible uses by ecosystems. Finally, Vassallo et al. (2013) applied emergy analysis to estimate the value of the main ecosystem services provided by the seagrass *Posidonia oceanica*. The estimated value resulted equal to 172 €·m^{-2}·a^{-1}. Sediment retained by the meadow resulted to be the most relevant input, composing almost the whole *P. oceanica* value. The study allowed also performing remarks about economic losses arising from meadow regression through a time comparison of meadow maps.

This procedure, representing an operative tool to provide a synthetic monetary measure of ecosystem services, has been preliminarily applied to other benthic habitats in a marine protected area (MPA) in the NW Italy in 2010 by Paoli et al. (2010) and presented to the workshop *Challenges for a Systemic Environmental Monitoring and Adequate Indicators*: almost 25% of total MPA value was due to the coralligenous, which also showed the greatest value per unit area among the habitats considered.

In 2013, the Italian Ministry of the Environment and Protection of Land and Sea financed a 4-year research program focused on the development of an environmental accounting system in the Italian marine protected areas (MPAs). The main goal of the project consists in the assessment of the ecological and economic value of the MPAs as well as environmental benefits they generate together with the environmental costs they support. The accounting, particularly addressed to ecosystem services valuation, is realized by the adoptions of a method founded on two complementary pathways: ecological and economic. The ecological accounting branch is based on the use of emergy, accounting for both the assessment of the ecological value of ecosystems and related flora and fauna and the environmental costs of the human activities conducted in the MPAs. From this approach, interesting findings will hopefully arise about the value of habitats contained in Mediterranean MPAs, such as the coralligenous, opening the way for practical application of such a procedure in environmental accounting.

10 The Economic Value of Animal Forests

To date, the economic value of the animal forest has been calculated only for coral reefs. Various estimates of their value have been attained applying classical methods for economic evaluation of goods and services.

Even if coral reefs represent only 0.2% of marine ecosystems, they contribute to 1.8% of the global gross national product. In general, economic estimates of the value of coral reefs include economic revenues from three main sectors: tourism, fisheries, and coastal protection. Sometimes also biodiversity and amenity are considered.

The annual value of coral reefs has been estimated by Cesar et al. (2003) as being equal to 29.8 billion $\text{US\$} \cdot \text{a}^{-1}$ and to 1050 $\text{US\$} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$: 32% of this value is ascribable to tourism and recreation and another 30% to coastal protection, while fisheries and biodiversity account for slightly less than 20% each. Two estimates of coral reefs value have been realized by Costanza et al. (1997) and de Groot et al. (2012), both performing a synthesis of studies about the economic value of different biomes. The value estimated in 1997, equal to 8384 $\text{US\$} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$, reached 352,249 $\text{US\$} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$ in 2011. The gap between these two different valuations can be ascribed to some main reasons: the development of new and more complete estimates of the unit values of ecosystem services per ha, real changes in the functionality of ecosystems per ha, and, finally, changes in value per ha due to modifications in human, social, or built capital.

A number of researches have been addressed to the calculation of the value of coral reefs located in a particular area: these studies vary significantly in terms of the valuation techniques used, goods and services assessed, and assumptions made. As a consequence, the values and the contribution of different services and sectors seem to vary sensibly from different areas and estimates. The main results from a selection of these studies are presented in Table 2. In the majority of the cases considered, the greatest share of value is due to tourism and related activities, while the value per ha varies from a minimum of 372 € to a maximum of 48,480 € with an approximate average of 3436 €.

For other coral reefs in deep and cold waters, as well as for coralligenous reefs and vermetid reefs, precise estimations of the monetary value of ES they provide, both on an economic and ecologic base, are not yet available.

11 Conclusions and Future Directions

Some final remarks can be made about animal forests. The complexity of these systems generates an extremely complex set of functions and services. Quantitative valuations of this ability can be found and dispersed in the extended literature about coral reefs or in recent studies about cold/deep coral reefs, coralligenous reefs, and various invertebrate reefs, even if for the most part not directly related to the ecosystem function/services theory.

As far as the monetary valuation is concerned, a great variety of estimates can be found nowadays in studies realized about the economic value of coral reefs. These assessments have been achieved with those methods mentioned in this chapter as traditional methods for economic valuation of ecosystem services. In general terms, it can be stated that total values per year are frequently in the range of billions of US dollars. It appears evident the dominant contribution, in economic terms, of tourism and recreation. It should be highlighted that this scenario is probably influenced by the fact that methods considering also nonuse values, such as the contingent valuation method, are applied only when tourism and recreation are considered. This is proven also by the fact that when these methodologies are applied to evaluate nonuse values in general terms, the amounts calculated became comparable with those evaluated for tourism and recreation.

The lack of studies aimed at estimating the economic value of cold and deepwater coral reefs, as well as of coralligenous reefs and invertebrate reefs, should be remedied in the near future. Moreover it appears evident the claim for a globally accepted and recognized methodology. It is compulsory to introduce techniques able to consider not only the economic side of functions and services but also the environmental one and to make the calculated values comparable, based on the same scientific basis and methodological approach. In our mind, the emergy analysis is the tool able to summarize all these characteristics, and both system and classical methodologies should be developed in parallel, applying different traditional methods for the economic valuation of nature, in order to obtain complete information, from both the nature and the human side.

Table 2 Synthesis of main studies about economic value of coral reefs

Place	Tourism	Fisheries	Coastal protection	Other services	Annual value (€) per ha	References	Calculation method
Pacific	9	22	67	2	394–666	Pascal 2010	Avoided damage cost, replacement cost, market value
Pacific	84	1	NE	15	48,480	Cesar and Van Beukering 2004	Contingent valuation, direct and indirect expenditures, hedonic pricing, market price
Atlantic	42	8	39	11	NE	Carleton and Lawrence 2005	Unknown
Pacific	1	8	4	87	372	Spurgeon et al. 2004	Market value, substitute price, benefit transfer, contingent valuation, replacement cost, changes in productivity
Atlantic	54	8	38	0	1821	Burke and Maidens 2004	Revenues, replacement cost
Pacific	79	2	13	6	6951 (estimate)	Van Beukering et al. 2006	Value transfer, net factor income, travel cost method, avoided damage cost, and net factor income
Pacific	81	3	7	9	11,793 (estimate)	Van Beukering et al. 2007	Travel cost method, value transfer and net factor income, hedonic pricing, avoided damage cost
Atlantic	81	1	18	0	NE	Burke et al. 2008	Avoided damage cost, revenues
Pacific	51	2	3	44	765–4728	Van Beukering et al. 2011	Change in productivity, travel cost method, and willingness to pay

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Restoration of the Animal Forests: Harnessing Silviculture Biodiversity Concepts for Coral Transplantation

45

Yael B. Horoszowski-Fridman and Baruch Rinkevich

Abstract

Coral reefs and rain forests are among the most diverse and productive ecosystems on earth, sharing numerous ecological and functional properties. Decades of anthropogenic activities and the overexploitation of reef/forest resources have led to a worldwide rapid degradation of both ecosystems, threatening the continued function of these habitats and their ability to provide numerous goods and services. Inspired by silviculture, an emerging approach to reef restoration is the gardening coral reefs tenet, in which numerous new coral colonies are farmed in situ in mid-water coral nurseries and are subsequently available for transplantation on degraded reefs. As in forestation, transplantation of corals can be used as a sustainable tool that carries ecological engineering benefits, such as the reconstruction of rehabilitated coral reefs with a particular coral coverage and associated species' compositions, increased rugosity (3-d structural complexity), and enhanced biodiversity.

