Sergio Rossi · Lorenzo Bramanti *Editors*

Perspectives on the Marine Animal Forests of the World

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Sergio Rossi: I want to dedicate this book to my daughters Livia and Giulia and son Sandro. Another world is possible, but you have to fight. . .do not wait for others to solve the problem.

Lorenzo Bramanti: In memory of “Il Niso,” *the first Dr. Bramanti ever.*

Preface

The initial idea for the first sentence of this preface was to start with the well-known statement: "*we know more about the Moon and Mars than about the oceans*."

Each one of us has heard this sentence countless times in recent years, and we ourselves have used it at conferences and seminars, but just a couple of weeks ago I was reading a book written by an oceanographer (Eelco J. Rohling). The book speaks about the history of the oceans (*The Oceans: A Deep History*) and starts stating that we know a lot about the oceans.

This statement became the argument of several chats between the editors of this book, and we ended up with a question: "If people know more about the Moon and Mars than about the oceans, what we marine scientists have done during the last 20 years?" We then started some reflections and back-of-the-envelope calculations.

We have studied the ocean for more than 20 years and some of the authors of the chapters of this book even longer.

Each chapter of the book includes approximately 60 scientific publications related to the ocean in the reference list, which makes almost a thousand scientific papers.

If we do the same with the scientific production (papers, book chapters, reports, etc.) of all the 70 contributors of this book along their careers, we would easily sum up to tens of thousands of publications related to the ocean.

Let us look again into the bibliographic list of this book and we will find works published as early as in the 1950s. Not to mention seminal works such as the monography on *Corallium rubrum* (the Mediterranean red coral) by Henri Lacaze-Duthiers in 1864, which is still used as a reference for the research on this species.

Moreover, the contributors of this book are only a small fraction of the thousands of scientists who every day, for several hundreds of years, produce knowledge about the ocean. This means that we actually do know a lot about the ocean. So, why people always state the contrary? Why there is so little awareness of the immense amount of knowledge we have about the ocean?

It is true that we still need a deeper knowledge about the marine habitat distribution and health status: we ignore most of it. It is also true that terrestrial ecology is always two to three steps ahead of marine ecology. However, we know a lot about marine environment.

On the basis of that evidence, we concluded that the responsibility is on us, marine scientists, each one of us focused on our own domain, focusing on a small group of species, on a limited geographic area, on a single ecological or physiological process. But it is not just our fault. Not a lot of people have the opportunity to SCUBA dive and see for themselves what lies beneath the surface of the ocean. Thanks to Captain Jacques Cousteau, "The *Silent World*" was one of the first movies using underwater cinematography and finally showing the underwater world in color, in 1956, when the ocean has already been studied for hundreds of years.

These considerations have reinforced our belief that a holistic and interdisciplinary approach combined with a powerful and recognizable image would have been the key to communicate how much we know about the ocean and, at the same time, how much we should know to avoid destroying the marvels it contains and the services it provides to mankind.

The forest is a powerful and recognizable image. Everyone knows how a forest looks like, and it is difficult to find someone not aware of the problems linked to the loss of forests. The vast ocean benthos is dominated by marine animal forests, composed of benthic suspension feeders (active or passive) that add complexity, interact with the water column, shelter a large number of species, and act as carbon immobilizers. These three-dimensional living structures are disappearing so fast that we are not fully understanding their role in the biosphere, but we are decimating their sophisticated architecture. We know a lot about the marine forests, but there are still a lot of questions to be answered, and we are running out of time to predict their importance as ecosystem service providers.

"*Perspectives on the Marine Animal Forest*" is the sequel, or rather a complement of a previous Reference Book, *Marine Animal Forest*, a tribute to these sets of benthic habitats.

In this edition, we tried to fill in some gaps of knowledge, especially highlighting some topics that were not taken into account in the first bibliographic work and that we consider essential for a wider view of these vast sets of habitats. In the spirit of a holistic and interdisciplinary approach, the first chapter of the book has not been written by a marine scientist. An anthropologist (Prof. D. Torri) explores the role of corals in the legends and spiritual life of some human populations living in the tropics.

After this introductory chapter, we dedicate two chapters to the exploration of different marine animal forests of the world, in South Africa (Samaai et al.) and in the Persian Sea (Bouwmeester et al.), highlighting the importance of the environmental conditions to understand not only the ecosystem functioning but also the distribution of the benthic suspension-feeding organisms.

Chapters “Marginal Reefs in the Anthropocene: They Are Not Noah’s Ark”, “Animal Forests in Submarine Caves”, and “The Tubeworm Forests of Hydrothermal Vents and Cold Seeps” are dedicated to not common marine forests. Soares et al. dive in the so-called marginal reefs, which are not as well described as the shallow tropical coral reefs that attracted the attention of scientists during the last few decades. Following the path, Belmonte at al. and Tunnicliffe and Cordes tell us about what are probably the lesser-known marine animal forests: those present in the submarine caves and in the hydrothermal vents.

After the exploration of not common marine forests, the book makes an in-depth revision of two of the most neglected taxonomic groups in the marine animal forests: the bryozoans and the polychaetes. Lombardi et al. stress the past and present importance of bryozoans, depicting also the future of these bioconstructors that in some areas may be dominant. Also, polychaetes may become dominant depending on the environmental and biological factors, as highlighted by Giangrande et al., who show how these annelids may become architects of the benthos.

In Chapters “Chemical War in Marine Animal Forests: Natural Products and Chemical Interactions”, “The Nursery Role of Marine Animal Forests”, and “Marine Animal Forests as Carbon Immobilizers or Why We Should Preserve These Three-Dimensional Alive Structures”, we start exploring some of the functions of the marine animal forests. Avila makes an in-depth revision of one of the most complex and unexplored issues: the natural product synthesis and their role in the chemical interactions of benthic suspension feeders, while Cau et al. focus on the role of marine animal forests as nursery grounds, a very novel approach that strengthens the importance of these three-dimensional living structures as biodiversity and biomass promoters. Rossi and Rizzo stress the importance of worldwide marine animal forests as carbon immobilizers, a neglected yet important ecosystem service.

In the “From Trees to Octocorals: The Role of Self-Thinning and Shading in Underwater Animal Forests” chapter, Nelson and Bramanti focus on one of the most known marine animal forests, the beautiful gorgonian forest, showing parallel functions and processes between trees and gorgonians: a comparison between terrestrial and marine forests.

In Chapters “Invasive Alien Species and Their Effects on Marine Animal Forests”, and “Plastics, an Additional Threat for Coral Ecosystems”, we explore the impacts, with Creed et al. paying attention to invasive alien species and focusing especially on ecosystem functioning and biodiversity guilds, and Lartaud et al. showing how plastic pollution affects benthic suspension-feeding communities, a novel and synergistic problem that is added to other local and global impacts.

The last two chapters are dedicated to solutions. There is the contribution of Castellan et al. which proposes studying the demography and biodiversity of animal forests through the standardization of remotely operated vehicle (ROV) image analysis, a step that will be mandatory to obtain maps of these habitats and quantify the impacts in different parts of the ocean. Finally, Zorrilla-Pujana highlights the importance of citizen science and scientific outreach in the conservation and management of marine animal forests. A tool that has been considered essential in several research and management programs to minimize the human impacts on different habitats.

We hope that at the end of this journey accompanied by anthropologists, ecologists, chemists, physics, geologist, etc., the reader will end up with the awareness that although there is still much to discern and understand about how the ocean works, what we know is still a lot, probably quite more than what we know about Mars and the Moon.

Lecce, Italy — Sergio Rossi
Banyuls sur Mer, France — Lorenzo Bramanti

Contents

The Coral Tree at the End of the World: Introductory Notes to Coralline Mythology and Folklore from the Indian and Pacific Oceans

D. Torri

> *In order for Z to control the rain, he must stay awake all night,*
> *chanting the spell over and over into a piece of black coral.*
> *(Weiner 1983: 703)*

Abstract In line with the more recent trends in anthropology, addressing multispecies' encounters and entanglements, this chapter aims to explore the role of corals and coral reefs in the mythology and folklore of some coastal and insular communities of the Pacific Ocean. From Maldives to Hawaii, in fact, we find several motifs, myths, tales, songs, and fables describing patterns of interaction between human and coralline non-human. From landscape to jewel, from animal to magical artefact, and even to gods and goddesses, coral is a pervasive element not only of the maritime communities' environmental dimension but also of their folkloric, religious, and ritual spheres. Drawing from ethnographic literature, this chapter highlights some of the coral-centered topics as they appear in a variety of sources from diverse cultures of Asia and Oceania.

Keywords Anthropocene · Deities · Multi-species anthropology · Mythology · Non-human · Religion · Coral reef

1 Introduction

While the debate on the actual starting point of the Anthropocene as a geological epoch is still being discussed, there can be few doubts that human beings have become a major geological force directly driving, or laterally causing, deep and severe changes to the various ecosystems of the globe. New trends in anthropolog-

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ical thought and discourse challenge previous assumptions about a nature-culture[1] divide (Descola and Pálsson 1996), or, even more radically, human/non-human[2] (De Castro 1998): it has to be acknowledged, in fact, that such a division appears to be far from universal and even meaningless for several indigenous people. It is not a coincidence that both Philippe Descola and Eduardo Viveiros de Castro[3] fieldworked among indigenous people inhabiting the Amazonian forest and engaging daily with hosts of other-than-human agencies. Quite interestingly, the new approach is taking into account multiple perspectives, in an effort to map the multi-sided entanglements characterizing life (and death) on planet Earth. Examples of this new wave are already visible: from the entanglement between humans and mushrooms (Tsing 2015) to *forest thinking* (Kohn 2013), from earth-beings (de la Cadena 2010, 2015) to cosmopolitics[4] (Stengers 2010, 2011), and various other authors engaging in multi-species ethnography.[5]

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[1] The distinction between nature and culture, which constitutes the backbone of Western modernist and scientific worldview, is grounded on a marked dualism. This dualism is far from universal, as amply demonstrated by the collection of essays edited by Descola and Pálsson already in 1996. The selected essays focused on diverse, and differentiated, approaches to the nature-culture dichotomy, or, better said, interface. Drawing from examples and case studies ranging from Amazonia to rural Japan, but also molecular biology and physics, the book offered new insights and open the path toward collaborative and interdisciplinary research teams working on a topic which became more and more important as times went by. The book addressed posed some ambitious questions and asked for bold answers, clearly stated in the introduction: "Are the different cultural models of nature conditioned by the same set of cognitive devices? Are we to replace the historically relative nature-culture dualist category with the more general distinction between the wild and the socialised? Do non-western cultures offer alternative models for rethinking universality and the issue of moral attitudes towards non-humans?" (Descola and Pálsson 1996: 2).

[2] Eduardo Viveiros de Castro, a brazilian anthropologist who worked extensively among amazonian indigenous people, developed a theory which may be defined, as it is called in his essays (1998, 2012), *amerindian perspectivism*. This theory is grounded on the assumption, drawn from amazonian indigenous people, that every being perceives the cosmos from its position in it. This position is always located at a deictic center, and the perspective associated with it is influenced by the body. So, while the western discourse, for example, recognizes a unified "nature" and multiple "cultures," indigenous people of the Amazon perceive a unified "culture" but different "natures" (i.e., bodies). This is the reason why in their mythologies, tales, legends but also experiences, animals can, and do, speak and sometimes exchange positions with the humans.

[3] Drawing from her fieldwork in Peru, and especially working with Andean shamans, Marisol de La Cadena describes collectives of beings, humans, and other-than humans. Among these, the *tirakuna* ("earth-beings") play a prominent role in the society. Local communities are in fact "composed of a constellation of sentient entities known as *tirakuna*, or earth-beings with individual physiognomies more or less known by individuals involved in interactions with them" (de la Cadena 2010: 341–342).

[4] Isabelle Stengers, a Belgian philosopher of science, has devoted her attention to the composition of a common world in which humans and other-than humans are deeply intertwined and interconnected. From this acknowledgement she calls for a bridging of the gap between the human and the non-human. This process of composition is called cosmopolitics (Stengers 2010, 2011).

[5] Multi-species ethnography can be defined as the "investigation of social and cultural phenomena are attentive to the agency of other-than-human species, whether they are plants, animals, fungi, bacteria, or even viruses, which confound the species concept" (Locke and Münster 2015). See also below.

Despite the relevance of this paradigmatic shift in anthropological thought, which is certainly linked to what has been defined the *ontological turn*,[6] we should also be reminded that some very similar conceptions—or should we say knowledge—were often included, embedded and reflected upon in indigenous ontologies, and embodied in several practices throughout the world. For a long time dismissed as imperfect, wrong, or superstitious way to look at the world, indigenous emic[7] views almost invariably acknowledged the fact—or should we say the basic truth—that landscape was always more than the simple, passive background upon which humans inscribed, carved, or wrote their histories. In addition, equally obvious is that clouds, seas, mountains, rivers, trees, animals, and other invisible entities were to be treated as persons, as recent developments in the legal field from several countries seem to show.

While the general public of Western newspapers may smile, or even laugh, when reading that basic human rights have been extended to a river[8] or a mountain, or to the *pachamama*[9] like in Ecuador and Bolivia, several members of indigenous communities all the world over lived for generations with the notion that "the world is full of persons, only some of whom are human" (Harvey 2005: ix). As a researcher on shamanism, which I have been investigating for more than two decades by now,[10] I was ready to accept the tenets of the ontological turn, notwithstanding its critics. Despite being challenged as a form of idealism, or a by-product of academic thought, the ontological turn was finally confirming something that was

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[6] In anthropology, the *ontological turn* calls for a diverse approach toward other conceptions of being and reality, namely, those advocated by many of the indigenous people with whom the anthropologists have been working with. In some cases, not everything should be understood as a metaphor, or a belief, or a way to describe the same reality: radical difference, or alterity, has to be taken seriously into account. The ontological turn has been severely criticized by some scholars for being essentialist, anti-scientific, and, at the best, a form of idealism. For a general introduction to the ontological turn, see, among others, Heywood (2012), Kohn (2015), and Holbraad and Pedersen (2017).

[7] In anthropological theory and related jargon, the word *emic* is used to denote the "insider's view," while the observer's view (and analysis) is called *etic*.

[8] In 2019, the government of New Zealand recognized to the river Whanganui the status of a legal person. This recognition was the direct outcome of a campaign by Maori activists. Similar campaigns are being led by indigenous people in many countries, to protect sacred and ancestral environments from exploitations by multinational companies or the states.

[9] *Pachamama* is the name under which "Mother Earth" is revered among andean indigenous peoples. Her basic rights are granted by the art: seven of the Ecuador Constitution, while in Bolivia a special set of laws has been promulgated to protect her.

[10] My first fieldwork experience was in 1997, when I visited the villages of the Lepcha people of Sikkim and northern districts of West Bengal (India) to study their indigenous shamanic religion. Lepcha shamans, called *bongthing and mun* engage, establish and maintain relations with a host of other-than-human entities of the environment and especially with mountain deities associated with Himalayan peaks, lakes, and rivers. Later on, I expanded my area of fieldwork to include the high valleys of Nepal, where I have been working with other indigenous people's shamans, namely, the Hyolmo, Tamang, and Tharu people. In Nepal I have been also studying with Tibetan oracles, who are also considered to be the spoke-persons of mountain deities.

already evident for me and for several anthropologists working with indigenous people, and especially with shamans. The world is a relational place, and the circles of relations (which involve exchange, negotiation, and conflict) extend far beyond the sphere of the humans (Bird-David 1999). According to new interpretations, what was previously defined *animism* (Tylor 1871) is to be understood as a relational epistemology involving multiple actors, and, as Graham Harvey properly remarked, acknowledging that personhood is not to be limited to humans only (Harvey 2005). Quite interestingly, the Anthropocene debate brings into contact, and conflict, secular and non-secular approaches, at the same time when indigenous people themselves embrace scientific ontology to corroborate and support the struggle to protect their own environments from pollution, extractivism, and exploitation.

With the emergence of the Anthropocene and related discourses, corals surfaced once again from the marine depths to become good to think with. Emerging from the sea depths or shallow waters, amidst the waves of an ever-raging clash of epistemologies/ontologies, corals stand as visible cornerstones of marine eco-systems but also as clear markers and signs of human/non-human entanglements. Coral is always plural, not only biologically, but also semantically: landscape, being, amulet, stone, deity, spirit, tear, poison, myth, and fire. Coral is a multi-sited repository of meaningful nodes articulating different ways of being human or non-human and entangled narratives about life, body, thought, sign, possibility, and tragedy. An example of this meaningful web is the well-known myth of Medusa, the Gorgon, beheaded by Perseus. Medusa was one—and the only mortal one—of three sisters, daughters of marine deities Phorcys and Ceto. After being killed by Perseus to fulfill his quest, he took the snake-haired severed head of Medusa. The head retained some of the magical and terrifying qualities of the Gorgon. From the blood of Medusa dripping from her severed neck, the flying horse, Pegasus, was born, together with Crisaore, both sons of Poseidon,[11] the chief deity of the sea. The poet Ovid says that when the hero wanted to lay down the head of the Gorgon, by now a terrific weapon employed by him to petrify his enemies, he prepared some marine weeds and algae to protect the head from the contact with sand. When he put the head on the cushion he had prepared, the weeds petrify, due to absorption of the power of Medusa still retained by the blood dripping from her severed neck. The nymphs, curious about this phenomenon and amused by it, tried repeatedly to obtain the same result with several submarine plants, thus creating the corals (Ovid 1998: IV, 740–752).

This story explains the double essence of corals as perceived by the ancient Greeks and Romans, specifically, as a stone deriving from a plant, for they believed that a submarine plant was petrified by the contact with air. The process of petrification was the long-lasting result of the contact with the pristine power of the Gorgon, at the time of the myth. But there is much more than simply a natural observation enshrined in this myth, for in mythology much more is hidden, and revealed to the wise, than a story about origins, or a fanciful and amusing tale filled with supernatural events to scare the children. In particular, the story of Perseus and

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[11] because, according to a version of the story, Poseidon had a love affair with Medusa.

Medusa is a story about death and life, mortality and immortality, of sea-deities and their progenies, of transmutation of substances and metamorphosis of beings, and much more. Coral is that whole story condensed, and this is why even the smallest part of it retains the magic qualities associated with it by virtue of its mythical antecedents and origins.

A social history of corals is yet to be written, and it surely will have to be the endeavor of a multi-disciplinary team of scholars, including of course marine biologists and historians of land and maritime trade, archeologists, scholars of religions and mythologists, anthropologists, specialists in the field of amulets, and perhaps more. For the ethnography part, it would be good to tackle the topic through the approaches just now being established by the so-called discipline of *multispecies ethnography*:

> We define "multispecies ethnography" as ethnographic research and writing that is attuned to life's emergence within a shifting assemblage of agentive beings. By "beings" we are suggesting both biophysical entities as well as the magical ways objects animate life itself. Much of the literature considered multispecies ethnography has focused on the relations of multiple organisms (plants, viruses, human, and nonhuman animals), with a particular emphasis on understanding the human as emergent through these relations ("becoming"). (Ogden et al. 2013: 6)

That is an ethnography finally looking beyond the human, for the human is just a part of wider assemblages of existing eco-systems, each part thriving, conflicting, using, dying, and negotiating with all the others in a unified field characterized by balance and unbalance, in a constant process of dynamic entanglements.

2 Coral as Landscape

Corals have long been part of the anthropologists' landscapes. At least since Bronisław Malinowski[12] published the third volume of his works devoted to the social life of the Trobriand islanders, titled *Coral Gardens and Their Magic: A Study of the Methods of Tilling the Soil and of Agricultural Rites in the Trobriand Islands* (1935). The book is also considered a masterpiece of ethnographic writings and deals with agricultural practices and the religious and magic rituals associated with it. The whole landscape is described by him as a "flat, even, coral foundation, covered for the most part with fertile black soil, interspersed with patches of swampy ground, and of drier, stony soil" (Malinowski 1935: 57), crossed by a coral ridge (*rayboag*) covered by a dense forest. Here and there, there are also villages and sacred groves (*boma*), mangroves and pools, and coral outcrops. This coralline

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[12] Bronisław Kasper Malinowski (1884–1942) can be considered one of the founding fathers of contemporary anthropology. His theory is known as *functionalism*, and according to him human culture developed in order to satisfy basic needs of the individual and of the society. He was also influential in setting the standard for ethnographic fieldwork, based on what he called *participant observation*.

landscape constitutes the background of every activity of the Trobrianders, whose life we can define as emplaced between corals and sea. Both the environments are to be engaged with a set of specific techniques, based on direct, empirical knowledge. And yet, for the anthropologist, this set of knowledge is essentially a form of magic. In the classic formulation of Sir George James Frazer, magic is to be understood as proto-science: the effort to control the environment and its agencies through a set of techniques. Gardening is magic, that is, to ensure a bountiful crop, the gardener-magician has to master a wisdom involving technical and spiritual knowledge, engaging in transaction with the other-than-human agents of the landscape, or the *baloma*— the spirits of the dead.

That these techniques were based on empirical observations, it is evident from the detailed terminology describing the environment itself with extreme accuracy. While a linguistic analysis lies beyond the immediate aims of this chapter, a brief survey will be sufficient to show the level of engagement between the humans and their environment in the specific context analyzed by Malinowski at the beginning of the twentieth century. The basic distinction to be found is the quite obvious one between *pwaypwaya*, land, or soil, and *bwarita*, the sea in general, and *lumata*, the open sea. The land is also further divided into *valu* (village, the inhabited land), *oligala valu* (the area close to the village), and *odila* (the space outside the village area). This threefold repartition clearly points to the classic division of human and non-human space, with a liminal buffer zone. Despite a conceptual homogeneity, these areas are open to discontinuities, as expressed by the categories of *weyka* (village grove), *boma* (sacred grove, but literally taboo), and *kapopu* (uncut forest). The landscape is further differentiated into the already mentioned *rayboag* (the forested coral ridge), *dumya* (swamps), *pasa* (mangrove swamp), *kanakenuwa* (beach), *kolawala* (the sandy beach between mangroves), and *momola* (the seashore). The land is further characterized according to its characteristics in cultivable, for which the same word *pwaypwaya* is used, or uncultivable, *rasarasa* (wasteland) or *sagala* (barren soil). The uncultivable is then further divided into *dakuna* (stone or stony soil), *kanakenuwa* (sandy soil), *pasa* (brackish mud), and *pododoweta* (ooze). Similarly, the fertile, cultivable soils are defined according to their organoleptic properties as *galaluwa* (black heavy soil), *butuma* (red light soil near the coral ridge), *kawala* (black soil near coral ridge), *dumya* (greasy swampy soil), *sawewo* (soil found in the holes of the coral ridge), *mo'a* (dry light soil near the *rayboag*), and *malala* (poor stony soil). The cultivable land is the one transformed by the activities of the gardener-magician into *baleko* (plot of cultivated land) or *buyago* (garden).

Quite literally, the whole life of the islanders described by Malinowski takes place on a coralline support, and it flourishes, blooms, and wither in its earthy or forested interstices. If we zoom out of a purely anthropocentric perspective, human beings are entangled, and embedded, into a living ecosystem, and definitely part of it. The special place occupied by corals in this ecosystem is linguistically highlighted by a specific terminology differentiating, for example, between the words *dakuna* as a general term for rock or stone, i.e., dead coral, and *vatu*, "coral boulder attached to the bedrock" (Malinowski 1935: 82), *rayboag*, "round boulder" (ibidem), and *kaybu'a*, "round boulder." Other stones, of different origin, have diverse designations. Coral boulders have a special role, or place, in magic rituals related to the inauguration of the magic gardens. Of particular relevance to the present discussion is the magic word *vatuvi*, whose obscure etymology could perhaps suggest, obliquely, to the qualities inherently possessed by corals that the magician-enchanter hopes to transfer into his doings. As one spell recorded by the anthropologist recites:

> Vatuvi, vatuvi, vatuvi, vatuvi,
> Vitumaga, i-maga,
> Vatuvi, vatuvi, vatuvi, vatuvi,
> Vitulola, i-lola.
> Show the way, show the way,
> Show the way, show the way,
> Show the way groundwards, into the deep ground,
> Show the way, show the way,
> Show the way, show the way,
> Show the way firmly, show the way to the firm moorings. (Malinowski 1935: 261)

Could it be that the power of the magic spell is drawing from the coralline qualities, especially from its foundational characters, i.e., emerging from the sea depths and firmly standing in the middle of the ocean, notwithstanding waves and storms, and ultimately enabling and making possible the human life? Without being able to prove it, Malinowski nonetheless acknowledges this possibility:

> I doubt very much whether vatuvi is etymologically connected with the word vatu, ‘coral boulder’. But considering the richness with which even fortuitous associations enter into words of magic, it is not impossible that the feeling of strength, depth and stability connected with the term vatu, ‘coral boulder’, ‘coral reef’, are active in the magical functioning of vatuvi. By this I mean that the strength of the ‘deeply anchored’ coral boulder flavours the more immediate meaning of vatuvi, ‘setting on the right way’, ‘setting up’, ‘showing the way’. (Malinowski 1935: 260)

The word *vatuvi*, we are told, is a purely magic word, with no grammatical use in daily language. It resonates with other common verbs like *vituvatu* (“to put together”) or *vatowa* (“to erect”). Are coralline qualities invoked and conjured to provide firmness and stability to the gardens? Are they evoked to infuse the crops with their ability to rise and grow? If we take into account the workings of magic thought, which Malinowski inspirer, George G. Frazer, defined *sympathetic magic* (Frazer 1894), it makes perfect sense. And, in line with contemporary anthropological debates, landscape is not passive: it has agency.

Moving away from the Trobriands, we find coralline landscapes possessing interesting qualities in Maldivian folklore (Romero-Frias 2012). Here, the reef is, in itself, the boundary between the domesticated and the untamed seascape. The coral reef is an ambiguous, ambivalent place. This duality is expressed by the two terms differentiating it into *eterevaru*, the lagoon-facing side, and *fuṭṭaru*, its ocean side. Many folktales and legends report of uncanny encounters with the other-than-human entities inhabiting this liminal area, or the ghosts of the drowned dead, forever trapped and unable to finally leave the human dimension. In addition, several tales deal with the presence of *faru fureta*, the reef monster. In these cases, the agency of the land- and sea-scape is expressed directly through ominous tales, which, as in many other cases of folklore stories from other parts of the world, well serve the purpose to highlight the direct outcomes of the engagement, on wrong terms, between human beings and the non-human. The greedy fisherman, the ghost of a murdered maiden, the spirits of the sea, the dangerous demons of the ocean, the reef monster, are all actors of the multiplicity of stories and lives, taking place between the shoreline and the open sea. The reef, after all, is not only the sediment of the skeletal remains of innumerable generations of polyps but also a repository of the tangible and, in the case of stories, intangible remains of all those humans and non-humans who trod, swam, feed, grew, and died in and around it.

3 Coral as Sacred Place

Certain places, here and there, have peculiar qualities in relation to human and non-human entanglements. In those places, material objects point to immaterial relational nodes, connecting human beings to the field of what has been termed the sacred. While a discussion on the essential traits of the sacred is surely out of the purposes of this chapter, I will limit myself to provide a very basic definition: the sacred is a specific form of relation between human and non-human. This relation is codified: it entails form of communications between diverse agents, and specific places, which are surcharged with meaning, where this peculiar communication happens. While a certain sacred quality is inherently attached to the coral gardens of the Trobriands, the most massive coralline monument of the Pacific is surely the so-called “Burden of Maui” of Tonga, sometimes defined, in Western sources, as “the Stonehenge of the Pacific.” The monument, located 32 km away from the capital city of the island, is indeed impressive. It consisted of three stones, technically called a trilithon in archeological jargon. The demigod Maui is one of the most popular character of Polynesian mythological narratives. Also known as Maui of a Thousand Tricks he is considered the archetypal cultural hero, who “fished up the islands of the Pacific, stole fire for humans, slowed down the sun, and unsuccessfully sought immortality for mortals” (Craig 1989: 165). In Tonga, legends about Maui are directly linked to the creation of the archipelagos, as he fished one by one the diverse islands that later became his home. The local topography is related to events of his adventures and deeds (Craig 1989: 167). The monument called the “Burden of Maui” dates, according to scholars, to the thirteenth century, and the three stones constituting it are, in fact, coral:

> Two enormous coral slabs, each weighing approximately 35 tons, stand upright between 14 to 16 feet and are approximately 10 to 12 feet apart, 8 to 10 feet wide, and 4 feet thick. When erected, deep notches were carved in the tops of the slabs to hold a third stone (the lintel), which itself weighs approximately 10 tons and is 24 feet long, 4 to 5 feet wide, and 2 feet thick. (Craig 2004: 127)

According to the findings of a team of scholars sponsored by the king of Tonga in 1967, it seems that the sacred complex was a site for astronomical observations. Shortly after, in 1972, the location and its surrounding were declared a national park.

While Maui is surely revered in local mythologies, Pacific religious systems also have several deities whose coralline nature is self-evident even from their names. In Hawaiian mythology, for example, we find the goddess Hina-'opū-hala-ko'a, literally translated as "Hina of the coral stomach" or "Hina of the coral reef," sometimes also called Hina-hele ("Travelling Hina"). According to some sources, she is the deity presiding over corals and spiny, marine creatures. It was from shells taken from her that Maui carved his hook, with which he fished the islands from their underwater locations (Beckwith 1940: 219). She is also the wife of Ku'ula ("Ku the red"), as the god of fish and patron deity of fishermen is called. It should be noted that the red is, among all the colors, considered the most sacred one in the Hawaiian tradition. Ku'ula is the lord of all the fishes in the sea, and his cult was centered on sacred shrines where people addressed prayers and left offerings to him. These shrines were called Ko'a Ku'ula. In Hawaiian language, the word *ko'a* has at least three meanings: (1) coral, (2) fishing ground, and (3) a "shrine often consisting of circular piles of coral or stone, to make fish multiply" (Pukui and Elbert 1986: 156).

En passant, we'll note that even here we find a diversification of coralline landscapes, with the word *kohola* for the outer coral reef, *hālelo* for a coral sea cavern, and *ko'akā* for a coral shoal. These environments are often associated with non-human entities, as in the case of the *'aumakua*, special fishes—often sharks—establishing strong relationships with certain individuals, who worship and regularly fed them. Another interesting case is represented by salt or freshwater ponds, which are believed to be the domain of the *menehunes*, as the fairy folk of the Hawaiian people are collectively known. Coming back to the topics of shrines, in Polynesia we often find sacred places called *marae* ("temple"; Fig. 1) which are usually in the forms of platforms or magic squares constituted by four coralline upright slabs encircling an empty space and an upward opening (Stimson and Marshall 1964: 69). The communities used to gather in these places, under the guidance of one or more religious specialists, to communicate with their deities and ancestors and to perform rituals and sacrifices to appease them. The sacred space is a micro-cosmos in itself: to possess magical qualities, it must be including, on a smaller scale, everything that exists. It is, in short, a miniature image of the cosmos. This is the reason why actions performed there have effects on things and events happening far away, or in the spirit realm, or influencing the behavior of animals and plants, winds, waves and rain, the ancestors, and the deities. For the same reason, this space is limited, closed—to make a comparison, the ancient Greek *temenos*, the sacred enclosure, was similarly marked. And the performance of every act, the uttering of every word, must be strictly controlled and regulated, in order not to cause unintended consequences.

Fig. 1 Marae Ahu-o-Mahine, Moorea (French Polynesia). Photo credit: Sigfrido Zimmermann

Quite interestingly, corals appear also in connection with the sacred figure of Mata Peto ("Dog's Face") on the Marquesas island. This *tiki* is carved out of a single column of basalt, on which stands a single head with two faces, facing opposite directions. According to scholars, the meaning of this statue is still unclear: it could be associated with twin gods, or brothers, or even to a legendary couple of freshwater eels inhabiting the waterfall of Taipivai (Humphrey and Suggs 1995: 13). At the base of the statue, we find some shells and a branch of coral. According to Karl von den Steinen, coral was often associated with marine deities, and its presence near sacred places is to be considered almost the norm: in describing a fisherman shrine in the Marquesas, he noted the presence of coral branches as support for other floral offerings (von den Steinen 1928: iii; also quoted in Humphrey and Suggs 1995: 19). In reviewing ethnographic literature dealing with the use of corals in ritual contexts, Lisa Humphrey and Robert C. Suggs also note that:

> Further, Handy (1938: 236) notes that branches played a very important role in imparting *mana* to *tona po* houses, where sacred chants were sung near or on *me'ae* (temple) platforms. The coral branches were hidden under the ridge thatch and were carefully disposed of, after the conclusion of the ceremonies, probably in temple enclosures. (Humphrey and Suggs 1995: 15)

Offering of coral branches to temple and shrines of the maritime deities was also common over a wide area of the Pacific upon returning from a sea travel, and, according to T. Henry, ignoring or forgetting to perform this ritual was considered potentially lethal and leading to a violent death (Henry 1951: 187).

4 Coral as Being

While Western mythologies—and natural sciences—focused on coral as a stone, as a petrified plant (*lithophyte*), or as a *zoophyte*, at least until the researches of John Ellis (1710–1776), in Pacific Asia its animal nature was probably acknowledged much earlier. For example, in the song of the creation of the Hawaii, which narrates the origin of the world, the coral polyp is one of the first beings to emerge from the previously endless darkness. The song of the creation, called the *Kumulipo*, offers a detailed description of the creative process: from darkness (*pō*), Kumulipo (male) and Po'ele (female) emerge, and subsequently all the other beings came into existence. The polyp is the first, as the myth seems to move from the smaller to the bigger:

> The slime, this was the source of the earth
> The source of the darkness that made darkness
> The source of the night that made night
> The intense darkness, the deep darkness
> Darkness of the sun, darkness of the night
> Nothing but night.
> The night gave birth
> Born was Kumulipo in the night, a male
> Born was Po'ele in the night, a female
> Born was the coral polyp, born was the coral, came forth
> Born was the grub that digs and heaps upon the earth, came forth
> Born was his [child] an earthworm, came forth
> Born was the starfish, his child the small starfish came forth
> Born was the sea cucumber, his child the small sea cucumber came forth (...). (Beckwith 1972: 58–59)

The *Kumulipo* song was composed in 1700, and it was not intended for larger audiences, since it was recited in public only in two occasions (Craig 2004: 47). The *Kumulipo* is, in fact, a myth establishing the genealogy of the royal family and its connection with the same generative powers of the times of the beginning. It was in fact part of the spiritual heritage of the family of king Kalākaua (1836–1891) and his sister, Queen Lili'uokalani (1839–1917), first translated it into English in 1897. Composed for the birth of the chief Ka-'i-'i-mamao in 1700, it was recited the first time during his funeral ceremonies and then the second time in 1779, at the presence of James Cook, probably to reinforce the claim to legitimacy of the local royalty in front of an emissary of a foreign power, which was also the reason it was made public later on by king Kalākaua (Craig 2004: 150). Yet, it is important to us, in the present discussion about corals, since it testify the relevance of coral polyps as the first of the sea creatures to exist, after the emergence of the male and female creative powers. As Martha Beckwith, who published a new English edition with a commentary in 1951, noted, the song describes the genealogy of the royal family, as mentioned before, connecting it to the primordial events of the creation, in a strictly evolutionary way. The creatures are generated one after the other, generation after generation, from the time of an eternal darkness, followed by the emergence of sea creatures, the creation of earth and sky, terrestrial animals, and finally the human beings, to be completed, and crowned, by the appearance of the royal family (Beckwith 1951, 1972). That is to say, that the coral polyp is a direct ancestor of the human being.

Several gods are associated with corals, as we have seen before also in the cases of Hina and Ku'ula. Among Pacific deities, we find also, for example, the Samoan war god Fe'e, who was found in the middle of the ocean by the god Tagaloa, the supreme deity of the Samoans: Fe'e was floating amidst the waves on a coral piece, and, because he had no parents, Tagaloa took him to Manu'a (Freeman 1944: 133–134). Fe'e seems to be associated not only with war but also with the underworld. On the hills of the island of Upolu, a site exists which is called "'O le Fale o le Fe'e—literally, The House of the Cuttlefish (or Octopus)" (Freeman 1944: 121). In close proximity, several coral boulders lay in disarray, and the legend says that they were brought from the reef by subjugated deities, willing to show their submission to the god Fe'e. This deity role is consistent with his animal aspect (the octopus) and its association with the coral reef: as in the cases previously examined, the reef is emerging from the abyss, thus showing an association with the oceanic depths, while among the Samoans household and village gods (who were often connected to the ancestors' cult) were usually incarnated into cuttlefishes and octopuses (Williamson 1924: 230; Turner 1884: 59, 72, 74).

5 Conclusions

> Coral reefs are monsters. Their polyps rise from reefs of their own making—but not just their own. Like the mythical chimeras of ancient Greece, beasts made up of the head of a lion, the body of a goat, and the tail of a snake, coral reefs are made of mismatched parts— animal, plant, and more—that hang together in fragile coordinations. (Gan et al. 2017: G4)

This chapter aimed to be no more than an introductive collection of sparse notes on the anthropology of corals, or a social history of corals, taking into account, and possibly merging, different strands of thoughts, artifacts, practices, and ideas. On the one side are pacific and Polynesian ethnographies from the twentieth century, with all the limitations they include, and, on the other, the emerging field of multi-species ethnography and the ontological turn. Everything is calling, if not crying, for an anthropology beyond the human, since it is not possible anymore to ignore the meaningful system of entanglements in which, or through which, multi-species assemblages exist. With the mounting evidence for global warming, with the acidification of oceans as a corollary, and the ensuing degradation of marine ecosystems in general and coral reefs in particular, I want to draw the attention toward the study of the entanglement between humans and corals across diverse epochs and different contexts. Humans have been, after all, living with corals for a long time, and corals have gained a long-standing reputation among humans at every level. Corals are also a very interesting metaphor, useful to highlight other concepts too. The reef in itself is a culture of sort, being the result of a cumulative process of sedimentation of past generations, whose births and deaths provide the skeleton, or the structure, of the colony. On this skeleton, not only the polyps live and thrive but also myriads of other beings, both animals and plants. The reef is a holobiome, where the boundaries between individuals are thin and porous. While natural sciences show us that every being is in fact is a holosymbiont—a community of living beings—the anthropologist Marilyn Strathern postulated something similar in the field of social sciences, too. According to her, we should abandon the idea of individuals to accept and welcome the notion of dividualism: being essentially relational, every being is constituted by the web of relations it entertains with every other being. As Donna Haraway claims in her latest work, "we are all corals now" (Haraway 2016: 80), and as such we should make kin with companion species to survive, as species, in the wake of (dark) things to come. Throughout her book, corals act as a powerful metaphor. While evoking the Lovecraftian Ancient One of the Abyss, Cthulhu, with the concept of Chthulhucene, she subverts it by inserting an extra "h," and transforming it in something related to the ancient Greek notion of *chthonios*, which she translates as "of, in or under the earth and seas" (Haraway 2016: 53–54). To the misanthropic monster of Lovecraft, she opposes the pre-patriarchal Gorgonian deities, like Medusa:

> (…) from the blood dripping from Medusa's severed head came the rocky corals of the western seas, remembered today in the taxonomic names of the gorgonians, the coral-like sea fans and sea-whips, composed in symbioses of tentacular animals cnidarians and photosynthetic algal-like beings called zoo-anthellae. (Haraway 2016: 54)

This is the sort of productive entanglement we should look at, she affirms, beyond a merely anthropocentric, male-dominated, and crudely exploitative perspective. Even more importantly, "coral reefs are an immense model for studying holobiome formation at the ecosystem level" (Haraway 2017: 30) and "like Anna Tsing's refugia in forests of the land, coral reefs are the forests of the sea, critical to resurgence for humans and nonhumans" (Haraway 2017: 35). The reef is a perfect nonlinear model of clustered holobiontic lives and a successful example of symbiotic processes. Human beings, together with the widely diverse hosts of denizens of marine ecosystems, benefit from each other in unexpected ways. A well-known Maldivian tale could aptly highlight the overarching role of reefs in fostering life. A tale collected by Xavier Romero-Frias tells the story of the famous sailor Boḍu Niyami, who, trailing a fish head across the ocean, ended up to the place where the world ends and masses of water fall down the edge, into the abyss. On that very place, a coral tree emerges from the abyss, and it is known as *Dagas*, or the coral tree at the end of the world. It is a giant black coral (*Antipatharia*), called *enderi* in Maldivian language. Boḍu Niyami and his sailors manage to secure the ship with a rope to a branch of the tree and managed to stay away from the fateful fall into the void. The morning after, they found themselves amidst gentle waves and breezes, floating in waters full of fishes never seen before. Sailing back toward home, they found the fishes were following them, so abundant that the water around the ship was reverberating from the sunlight reflecting on the fishes. After many adventures on the high seas, they reached home safely. And since that time, the wondrous fish (skipjack tuna, *Katsuwonus pelamis*) was the main food of the Maldivians (Romero-Frias 2012: 52–55).