Forest restoration initiatives have been underway for over a century, leading to the development of consolidated silviculture rationales. In contrast, many theoretical aspects have yet to be elucidated in the newly emergent discipline of active reef restoration. Due to the numerous similarities between coral reef and forest ecosystems, as well as between their restoration approaches, insights regarding the use of tree plantations for forest restoration could substantially advance the restoration of coral reefs. Here, we synthesize recent advances in farmed coral transplantation and discuss the influence of active reef restoration on biodiversity

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outcomes. We particularly focus on diversity estimates at the population genetics, species, and ecosystem levels, consulting forest restoration literature for rationales, tools, and recommendations that can be harnessed in the gardening approach for active reef restoration.

Keywords
Biodiversity • Gardening approach • Active reef restoration • Marine silviculture • Tree plantation • Forest restoration • Coral transplantation

Contents

1 Introduction

Coral reefs and rain forests are two ecosystems that share numerous ecological and functional properties (Connell 1978). They are among the most diverse biomes on earth, and they provide vital goods and services to human populations, including food, livelihood, cultural values, and monetary fluxes from recreational activities. Forests also supply fiber, timber, and wood for fuel, while reefs protect adjacent coastal areas from erosion and provide important sources of protein to hundreds of millions of people (Chazdon 2008; Rinkevich 2008). The numerous goods and services supplied by forests and reefs rely on the existence of their building blocks, which are trees and hermatypic corals, respectively – sessile ecosystem engineering organisms that follow similar architectural patterns (Epstein et al. 2003; Lartaud et al., this volume). These habitat constructors alter the physical characteristics of the environment and create new living spaces and a surplus of ecological niches. The three-dimensional complex topographic reliefs that trees and hermatypic corals create are crucial for the existence of the multitude of associated fauna and flora and provide essential breeding, nursing, and feeding sites for a myriad of organisms (Graham and Nash 2013).

Regrettably, decades of anthropogenic activities, overexploitation of forest/reef resources, and intensifying climate changes have led to a worldwide rapid degradation of both ecosystems, threatening their continued functioning. On land, the conversion of forest areas into farmlands, forest fragmentation, extensive logging, cattle grazing activities, and the enhanced frequencies and magnitudes of perturbations (e.g., fire, floods) have substantially impacted soil quality and hydrological processes, leading to habitat and biodiversity losses (Chazdon 2003, 2008; Rodrigues et al. 2009, 2011; Bullock et al. 2011; Latawiec et al. 2015). Likewise, the chronic impacts of overfishing and pollution, coupled with major coral bleaching events and the outbreaks of diseases, have led to extensive coral mortalities, changes in species composition and recruitment failures (Graham et al. 2014), the loss of reef resilience, and irreversible phase-shift scenarios (Rinkevich 2015a).

In response to these outcomes, forest restoration initiatives have been underway for over a century (Rodrigues et al. 2009), supported by numerous silviculture concepts and practices (Lindenmayer and Hobbs 2004; Lamb et al. 2005; Carnus et al. 2006; Brockerhoff et al. 2008; Chazdon 2008; Rodrigues et al. 2011). An increasingly sanctioned approach to the reforestation of degraded forest areas is the use of tree plantations (also referred to as “plantation forests/planted forests”, cultured forest habitats established for afforestation/reforestation purposes using planting, seeding, or both; Carnus et al. 2006). The planted trees reshape the altered physical and chemical conditions of the degraded sites, enabling the return of the original communities of the forest habitat through natural succession or human-assisted processes. According to Chazdon (2008), plantations constitute 4% of the world’s forested area, and their planting rates are increasing by 2.8 million ha/year (~2%). Although many of the world’s plantations are established for commercial production, considerable areas are set aside for the conservation of endangered species and biodiversity (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008), and they evolve with time and through succession processes into “natural forests” (Chazdon 2003; Rodrigues et al. 2009), even though they represent biologically depleted ecosystems (Latawiec et al. 2015). Using plantations in restoration acts enables the mitigation of many hindrances to ecological succession, while indirectly supporting natural recovery, averting ecological phase shifts and ultimately restoring ecosystem services and biodiversity (Brockerhoff et al. 2008; Paquette and Messier 2010).

Reef restoration, in contrast, is a novel ecological discipline that has been receiving increasing attention over the past two decades, though many of its theoretical and practical aspects have yet to be elucidated. Following the realization that passive rehabilitation measures are providing insufficient outcomes, much effort is being devoted to the development of effective active reef restoration tools (Lirman et al. 2010; Young et al. 2012; Rinkevich 2014, 2015a). One of these emerging tools is the marine silviculture approach, also known as gardening coral reefs (Rinkevich 1995, 2005, 2006, 2008, 2014, 2015a, b). Inspired by silviculture rationales and methodologies, this practice has two phases. In the first phase, numerous new coral colonies are farmed in designated underwater coral nurseries, which are made available in the second phase for transplantation onto degraded reef areas (Fig. 1). As in terrestrial forestation, coral transplantation incorporates ecological engineering tools, for example, the use of specific coral species and various genotypes, sizes and compositions of transplants, emerged seascapes, and more.

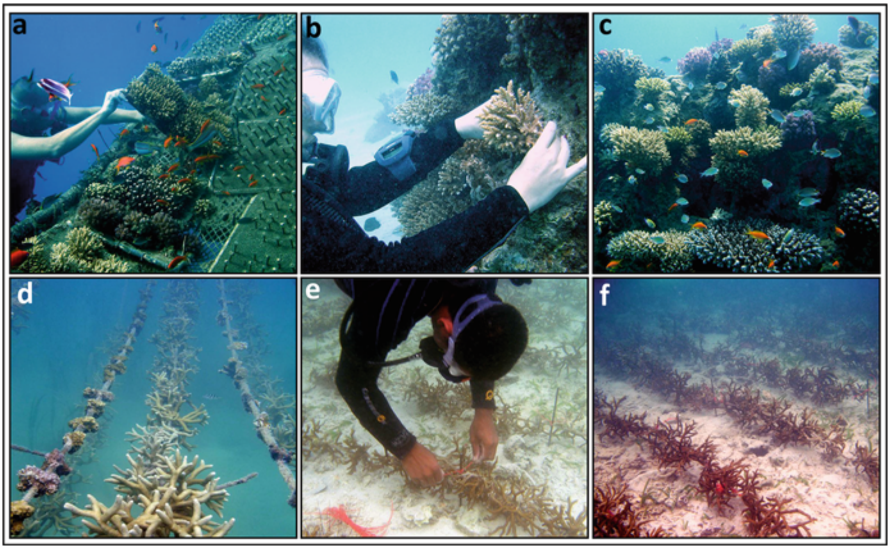

Fig. 1 The gardening coral reefs approach, a two-phase methodology (coral farming and coral transplantation) inspired by silviculture rationales, was tested first in the Red Sea (**a**–**c**) and then in reef sites worldwide, including the Philippines (**d**–**f**). Two nursery types and two transplantation methodologies are shown: (**a**) new coral colonies of various species cultured in the *mid-water* coral nursery at Eilat (Israel, Red Sea), showing small farmed fragments (*right side*) and adult colonies ready for transplantation (*left side* and tray held by the scuba diver). (**b**) Transplantation of a nursery-grown *Acropora valida* colony on a degraded knoll at Dekel Beach, Eilat. The colony has been reared in the nursery on a plastic peg that is inserted into a drilled hole within the rocky substrate. (**c**) A transplanted knoll at the Dekel Beach, completely covered by nursery-grown coral transplants of various coral species, 1.5 years after transplantation. This figure depicts the recruitment of coral-dwelling fish that reside in the restored knoll. (**d**) New coral colonies of *Montipora digitata*, *Porites rus*, and *Pavona frondifera* cultured at the rope coral nursery of Bolinao (Philippines). Each rope holds colonies (various genotypes) of a single species that was initiated from small inserted fragments that grew and developed into large colonies. (**e**) Transplantation of the rope nursery of *Montipora digitata* colonies on a degraded sandy substrate in Santiago lagoon, Bolinao. The ropes, which are covered with the farmed corals, are secured individually with cable ties to iron bars anchored into the substrate. (**f**) Another case of rope nursery transplantation on the soft bottom of a degraded area in Santiago lagoon, covered by parallel rows of *Montipora digitata* (Photographs **d**–**f** by Gidi Levy)

Due to the numerous structural and functional similarities between the rain forest and the coral reef ecosystems, as well as between the restoration approaches (Epstein et al. 2003; Rinkevich 2006), insights gathered over decades regarding the use of plantations in forest restoration could substantially advance the restoration of coral reefs (animal forests). Below, we will discuss the rationales for farmed coral transplantation and review the current knowledge on transplanting nursery-grown corals. By reviewing the use of tree plantations for forest restoration and by identifying key issues related to biodiversity conservation, we will attempt to highlight tools, rationales, and lessons of silviculture that can be harnessed in the "gardening coral reefs" approach.