In the changing landscapes of the Anthropocene, only the alliance between different species—and not the domination of "nature" under the human master and commander—could ensure systemic survival. While Haraway is an intellectual provocateur from an academic milieu, a similar way of thinking has been common since time immemorial among many indigenous people across the globe. What was quite erroneously defined by Tylor as animism at the end of the nineteenth century was in fact the pure and simple acknowledgment that human beings spend their life together, and not in opposition, with other entities and that these entities have agency. As pointed out by Frédéric Torrente, Polynesian systems envision a unified cosmos, based on an understanding of a continuity of sort which encompasses human beings, animals, botanical species, and inorganic matter:

> Each species of creation owned a visible shape, issued from the depths (*tupu*) and a specific appearance (huru) visible to humans, as a kind of container, an envelope, a shell. This contained an invisible interiority made of many vital elements. First, the *vārua*, sort of an ever-unseen double living inside this body that could survive the death of its envelope. This was the living factor behind the animation of each physical body, which explains the personification of elements seen in the natural environment, such as coral. (Torrente 2016: 41)

Framed in religious, magic, or spiritual discourses, indigenous relations to the environment, and to companion species, were relational in a very direct way and not exploitative. In his by now famous critique of Frazer's idea of animism as wrong understanding of the environment they live in, Ludwig Wittgenstein's statement retains all its validity: if, for example, a certain group of people worship oak trees, it is not because they live and understand their world according to phantasy but more simply, and even more pragmatically, because of the fact "that they and the oak were united in a community of life, and thus that they arose together not by choice, but rather like the flea and the dog. (If fleas developed a rite, it would be based on the dog)" (Wittgenstein 1993: 139).

In the few examples provided in the previous pages of this chapter, I tried to show exactly this. Corals were multiple "things" and had multiple meanings to people of the Pacific: animal and landscape, deity and monster, danger and richness, and magic and fertility. This multiplicity of meanings is of course the result of a deep, and extremely intimate, entanglement, but it is also of the recognition that every relation, with every part of the cosmos, is never unidirectional. Our relation with the environment always implies a reciprocity of sort, and consequences we cannot ignore, for we live in complex assemblages and geometries of interdependences. The loss of one element could have unimagined outcomes:

> The problem is not just the loss of individual species but of assemblages, some of which we may not even know about, some of which will not recover. Mass extinction could ensue rom cascading effects. In an entangled world where bodies are tumbled into bodies (see our Monsters), extinction is a multispecies event. The extinction of a critical number of species would mean the destruction of long-evolving coordinations and interdependencies. While we gain plastic gyres and parking lots, we lose rainforests and coral reefs. (Gan et al. 2017: G4)

We may be laughing, when reading that “a number of other fish are not allowed to the magician, some of them because they are of dark or black colour, some of them because they live in the coral outcrops of the reef” (Malinowski 1935: 107), and yet, perhaps, the magician may still know better.

References

Beckwith MW (1940) Hawaiian mythology. Yale University Press, New Haven

Beckwith MW (1951) The Kumulipo. A Hawaiian creation chant. Chicago, University of Chicago Press

Beckwith MW (1972) The Kumulipo: a Hawaiian creation chant. University Press of Hawaii, Honolulu

Bird-David N (1999) “Animism” revisited: personhood, environment, and relational epistemology. Curr Anthropol 40(1):67–91

Craig RD (1989) Dictionary of polynesian mythology. Greenwood Press, New York

Craig RD (2004) Handbook of Polynesian mythology. ABC-CLIO, Santa Barbara

De Castro EV (1998) Cosmological deixis and Amerindian perspectivism. J R Anthropol Inst 4 (3):469–488

de la Cadena M (2010) Indigenous cosmopolitics in the Andes: conceptual reflections beyond “politics”. Cult Anthropol 25(2):334–370

de la Cadena M (2015) Earth beings: ecologies of practice across Andean worlds. Duke University Press, Durham

Descola P, Pálsson G (1996) Nature and society. Anthropological perspectives. Routledge, London

Frazer JG (1894) The Golden Bough. A study in comparative religion. Macmillan, New York

Freeman JD (1944) O le fale o le fe’e. J Polynesian Soc 53(4):121–144

Gan E, Tsing AL, Swanson HA, Bubandt N (2017) Arts of living on a damaged planet. Ghosts and monsters of the anthropocene. University of Minnesota Press, Minneapolis

Handy WC (1938) L’art des îles Marquises. Les Éditions d’art et d’histoire, Paris

Haraway DJ (2016) Staying with the trouble: making kin in the Chthulucene. Duke University Press, Durham

Haraway DJ (2017) Symbiogenesis, sympoiesis, and art science activisms for staying with the trouble. In: Gan E, Tsing AL, Swanson HA, Bubandt N (eds) Arts of living on a damaged planet. Ghosts and monsters of the anthropocene. University of Minnesota Press, Minneapolis, pp 25–50

Harvey G (2005) Animism: respecting the living world. Wakefield Press, Kent Town

Henry T (1951) Tahiti aux temps anciens. Société des Océanistes, Paris

Heywood P (2012) Anthropology and what there is: reflections on ‘ontology’. Camb J Anthropol 30 (1):143–151

Holbraad M, Pedersen MA (2017) The ontological turn: an anthropological exposition. Cambridge University Press, Cambridge

Humphrey L, Suggs RC (1995) Mata Peto: an unusual Marquesan Tiki. Pacific Arts (11/12):10–19

Kohn E (2013) How forests think: toward an anthropology beyond the human. University of California Press, Berkeley

Kohn E (2015) Anthropology of ontologies. Annu Rev Anthropol 44:311–327

Locke P, Münster U (2015) Multispecies ethnography. Oxford University Press, Oxford

Malinowski B (1935) Coral gardens and their magic: a study of the methods of tilling the soil and of agricultural rites in the Trobriand Islands. Routledge, London

Ogden LA, Hall B, Tanita K (2013) Animals, plants, people, and things: a review of multispecies ethnography. Environ Soc 4(1):5–24

Ovid (1998) Metamorphoses. Wordsworth Editions, Ware

Pukui MK, Elbert SH (1986) Hawaiian dictionary: Hawaiian-English, English-Hawaiian. University of Hawaii Press, Honolulu

Romero-Frias X (2012) Folk tales of the Maldives. Nias Press, Copenhagen

Stengers I (2010) Cosmopolitics. University of Minnesota Press, Minneapolis

Stengers I (2011) Cosmopolitics II. University of Minnesota Press, Minneapolis

Stimson JF, Marshall S (1964) Dictionary of some Tuamotuan dialects of the Polynesian languages. Peabody Museum, Salem

Torrente F (2016) Ancient magic and religious trends of the *rāhui* on the atoll of Anaa, Tuamotu. In: Bambridge T (ed) The rahui. Legal pluralism in Polynesian traditional management of resources and territories. Australian National University Press, Acton

Tsing AL (2015) The mushroom at the end of the world: on the possibility of life in capitalist ruins. Princeton University Press, Princeton

Turner G (1884) Samoa, a hundred years ago and long before: together with notes on the cults and customs of twenty-three other islands in the Pacific. Macmillan, London

Tylor EB (1871) Primitive culture: researches into the development of mythology, philosophy, religion, art, and custom. J. Murray, London

von den Steinen K (1928) Die Maŕquesaner und ihre Kunst: Studien über die Entwicklung primitiver Südseeornamentik nach eigenen Reiseergebnissen und dem Material der Museen (vol 2). D. Reimer (E. Vohsen), Berlin

Weiner AB (1983) From words to objects to magic: hard words and the boundaries of social interaction. Man 18(4):690–709

Williamson RW (1924) The social and political systems of Central Polynesia. Cambridge University Press, Cambridge

Wittgenstein L (1993) Remarks on Frazer’s Golden Bough. Brynmill Press, Norfolk

The Marine Animal Forests of South Africa: Importance for Bioregionalization and Marine Spatial Planning

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Abstract Marine animal forests, although among the most diverse ecosystems worldwide, remain obscure in terms of their diversity and functioning. Their spatial extent, diversity and function within the larger marine ecosystems remain poorly known; mainly due to a lack of traditional taxonomic expertise and the challenges associated with non-destructive sampling submarine habitats beyond the reach of SCUBA divers. In South Africa, information on marine benthic invertebrate biodiversity and taxonomy has been limited and fragmented, with more than 80% of samples collected shallower than 100 m. In the last decade, systematic surveys

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employing modern marine sampling equipment such as ROVs, jump cameras and towed cameras accelerated the discovery of marine animal forests within the South African Exclusive Economic Zone. Extensive marine animal forests have been found in both the Benguela and the Agulhas current systems, which dominate South African waters. The general distribution and diversity of benthic suspension feeders (e.g. sponges, scleractinian corals, octocorals, ascidians and bryozoans) is comparatively well established and has been used in marine spatial planning and the establishment of a network of offshore Marine Protected Areas. The proclamation of these Marine Protected Areas (MPAs) along with the identification and mapping of Vulnerable Marine Ecosystems and Ecologically and Biologically Sensitive Areas along with potential threats (e.g. trawling, invasive species, mining, climate change and petroleum and gas exploration) forms part of South Africa's strategy to manage its waters and preserve these illusive marine ecosystems.

Keywords Sessile marine invertebrates · Sponges · Cnidarians · Bryozoans · Ascidians · Benthic biodiversity · Conservation · Marine environment · South Africa

1 Introduction

Unlike terrestrial ecosystems, the biomass of most marine ecosystems is dominated by animals (Rossi et al. 2017). Sessile animals are ubiquitous in the oceans from intertidal rocky shores to abyssal depths, from the poles to the tropics, and from high to low salinity environments; they are even found in kelp beds, mangroves and among sea grasses. A pervasive organizational feature of marine sessile invertebrates is their ability to form dense communities and mass aggregations, which can dominate the marine seascape and significantly alter the surrounding environment.

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As these communities feed on suspended particles and organisms from the water column, they transfer energy and material from the water column into biogenic structures loosely resembling terrestrial forests. These "animal forests" are typically composed of assemblages of anthozoans or sponges forming the matrix for a diverse community of other benthic invertebrate taxa.

While they are among the most diverse ecosystems worldwide, understanding the diversity and functioning of most marine animal forests assemblages remains obscure. This can be ascribed to several reasons: inaccessibility and limited opportunities to sample deeper-water assemblages beyond scuba diving depth, challenges of sampling these fragile habitats without damaging them as well as lack of relevant taxonomic expertise. In the Southern Hemisphere in particular, deep-sea benthic invertebrate taxonomy and biodiversity information is limited. In South Africa, for example, systematic surveys of offshore benthic invertebrate communities only commenced in 2011, to support the classification and mapping of these ecosystems towards a comprehensive offshore Marine Protected Area network rollout. Prior to this, South Africa's offshore biodiversity was considered poorly studied with more than 80% of samples collected at depths shallower than 100 m (Griffiths et al. 2010).

While there is a scarcity of information and knowledge of the deep water marine fauna of South Africa, to date, nearly 17,000 records of occurrence and biomass for South African offshore benthic invertebrates are accessible (Atkinson and Sink 2018). In addition, 410 taxa have recently been described to genus and species level in a recent guide to the offshore Invertebrates of South Africa (Atkinson and Sink 2018). From this, the general distribution and diversity of benthic suspension feeders (e.g. sponges, scleractinian corals, octocorals, ascidians and bryozoans) in South African waters, and the locations of animal forests, have been relatively well established. These data have been compiled into various field guides and databases through collaborations with taxonomists and ecologists (Branch et al. 2016; Atkinson and Sink 2018).

In this chapter we provide an introduction to deep- and shallow-water marine animal forests in South Africa, focussing on examples from different ecoregions. The diversity and ecology of the animal communities that constitute these forests are described, as well as the ecosystem services and economic opportunities that they provide. We further discuss conservation and management alternatives for marine animal forests in South Africa, in the context of the major threats to their integrity and perseverance.

2 Oceanography, Biogeography and Biodiversity of Mainland South Africa's Exclusive Economic Zone

Mainland South Africa has a territorial sea and Exclusive Economic Zone (EEZ) of ca. 1,072,700 km^2 and a coastline of nearly 3000 km long (Fig. 1), excluding the Prince Edward Islands—South African territory situated in the Southern Ocean. The EEZ extends to a maximum depth of 5700 m and overlaps two oceans,

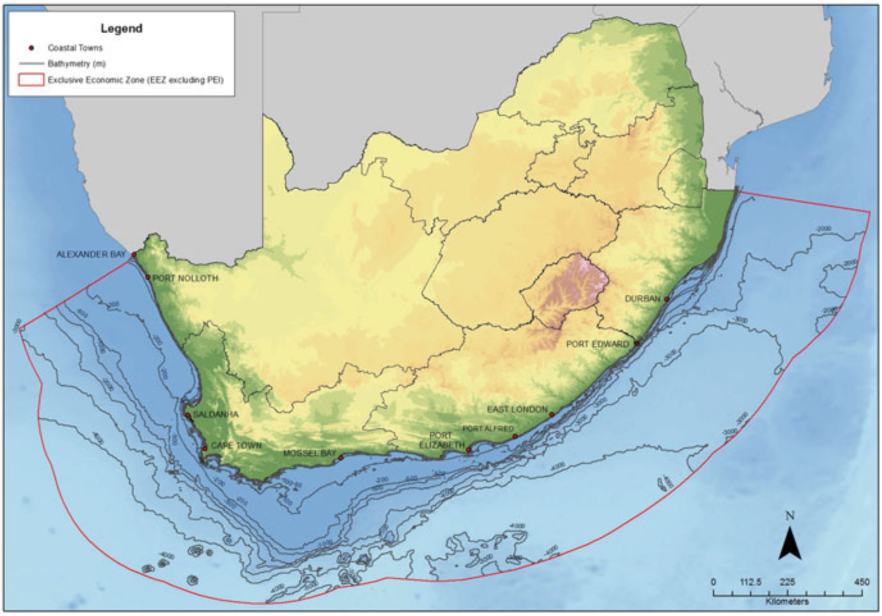


Fig. 1 Map of South Africa. The warm Agulhas Current flows on the east coast towards the south coast and the cold Benguela Current flows on the west coast. Map created ex-novo by Dr. Lauren Williams

namely, the Indian Ocean in the east and the Atlantic Ocean in the west. The continental shelf is narrow along the east coast, but much wider in the west, and especially to the south, where it extends into the large, shallow Agulhas Bank which forms an extension of the African continent. The oceanography of the east coast is dominated by the fast, southwestward flowing, Agulhas Current. This warm current, which is one of the most powerful ocean currents in the world, originates at the southern end of the Mozambique Channel and flows almost continuously from Delagoa Bay to the southern end of Africa. In the southeast Atlantic Ocean (south of Cape Agulhas), the Agulhas Current retroflects (turns back on itself) and in doing so, periodically pinches off eddies (rings) of “warm” water that enter the northward flow of the Benguela Current, the dominant current off the west coast of South Africa. The Benguela Current constitutes the eastern branch of the South Atlantic Gyre, reinforced by the Antarctic Circumpolar Current. It is characterized by intensive wind-driven upwelling resulting in high productivity which is reflected in the high abundance of fish, dense shellfish and thick kelp beds found in the waters off the west coast (Branch and Branch 2018).

As a consequence of the complex ocean water movements and resultant geographical differences in oceanographic properties, six broad biogeographic marine regions have been classified across South Africa, namely, the Southern Benguela, Agulhas, Natal, Delagoa, Southeast Atlantic and Southwest Indian ecoregions (Sink et al. 2012a). The Benguela, Agulhas, Natal and Delagoa ecoregions consist of the

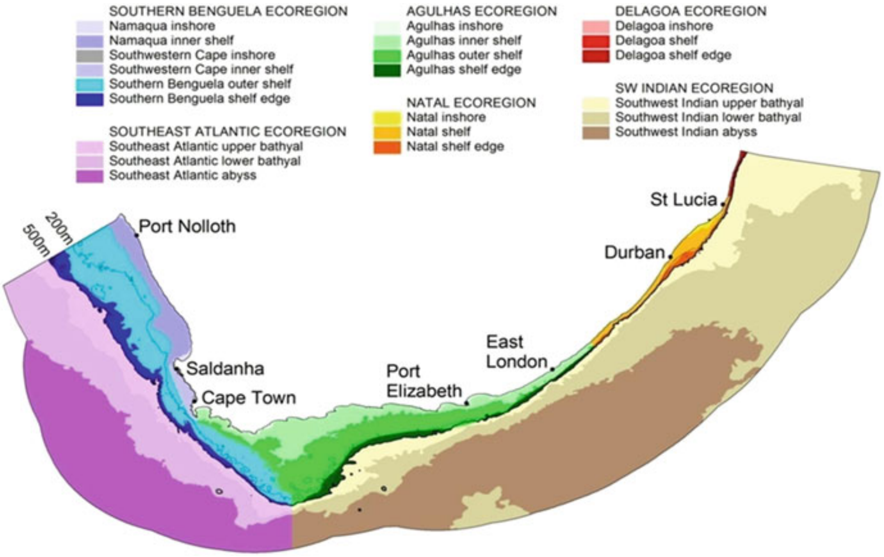


Fig. 2 Six marine ecoregions with 22 ecozones incorporating biogeographic and depth divisions in the South African marine environment (redone from Sink et al. 2012; Fig. 4). Permission was granted by Dr. Kerry Sink, lead author of the National Biodiversity Assessment published by the South African National Biodiversity Institute, Department of Environment, Fisheries and Forestry

coastal areas, the continental shelf and the shelf edge, whereas the deep-sea Southeast Atlantic and Southwest Indian ecoregions include the upper and lower bathyal zones and the abyss, where most of the seamounts are found (Fig. 2). The two offshore regions have primarily been characterized in terms of physical criteria (e.g. temperature, depth, substratum), while the four coastal ecoregions have additional faunistic and floristic detailed descriptions.

Biogeographical marine assessments that have been conducted in South Africa (Lombard et al. 2004; Majiedt et al. 2013; Sink et al. 2011, 2012a) have also recognized three broad zones, based on depth, namely, coastal, benthic and pelagic. Between the intertidal and the 30 m depth contour where there is significant photic influence, benthic and pelagic habitat have been considered to be coupled together as part of the coastal zone. Offshore of the 30 m contour, coupling is considered to be weaker, and the benthic and pelagic are considered separate zones for the purposes of the assessments. The intersection of these zones with ecoregions provides for the delineation of ecozones, of which there are 22.

Biogeographic transition areas typically contain organisms from each of the neighbouring areas as well as endemic species specifically adapted to the conditions of the transition zone. Consequently, biogeographic transition areas are typically areas of high diversity. For example, the western biogeographic transition zone (located between Cape Point and the area immediately east of Cape Agulhas) is characterized by the greatest turnover in marine species composition in South Africa (Awad et al. 2002; Bolton and Anderson 1990; Bolton and Stegenga 2002), a phenomenon known as *meso-scale* diversity (Hooper and Kennedy 2002; Anderson et al. 2009). This is caused by the presence of a high number of range-restricted endemic species that are found only along a very short section of the coast (and possibly offshore) in this area (Awad et al. 2002; Anderson et al. 2009). Among the areas within this transition zone, the Agulhas inshore ecozone has been singled out as having the greatest number of range-restricted endemics and highest diversity (Awad et al. 2002; Bolton and Stegenga 2002; Turpie et al. 2000). In particular sponges, octocorals, ascidians, anemones (Awad et al. 2002; Samaai 2005; Acuña and Griffiths 2004) and coastal fishes (Sparidae spp.) (Turpie et al. 2000) exhibit a high degree of endemism with numerous species restricted to the Agulhas ecoregion. Furthermore, many other species have the centre of their distributions within the region, such as coralline algae, bivalves and bryozoans.

In general, South Africa's waters are deemed to be rich in biodiversity, with ecosystem types ranging from tropical coral reefs to cool-water kelp forests, and some 13,000 species of free-living marine animals have been recorded/described so far (Griffiths et al. 2010). Importantly, approximately 30% of the known species are considered to be endemic (Griffiths et al. 2010). The high species diversity may largely be attributed to the habitat diversity of the region, which incorporates cool temperate, warm temperate and subtropical biogeographic provinces (Sink et al. 2012a; Awad et al. 2002; Bolton and Stegenga 2002; Turpie et al. 2000; Samaai 2005). Endemism is particularly high in the Agulhas ecoregion across a number of marine taxa such as isopods (84%) (Awad et al. 2002), marine mites (50%) (Proches and Marshall 2002), amphipods (40%), bivalves (45%) and sea anemones (49%) (Acuña and Griffiths 2004), with lower levels for ascidians (5%) and echinoderms (19%). The high levels of endemism are often attributed to the geographical isolation of this bioregion on the tip of the African continent (Samaai 2005). The Benguela (Namaqua and Southern Benguela ecoregions) and Agulhas (Agulhas ecoregion) current systems are important causal agents for connectivity (see Gibbons et al. 1995). Decreasing endemism from the apex of the African continent alongshore in both easterly and westerly direction may also be attributed to several factors. For the west coast, the relatively recent age of the Benguela Current (Bolton and Anderson 1997; Gibbons et al. 1995), its physical interactions with other water masses (Shannon 1985) and the instability of the physical environment may all reduce endemism. The low proportion of endemic species on the east coast might also be attributed to recruitment of widespread Western Indian Ocean and Indo-Pacific species into this region. The Agulhas Bank is also the centre of abundance for a number of South African warm temperate reef fish and benthic invertebrate species (Awad et al. 2002; Turpie et al. 2000). While notable efforts have been (and continue to be) made to document the region's taxonomic richness, many taxonomic groups remain poorly described, and some (e.g. Tardigrada, Kinorhyncha, Sipuncula) have not been studied for over 50 years (Gibbons et al. 1999; Griffiths et al. 2010).

South African marine systems have been severely impacted and degraded due to development, mining, pollution and fishing, causing the depletion of key species and the disturbance of ecosystems, yet our understanding of offshore sessile benthic invertebrate biodiversity on the continental shelf around South Africa is still in its infancy. This limits our ability to prioritize sensitive areas for conservation, to utilize resources for economic potential (biodiscovery) and to fulfil the demands of international agreements in terms of protection of representative marine biodiversity.

Although not the result of a dedicated research focus towards animal forests in South Africa, there have been a number of initiatives over recent years to locate and record subaquatic features that constitute ecologically and biologically sensitive areas, many of which potentially constitute marine animal forests. Research scuba diving, submersible and remotely operated vehicles (ROV) surveys, ROV and diving footage from mining companies, geological surveys and scientific research expeditions deploying tow cameras and benthic sleds, supplemented by specimen collections in museums, have helped to identify and locate potential marine animal forest sites throughout South Africa's oceans. Several marine animal forests dominated by different taxa were confirmed, revealing a startling diversity among different types of organization. We will review the diversity and ecology of these animal groups in South African waters.

3 Marine Animal Forest Ecosystems: Marine Benthic Eco-engineers in South Africa

South Africa has several marine animal forest ecosystems (MAFEs) within its territorial sea and EEZ. Sponges, cnidarians (stony corals, black corals, stylasterine lace corals, octocorals and sea anemones), bryozoans and ascidians are the main structuring species in marine animal forests in shallow- and deep-water ecosystems in South Africa. Museum records, ROV footage, submersible footage, geological surveys and scientific research expeditions have helped to identify some of these potential MAFEs, drawing from previous research to identify Vulnerable Marine Ecosystems in South Africa (Sink and Samaai 2009) and from new deep-water surveys and taxonomic studies on key invertebrate groups. We review the diversity and ecology of these animal groups in South African waters.

3.1 Sponge Grounds

Sponges are sessile aquatic organisms that are distributed in almost all aquatic environments and are important components of benthic communities (Hooper and Van Soest 2002; Van Soest et al. 2012). They fulfil many roles in these habitats, providing substrate for colonization, shelter and food for several groups of organisms, which contribute significantly to biodiversity maintenance. Due to their sessile and active filter feeding nature, sponges are also good ecological indicators and have been touted as useful pollution biomonitors. Furthermore, because they produce a range of bioactive compounds with considerable pharmacological importance, they possess a high economical potential (Joseph and Sujatha 2011).

Table 1 Literature on South African sponges (recreated from Samaai et al. 2019)

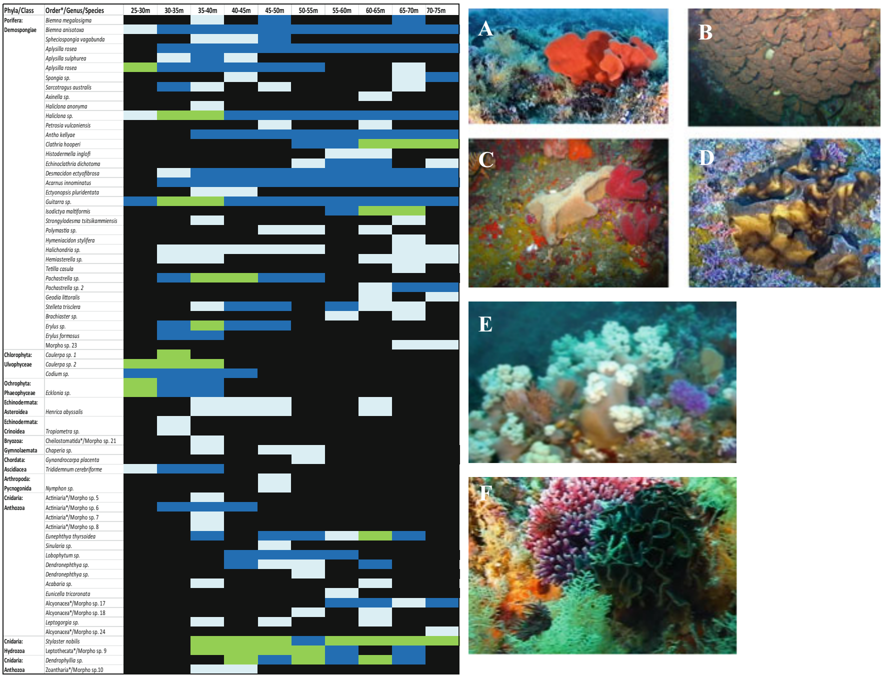
Region	Sponge literature
South Africa	Ehlers (1870), Carter (1871), Gray (1873), Vosmaer (1880), Kirkpatrick (1900, 1901, 1902a, 1902b, 1903, 1904, 1908, 1913), Sollas (1908), Stephens (1915), Burton (1926, 1929, 1931, 1933a, 1933b, 1936, 1958), Lévi (1963, 1967), Borojevic (1967), Day (1981), Schleyer (1991), Pettit et al. (1993), Rudi et al. (1993, 1994a, 1994b, 1995), Barkai et al. (1996), Hooper et al. (1996a, b), SaMcPhail et al. (1998), Samaai et al. (2003), Samaai (2004a, b), Samaai and Gibbons (2005), Samaai et al. (2006a, 2000b), Sink et al. (2006), Tronchin et al. (2006), Samaai et al. (2009), Branch et al. (2010), Samaai et al. (2017), Samaai et al. (2019), Samaai et al. (2018) (Sponge guide)

Sponges are considered to be among the earliest and most basic metazoans. The phylum Porifera has four classes, namely, the Calcarea, Demospongiae, Hexactinellida and Homoscleromorpha. Globally, there are around 9360 extant sponge species, with the vast majority (83%) belonging to the class Demospongiae. South Africa has recorded 374 sponge species (Samaai pers. comm.; Table 1) comprising around 4% of sponge diversity worldwide (Van Soest et al. 2019). The biogeographical pattern shows distinct peaks of sponge species richness on the south coast with richness declining towards the cool temperate west coast and the sub-tropical east coasts (Samaai 2005). The ecoregion with the highest number of reported marine sponges species is Agulhas (203 species), followed by Southern Benguela (194 species), Natal (178) and Delagoa (45 species).

The Agulhas ecoregion also has the highest number of apparent endemics (approximately 71 species), with an average of 57% of apparent endemic species recorded for South Africa (Samaai 2005). The hard reefs on the Agulhas Bank (e.g. Alphard Bank) is characterized by a dense population of the kelp *Ecklonia radiata* to a depth of 35 m (Makwela et al. 2016). The deeper zones are however dominated by diverse and abundant sponge assemblages. The coastal regions of the Agulhas ecoregion (i.e. the south and southeast coasts of South Africa) are recognized as global hotspots for latrunculid sponges (Samaai 2002; Samaai and Kelly 2002; Matcher et al. 2017; Van Soest et al. 2019). The area with the highest number of species recorded for South Africa is the Agulhas inner shelf (13 species), and the lowest number of species recorded from the outer shelf, shelf edge, bathyal and abyssal plains within the EEZ.

The highest abundance of sponges was found at the 40–50 m depth range, while in the 60–80 m depth range the presence of large sponges such *Spheciospongia vagabunda*, *Desmacidon ectyofibrosa* and *Echinoclathria dichotoma* progressively increases (Fig. 3). Vlak Bank, a south coast inshore reef, is dominated by massive growth forms of wall sponges (*Spirastrella* sp., *Desmacidon ectyofibrosa* and *Cliona* sp.), seafan (*Eunicella* spp.) and red algae between 20 and 30 m depth. Martha's Reef is sponge-dominated but the sponges were mostly small, erect or spherical and included some encrusting forms (Makwela et al. 2016).

During 100 ROV surveys off the Amathole region, East London (Agulhas ecoregion), where the first coelacanth was caught, still images and video footage



Phyla/Class	Order*/Genus/Species	25-30m	30-35m	35-40m	40-45m	45-50m	50-55m	55-60m	60-65m	65-70m	70-75m
Porifera: Demospongiae	*Biemna megalosigma*	⬛	⬛	⬜	⬛	🟦	⬛	⬛	⬛	🟦	⬛
	Biemna anisotoxa	⬜	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Spheciospongia vagabunda	⬛	⬛	⬜	⬜	🟦	⬛	⬛	⬛	⬛	⬛
	Aplysilla rosea	⬛	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Aplysilla sulphurea	⬛	⬜	🟦	⬜	⬛	⬛	⬛	⬛	⬛	⬛
	Aplysilla rosea	🟩	🟦	🟦	🟦	🟦	🟦	⬛	⬛	⬜	⬛
	Spongia sp.	⬛	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬜	🟦
	Sarcotragus australis	⬛	🟦	⬜	⬛	⬜	⬛	⬛	⬛	⬜	⬛
	Axinella sp.	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬛
	Haliclona anonyma	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Haliclona sp.	⬜	🟩	🟩	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Petrosia vulcaniensis	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬜	⬛	⬛
	Antho kellyae	⬛	⬛	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Clathria hooperi	⬛	⬛	⬛	⬛	⬛	🟦	🟦	🟩	🟩	🟩
	Histodermella inglofi	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬜	⬛	⬛
	Echinoclathria dichotoma	⬛	⬛	⬛	⬛	⬛	⬜	🟦	🟦	⬛	⬜
	Desmacidon ectyofibrosa	⬛	⬜	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Acarnus innominatus	⬛	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Ectyonopsis pluridentata	⬛	⬛	⬜	⬜	⬛	⬛	⬛	⬛	⬛	⬛
	Guitarra sp.	🟦	🟩	🟩	🟦	🟦	🟦	🟦	🟦	🟦	🟦
	Isodictya maltiformis	⬛	⬛	⬛	⬛	⬛	⬛	🟦	🟩	🟩	⬛
	Strongylodesma tsitsikammiensis	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬜	⬛
	Polymastia sp.	⬛	⬛	⬛	⬛	⬜	⬜	⬛	⬜	⬛	⬛
	Hymeniacidon stylifera	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛
	Halichondria sp.	⬛	⬜	⬜	⬜	⬜	⬜	⬛	⬛	⬜	⬜
	Hemiasterella sp.	⬛	⬜	⬜	⬛	⬛	⬛	⬛	⬜	⬜	⬜
	Tetilla casula	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛
	Pachastrella sp.	⬛	🟦	🟩	🟩	🟦	🟦	⬛	⬛	⬛	⬛
	Pachastrella sp. 2	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	🟦	🟦
	Geodia littoralis	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬜
	Stelleta trisclera	⬛	⬛	⬜	🟦	🟦	⬛	🟦	⬜	⬜	⬛
	Brachiaster sp.	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬜	⬛
	Erylus sp.	⬛	🟦	🟩	🟦	🟦	⬛	⬛	⬛	⬛	⬛
	Erylus formosus	⬛	🟦	🟦	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Morpho sp. 23	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬜
Chlorophyta: Ulvophyceae	*Caulerpa sp. 1*	⬛	🟩	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Caulerpa sp. 2	🟩	🟩	🟩	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Codium sp.	🟦	🟦	🟦	🟦	⬛	⬛	⬛	⬛	⬛	⬛
Ochrophyta: Phaeophyceae	*Ecklonia sp.*	🟩	🟦	🟦	⬛	⬛	⬛	⬛	⬛	⬛	⬛
Echinodermata: Asteroidea	*Henrica abyssalis*	⬛	⬛	⬜	⬜	⬜	⬛	⬛	⬜	⬛	⬛
Echinodermata: Crinoidea	*Tropiometra sp.*	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛
Bryozoa: Gymnolaemata	Cheilostomatida*/Morpho sp. 21	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Chaperia sp.	⬛	⬛	⬜	⬛	⬜	⬜	⬛	⬛	⬛	⬛
Chordata: Ascidiacea	*Gynandrocarpa placenta*	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬛	⬛
	Trididemnum cerebriforme	⬜	🟦	🟦	⬛	⬛	⬛	⬛	⬛	⬛	⬛
Arthropoda: Pycnogonida	*Nymphon sp.*	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛
Cnidaria: Anthozoa	Actiniaria*/Morpho sp. 5	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Actiniaria*/Morpho sp. 6	⬛	🟦	🟦	🟦	⬛	⬛	⬛	⬛	⬛	⬛
	Actiniaria*/Morpho sp. 7	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Actiniaria*/Morpho sp. 8	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛	⬛	⬛
	Eunephthya thyrsoidea	⬛	⬛	🟦	⬛	🟦	🟦	⬜	🟩	🟦	⬛
	Sinularia sp.	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬛
	Lobophytum sp.	⬛	⬛	⬛	🟦	🟦	🟦	🟦	⬛	⬛	⬛
	Dendronephthya sp.	⬛	⬛	⬛	🟦	⬜	⬜	⬛	🟦	⬛	⬛
	Dendronephthya sp.	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬛	⬛
	Acabaria sp.	⬛	⬛	⬜	⬛	⬛	⬛	⬛	⬜	⬛	⬛
	Eunicella tricoronata	⬛	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬛	⬛
	Alcyonacea*/Morpho sp. 17	⬛	⬛	⬛	⬛	⬛	⬛	🟦	🟦	⬜	🟦
	Alcyonacea*/Morpho sp. 18	⬛	⬛	⬛	⬛	⬛	⬜	⬛	⬜	⬛	⬛
	Leptogorgia sp.	⬛	⬛	⬜	⬛	⬜	⬛	⬛	⬜	⬛	⬛
	Alcyonacea*/Morpho sp. 24	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬛	⬜
Cnidaria: Hydrozoa	*Stylaster nobilis*	⬛	⬛	🟩	🟩	🟩	🟦	🟩	🟩	🟩	🟩
	Leptothecata*/Morpho sp. 9	⬛	⬛	🟩	🟩	🟩	🟩	🟦	⬛	🟦	⬛
Cnidaria: Anthozoa	*Dendrophyllia sp.*	⬛	⬛	⬛	🟩	🟦	🟩	🟦	🟩	🟦	⬛
	Zoantharia*/Morpho sp.10	⬛	⬛	⬜	⬜	⬛	⬛	⬛	⬛	⬛	⬛

Fig. 3 Table indicating invertebrate and algal species occurring between 25 and 75 m depth on Alphard Bank. Common invertebrates found at varying depths, (**a**–**d**) sponges, (**e**) sea anemones, (**f**) bryozoan and noble coral (unpublished data). The figure was created ex-novo, using data and images belonging to the author Dr. Toufiek Samaai and Dr. Sven Kerwath collected during DEFF benthic surveys. Colour coding depicts the following: light blue = rare; blue = common; green = abundant; black = absent.

were taken of the shelf between 30 and 300 m (Fig. 4a). Large sponges dominated the shallow reef habitats (30–40 m) and included prolific sponges in the genera *Cliona* (large bowl shape), *Isodictya* (fan sponges) and *Suberites* and a number of new *Tsitsikamma* sponges (Figs. 4b and 5a–c). The shallow reefs were also colonized by hydroids, scrolled bryozoans, seafans and seawhips (*Homophyton verrucosum*, *Leptogorgia* spp. and other octocorals) (Fig. 4c). The deeper rocky areas were colonized by dense sponge communities and populations of seafans, soft corals and non-reef-building scleractinian corals (Fig. 11g). Some soft-sediment areas were characterized by sea pens (Fig. 4d). Bryozoa, ascidians and crustaceans were also common. The rocky shelf areas in KwaZulu-Natal and the Eastern Cape can be considered as sponge (and other invertebrate) hotspots. Dense filter feeding communities on the shelf edge suggest that the topography and associated oceanographic processes may concentrate food to support filter and plankton feeding biota.