2 Farmed Coral Transplantation: Aims and Recent Advances

Changes to the physical and biological properties of an ecosystem (e.g., changes to the light intensity that reaches substrates following tree clearing in forests or loss of branching corals in coral reefs; Fig. 2) are a major barrier to the natural rehabilitation of degraded areas (Lugo 1997). Furthermore, the natural recruitment of coral larvae in the coral reefs, like of tree propagules in the forests, depends on larval/seed survival, which are processes that rely on the right substrates' physical and biological properties and are also characterized by large post-settlement mortalities (Rinkevich 2005). Thus, the transplantation of adult coral colonies on degraded reefs allows (i) the reshaping of local environmental conditions (Rinkevich 2008; Fig. 2) and (ii) the augmentation of degraded biodiversity while bypassing mortalities characteristic to early stages (Rinkevich 2005). While the latter is more straightforward, the remodeling of the local conditions of impacted reef areas via coral transplantation is not clear, as it is rooted in silviculture rationales (which have yet to be studied in coral reefs).

In forest restoration, the ecological engineering tool of tree plantations is often used in order to recreate suitable conditions for the initiation of native communities via natural processes (Lugo 1997; Lamb et al. 2005; Chazdon 2008). In these cases, plantations are composed of monocultures or mixed stands of native, sometimes even exotic, species, selected based on ecological engineering criteria and their ability to adapt to the new and modified conditions of the degraded site (Kelty 2006). Following tree transplantation, canopies alter the understory environmental settings, such as light intensity, temperature, and humidity, while the planted trees further stabilize the soil, improving nutrient and organic matter contents as the aboveground litter accumulates (Brockerhoff et al. 2008), lessening the likelihood of takeover by opportunistic plants (Chazdon 2003) and negating phase-shift scenarios. Such plantations generate a foster ecosystem with microclimates that facilitate the recruitment of ecosystem biodiversity (Chazdon 2003; Carnus et al. 2006; Brockerhoff et al. 2008), creating a tool that can be harnessed to reef restoration by transplanting large numbers of nursery-grown adult corals (Fig. 2). Thus, farmed corals could be used not only to reinforce poor local coral populations or to support coral-associated species but also to change the seascape and prevent phase shifts to non-coral-dominated structures, alleviating ecological barriers to reef regeneration (Rinkevich 2014).

Research in the newly emerged discipline of farmed coral transplantation has explored feasibility aspects and methodological issues, such as the attachment of transplanted corals to substrates (Edwards et al. 2010; Shaish et al. 2010a, b; Bowden-Kerby and Carne 2012; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Rinkevich 2014; Horoszowski-Fridman et al. 2015; and unpublished; Fig. 1), the choice of coral species, and their survival (Putchim et al. 2009; Muko and Iwasa 2011; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Shaish et al. 2010a, b; Gomez et al. 2014; Horoszowski-Fridman et al. 2015). One third (26/86; Table 1) of the coral species cultured in coral nurseries worldwide (Rinkevich 2014) was used in transplantation,

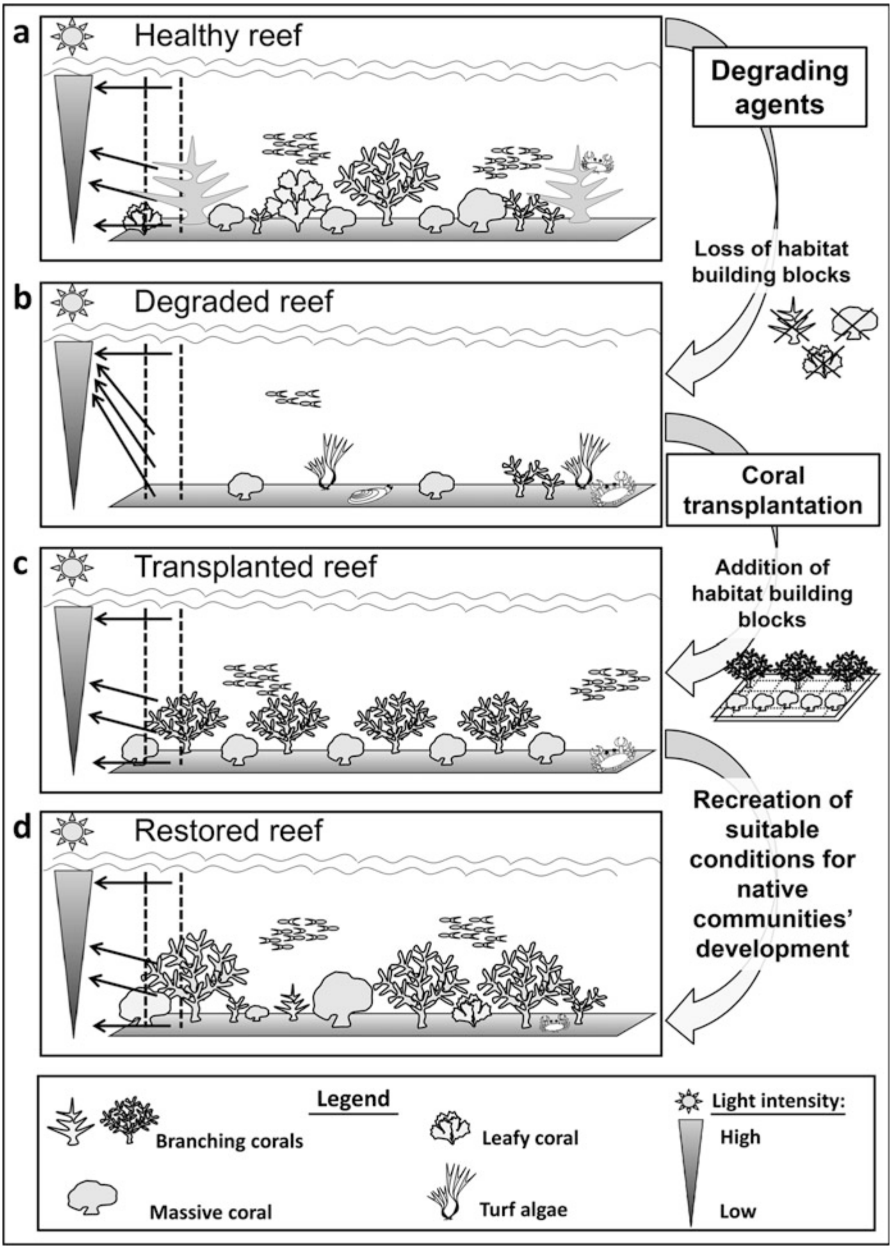

Fig. 2 Reshaping local environmental conditions in a degraded reef via coral transplantation – an example of changes in light intensity. (**a**) An illustration of light intensity (indicated by *black arrows*) at four levels along a healthy reef's water column: below water surface, upper colonial plane, mid-colonial plane, and substrate. (**b**) Caused by the loss of coral coverage, the irradiation level on the substrate and mid-colonial/upper colonial planes was modified by the removal of coral

and those species revealed variable yet remarkable abilities to acclimate and thrive on degraded reefs. Nursery-grown transplants grew on restored reefs (Putchim et al. 2009; Edwards et al. 2010; Shaish et al. 2010b; Nakamura et al. 2011; Bowden-Kerby and Carne 2012; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014), in some cases maintaining the augmented growth rates recorded in the coral nursery (Horoszowski-Fridman et al. 2015) even while directly affected by seasonality and environmental conditions (Shaish et al. 2010a) or by the appearance of corallivorous organisms (Horoszowski-Fridman et al. 2015). Transplanted corals also contributed to reef reproduction by broadcasting gametes (Guest et al. 2014) or by larval release (Horoszowski-Fridman et al. 2011).