During submersible surveys of the shelf edge and submarine canyons (Fig. 6c) in Sodwana Bay and Trafalgar on the east coast of South Africa, beds of glass sponges

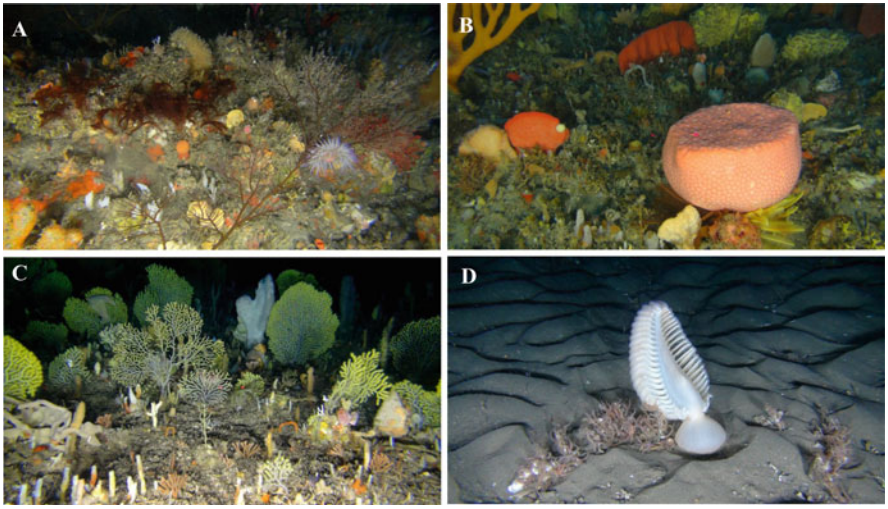


Fig. 4 (**a**) Amathole deep reef invertebrate community (Agulhas ecoregion); (**b**) sponges; (**c** and **d**) seafans and sea pen. The figure was created ex-novo, using images from the Imida project, African Coelacanth Ecosystem Programme (ACEP; Grant Number 97969). The PI of the project is Dr. Sven Kerwath

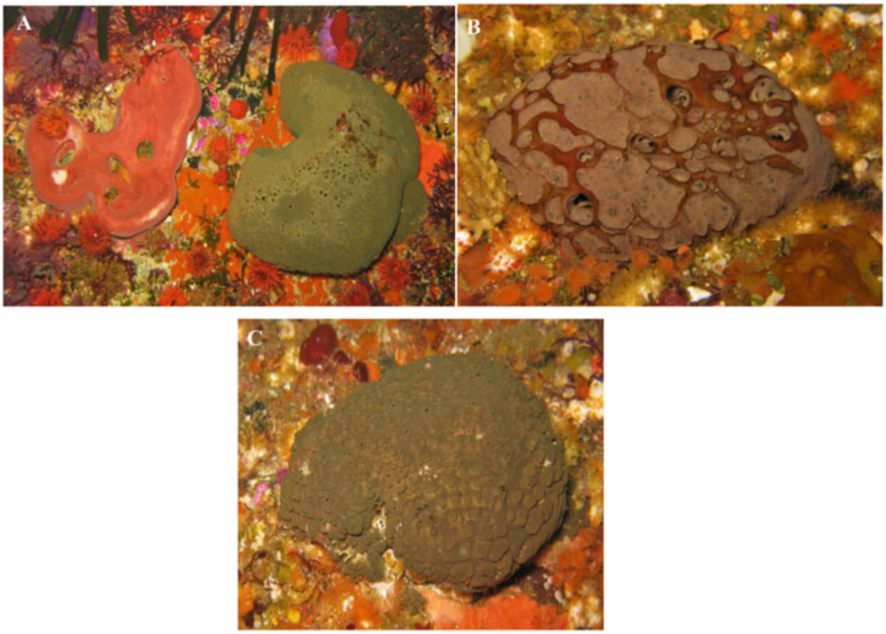


Fig. 5 Diversity of Latrunculiidae sponges. (**a**) *Latrunculia lunaviridis*; (**b**) *Latrunculia gotzi*; (**c**) *Tsitsikamma favus*. The figure was created ex-novo, using images belonging to the Coral Reef Research Foundation (CRRF), Dr. Toufiek Samaai and Dr. Ali Gotz, respectively. Permission was granted by Dr. Gotz (SAEON) and Lori Jane Bell Colin (CRRF)

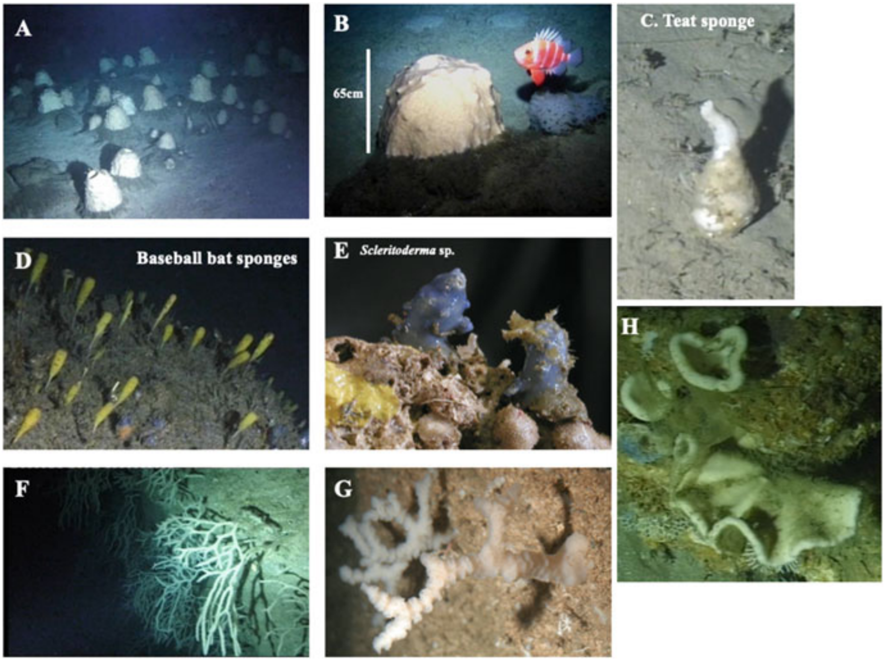


Fig. 6 Sponge communities in the iSimangaliso Wetland Park in northern KwaZulu-Natal. (**a**) Dense aggregations of *Pheronema* on the shelf edge at 130 m between Jesser and Wright canyon. This species stands as much as 60 cm off the substrate (**b**) and is used for shelter by many species including this bigeye *Pristigenys* species. On the upper and lower canyon slopes *Hyrtios* sp. (**c**), *Echinostylinos* sp. (**d**), the Lithistida *Scleritoderma* sp. (**e**), *Sclerothamnus* sp. (**f**, **g**) and *Pachastrella* sp. form dense aggregations. *Sclerothamnus* sp. nov. is extremely fragile. The figure was created ex-novo, using images in the collection of Dr. Kerry Sink, courtesy of the Jago submersible team during the African Coelacanth Ecosystem Program expeditions 2002–2004. Permission was granted by the ACEP manager, Dr. Angus Patterson, to use the images

Pheronema sp. were observed (Fig. 6a, b). These abundant sponges formed a distinct habitat at depths between 130 and 160 m (Fig. 6a, b) where they grow up to 65 cm high and 50 cm in diameter. The dense cover of *Pheronema* sponges (up to 17 individuals/m) of different sizes provides spatial complexity that benefits associated fauna. Many juvenile fishes have been seen in the complex structures provided by the sponges, suggesting a possible nursery function for the sponge beds. Apart from these *Pheronema* grounds, a common feature on the canyon walls and cliffs in the 160–300 m depth range with a peak between 180 and 210 m was the presence of very fragile dichotomously branching *Sclerothamnus* sp., a glass sponge that extends up to 80 cm in length (Fig. 6f, g). A lithistid sponge (rock sponge) was relatively abundant on the deeper rocky outcrops in the upper slopes of the canyon (Fig. 6e). Deeper than 140 m the sponge fauna becomes gradually more diverse. On the rocky outcrops of the sandy plain region, a yellow club-shaped species of *Echinostylinos* sp. was very common (Fig. 6d). At about 140 m, the most common taxa were species of *Hemiasterella* and *Halichondria* (Samaai et al. 2010). Other species recorded from the submarine canyon (Wright Canyon) were *Pachastrella monilifera* (Fig. 6h), *Hemiasterella vasiformis*, *Hymeniacidon caliculatum*, *Topsentia pachastrelloides*, *Psammocinia* cf. *arenosa*, *Poecillastra compressa*, *Clathria (Clathria) lissocladus*, *Isodictya frondosa*, *Myxilla (Ectyomyxilla) kerguelensis* and *Coscinoderma* cf. *nardorus*. The genus *Clathropella* was recorded for the first time in South Africa (Sink et al. 2006).

The distribution of species on the west coast reflects a different pattern. In the 100–500 m depth range of the Benguela region off west coast South Africa and Namibia, a massive lobe-shaped demosponge *Suberites dandelenae* is common in unconsolidated seabed habitats, constituting true, usually mutually exclusive facies (Samaai et al. 2017; Uriz 1988) (Fig. 7a–d). During various trawl surveys on the west coast (with the research vessels Dr. Fridtjof Nansen and RV Africana), more than 6 tons/km^2 of sponge material were obtained during several hauls within depths ranging 120–275 m. The greatest mass of sponges collected was 18 tons/km^2, from a depth of 138 m offshore of Doring Bay (2006–Cruise 402, Station 1250). The three localities offshore of Port Nolloth produced 3–3.5 tons/km^2 of sponges collected on average, while 6 tons/km^2 of sponges were obtained from one site at a depth of 195 m in the proposed Namaqualand MPA (Nansen Cruise 402, Station 1196, 2006) (Samaai et al. 2017) (Fig. 7b).

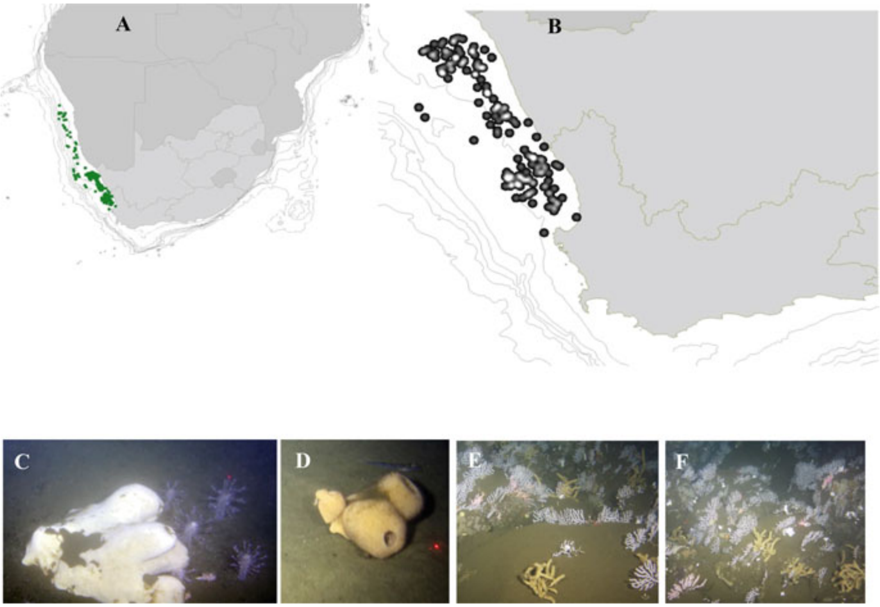


Fig. 7 (**a**) Geographical distribution of *Suberites dandelenae* along the west coast of South Africa; (**b**) Heatmap indicating high abundance; (**c**, **d**) in situ photo of *Suberites dandelenae*; (**e**, **f**) in situ photo of *Fibula ramosa* and stylasterids. The figure was created ex-novo. Underwater images taken and provided by Ms Zoleka Filander, Oceans and Coasts Research, DEFF

Though not a reef builder, *S. dandelenae* can be habitat forming (Fig. 7c, d). The sponge grounds constitute an ecologically important habitat of great complexity for fishes and both motile and sessile invertebrates, and they may play an important role in the ecology and diversity of the west coast region. Indeed, their presence could indicate a potential Vulnerable Marine Ecosystem (VME) or an Ecologically and Biologically Significant Area (EBSA) in the sense of their fragility and slow recovery (Samaai et al. 2017). It remains unclear what the particular conditions are that have favoured the impressive aggregation of *S. dandelenae* in the 100–200 m depth range. As a well-developed organic body characterizes this sponge by having a massive silica skeleton, it would be expected to require large amounts of dissolved silicon for growth and build its skeletal framework. However, average silicate concentrations where the sponges are found were low, even in areas where the sponge occurs in far lower abundance. The data suggests that dissolved silicon availability in the southern Benguela may not be wholly accountable for the occurrence of *S. dandelenae*.

Other abundant sponge species on the west coast are *Rossella antarctica*, *Hamacantha* (*Vomerula*) *esperioides* and *Fibulia ramosa* (Figs. 7e, f and 8a–g) (Samaai et al. 2017; Uriz 1988). These sponges are also non-reef builders but are habitat forming and likely occur in reef and soft-sediment environments. Their

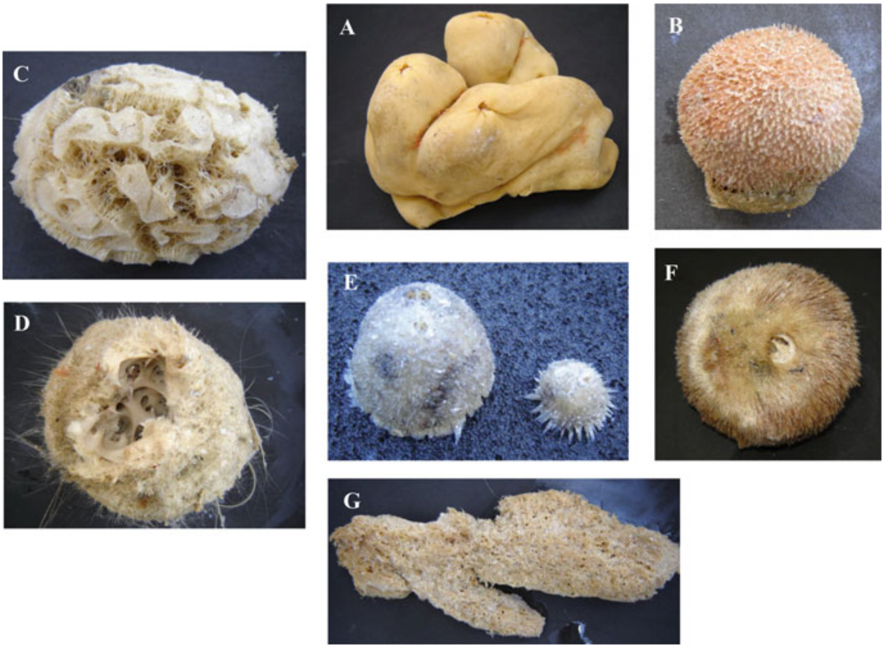


Fig. 8 Samples of sponges collected during trawl surveys on the west and south coasts. (**a**) *Suberites dandelenae*; (**b**) *Tethya* sp.; (**c**) *Mycale (Mycale) anisochela*; (**d**) *Rossella antarctica*; (**e**) *Tetilla casula*; (**f**) *Tetilla capilosa*; (**g**) *Isodictya* sp. The figure was created ex-novo. Images provided by Dr. Lara Atkinson, SAEON

populations constitute ecologically important deep-water habitats of great complexity for fish and both motile and sessile invertebrates and play an important role in the ecology and diversity of the deep sea. *Rossella antarctica* is more abundant at deeper depths and in soft substrates and is more common on the west than south coast, where it occurs on the shelf edge (Samaai et al. 2017).

Also, on the west coast, submersible footage from Cape Canyon off Cape Columbine shows a high diversity and abundance of sponges, many of which are also habitat forming but these are unlike the homogenous nature of the *Pheronema* beds occurring on the shelf edge of the east coast. Most abundant sponge species occurring in the Cape Canyon are *Hamacantha (Vomerula) esperioides*, *Mycale (Mycale) anisochela* and *Tethya* sp. (ball sponges).

Currently, only eight species of hexactinellid sponges are described from the Atlantic and Southern Indian oceans of South Africa, none of which have reef-building characteristics.

The potentially high importance of sponges to benthic ecosystems, as well as the potential for high impacts of bottom trawling on sponge grounds, indicates that maintaining healthy sponge assemblages should be an important priority for marine conservation planners. Successful management will need to be underpinned by additional research that better identifies the ecological roles of sponges and their distributions over local and broad environmental scales**.** The patterns of sponge diversity observed are therefore applied to support the future management and monitoring of marine benthic biodiversity in South Africa, particularly noting the importance of spatial scale in biodiversity assessments and associated management strategies.

3.2 Shallow-Water Subtropical Coral Communities

Tropical coral reefs are considered the “rainforest of the sea” and are among the marine ecosystems with the highest biodiversity. East Africa has a rich tropical coral fauna that extends to the high-latitude reefs along the South African east coast (Fig. 9). Here at the southern-most extent of coral communities within the Western Indian Ocean (WIO), they form a veneer on limited, Late Pleistocene reefs, rather than forming the hermatypic aragonite reef complexes found in the Great Barrier Reef (Schleyer 1999; Porter and Schleyer 2017). The coral communities consist largely of widely distributed Indo-Pacific species but include a few endemic species and are dominated by soft corals (Schleyer and Celliers 2003a, b; Porter and Schleyer 2017). The coral communities within Sodwana Bay form the central complex (Fig. 9) of the Northern KwaZulu-Natal reefs, with a northern complex that adjoins Kosi Bay and a southern complex that consists of Red Sands reef and Leadsman Shoal (Schleyer and Celliers 2003a, b, 2005). Substantial water movement occurs on the reefs, with the coast occasionally swept by an inshore meander of the southward flowing Agulhas Current (Lutjeharms 2006). The coral communities

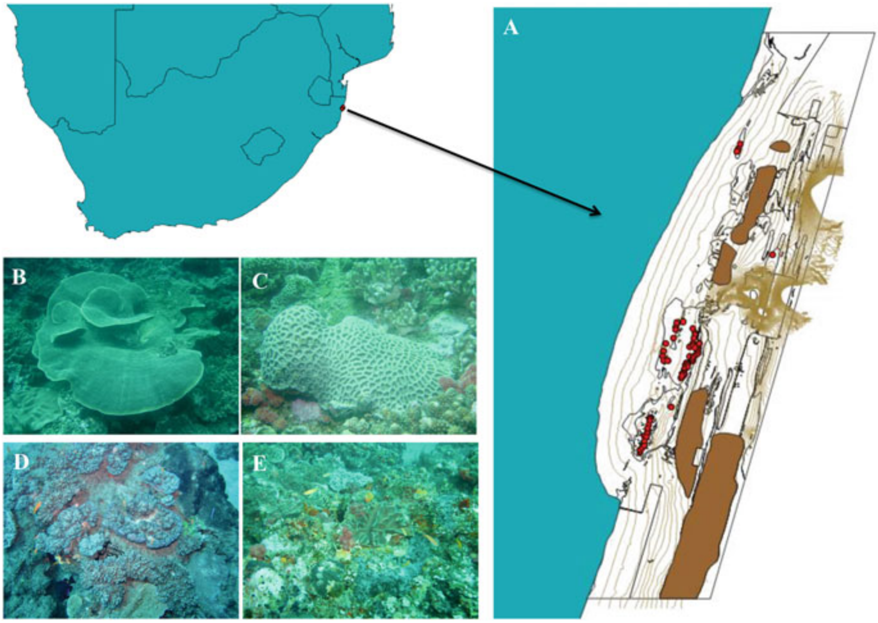


Fig. 9 (**a**) Sodwana Bay coral reef complex; (**b**–**e**) Corals from Sodwana Bay. The figure was created ex-novo

are protected within the iSimangaliso Wetland Park, a world heritage site in the Delagoa ecoregion South Africa.

Schleyer (1999) and Schleyer and Celliers (2005) provide species lists of the corals found in Northern KwaZulu-Natal region. The checklist also provides an indication of the high biodiversity on the coral habitats. The high-latitude coral communities of South Africa are well known for their extraordinary beauty and richness and are recognized as a centre of endemism that represents a high priority for conservation (Roberts et al. 2002).

3.3 Cold-Water Coral Reefs and Coral Communities

Cold-water coral reefs, like their tropical warm- and shallow-water counterparts, are built predominately by stony corals (Scleractinia) (Fig. 10a–g). A comparison between warm- and cold-water coral reefs is presented in Table 2. Reef-building and habitat-forming corals in cold waters are derived from several systematic groups belonging to the phylum Cnidaria. Deep-water cnidarians have been less studied than their shallow-water counterparts and are the focus of current research in South Africa.

Stony corals that occur in cold and usually deep waters with no or very little light are non-symbiotic. They lack the symbiotic light-dependent algae that are

Fig. 10 South African specimens of reef-building cold-water corals photographed from the invertebrate collection in the South African Museum (**a**–**d**) or from collections made in the southern Cape (**e**, **f**). (**a** and **b**) *Solenosmilia* cf. *variabilis*. Specimen A was sampled from 904 m on the eastern edge of the Agulhas Bank. A trawl sample with extensive framework reef-building coral is shown in E. This photo was taken during a demersal research survey from an approximate depth of 907 m (Photo courtesy of Dave Japp). Images (**a**–**e**) from Sink and Samaai (2009). (**f** and **g**) Reef with dense azooxanthellate corals found in the deep shelf edge off the south (**f**) and southeast (**g**) coasts (credit ACEP Deep Secrets and Imida projects, respectively). The figure was created ex-novo, using images in the collection of Dr. Kerry Sink, and images from the ACEP Imida & ACEP Deep Secrets (Grant Number 97971) projects Permission was granted by Dr. Kerry Sink and Dr. Sven Kerwath, the PIs of the two projects

characteristic of warm-water corals. At present about 1334 stony coral species are described of which the majority, 672 species, belong to the non-symbiotic group (Cairns 2001). Only 26% of non-symbiotic corals exist in water depths shallower than 40 m, while the majority thrive in deeper waters down to abyssal depths, with the deepest reported at 6328 m depth (Freiwald et al. 2004).