The successful integration of coral transplants into degraded reefs has resulted in the provision of new ecological niches for reef-dwelling fauna (Fig. 1c). Nursery-grown *Stylophora pistillata* and *Pocillopora damicornis* transplants in the Red Sea created new living spaces for a range of reef-associated invertebrate species, such as boring and surface inhabitants (e.g., *Trapezia* crabs, *Alpheus* shrimps, *Spirobranchus* worms, and *Lithophaga* bivalves; Horoszowski-Fridman et al. 2015). The transplantation of *Montipora digitata* and *Porites cylindrica* corals on damaged sites in the Philippines resulted in the return of reef fish communities (Shaish et al. 2010b; Gomez et al. 2014). In Tanzania, fish- and coral-associated invertebrates were recruited to the presence of transplanted *Acropora muricata*, *Acropora nasuta*, *Acropora hemprichii*, *Pocillopora verrucosa*, *P. cylindrica*, and *Millepora* sp. (Mbije et al. 2013).

Recent studies conducted in several countries worldwide also evaluated economic aspects of farmed coral transplantation, revealing that expenditure vary depending on the source of the coral transplants (e.g., sexually vs. asexually propagated colonies), the distance between the restoration sites and the coral nurseries, the transplantation methodology, and the labor/local economy of the concerned country (Edwards et al. 2010; Nakamura et al. 2011; Villanueva et al. 2012; Young et al. 2012; Mbije et al. 2013; Guest et al. 2014; Horoszowski-Fridman et al. 2015; Rinkevich 2015b). Concentrating on the more recently developed methodologies, the costs of farmed coral transplantation (including the nursery culture phase) can be minimized to 0.5US$ per each asexually propagated coral colony, equaling the costs of silviculture practices (Rinkevich 2015b; see also Rodrigues et al. (2011) for an example of forest restoration costs).

Fig. 2 (continued) colonies following reef degradation. (**c**) The transplantation of coral colonies is used to modulate the local physical conditions of restored reefs. (**d**) The light intensity at the substrate, mid-colonial, and upper colonial planes is adjusted to pre-degradation levels. Once the physical characteristics of the impacted reef are reinstated, the development of native reef communities through natural processes as time progresses is made possible

Table 1 A list of the farmed coral species used in transplantation acts

No.	Coral species	Location	References
1	*Acropora cervicornis*	C&WA	Young et al. (2012)
2	*Acropora digitifera*	S	Edwards et al. (2010)
3	*Acropora formosa*	P	Shaish et al. (2010a)
4	*Acropora grandis*	TH	Putchim et al. (2009)
5	*Acropora hemprichii*	TA	Mbije et al. (2013)
6	*Acropora humilis*	I	Horoszowski-Fridman et al. (2011)
7	*Acropora hyacinthus*	S	Edwards et al. (2010)
8	*Acropora millepora*	P	Guest et al. (2014)
9	*Acropora muricata*	F, S, TA, TH	Putchim et al. (2009), Edwards et al. (2010), Mbije et al. (2013)
10	*Acropora nasuta*	S, TA	Edwards et al. (2010), Mbije et al. (2013)
11	*Acropora palmata*	C&WA	Young et al. (2012)
12	*Acropora pharaonis*	I	Horoszowski-Fridman et al. (2011)
13	*Acropora tenuis*	J	Nakamura et al. (2011)
14	*Acropora valida*	I, P	Villanueva et al. (2012), Horoszowski-Fridman et al. (2011)
15	*Acropora variabilis*	I	Horoszowski-Fridman et al. (2011)
16	*Acropora samoensis*	S	Edwards et al. (2010)
17	*Echinopora lamellosa*	P	Shaish et al. (2010a)
18	*Favia favus*	I	Horoszowski-Fridman (unpublished), Edwards et al. (2010)
19	*Merulina scabricula*	P	Shaish et al. (2010a)
20	*Millepora dichotoma* and *Millepora sp.*	I, TA	Horoszowski-Fridman et al. (2011), Mbije et al. (2013)
21	*Montipora digitata*	P	Shaish et al. (2010a, b)
22	*Pocillopora damicornis*	I, P	Shaish et al. (2010a), Horoszowski-Fridman et al. (2011, 2015)
23	*Pocillopora verrucosa*	TA	Mbije et al. (2013)
24	*Porites cylindrica*	P, TA	Mbije et al. (2013), Gomez et al. (2014)
25	*Porites rus*	P	Shaish et al. (2010a)
26	*Stylophora pistillata*	I	Horoszowski-Fridman et al. (2011, 2015)

C&WA Caribbean and Western Atlantic, *F* Fiji, *I* Israel (Red Sea), *J* Japan, *P* Philippines, *S* Seychelles, *TA* Tanzania, *TH* Thailand

3 Addressing Biodiversity Concerns in Coral Transplantation: A Take-Home Lesson from Silviculture

Biological diversity, at all organizational levels, is adversely affected by habitat degradation (Carnus et al. 2006; Bullock et al. 2011). The impoverishment of coral reef biodiversity impacts the habitat's ability to withstand stressors, respond to changing conditions, and sustain ecosystem services (Pratchett et al. 2014). Active reef restoration attempts to reverse these diminution trends in biodiversity. In particular, the diversity estimates at the population genetics, species, and ecosystem levels are relevant to discussions regarding the impacts of active reef restoration on biodiversity outcomes, features that are discussed below.

3.1 Genetic Diversity

A growing number of studies employ genetic analyses at the population level to better understand the processes involved with human activities and restoration activities (Shearer et al. 2009; Schopmeyer et al. 2012). The genetic diversity of each single population has profound impacts on disease resistance and the ability to stand environmental perturbations, including global change impacts (Carnus et al. 2006). Thus, whereas coral populations worldwide are genetically diverse (Shearer et al. 2009), the repopulation of degraded reefs with nursery corals grown from a limited number of clonal genotypes (the most rapid and cost-effective practice for the production of a large pool of nursery-grown corals; Rinkevich 1995, 2015a, b) could result in restored populations with a diminished genetic diversity compared to the original populations, lowering their adaptability capacities and ability to face unexpected stressors. That is the reason why consideration on the genetic diversity of farmed corals is given at the coral nursery stage so as to maintain the capacities and resilience of the reconstructed reefs (Rinkevich 1995, 2014, 2015a; Baums 2008; Shearer et al. 2009 Bowden-Kerby and Carne 2012). Thus, concerns for reduced population genetics have emerged following the use of transplants generated from asexual propagation (Baums 2008; Table 2).

Similar concerns were implied in silviculture, where selection programs have gradually decreased the genetic diversity of planted tree stocks, and, together with the generation of clonal plantations from a reduced number of genotypes, have impacted the forests' capacity to withstand environmental changes and perturbations of both biotic and abiotic nature (Carnus et al. 2006). In order to reduce the threats associated with clonal plantations, it is now recommended to use clonal mixtures of 30–40 genotypes of the planted tree species. In the same way, Shearer et al. (2009) have suggested using 10–35 coral colonies so as to retain 50–90% of the allelic diversity of these populations. Quantifying levels of species-specific allelic diversity and preserving the genetic integrity of damaged populations should become a part of reef restoration goals, integrated into restoration strategies and management (Table 2).

The reduced genetic heterogeneity in transplanted coral colonies may also hamper reproductive efforts and fecundity due to reduced fertilization rates, following self-fertilization sterility phenomena and inbreeding depression (Shearer et al. 2009; Iwao et al. 2014; Table 2), processes that are of particular relevance in genetically isolated populations. A recent study (Iwao et al. 2014) has suggested using more than six donor colonies in order to optimize the fertilization rates once cultured colonies reach reproductive stages. Another approach that has been successfully tested in silviculture acts and can be easily adapted to reef restoration is "enrichment

Table 2 Concerns, opportunities, and silviculture tools related to the genetic diversity of nursery-farmed corals

Concerns associated with the use of clonal coral transplants
1. Decreased adaptability to environmental (e.g., temperature increase), anthropogenic (e.g., sedimentation), and biological (e.g., competition, diseases) challenges
2. Hampered reproductive efforts, fecundity and success rates, inbreeding depression
3. Modification of coral population genetic structures due to (a) the use of a restricted number of genotypes, (b) the provenance of the donor colonies, (c) genetic bottleneck, (d) genetic drift, (e) gene flow over geographic scales
4. Impacts on associated reef fauna
Opportunities associated with farmed coral transplants
1. Selection of genotypes of interest, primarily those that can better withstand global change impacts
2. Integration of resilient varieties into degraded reefs
3. Counteracting the occurrence of ill-adapted local populations in degraded reefs
4. Enhancement of the genetic diversity of remnant natal populations on degraded reefs
5. Increasing the density of sexually mature adults for the purpose of enhancing local reproduction on degraded reefs
6. Using coral nursery and transplant pools as genetic repositories for reintroducing lost alleles
Silviculture tools and recommendations to be applied in the transplantation of farmed coral colonies
1. Determination of the minimal (and optimal) number of donor colonies used for the generation of clonal transplants, alleviating the risks associated with genetic diversity
2. Determination of the minimal (and optimal) number of donor colonies used for the generation of clonal transplants, offering optimization of reproductive efforts
3. Complementing transplantation of asexually produced colonies with sexually generated transplants
4. Using ecosystem engineering tools that enhance/assist local coral reproduction (e.g., employing coral nursery as "planulae hubs," transplantation of gravid colonies, etc.)
5. Using the native populations of degraded reefs (or as similar as possible) to generate transplant pools
6. To ensure that the genotypes used to generate clonal transplants can cope with the emerging environmental/biological conditions
7. Maintaining landscape connectivity in order to allow the expansion of adapted genotypes in the face of altered environmental conditions

planting" (Lamb et al. 2005; Paquette and Messier 2010), the improvement of biodiversity or the percentage of desirable species/genotypes in a forest by increasing the planting density in an already growing forest stand. In addition, other ecosystem engineering tools that support an enhanced sexual propagation of transplanted coral colonies at degraded reef sites (Table 2), such as the use of coral nurseries as planulae hubs (Rinkevich 2015a) or the transplantation of gravid corals at the onset of the reproductive season (Horoszowski-Fridman et al. 2011), would result in enhanced genetic diversity in the restored reefs.

The modification of restored reef coral population genetics is an additional issue of concern. The transplantation of colonies with low genetic heterogeneity could lead to situations of bottlenecks and genetic drifts (Table 2), where local genotypes could be lost. Furthermore, transplanting corals that originate from coral populations that are genetically disparate from those of the transplanted sites (a potential constraint imposed by the scarcity of donor colonies at damaged sites) could lead to "anthropogenic"-guided gene flow, which would modify the genetic structure of local coral populations or replace local genotypes altogether, a phenomenon that may result in the loss of local micro-adaptations or in reduced phenotypic responses to various environmental challenges. To meet these threats, forest restoration approaches recommend using stocks of local species and natal genotypes, so as to avoid genetic modification and preserve the genetic structures of the local populations (Carnus et al. 2006; Brockerhoff et al. 2008; Rodrigues et al. 2009; Table 2). Plant studies have also revealed that the population genetics of plant species directly affect the diversity of the associated biota (Whitham et al. 2003). For example, increasing the transplants' genotypic diversity from monocultures to eight genotypes (Johnson et al. 2006) in evening primrose, *Oenothera biennis*, and from monocultures to 12 genotypes in tall goldenrod, *Solidago altissima* (Crutsinger et al. 2006), resulted in a significant increase in arthropod species richness, remodeling the associated communities and trophic webs. In *Zostera marina* seagrass-transplanted plots, a comparison of single vs. six genotype compositions revealed that enhanced genotypic diversity increased the abundance of the associated epifauna (Reusch et al. 2005), supporting the concept of the "minimum viable interacting population" (Whitham et al. 2003). Whether such effects exist in coral reefs (Table 2) is yet to be determined, since to our knowledge, the relationship between the intraspecific diversity of corals and the diversity of their related communities has not been studied in detail.

Nursery-farmed coral transplants may otherwise positively impact reef biodiversity outcomes (Table 2). First, coral nurseries can be used for the selective amplification of genotypes of interest and for creating cohorts of transplants that are resistant to future threats, including global change impacts (e.g., bleaching-resistant coral colonies; Bowden-Kerby and Carne 2012), as recommended in silviculture (Tepe and Meretsky 2011). Like in silviculture strategies (Carnus et al. 2006), coral nurseries can also be used to generate resilient varieties of corals through approaches such as assisted evolution (i.e., the acceleration of naturally occurring evolutionary processes like selection, mutations, acclimatization, symbiont community change, etc.), assisting with their integration into degraded coral communities. The transplantation of nursery-grown coral colonies can also alleviate constraints of local sexual reproduction repression that result from the reduced densities of remnant corals on degraded reefs. This may be further supported by floristic evidence showing that densely planted populations have a reproductive advantage over sparsely planted populations of the same size (Morgan and Scacco 2006). It should be noted that transplanting large farmed colonies rather than small colonies or coral fragments increases the capability of the transplants to participate in the local corals' reproduction at their new resident reefs (Horoszowski-Fridman et al. 2011), further improving the restored reefs' natural resilience. Additionally, coral nurseries can function as genetic repositories (Table 2) that preserve genetic material lost as a result of natural catastrophes (Schopmeyer et al. 2012). Then, the lost alleles and species can be reintroduced back into degraded populations, including those of other reef-associated species that are constantly recruited to the nurseries (Shafir and Rinkevich 2010); the simultaneous transplantation of farmed corals together with the recruited reef biota is a phenomenon not recorded in the transplantation of trees that are farmed in nurseries under sterile conditions.

3.2 Species Diversity

The loss of species diversity is a major threat to ecosystem functioning and resilience, as it supports many of the habitat's ecological processes, goods, and services (Paquette and Messier 2010; Bullock et al. 2011). Active reef restoration carries impacts on species diversity in the restored reefs through several pathways, some of which are discussed below.

The attributes of transplanted corals: The ability to modify the damaged site, to provide living space, and to facilitate the establishment of both native and dependent reef species can vary according to the corals' species-specific characteristics, including the autogenic and allogenic ecological engineering properties. Therefore, the attributes of the selected transplanted species may disparately influence the reef's biodiversity, a notion well established in silviculture, where diverse and even contrasting understory conditions are achieved according to the tree species' features (Lugo 1997). As an example, different leaf size and branching patterns may create understories with different light intensity and quality (Lemenih et al. 2004), resulting in microenvironments that support or contain the existence of other forest-associated species. Likewise, the autogenic and allogenic ecological engineering properties of transplanted coral species may impose differential impacts on reef fauna abundance and diversity, also leading to different reef physiognomy. For example, compared to massive colonial forms, branching species contribute enhanced three-dimensional complexities for reef-dwelling invertebrates and fish. Branching coral species have vaster impacts on the reef's relief complexity (Pratchett et al. 2014), a quality that promotes the attraction of grazers and in turn facilitates coral spat recruitment and their survivorship by reducing competitive macroalgae (Bozec et al. 2013).