The most significant reef-building and habitat-forming Cnidaria are the colonial stony corals (Scleractinia), true soft corals (Octocorallia), black corals (Antipatharia) and calcifying stylasterine 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 (see Table 2). These cold-water coral structures act like islands in the normally flat, featureless unconsolidated sediment surroundings and harbour a distinct and rich community by providing niches and nursery grounds for a variety of species, including commercial fish species (Freiwald et al. 2004).

Table 2 Comparison between cold-water and warm-water coral reefs (taken from Freiwald et al. 2004)

	Cold-water coral reefs—deep-water	Warm-water coral reefs—shallow-water
Distribution	Global—potentially in all seas—and at all global, in subtropical and tropical	Global—in subtropical and tropical seas between 30°N and 30°S
Depth	Deep water	Shallow reefs
Temperature range	Temperature range 4°–13 °C 20°–29 °C	Temperature range 4°–13 °C 20°–29 °C
Depth range	39–3383 m	0–100 m
Symbiotic algae	No	Yes
Nutrition	Uncertain, but probably suspended organic matter and zooplankton	Suspended organic matter and photosynthesis
Reef composition	Mostly composed of one or a few species	Mostly composed of numerous species
Age of living reefs	Up to 8500 years	Up to 9000 years

Cold-water corals are slow growing, recognized as vulnerable and extremely fragile (FAO 2008; Lartaud et al. 2017), playing an important role as structural elements that enhance habitat complexity and heterogeneity (FAO 2008; Buhl-Mortensen et al. 2010) and should be protected from damage by bottom trawling fishing or deep-sea mining in key areas (Freiwald et al. 2004).

Museum records indicate that there are at least three species of reef-building cold-water coral known from South Africa (Fig. 10a–d; Tables 3 and 4). Within the collections at Iziko Museums, the first colony of *Solenosmilia* was collected in 1901 in 549 m off the Buffalo River; however this record could not be precisely mapped (Sink and Samaai 2009) (Table 4). More recent collections were made during deep demersal research cruises off the western and eastern Agulhas Bank (Sink 2016, Deep Secrets cruise report). Uriz (1988) reported the presence of semifossil coral on the west coast from Spanish cruises noting—“The bottom is relatively uniform, mud or sand mixed with mud with scattered rocky bars frequently colonized by banks of semifossil coral”. Zibrowius and Gili (1990), working on samples from the same cruises, also reported cold-water corals from the north-west coast of South Africa in the 145–1412 m depth range (Valdivia cruises Benguela V and VI, 6 stations) although many of these species are not considered to be reef-building. Cairns and Keller (1993) also reported on cold-water corals from South Africa but focussed on the Indian Ocean component. Submersible footage taken in 2001 in the proposed Ibhubesi gas development area off the west coast also documented a cold-water coral reef (undocumented footage reported by Sink and Samaai 2009). Footage quality was poor but the ROV pilot annotated the footage and showed sonar images indicating the presence of the reef. This suggested presence of a cold-water coral reef system in the 300–400 m depth range off Namaqualand warrants further investigation. Cold-water coral samples were also collected during a trawl impact

Table 3 Records of reef-building cold-water corals from South Africa based on specimens holdings of Iziko Museums as reported by Sink and Samaai (2009)

Species	Type locality	South African distribution	Depth range	No. of SA records	Worldwide distribution	Number of synonyms	Species status/ reference
Desmophyllum pertusum	Northern Hemisphere	Off Dassen Island—Dwesa (central Transkei)	500–520 m (depth available for only 1 record)	3	Semi-cosmopolitan?	18	Questionable in South Africa
Solenosmilia variabilis	Nova Scotia	Kleinsee—Leven Point (north of Cape Vidal, KwaZulu-Natal)	86–930 m	13	Semi-cosmopolitan?	1	Questionable in South Africa
Goniocorella dumosa	Indonesia	Kleinmonde—Leven Point (north of Cape Vidal, KwaZulu-Natal)	86–900 m	6	New Zealand, Indonesia and Korea	2	Questionable in South Africa

Table 4 Specimen occurrence records of reef-building cold-water corals based on the holdings of Iziko Museums

Species	Catalogue Number	Coordinates/ locality	Depth range (m)	Date collected	Station number	Determined by	Actual species status
Desmophyllum cf. *pertusum*	SAM H 1608	wnw Dassen Island	Unknown	25-Feb-65		?	Questionable—species to be determined
Desmophyllum cf. *pertusum*	SAM H 1606	w of Cape Town	Unknown	22-Sep-65		?	
Desmophyllum cf. *pertusum*	SAM H 3129	−32.25°S; 29.15167°E	500–520 m	25-Jun-79	sm234	?	
Goniocorella cf. *dumosa*	SAM H 3189	−30.72°S; 30.81333°E	780 m	11-May-77	sm131	Zibrowius	Questionable—species to be determined
Goniocorella cf. *dumosa*	SAM H 3185	−27.99167°S; 32.81333°E	550 m	22-May-76	sm85	Zibrowius	
Goniocorella cf. *dumosa*	SAM H 3188	−30.89°S; 30.52833°E	850 m		sm129	Zibrowius	
Goniocorella cf. *dumosa*	SAM H 3187	−31°S; 30.45333°E	900 m	12-May-77	sm134	Zibrowius	
Goniocorella cf. *dumosa*	SAM H 3816	−33.65667°S; 27.195°E	86 m	31-May-78	sm184	Zibrowius	
Goniocorella cf. *dumosa*	SAM H 3190	−33.32667°S; 27.87333°E	760 m	28-May-78	sm174	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3179	−33.65667°S; 27.195°E	86 m	31-May-78	sm184	Zibrowius	Questionable—species to be determined
Solenosmilia cf. *variabilis*	SAM H 4448	−47.02967°S; 37.95°E	680 m	Not recorded	?	Marion is—determined by Branch M.?	Questionable—species to be determined
Solenosmilia cf. *variabilis*	SAM H 3142	−33.1°S; 28.13833°E	Unknown		sm165	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3158	−32.91667°S; 28.51667°E	630 m	25-May-78	sm162	Zibrowius	

(continued)

Table 4 (continued)

Species	Catalogue Number	Coordinates/ locality	Depth range (m)	Date collected	Station number	Determined by	Actual species status
Solenosmilia cf. *variabilis*	SAM H 3140	−33.32667°S; 27.87333°E	760 m	28-May-78	sm174	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3037	−30.89°S; 30.52833°E	850 m	11-May-77	sm129	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3035	−30.81833°S; 30.595°E	830–930 m	11-May-77	sm128	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 1397	Buffalo N 15 miles bearing	567 m	24-Apr-01	PF12846	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3034	−31°S; 30.45333°E	900 m	12-May-77	sm134	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3141	−32.47667°S; 28.98°E	710–775 m	24-Jun-79	sm226	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3036	−30.72°S; 30.81333°E	780 m	11-May-77	sm131	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 2840	−27.99167°S; 32.68°E	550 m	22-May-76	sm85	Zibrowius	
Solenosmilia cf. *variabilis*	SAM H 3191	−34.705°S; 25.27833°E	904–907 m	05-May-93	A14846	Net chewer—live	

study on the west coast of South Africa. Two grab samples collected on soft bottom habitats had 1.7 and 1.2 kg of *Desmophyllum* cf. *pertusum* fragments (Atkinson 2010) (Fig. 10e; Tables 3 and 4). These fragments were recently dead and may have been transported to the site. These isolated records of cold-water corals dredged from the soft bottom habitat may suggest that coral habitats may be present on the west coast.

Three species of cold-water coral, *Desmophyllum* cf. *pertusum*, *Solenosmilia* cf. *variabilis* and *Goniochorella* cf. *dumosa*, were recorded off Buffalo River (500–520 m depth range) and north of Cape Vidal, KwaZulu-Natal (86–930 m depth range) (Tables 3 and 4) (see also Sink et al. 2018). The biology of *Goniochorella dumosa* is comparatively poorly understood. This coral is restricted to the southern hemisphere, mostly to New Zealand waters although it has been recorded from South African, Indonesian and Korean waters (Cairns and Kitahara 2012). The known bathymetric range is from 88 to 1488 m with a concentration around 300 and 400 m below sea level (Freiwald et al. 2004).

Furthermore, research trawl surveys by the Department of Agriculture, Fisheries and Forestry (DAFF) research trawl surveys encountered fragments of dead coral specimens of *D.* cf. *pertusum* on the west coast of South Africa from a depth range of 900–910 m (DAFF unpublished report). The first live cold-water corals were observed in situ in 2016, thus confirming the presence of corals in the region (Sink 2016, Deep Secrets cruise report). However, until further acoustic mapping, seabed images or several samples are acquired, we cannot be sure that the samples are not from isolated colonies or smaller thickets that are sometimes known to be associated with slope habitats. During a dedicated research project (2016–2018), historical cold-water coral sites on the west coast together with new deep-water sites on the southeast coast of South Africa were explored with a towed camera sled. During the Deep Secrets voyage, the first in situ photographic surveys of the coral habitats at Browns Bank on the west coast and between Port Elizabeth and Knysna were undertaken (Sink 2016). High live coral cover were observed at “Secret Reef”, at a depth of 330 m off Knysna.

Apart from this, the first in situ cold-water coral assemblages were observed with octocoral-dominated deep reefs, a steep cliff colonized by high cover of an unidentified Scleractinia of the Dendrophylliidae family at a depth between 70 and 103 m off East London (Amathole area), South Africa (Fig. 10g). However, samples collected at these sites did not comprise reef-building species.

Another framework-building invertebrate group that is known as the stylasterine corals (Fig. 11a–b) is frequently encountered in South African waters (Cairns and Zibrowius 2013; Sink et al. 2018; Atkinson and Sink 2018). These taxa are hydrozoans and are considered as one of the many cnidarian groups that constitute cold-water lace corals. Lace corals are calcified and have delicately branched skeletons and are often confused with stony corals. All lace corals living in cold and deep waters belong to the group of Stylasteridae with *Stylaster* being the better-known genus, but 20 species from 7 genera have been reported in South Africa (Cairns and Zibrowius 2013). One of the conspicuous components of the south coast is the shallow- and deep-water emergent stylasterid hydrocoral, *Stylaster nobilis* (noble

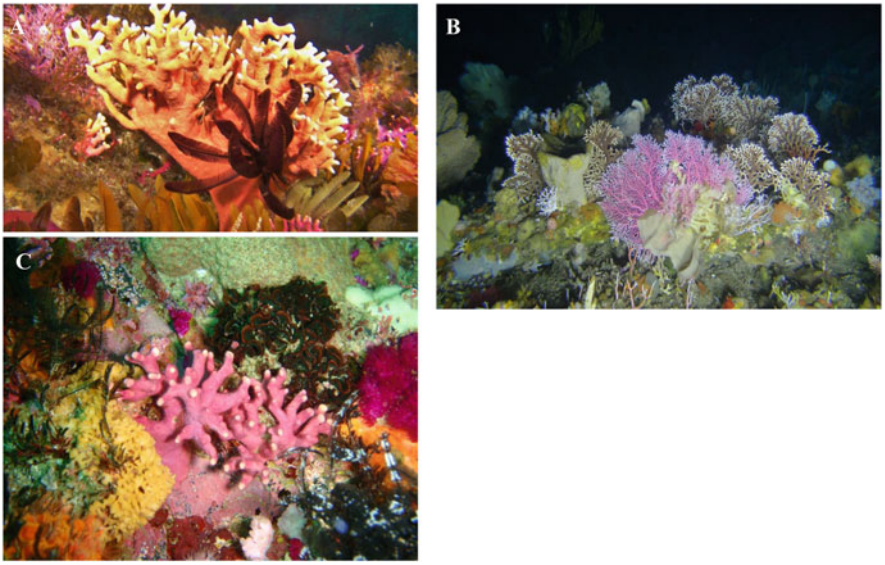


Fig. 11 *Stylaster nobilis*, the endemic milleporid hard coral from South Africa (**a**, **c**). Colonies of this size are reported to be over 100 years old. (**b**) shows other species in the *Stylaster* genus on the East London shelf edge (ACEP Imida Project). The figure was created ex-novo, using images from the Imida project, African Coelacanth Ecosystem Programme (ACEP; Grant Number 97969). The PI of the project is Dr. Sven Kerwath

coral), which is relatively common on shallow and deep reefs between the Cape Peninsula to Port Elizabeth in 5–200 m of water. This hydrocoral is endemic to South Africa, and it is reported to be very slow growing with colonies larger than 20 cm reported to be more than 100 years old (Branch et al. 2016). The structure of *S. nobilis* populations on the south coast is typical of modular marine invertebrates, with small colonies being the most abundant and larger colonies the least abundant. Considering the slow growth and the fragile nature of these corals, they are considered to be vulnerable and/or fragile species. These species are more prevalent in the Agulhas ecoregion, where dense colonies of lace corals are found offshore of Tsitsikamma, 12 mile reef, Alphard Bank and 45 mile reef on the Agulhas Bank. *Stylaster nobilis* has a delicate calcium carbonate skeleton and may be susceptible to ocean acidification and diver damage. Various sponge species are associated with the coral *Stylaster nobilis*, as well as various anemone species, bushy hydroids (*Eudendrium* sp.) and various bryozoan species.

Partial COI mtDNA gene sequences (650 bp) were identical for 17 specimens of pink-orange lace coral representing specimens with different colour morphs, growth forms and occurring either inshore (12 mile reef and Tsitsikamma) or offshore (Alphard Bank, 72 mile reef) on the Agulhas Bank. The high genetic similarity among sequences of *S. nobilis* and the fact that all haplotypes generated are novel indicate that all specimens sequenced belong to the same species, *S. nobilis* (Samaai unpublished data).

3.4 Octocoral Gardens

Octocorals include soft corals, gorgonians (seafans) and sea pens. Although South Africa has extensive octocoral collections and made important contributions to the taxonomy of this group (see publications by Gary Williams, South African Museum), there has been little research into octocoral communities. The known South African octocoral fauna constitutes approximately 204 species (Gibbons et al. 1999), of which 110 (54%) are endemic to South Africa (Gibbons et al. 1999). Submersible footage from the shelf edge and canyons in northern KwaZulu-Natal, off East London and from the Cape Canyon revealed diverse and dense assemblages of seafans and other octocorals (Figs. 4c, d, 12e, and 13). Deep reefs such as the Middle Bank reef in the Tsitsikamma National Park also support fragile seafans (Fig. 12b–d). In addition, in KwaZulu-Natal, Sink and Samaai (2009) reported dense

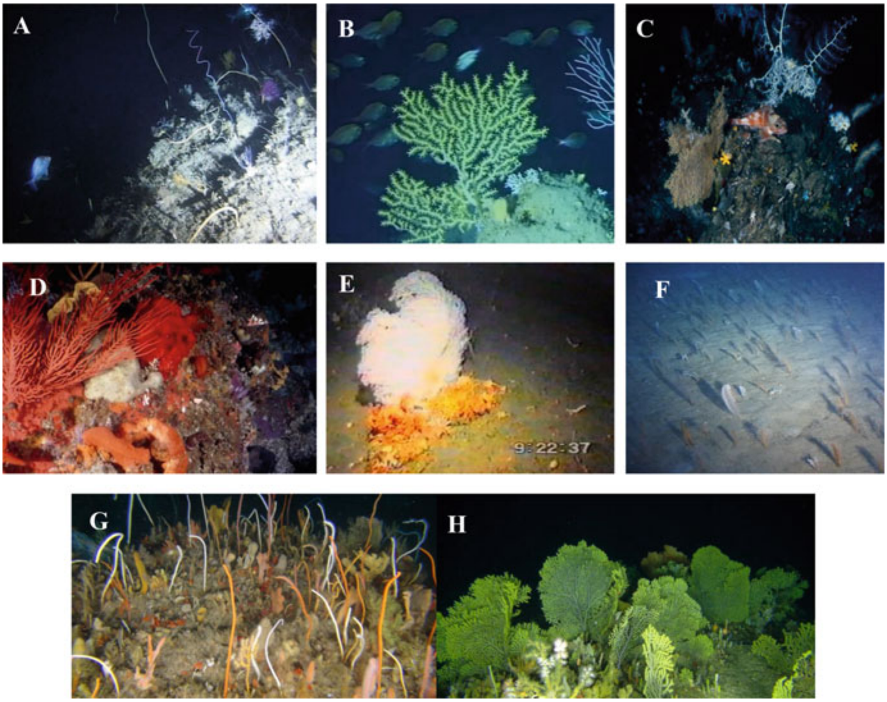


Fig. 12 Groves of seafans and octocorals from the iSimangaliso Wetland Park (**a**, **b**), the East London shelf edge (**c**), Middle Bank in the Tsitsikamma National Park (**d**) and Cape Canyon off Cape Columbine on the west coast (**e**). Sea pen aggregations were documented by submersible adjacent to the three largest submarine canyon heads off Cape Vidal and Sodwana Bay in KwaZulu-Natal (**f**). Images from Sink and Samaai (2009) courtesy of the Jago submersible team (**a**–**f**) and Diamond Fields International (**e**). More recently ROV surveys found high densities of seawhips (**g**) and seafans (**h**) in the Amathole Offshore MPA (Images from the ACEP Imida Project). The figure was created ex-novo, using images in the collection of Dr. Kerry Sink and Dr. Sven Kerwath

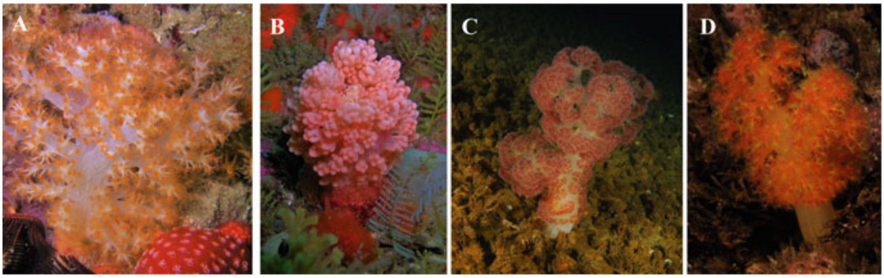


Fig. 13 The morphotypes of soft corals found in South Africa. The figure was created ex-novo. Permission to use images was granted by Peter Southwood

sea pen aggregations on the shelf adjacent to the three largest submarine canyon heads, Wright, Diepgat and Leven canyons (Fig. 12a). As octocoral communities have not been mapped, it is difficult to assess potential activities that may impact on this potential animal-dominated community. Ten taxa of octocorals are represented in the Wright Canyon collection (Sink et al. 2006).

The gorgonian *Nicella dichotoma* first described from Mauritius represents a new record for South Africa and a range extension for the species. *Homophyton verrucosum*, an endemic to southern Africa and is a common species in Northern KwaZulu-Natal, occurs in depths of up to 168 m, whereas the grey seafan, *Rumphella* sp., was previously recorded at depths of less than 25 m. Only one sea pen, *Pennatula murrayi*, was collected in Wright Canyon (Fig. 12f). Until now, only three species of antipatharian black coral have been recorded in South Africa, with three new taxa collected from Wright Canyon. In addition, other distinctive antipatharian species that are not represented in the marine invertebrate collection of the Iziko Museums but were documented in canyon footage (Sink et al. 2006).

Off the Amathole region, East London, at a depth of 23–40 m, the octocorals *Leptogorgia palma*, *H. verrucosum*, *Eunicella tricoronata*, flame octocorals and *Alcyonium* spp. are common in reef habitat. In the deeper reefs, seawhips *Helicogorgia* spp., unidentified seafans and other soft corals, and sponges dominate (Fig. 12g, h).

Awad et al. (2002) examined the distributions of 54 shallow-water octocoral species. They found that shallow-water octocoral species were concentrated along the south coast, which may be the centre of radiation for this group. The highest species richness was recorded at Port Elizabeth (25 species), and the lowest species richness occurred at Kosi Bay (1 species).