Diversity of transplanted coral species: The number of farmed coral species used for transplantation is expected to influence the coral species diversity and the reef-associated species diversity in restored reefs. As in forest restoration (Lamb et al. 2005), two strategies can be employed in order to reestablish coral biodiversity on denuded reefs using farmed coral colonies. The first uses the transplantation of a small number of fast-growing, early successional pioneering coral species in order to quickly cover a vast area of the degraded reef, forestalling community phase-shift developments. While this was not tested yet in reef restoration practices, evidence from silviculture studies attests to the ability of this approach to positively impact biodiversity (Lamb et al. 2005; Brockerhoff et al. 2008). The success of such a strategy in reestablishing species diversity depends mainly on the ability of organisms to recruit to the restored zone from the surrounding areas (Lamb et al. 2005).

When using this approach, one can predict stochastic outcomes, leading to a significantly modified biodiversity compared to that of the original population.

The second approach uses the transplantation of a large number of coral species to bypass the natural succession sequence and to increase species diversity while also contributing to the habitat's niche diversity. This enables the generation of a buffer effect in the face of environmental variations, caused by a differential responses of different species to fluctuating environmental conditions (e.g., different bleaching susceptibilities; see also "the insurance hypothesis of biodiversity" in Dizon and Yap 2005 and references therein). This approach has been studied in silviculture, where it is highly recommended to use a high number of tree species when planning forest restoration activities (Kelty 2006). This approach has also led to an enhanced abundance and diversity of ecological niches (Rodrigues et al. 2011). The species mixtures chosen for transplantation together with inter-/intra-competitive interactions determine the final community assembly and species diversity. It is also postulated that, as in forests (Kelty 2006; Paquette and Messier 2010), the larger the variety of transplanted coral species, the lower the risks for diseases and corallivory incidents.

As coral mariculture is a relatively young practice, the limited ecological knowledge that is available regarding the nursery rearing and transplantation of numerous coral species is a hindrance for transplanting an increased number of coral species. Therefore, under certain circumstances, it would be beneficial to combine these two approaches in order to enhance the outcomes of farmed coral transplantation on reef biological diversity while at the same time optimizing the use of restoration resources.

Functional diversity: In silviculture, it is now becoming evident that the composition of particular faunal assemblages can have a major impact on restored habitats, and in some cases, the presence of such assemblages can be of greater importance for biodiversity conservation than the number of planted species (Lindenmayer and Hobbs 2004; Lamb et al. 2005). Therefore, integrating into farmed coral transplantation functional considerations, such as the use of species that present disparate ecological characteristics (e.g., allogenic and autogenic ecosystem engineers species), species that share similar effects on ecosystem processes, or species that respond to environmental fluctuations in various ways, could improve the impacts of restoration on reef biodiversity. Reef restoration, as in forestry (Carnus et al. 2006; Rodrigues et al. 2009; Paquette and Messier 2010), can make use of ecological considerations in order to enhance functional diversity, including the choice of species, transplants morphologies (massive, branching, encrusting), and biological traits (e.g., r vs. K selection strategies, semelparous vs. iteroparous species). The enhancement of functional diversity can also be supported by adopting the consideration of various ecological processes such as inter-/intraspecific competitive interactions, transitive vs. nontransitive hierarchies, leading to the formation of more stable ecosystems, as was confirmed in silviculture practices when species that have a complementary use of habitat resources were used (Carnus et al. 2006; Kelty 2006; Paquette and Messier 2010). Thus, in coral reef restoration, harnessing facilitative interactions between coral species or between corals and reef-dwelling organisms

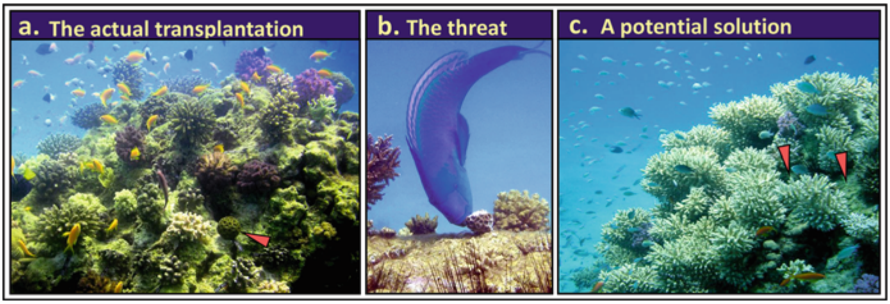

Fig. 3 Can facilitative interaction improve the survival of farmed transplants on degraded reefs? An example from Dekel Beach, Eilat (Red Sea, Israel), where colonies were transplanted directly onto bare knolls. (**a**) An overview of a transplanted knoll immediately following the transplantation of nursery-grown coral colonies of various species, including *Favia favus* colonies (massive form; *red arrow*). (**b**) Two days after transplantation, a *Favia* transplant is attacked by a parrot fish, who removed tissues and substantial parts of the colony's skeleton. (**c**) The integration of *Favia* transplants among previously planted dense plots of Acroporid branching coral species (*red arrows*) generates a physical barrier to fish attacks

(Dizon and Yap 2005; Bozec et al. 2013) could also contribute to the augmentation of functional diversity. An example of a case where facilitative interactions were used to ameliorate the integration of transplanted coral colonies into a restored reef can be seen in the restoration act performed in Eilat (Red Sea, Israel). Horoszowski-Fridman et al. (2015 and unpublished results) followed nursery-grown *Favia favus* colonies that were transplanted among other farmed coral species on bare substrate plots (Fig. 3a). The massive shaped *Favia* transplants were attacked within a few hours to a few days post transplantation by scarid fish that grazed on coral tissues, removing substantial parts of the peripheral corals' skeletons (Fig. 3b). Transplanting these massive corals among canopies of previously planted dense plots of branching Acroporid species (Fig. 3c) has significantly reduced fish attacks due to the limited accessible spaces between the new and the older transplants, which enhanced the survival rates of the *Favia* colonies.

Connectivity: When transplantation sites are isolated, the natural reintroduction of lost species native to the regenerating area may be restricted. As illustrated by forest restoration studies, the diversity (and abundance) of forest-associated plant and animal species are higher when tree plantations are located near remnant forests that serve as a source of propagules of native species (Lindenmayer and Hobbs 2004). Selecting coral transplantation sites that are connected to other reefs, capable of acting as local seeding sources of reef species and as hubs of "biocontrol" species (e.g., natural enemies of corallivorous and competing sessile organisms), could enhance the diversity of both the corals and their associated species.

The inclusion of coral-dwelling species naturally recruited to coral nurseries: Contrary to terrestrial nurseries, where the trees are farmed under sterile conditions, an in situ coral nursery is an open-to-the-environment site (Shafir and Rinkevich 2010; Rinkevich 2015a). As a result, substantial numbers of reef taxa larvae are attracted to the farmed coral colonies, including fish and invertebrates (thousands of specimens of more than 100 morphologically large species were recruited in the first five operational years in a nursery situated at Eilat, Red Sea; Shafir and Rinkevich 2010, and personal observations). Many of these species were transferred to the degraded reef together with the coral transplants, increasing the diversity and abundance of other reef-associated species in the restored area (unpublished). Clearly, the "free" use of reef-associated assemblages that are established in coral nurseries can enhance the biodiversity of transplanted areas, accelerating the recovery toward a self-sustaining reef ecosystem.