3.5 Sea Anemones

The term sea anemones are the common name for cnidarians belonging to the orders Actiniaria and Corallimorpharia. Actiniaria (sea anemones) are a small, yet

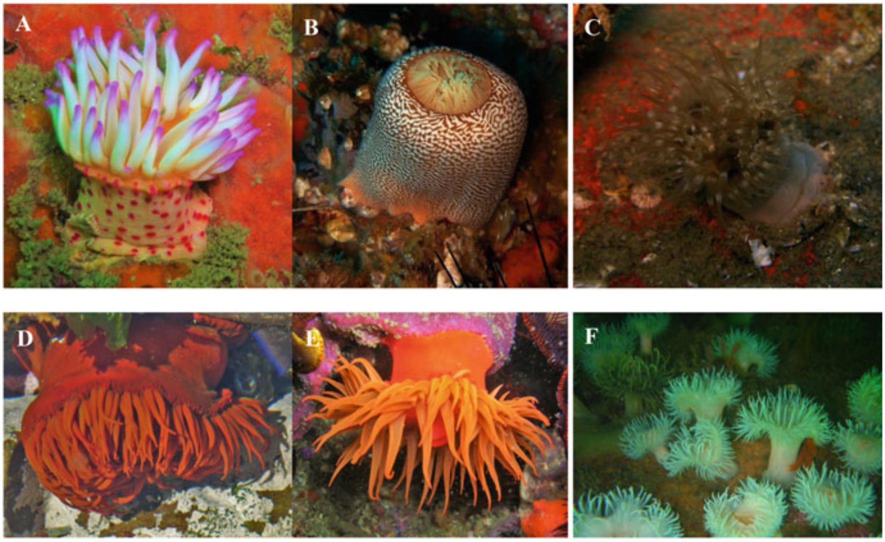


Fig. 14 The morphotypes of sea anemones found in South Africa. The figure was created ex-novo. Permission to use images was granted by Peter Southwood

moderately diverse, order in South Africa (Fig. 14). The most recent species list available is that compiled by Acuña and Griffiths (2004), who reported 49 species of sea anemones from South Africa. Laird and Griffiths (2016) increased the number of species recorded to 63 of which 46% are endemic, 29% non-endemic, 22% cosmopolitan and 3% introduced (Laird 2014). The ecoregion with the highest number of reported sea anemone species is the Agulhas (38 species), Natal (26 species), followed by the Southern Benguela (20 species) and Southwest Indian ecoregion (5 species), while the Delagoa ecoregion had the greatest number of cosmopolitan species with 11 (Laird 2014). Overall trends in species richness are unclear, but if anything, sea anemones are more diverse in the temperate south and southwest region of South Africa.

The families Actiniidae (16 species) and Hormathiidae (8 species) are the most diverse families of South African sea anemones, but the latter contains a much higher proportion of endemics. The deep-water distribution of Hormathiidae could be the explanation for this high apparent endemicity rate, since very few deep-sea samples have been collected in countries adjacent to South Africa (Acuña and Griffiths 2004). The list of Laird and Griffiths (2016) is incomplete and emphasizes the need to increase the sampling effort in the deeper regions of the EEZ. Gaps in sample coverage remain particularly obvious in deep-sea areas, particularly the bathyal and the abyssal (500–5000 m), the latter being largely unexplored. Geographically, the west and east coasts need to be more thoroughly sampled, while mesophotic and rariphotic reef habitats also need to be made a priority. On the west coast shelf (Namaqua and Namib ecoregions), Uriz (1988) reported that the soft sediments were characterized by low diversity and a sizable biomass of an

Actinauge-like actinian (sea anemone) found to be extremely abundant. The sea anemone beds occurred at the 400–500 m depth ranges (Uriz 1988).

High densities of anemones were observed on ROV footage off Port Elizabeth on the south coast (Sink 2016, Deep Secrets cruise report), but the species identity has not been confirmed. It is challenging to collect deep-water anemones and difficult to link in situ observations with trawled specimens. The species most commonly trawled in South Africa are *Bolocera kerguelensis*, *Actinauge granulata* and *Actinostola capensis* (see Branch et al. 2016; Sink et al. 2018; Atkinson and Sink 2018).

Although suitable ports for the proliferation of introduced species also lie on the east and south coasts, water temperature there is most likely too high for the invasion of *Sagartia ornata* and *Metridium senile*, which are the only anemone species that have been introduced to South Africa to date (Laird 2014).

3.6 Bryozoan Thickets

Bryozoans or “moss animals” are aquatic animals that are predominantly marine, with some estuarine and even freshwater forms (Hayward and Ryland 1999). The marine Bryozoa are adapted to live in marine habitats including the intertidal zone, continental shelf, deep ocean canyons and abyssal plains. Typically, these sessile colonial animals are found attached to diverse substrates ranging from, but not limited to, anthropologically produced structures to large rocks, shells, algae and even other bryozoans. Their ability to adapt to heterogeneous environments has driven a spectacular diversity within this monophyletic group.

The estimated 6500 globally known species of Bryozoa may be less than half the true number of species. The marine species of Bryozoa are classified in the orders Cyclostomatida, Ctenostomatida and Cheilostomatida (Hayward and Ryland 1999). The known South African bryozoan fauna constitutes approximately 282 species (Florence et al. 2007; Florence and Atkinson 2018; Boonzaaier et al. 2020), of which 67 (26%) were reported as new by Hayward and Cook (1979, 1983). Despite the importance of Bryozoa fauna in benthic communities, few studies have been carried out on bryozoans along the South African coast, compared to sponges. Despite zooids being microscopic, bryozoan colonies may range in size through five orders of magnitude from 0.2 mm to 2 m (Anderson et al. 2019). Large bryozoans often provide habitat for diverse associated assemblages, particularly for other bryozoans, molluscs, annelids, arthropods, cnidarians, sponges, echinoderms and macroalgae (Wood et al. 2012). Other ecological services of habitat-forming Bryozoa include sediment stabilization, reduction of current flow in and around the thickets and provision of three dimensionality, attachment surfaces and food (Anderson et al. 2019). Coastal Bryozoa thickets that have the appearance of brightly coloured coral reefs also have high aesthetic value for tourism, especially for to the diving and free-diving communities (Anderson et al. 2019).

In their recent study on the Abrolhos Shelf in the south Atlantic, Bastos et al. (2018) found that bryozoans accounted for up to 44% of the reef framework, while crustose coralline algae and coral accounted for less than 28 and 23% respectively. Habitat-forming bryozoans are particularly prevalent in New Zealand, Antarctica (Weddell, Lazarev and Ross Seas), the North Pacific around Japan, the northern Mediterranean and Adriatic and along the southern edge of the North Sea, through the English Channel and around the United Kingdom (Wood et al. 2012, 2013; Santagata et al. 2018). It is likely that bryozoans are significant generational contributors to biogenic reefs in both the tropical and temperate reefs of South Africa. In South Africa, however, there is no known published study on the distribution or extent of habitat-forming bryozoans, although potential habitat-forming bryozoan thickets have been observed and habitat-forming taxa are abundant.

Bryozoans are generally considered to be significant habitat formers if they are rigidly erect and widely distributed and provide three-dimensional structure (Anderson et al. 2019). Colonies can be encrustations that form thin or thick circular or irregular patches or erect and bushy tufts that resemble algae or hydroids, while others can form three-dimensional calcified coral-like structures (Smith and Gordon 2011). Through the utilization of available biominerals the Bryozoa conform to 17 widely accepted colony morphotypes (see Brown 1952; Moyano 1979; Stach 1936; Cook 1968). The primary colony morphotypes that meet these criteria for South Africa include (see Florence et al. 2007; Florence 2016; Florence and Atkinson 2018):

- Adeonelliform (Fig. 15a) including *Laminopora jellyae*
- Reteporiform (Fig. 15b) including *Reteporella lata*, *Schizoretepora tessellata* and *Aspidostoma livida*
- Membraniporiform (Fig. 15c) including *Calyptotheca porelliformis* and *Chaperiopsis multifida*
- Adeoniform including (Fig. 15d) *Gephyrophora polymorpha*

Other morphotypes that may, to a lesser extent, contribute to bryozoan thickets are less calcified but foliaceous and erect and include (see Florence et al. 2007; Florence 2016; Florence and Atkinson 2018):

- Buguliform (Fig. 15e) including *Virididentula dentata*, *Onchoporella bombycina*, *Flustramorpha marginata* and *Flustramorpha angusta*
- Cellulariiform (Fig. 15f) including *Menipea triseriata* and *Menipea crispa*
- Cellariform (Fig. 15g) including *Margaretta levinseni*
- Flustriform (Fig. 15h) including *Gregarinidra spinuligera* and *Alcyonidium rhomboidale*

The species mentioned above have wide spatial and bathymetric ranges (Florence et al. 2007; Florence 2016; Florence and Atkinson 2018). However, there is a paucity of knowledge regarding full-scale spatial and bathymetric analysis of

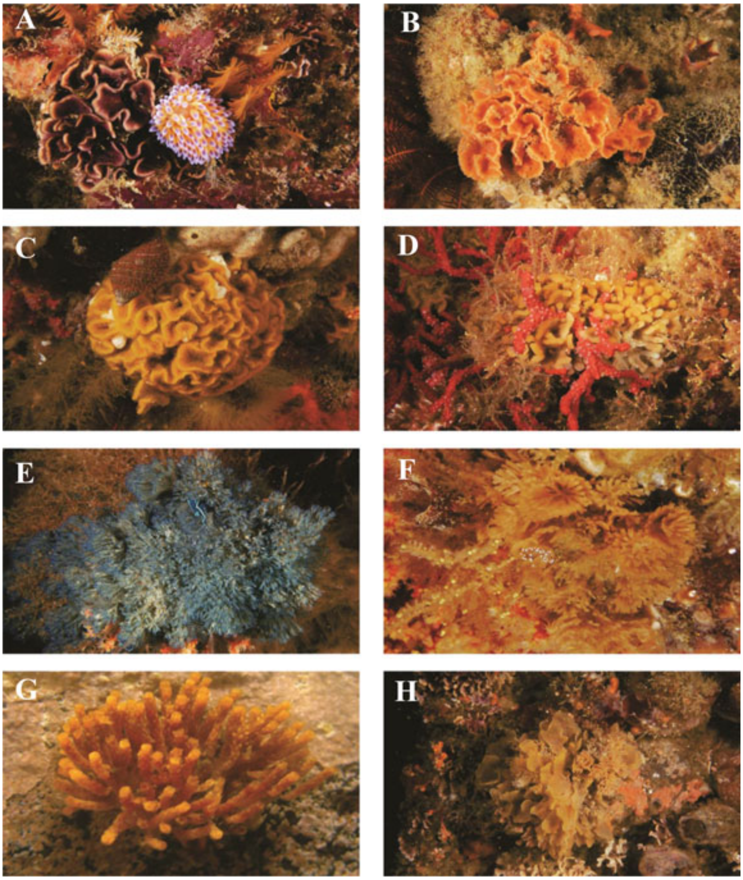


Fig. 15 Examples of key habitat-forming bryozoan colony morphotypes. (**a**) *Laminopora jellyae* (Adeonelliform) being grazed upon by *Bonisa nakaza* (Gas Flame Nudibranch), (**b**) *Schizoretepora tessellata* (Reteporiform) the "false lace coral" is prevalent in large numbers on subtropical temperate reefs, (**c**) *Chaperiopsis multifida* (Membraniporiform) provides microhabitat due to its 3D "honeycomb" structure. (**d**) *Gephyrophora polymorpha* (Adeoniform) provides attachment substrate for hydroids and other cnidarians. (**e**) *Virididentula dentata* (Buguliform) forms large, lightly calcified, tufts resembling algae; (**f**) *Menipea triseriata* (Cellulariiform) an algae-like tuft that provides refugia for small molluscs, crustaceans and fishes; (**g**) *Margaretta levinseni* (Cellariform) is a tree-like bryozoan; (**h**) *Alcyonidium rhomboidale* (Flustriform) forms large, gelatinous, colonies that traps sediment between its "fronds". Photographs taken by Piotr Kuklinski, IOPAS and Wayne Florence, Iziko Museums. The figure was created ex-novo. Permission to use images was granted by Dr. Wayne Florence and Prof. Piotr Kukliński

South African Bryozoa that urgently requires attention. Beds of Bryozoa are known to occur on the continental shelf, at 200–500 m depth range on both the west and south coasts (see Atkinson and Sink 2018). However, there is little information about shelf edge and slope communities even though a few species were recorded at 700–900 m.

3.7 Ascidians

Ascidians (Phylum: Chordata, Class: Ascidiacea), or sea squirts, are the largest and most diverse class of the subphylum Tunicata (also known as Urochordata). They comprise approximately 3000 accepted species found in all marine habitats (Shenkar and Swalla 2011). The most recent species list available is that recorded in Monniot et al. (2001), who reported 82 species of shallow-water ascidians from South Africa. Monniot et al. (2001) also make reference of an additional 63 species not described in their monograph. The known South African ascidian fauna constitutes approximately 145 species (Gibbons et al. 1999; Monniot et al. 2001; Parker-Nance and Atkinson 2018), of which approximately 30% are reported from deeper waters (Monniot et al. 2001). Of the 145 species, 81 species (56%) were found to be endemic to South Africa (Gibbons et al. 1999; Awad et al. 2002). The rate of endemism found for the South African ascidian fauna is relatively equal in comparison to other regions. For example, similar rates of endemism were found in New Zealand (43%), the Antarctic region (44%) and the Eastern Mediterranean (40.9%). There are 227 species of ascidians described in South Africa (Griffiths et al. 2010).

Furthermore, Parker-Nance and Atkinson (2018) list eight deep-water ascidians collected from the shelf, shelf edge and slope regions of the south and west coasts of South Africa. On the west coast shelf, Uriz (1988) reported high densities of a solitary ascidian (*Molgula scutata*) being abundant between 400 and 500 m depth ranges in the northern Benguela, with Parker-Nance and Atkinson (2018) noting that this species also occurs on the Agulhas Bank but in water depths shallower than 100 m depth. *Ascidia incrassate* and *M. scutata* are the only endemic deep-water species (Parker-Nance and Atkinson 2018).

Awad et al. (2002) examined the distributions of 134 shallow-water ascidian species. They found that shallow-water ascidian species were concentrated along the south coast, with the highest species richness occurring at False Bay (58 species). The west coast was species poor with only five species recorded from the Orange River down to Saldanha Bay. Ascidian species also declined eastwards from False Bay (Awad et al. 2002). The growing recognition of ascidians as a subject for research in the fields of ecology and evolution, and especially their promising potential for new pharmaceutical compounds, greatly emphasizes the need for future studies of the ascidian fauna of South Africa. The primary colony morphotypes are shown in Fig. 16.

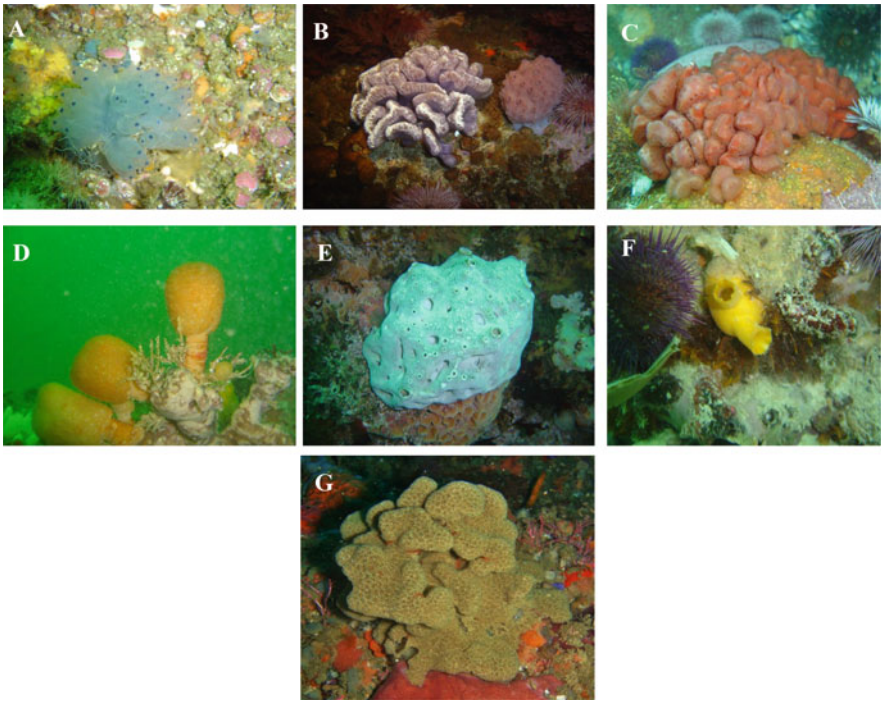


Fig. 16 The morphotypes of ascidians found in South Africa. The figure was created ex-novo. Permission to use images was granted by Peter Southwood

4 Threats to South African Marine Animal Forests and Their Mitigation

4.1 Seabed Impacts Caused by Offshore Fishing and Mining in South Africa

Primary industrial activities that pose a risk to animal forests in South African waters include the demersal trawl, crustacean trawl, demersal longline and rock lobster trap fisheries, as well as extractive mining operations, specifically for marine diamonds, petroleum (oil and gas) and minerals (Atkinson and Sink 2008). Most of these industrial activities are known to negatively impact seabed communities with considerable research done to quantify their impacts and develop mitigation measures or best practice guidelines to minimize damage (Grieve et al. 2015; Cordes et al. 2016; Kaiser et al. 2016; Miller et al. 2018). These industries provide critical economic value for South Africa, and socio-economic benefits must be considered when implementing impact mitigation measures. Some management measures are in place in South Africa to mitigate the deleterious effects of disturbance caused by industrial activities of such industries, including substantive measures implemented by the hake trawl fishery who hold Marine Stewardship Council (MSC) certification. There is work underway to ensure such industries continue to strive towards global best practice and take into account cumulative impacts.

Globally, demersal trawl fisheries are known to impact the seabed and benthic communities with a vast amount of scientific research having focussed on the subject (Hughes et al. 2014; Hiddink et al. 2017). Although such fisheries generally take place in unconsolidated, homogenous habitats, there are areas where sensitive, biogenic ecosystems continue to be impacted by trawl fisheries (e.g. seamounts and deep cold-water coral reefs, Clark et al. 2015). The South African demersal trawl fishery has been operational for more than 100 years (Payne 1989) and continues to be the most financially lucrative fishery in the country having important socio-economic benefits (Durholtz et al. 2015; Lallemand et al. 2016). Nonetheless, the fishing activity of dragging large, heavy nets, with footrope gear designed to roll along the seafloor, will damage any structurally complex and fragile biota and ecosystems, when encountered. The South African offshore trawl fishery targets two species of hake (*Merluccius capensis* and *M. paradoxus*) and operates along the deep, offshore shelf edge of the west and south coasts and the inshore region of the Agulhas Bank (Durholtz et al. 2015). Other benthic fish species are caught as trawl bycatch and retained if commercially valuable (e.g. kingklip, monk, sole, angelfish, horse mackerel), otherwise discarded. An analysis conducted by Sink et al. (2012a) reported that 27 of 136 mapped marine habitat types are exposed to trawling in South Africa's EEZ with 12 of these being likely to host dense aggregations of fragile, sessile animals forming biogenic features. These include canyons, steep slopes and rocky and gravel areas that are known to provide habitat for vulnerable, slow-growing, sessile species and are areas essential for fish reproduction and juvenile fish protection.

In 2004, the South African trawl fishery achieved Marine Stewardship Council (MSC) certification, with successful recertification in 2011 and 2015 (Lallemand et al. 2016). A fish product with an MSC eco-label has the financial benefit of attracting a higher market price. However, to retain MSC certification, a fishery has to meet certain criteria, including complying with international best practice in mitigating ecosystem impacts (Martin et al. 2012). As a result of the South African trawl fishery's MSC eco-label, the fishery voluntarily agreed to freeze their footprint in 2008 (subsequently enforced through permit conditions), thereby preventing further spatial expansion of this fishery (Durholtz et al. 2015).