3.3 Ecosystem Diversity: Structural Complexity and Habitat Diversity

In forest restoration, the spatial and structural diversity of plantations are as vital to the ecosystem biodiversity as the chosen planted species are (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008). The same holds true for restored reefs, where the diversity and abundance of the whole spectrum of reef organisms are strongly linked to habitat complexity (Chabanet et al. 1997; Pratchett et al. 2014). As complexity is increased at the ecosystem level, reef heterogeneity provides a larger variety of ecological niches and habitats, supporting ecosystem services and resilience (Bozec et al. 2013; Pratchett et al. 2014). As is recommended for silviculture practices (Lindenmayer and Hobbs 2004; Carnus et al. 2006), reef ecosystem diversity should be considered on two spatial scales: a local level, i.e., the structural complexity of the transplanted reef, and a regional level, i.e., how restored reefs are ordered, arranged, and integrated into the ecosystem's landscape.

On a local scale, the reef's structural complexity can be strengthened by transplanting species of various coral morphologies (e.g., branching, massive, or encrusting forms; Table 3), as is practiced in silviculture with different tree forms (Lindenmayer and Hobbs 2004). In the same way, the spatial arrangement of the coral transplants in the restored reefs and the variable spacing designs have direct bearings on topographic complexity and reef heterogeneity (Fig. 4). In plantations established for restoration purposes, spatial heterogeneity is increased by planting trees in variable spacing designs that combine dense and spaced plots (Carnus et al. 2006). Plantation heterogeneity is also augmented by using transplants of different size-classes and spatially dispersing them within the restored plots, as tree-associated organisms favor properties allied to different age-classes of trees (e.g., hollows, large branches, bark accumulation; Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008). Additionally, when plantations are managed for biodiversity purposes, structures like horizontal and vertical dead trees, logs, and snags are also given importance as they constitute important components for some forest species (Carnus et al. 2006). Canopy gaps are also used as an applied tool to influence the understory's microclimate (e.g., soil temperature and moisture, the amount and quality of light that reaches the forest floor), modulating the colonization, survival, and growth of the regenerating forest biota (Lemenih et al. 2004). The rationales of these practices can also be adapted for reef restoration (Table 3),

Table 3 Coral transplantation measures that allow the advancement of habitat diversity on local and regional scales, inspired by silviculture practices and rationales

	Coral transplantation strategies for enhanced habitat diversity
Local scale	Using various coral colony morphologies simultaneously
	Considering the site-specific variable spacing of coral genotypes/species within and between planted plots
	Using variable size-classes of coral transplants
	Integration of coral skeletons
	Inclusion of bare substrate patches
	Considering various typographic arrangements of transplants (e.g., in aggregates, in order, or in random)
	Development of planting strategies that favor high reef biodiversity (e.g., functional groups, island planting design)
Landscape scale	Creation of buffer and transition zones
	Increasing landscape connectivity by forming biological corridors/stepping stones
	Provision of enlarged or supplementary habitats
	Increasing the structural and functional complexity of the landscape

Lemenih et al. (2004), Lindenmayer and Hobbs (2004), Lamb et al. (2005), Carnus et al. (2006), Brockerhoff et al. (2008), Chazdon (2008), Rodrigues et al. (2009, 2011), Paquette and Messier (2010), Holl et al. (2011), Latawiec et al. (2015)

as coral-related features such as colonial sizes and architectural complexity affect the presence, abundance, and diversity of the associated fauna, including fish and invertebrates (Chabanet et al. 1997).

As the use of coral colonial structures, sizes, and positioning may lead to discrete topographies, structural complexities, habitat diversity, and whole ecosystem diversity changes (Fig. 4), these lessons ascertained from silviculture should be taken into consideration when performing active reef restoration. Two strategies developed for silviculture, the “functional group design” (Rodrigues et al. 2009, 2011) and the “island planting” design (Holl et al. 2011), could be of particular interest to coral transplantation schemes. Following the first transplantation design (Rodrigues et al. 2009, 2011), farmed coral species would be divided into two functional groups, “filling” and “diversity.” The “filling” group consists of coral species that exhibit fast growth and high coverage capabilities (i.e., branching species), allowing a quick reef recovery while providing structural heterogeneity and an unfavorable, challenging environment for competing macroalgae and other sessile coral competitors while at the same time generating improved microclimatic conditions for the “diversity” group. The “diversity” group consists primarily of slow growth/low structural complexity coral species, which represent a wide range of colonial forms (e.g., massive, leafy, encrusting). The transplantation of this coral species assemblage is meant to enhance species diversity and functional diversity at the restored reef, while also augmenting the perpetuation probabilities of the reconstructed reef. As with tree transplantation, the transplantation design of planted corals should start with a large number of individuals from the “filling” group species and few individuals from

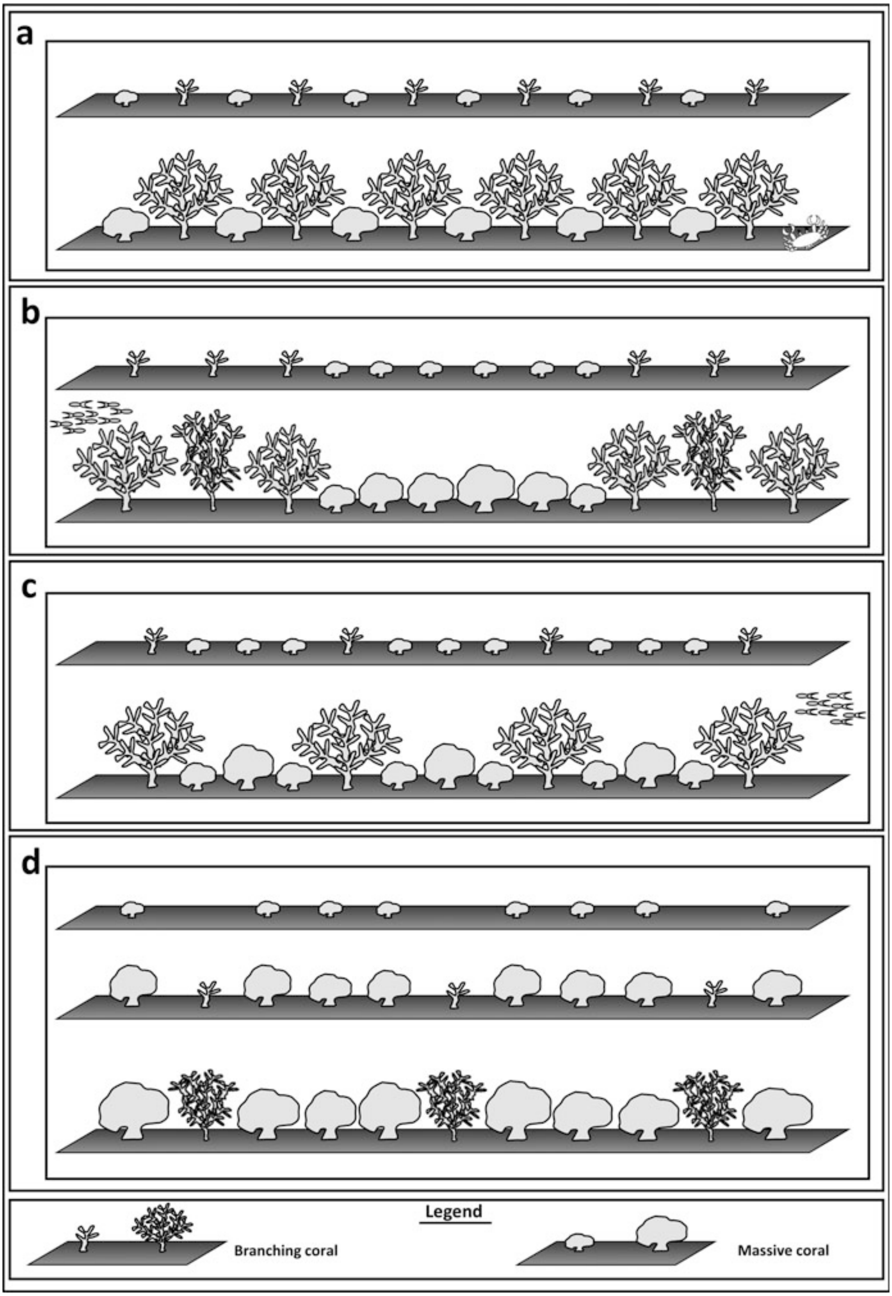

Fig. 4 Schematic illustrations of four transplantation designs, each containing two coral species (one branching and one massive), leading to discrete reef topographies. Each case (**a–d**) reveals arrangements at the transplantation stage (*upper line*) as well as expected topographical reef complexity scenarios (*lower line*), based on the biological features of the transplant species, i.e.,

each species of the "diversity" group. The initial recovery that follows the growth of the "filling" species would foster the growth and establishment of the "diversity" species.

The "island planting" transplantation design (Holl et al. 2011) argues for a transplantation layout in small patches (i.e., islands) in order to stimulate recovery by nucleation. Following results from silviculture, this planting design would promote a reduced long-term effect of planted corals on final species composition compared to the "functional groups design," creating restored reefs with a higher resemblance to the surrounding reefs. Determining the optimal patch size of each island is of importance in order to decrease possible edge effects on coral growth and survival, increase facilitating interactions, and maximize the ability of transplanted "coral island" plots to spread. Such a design could further facilitate coral recruitment by augmenting the grazing levels around the dense patches (Bozec et al. 2013).

An additional avenue for influencing reef biodiversity through the enhancement of spatial heterogeneity is to envisage coral transplantation in the context of the landscape. As in silviculture (Carnus et al. 2006), transplanted reefs can be positioned within the landscape mosaic according to various scenarios, and like in forests (Lamb et al. 2005), the ability of the separately restored reef patches to complement each other on a regional scale can further impact reef restoration outcomes for biodiversity. Given the wide spatial scale at which reef degradation is taking place, performing coral transplantation acts at the entire landscape level is not always a realistic goal. Therefore, designing site-based operations within regional contexts and managing them within the consideration of the whole heterogeneous mosaic landscape may provide opportunities to meet the restoration goals while maintaining ecological functioning, services, and biodiversity. Numerous take-home lessons can be drawn from silviculture, ameliorating the abilities of coral transplantation to increase heterogeneity on the landscape level and consequently increase reef biodiversity (Table 3). Plantations are often located at forest margins, where they constitute a transition zone between woodlands and open landscapes (Brockerhoff et al. 2008). They are also used to create buffer zones and biological corridors/stepping stones, with the purpose of increasing landscape connectivity (Lindenmayer and Hobbs 2004; Carnus et al. 2006; Brockerhoff et al. 2008; Chazdon 2008; Latawiec et al. 2015). Plantations are also managed with the purpose of increasing the landscape's structural and functional complexity by juxtapositioning different plantation types, sizes, and shapes within and between the degraded zones and remnant forests (Brockerhoff et al. 2008; Paquette and Messier 2010). Correspondingly, farmed coral transplants could also be used to extend the margins of still functioning

Fig. 4 (continued) the faster growth and significantly larger ecological volumes of the branching species compared to the massive species. (**a** and **b**) Equal numbers of colonies from each species, transplanted (**a**) alternately or (**b**) in aggregations. Colonial growth and reef structural complexity can also be modulated by varying the ratios between the species, for example, (**c**) reducing the amount of fast-growing, voluminous branching species compared to the massive, slow growth species or (**d**) delaying their transplantation reefs in areas of intense human impact, offering a transit area with some buffering effects between adverse anthropogenic influences and the remnant reefs (Table 3). Following some silviculture rationales, coral transplants can also be used to create margins around marine protected areas, forming a gradient in the environmental conditions that preserves an artificial and permanent stage of natural succession as well as a supplementary habitat for edge-specialist and reef-generalist species. Nursery-grown coral transplants can further be used to alleviate connectivity limitations between sites, as they can alter the landscape's permeability (Table 3). Like trees in plantations (Lindenmayer and Hobbs 2004), even if the coral species selected are not suitable for the settlement of certain coral-associated species and will not create the original reef species composition, they may still enable or facilitate animal movement and migration between remnant reef patches. Combining the transplantation of farmed corals with the additional ecosystem engineering tools of the coral gardening approach, such as serially positioning mid-water coral nurseries to create novel biological corridors through stepping stone mechanisms (Rinkevich 2015a), could substantially alter the restricted connectivity between reef sites. Additionally, transplanted zones of different types, sizes, and shapes could be planned and integrated within and between remnant reefs, in order to increase the structural and functional diversity of the reef's landscape (Table 3).

4 The Reefs of Tomorrow: Successful Restoration in an Uncertain Future

An increasing number of terrestrial and marine ecosystems are being inevitably transformed due to anthropogenic influences and global change (Hobbs et al. 2009; Graham et al. 2014). In such a reality, one must deliberate whether the recovery and conservation of coral reef biodiversity should focus primarily on reinstating the primeval reef configuration. As the global degradation of coral reefs continues and environmental conditions are being affected by climatic variations, the recreation of past reefs will probably necessitate increasing inputs of energy and money and may even lead to unsustainable reefs that are ill adjusted to the current environmental conditions and unable to support species adaptation following global change impacts and anthropogenic outcomes. Rather than aiming for a static ecosystem state, a portfolio of different future ecosystem trajectories could be set as a reference system (Rodrigues et al. 2011), allowing for the selection and preservation of the desired biodiversity attributes. In human-impacted terrestrial landscapes, new reconstructed forests do not always have species compositions that are similar to old-growth forests, but they do recover many elements and features of their former ecological services and biodiversity (Lindenmayer and Hobbs 2004; Brockerhoff et al. 2008; Chazdon 2008). It is even becoming legitimate to integrate non-native species into new habitats if they support important ecosystem functions that would otherwise be lost in the degraded systems, for the purpose of protecting biodiversity (Hobbs et al. 2009; Walther et al. 2009). In human-impacted tropical marine landscapes, the predicted future threats of ocean acidification, elevated water temperatures, and disease outbreaks should be taken into account when planning the transplantation of farmed corals, in order to accommodate large fractions of threatened biodiversity. Coral nurseries could be used as a tool for maintaining stocks from a wide variety of sources (i.e., genetic and species repositories; Schopmeyer et al. 2012), especially if they are to become major suppliers of coral material for reef rehabilitation (as in silviculture). If reef restoration is to move from damage control to ecosystem engineering, the transplantation of denuded areas with farmed corals will allow the shifting species composition to be adjusted according to the new resulting conditions (as discussed in forestry; Tepe and Meretsky 2011).

As no single conservation action can benefit all species, the reef restoration toolbox should be capable of providing a portfolio of various rationales and methodologies tailored to different restoration goals, financial limitations, and local ecosystem conditions. Of the major challenges emerging in farmed coral transplantation, the most urgent are harnessing biodiversity goals and the need to increase the scale of the transplantation operations in order to draw alongside the pace and scale of reef degradation. At the same time, further consultation of forest restoration protocols may continue to advance reef restoration rationales and generate new ideas for coral reef rehabilitation. Our success in the hard task of preserving the invaluable biodiversity of coral reefs relies on the development of new approaches for generating well-conceived, self-perpetuating reef zones, designed to maintain a variety of ecological flows, supply habitats for a wide range of reef biodiversity, and provide various ecosystem services to reef organisms and human populations alike.

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5 Cross-References

▶ Growth Patterns in Long-Lived Coral Species

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Index

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