Other types of fishing activities in South Africa that may result in damaging interactions with sessile, fragile benthic species include the crustacean trawl fishery, demersal longline fishery and fisheries that deploy traps, such as the rock lobster fisheries (Atkinson and Sink 2008). South Africa's crustacean trawl fishery is restricted to localized areas of the KwaZulu-Natal province on the east coast. Here, trawls occur on the inshore mud banks and the offshore shelf edge (Sink et al. 2012b). The potential impact of this fishery on animal forest communities is highest in the offshore shelf edge area, which is rocky and likely to support fragile communities. The fishing effort of South Africa's crustacean trawl fishery is low with only three vessels reportedly operational in 2016 and the recent proclamation of the uThukela MPA further reducing trawl areas.

The longline and trap fisheries pose potential risk to snagging and breaking structurally complex and fragile benthic species. Demersal longline fishing, primarily targeting the Cape hake and demersal sharks, occurs on the west and south coasts of South Africa with effort concentrated on the shelf edge, usually on steep or rocky terrain that is not as accessible to trawlers (Atkinson and Sink 2008; Sink et al. 2012b). Although the primary environmental concerns of the demersal longline fishery are related to bycatch species, the weighted lines deployed by the fishery can damage sessile, emergent invertebrate species (Atkinson and Sink 2008). Trap fisheries operating in South Africa include the west and south coast rock lobster fisheries. The larger, heavier metal traps used by the offshore west coast rock lobster fishery are more likely to damage fragile benthic species in comparison to the smaller, plastic traps used for the south coast rock lobster fishery (Atkinson and Sink 2008).

Petroleum exploration and production activities are mostly concentrated on the Agulhas Bank; however, several wells have been drilled on the west coast, and large areas are under lease for production (Ibhubesi Gas Field) and further exploration (www.petroleumagencysa.com, 2019). Seabed impacts of these activities include localized habitat disturbance, smothering and risk of catastrophic pollution, should an oil spill occur as a result of an uncontrolled release of hydrocarbons (Sink et al. 2012b). The only known in situ research conducted in South Africa investigating benthic impacts of petroleum activities showed a limited area (<250 m radius) of impact around a wellhead (Sink et al. 2010). Nonetheless, should an area of petroleum interest intersect with that of a sessile, fragile community, it is likely that the seabed fauna will be negatively impacted or destroyed during exploration and/or extraction.

Diamond mining occurs in the intertidal, near-shore and shelf habitats along the north-west coast of South Africa and southern Namibia (Atkinson and Sink 2008; Sink et al. 2012b). Impacts on the ecosystem as a result of diamond mining activities include smothering of benthic communities from sediment plumes, alteration of seafloor composition and loss of unique habitat that may intersect with diamond concentrations. There is growing global interest in mining the seabed for a wide range of other minerals such as polymetallic nodules, sulphides, manganese and phosphates (Miller et al. 2018; Sharma 2017). Seabed areas that lie beyond national jurisdiction are governed by the United Nations Convention on the Law of the Sea (UNCLOS) with the International Seabed Authority (ISA) regulating mineral-related activities therein (Miller et al. 2018). Mining of seabed minerals has not yet taken place within South Africa’s EEZ; however, in 2012 and 2014, three prospecting rights for marine phosphate mining, covering a total area of 155,500 km^2 (±10% of the EEZ), were granted by South Africa’s Department of Mineral Resources (Centre for Environmental Rights, Safeguard Our Seabed Coalition, www.cer.org.za). South African stakeholders (environmental agencies and fishing sectors) raised issues of irregularities in granting these rights, and to date, no known prospecting has taken place. Considering the nature, spatial scale and extent of proposed seabed mining activities, in South Africa and internationally, large-scale loss of entire ecosystems, especially fragile, sessile communities, is inevitable with zero to little recovery potential (Van Dover et al. 2017).

4.2 Climate Change

In terms of a more acidic ocean environment, various taxa including corals, calcareous sponges and bryozoan will be negatively impacted since their ability to calcify will be impaired. This will have considerable impacts on animal forest communities including non-sessile species that inhabit animal forests for food or shelter (Sweetman et al. 2017). No in situ studies have demonstrated impacts or responses in animal forest communities of South Africa with respect to acidification to date. Changes in warm-, shallow-water coral communities in response to warming have been observed at Sodwana in Northern KwaZulu-Natal (Porter and Schleyer 2017). Whereas corals grow faster as temperatures rise, beyond some limit rising temperatures harm them by breaking down the relationship between the corals and their symbiotic zooxanthellae, which are then expelled, resulting in bleaching. Reef corals in Northern KwaZulu-Natal largely escaped the widespread, episodic warming events that caused bleaching and mass mortalities of corals across the tropics in several years during the 1990s and early 2000s; this was put down to moderating effects of local small-scale upwelling in summer that kept temperatures to below bleaching levels. However, in 2005 it was estimated that 16–60% of corals at Sodwana Bay were bleached following prolonged high temperatures.

Before this event, long-term monitoring at Sodwana Bay had showed that water temperatures rose 1 °C between 1994 and 2000 and then levelled off; this coincided with an increase in hard coral cover due to increased skeletal growth and a decline in soft coral cover (Porter and Schleyer 2017). The usefulness of benthic communities for such long-term investigations of climate change effects is well recognized, given the sessile nature and low mobility of most constituent taxa and the fact that many are long-lived and integrate the effects of environmental change over time. The need for more studies to monitor and investigate the responses of these communities to global changes including impacts on ecosystem structure and functioning, and especially in deeper ecosystems, is therefore emphasized.

5 Identifying and Protecting Important Areas of Marine Habitat and Biodiversity

5.1 *Marine Protected Areas*

In South Africa, the first Marine Protected Area (MPA) was declared in 1964—the Tsitsikamma National Park MPA. By 2009, 23 MPAs had been declared around South Africa, covering 23% of the length of the coastline of which approximately 10% was "no-take" area (Fig. 17). Following the declaration of the large Prince Edward Islands MPA in the Southern Ocean (2013), the overall level of protection in South African waters exceeded the 10% target of the 2020 Global Target in the Decadal Plan of the Convention of Biodiversity; however only 0.4% of the area of the mainland territory was protected. The full diversity of South Africa's marine systems was thus greatly under-represented in the MPA network, with 47% of recognized marine ecosystem types not represented at all, and offshore areas of the mainland's EEZ were especially lacking. To address this, a proposal for a network of new MPAs that would advance marine habitat representation and protection of threatened marine ecosystems and species was developed in 2014 and gazetted for public comment in 2016. In 2019, 20 new MPAs were finally declared, which brought overall protection of the mainland's ocean territory to 5% (Fig. 17).

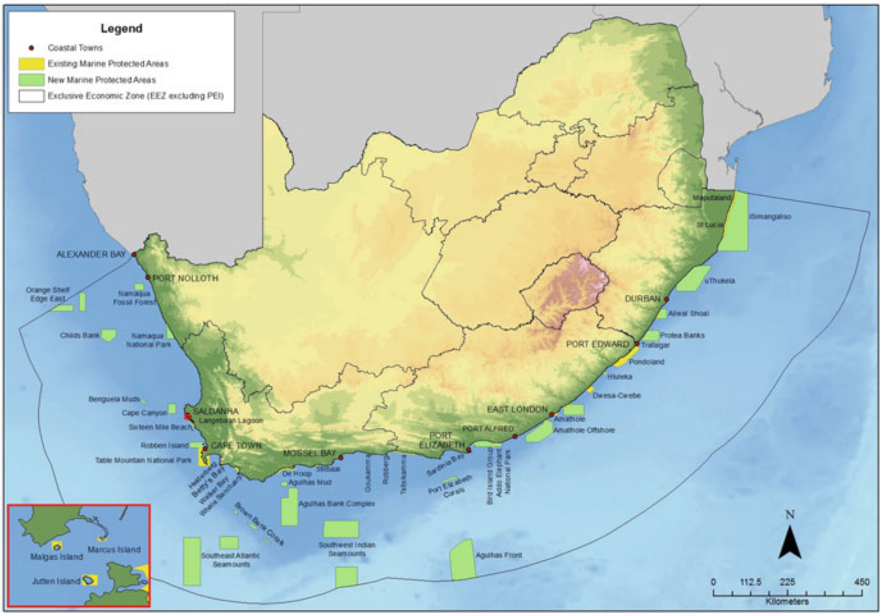


Fig. 17 New MPA network declared for South Africa. Map created ex-novo by Dr. Lauren Williams (sourced from https://egis.environment.gov.za/)

The sites and boundaries of new MPAs had been identified and developed using a Systematic Conservation Planning (SCP) that took into account established principles for protected area networks (e.g. comprehensiveness, adequacy, representativeness). Where possible, incurring social or economic costs to users of the marine environment was avoided through selection of less used sites, where there were alternatives, or through zonation whereby controlled use is allowed in some areas as long as it does not compromise the protection objectives of the MPA. Boundaries and zonations were refined during the consultation period.

The MPA network advanced ecosystem representation from 47% to 87%, with 51 ecosystem types receiving their first protection (Sink et al. 2019). Apart from increasing the representation of ecosystems under protection, the expanded network contributes to protection of threatened ecosystems and species, potential Vulnerable Marine Ecosystems (VMEs; see below section), supports fisheries management and ecotourism and provides a platform for research and monitoring in South Africa's ocean environment. Most of the new MPAs also included some degree of overlap with existing Ecologically or Biologically Significant Marine Areas (EBSAs; see below section), thus providing protection to key components of the EBSA network. Protection of animal forest communities including cold-water coral reefs and sponge grounds was key motivations for several of the new MPAs, including Namaqua Fossil Forest, Child Bank, Browns Bank Corals, Southwest Indian Seamount, Port Elizabeth Coral, Amathole Offshore, Protea Banks and the expanded iSimangaliso MPA. Protection of both shallow-water subtropical coral communities and deep-water corals and sponge grounds is achieved at the expanded iSimangaliso MPA in the north east of the country.

5.2 Ecologically or Biologically Significant Areas and Vulnerable Marine Ecosystems

Ecologically or Biologically Significant Areas (EBSAs) are a tool that draws attention to areas that have particularly high ecological or biological importance and that should be considered by decision-makers working towards ecosystem objectives, e.g. they could be treated with a higher than usual degree of risk averseness. Potential management interventions that are encouraged by the Convention on Biological Diversity (CBD) to manage EBSAs and their underlying features include MPAs and other effective area-based conservation measures (OECMs). That focussed portions of most of South Africa's EBSAs have been incorporated in the country's expanded MPA network (see above section) that supports the assertion that EBSAs can contribute towards achieving Aichi Target 11.

Descriptions of 17 areas that meet the criteria for EBSAs in South Africa were formally endorsed by the CBD Conference of the Parties in October 2014 (Fig. 18).

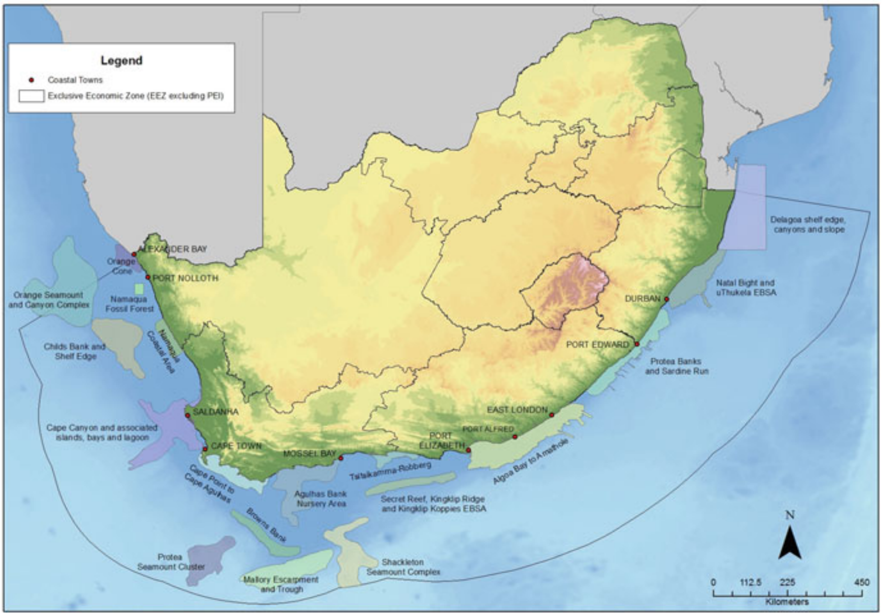


Fig. 18 Proposed EBSAs for South Africa. Map created ex-novo by Dr. Lauren Williams (sourced from https://cmr.mandela.ac.za/EBSA-Portal/MARISMA-Spatial-Data-Portal)

These included 11 EBSAs that were contained within the Exclusive Economic Zone (EEZ) and 6 that extended into other country's EEZs or into Areas Beyond National Jurisdiction (ABNJ). Since 2016 the country's EBSAs have been under review, and a SCP approach has been used to assist with identifying new potential areas, which were then assessed in terms of EBSA criteria, and also to delineate their boundaries or to revise the boundary delineations of existing EBSAs. As part of this process, descriptions of three newly described EBSAs (i.e. Protea Seamount Cluster, Seas of Good Hope, Tsitsikamma-Robberg) have been proposed. Eight of the existing or proposed EBSAs in South Africa have been motivated largely, or partly, on the basis of scoring highly in terms of the "vulnerability, fragility, sensitivity or slow recovery" EBSA criterion. For most, this was based on the presence of animal forest-type communities which are highly applicable to this category. Examples include structurally complex and habitat-forming cold-water corals, habitat-forming sponges, hydrocorals, gorgonians, bryozoans and others.

These animal forest communities are also highly consistent with the definition of Vulnerable Marine Ecosystems (VMEs), which are groups of species, communities or habitats that may be vulnerable to fishing activities. The key concepts of VMEs, namely, "vulnerability" and "significant adverse effects", are very much in line with the EBSA category "vulnerability, fragility, sensitivity or slow recovery". In particular VMEs describe habitat types that are easily disturbed by fishing activities and are slow to recover, or which may never recover, including features such as seamounts, banks, knolls, the slopes of oceanic islands, carbonate mounds, submarine canyons, trenches, manganese nodule habitats, hydrothermal vents and biogenic reefs such as cold-water corals, octocoral gardens and deep-sea sponge beds. Several of these such coral reefs, octocoral gardens and deep-sea sponge beds not only form complex animal structures but provide habitat and shelter for other animals, giving rise to complex and fragile communities.

While the guidelines for the identification and management of VMEs, which were developed by the Food and Agriculture Organization of the United Nations (FAO), were aimed at high seas fisheries and provide a voluntary tool through which to achieve this objective of better-managed fisheries and protected VMEs, the concept is also applicable to areas within national jurisdiction. Atkinson and Sink (2018) identified a number of deep-water taxa that are considered potential indicators of VMEs in South Africa (Table 5). This list contains species that form complex and emergent biogenic benthic structures, are typically fragile and therefore easily damaged by fishing gears and are likely to be long-lived and slow to recover.

5.3 Marine Spatial Planning

The recently proclaimed Marine Spatial Planning Act for South Africa provides an operational framework for MSP in South Africa (Government Gazette No. 42479). MSP is a process for allocating and siting ocean uses to avoid user conflict and ensure that trade-offs between ecosystem services are appropriately dealt with. As per the Act, marine plans will need to be informed on the characteristics of the ocean including species, habitats and ecosystems, as well as ecological processes. Therefore a critical component of the MSP process is the development of a national data- and information-gathering platform, in which existing knowledge on marine biodiversity, ecology, economics and societal impacts and their interactions are consolidated. A concern is that proper planning may be hampered by the current poor state of knowledge for several ecosystem types. This is the case especially for deeper, less accessible ecosystem types, some of which have hardly been sampled, if at all. These include ecosystems where animal forest communities may be found such as deep reefs, cold-water coral communities and submarine canyons. However, EBSAs, including several of which comprise animal forest communities, and the databases that have been amassed in the process of identifying, describing and revising them in recent years provide a useful spatial tool and ecological basis to inform MSP. This process is still in its infancy in South Africa.

Table 5 Potential VME taxa that may be indicators of Vulnerable Marine Ecosystems (VME) in SA EEZ, as defined by FAO (2009)

Taxa	Species	SA distribution record	Depth range	SA Endemic	Other distribution records?	Status/ reference
Porifera	*Hamacantha (Vomerula) esperioides*	West and south coasts	17–1117 m		South America	Valid
Porifera	*Fibulia ramosa*	West and south coasts	91–287 m		Prince Edward Island	Valid
Porifera	*Suberites dandelenae*	West coast	80–500 m	Yes	Namibia	Valid
Porifera	*Rossella* cf. *antarctica*	West and south coasts	8–2000 m		New Zealand, South America, Subantarctic, Antarctica	Questionable
Cnidaria	*Melithaea* spp.	West and south coasts			Indo-Pacific	Species to be determined
Cnidaria	*Thouarella* spp.	West and south coasts	100–900 m			Species to be determined
Cnidaria	*Bamboo coral* (Isididae sp.)	West and south coasts	200–4850 m		Cosmopolitan?	Species to be determined
Cnidaria	*Anthoptilum grandiflorum*	West and south coasts	200–2000 m		Cosmopolitan?	Questionable
Cnidaria	*Desmophyllum pertusum*	West and south coasts	39–2775 m		Semi-cosmopolitan?	Questionable
Cnidaria	*Solenosmilia variabilis*	South coast	220–2165 m		Semi-cosmopolitan?	Questionable
Cnidaria	*Goniocorella dumosa*	South and east coasts	86–760 m		New Zealand, Indonesia and Korea	Questionable
Cnidaria	Dendrophylliidae spp.	South coast	0–470 m		Indo-Pacific and Atlantic	Species to be determined
Cnidaria	*Enallopsammia rostrata*	South coast	Deeper than 110 m		Global 110–2165 m; New Zealand	Questionable
Cnidaria	*Stylaster nobilis*	West and south coasts	3–174 m	Endemic		Valid
Cnidaria	*Stylaster* spp.	West and south coasts		Endemic		Species to be determined

Cnidaria	*Errina* spp.	South coast	110 m			Species to be determined
Cnidaria	*Errinopsis* spp.	South coast	174–250 m		Subantarctic	Species to be determined
Cnidaria	*Inferiolabiata* spp.	South coast	<155 m			Species to be determined
Bryozoa	*Adeonella* spp.	West, south and east coasts	Shallow subtidal—880 m	Endemic		Species to be determined
Bryozoa	*Aspidostoma* sp. 1	South coasts	90–780 m			Species to be determined
Bryozoa	Phidoloporidae spp.	West, south and east coasts	2–775 m			Species to be determined
Hemichordata	*Cephalodiscus gilchristi*	Mostly south coast, also on west coast		Endemic		Valid

List compiled from Atkinson and Sink (eds) 2018

6 Conclusion

South Africa's seascape is host to a diverse range of animal forest assemblages, from high-latitude soft coral-dominated reefs along its eastern coast to cold-water coral assemblages fringing its continental shelf drop-off along the south coast and extensive, highly diverse sponge grounds on the Agulhas Bank and western shelf. There is limited knowledge on the extent of these assemblages, their species composition and their ecological function, but the information that exists suggests that many of these assemblages constitute both EBSAs and VMEs, making them a priority for protection from adverse anthropogenic impacts. The recently established offshore MPA network will preserve a number of these assemblages, broadly representative of their diversity and their distribution, but outside of these MPAs many of them may have already been impacted by mining and demersal fishing activities. In the last decade, there has been an increased effort to study these benthic assemblages with equipment such as ROVs, jump and tow cameras and benthic sleds. This is providing for the first time visual imagery of the in situ structures and organizations of South African animal forests. Some of these assemblages resemble shrublands, and some are more analogous to thickets, whereas others form a true canopy more synonymous with that of a terrestrial forest, albeit on a scale that is one magnitude lower (centimetres to metres vs. metres to tens of metres for a terrestrial forest). These research initiatives are providing new insights into their ecology with indications that these habitats not only harbour an increased diversity when compared to their surroundings but also provide refuge, areas for reproduction and nursery grounds for a range of fish species, some of which are threatened and some of which are commercially important. Continued investigation into the ecology and distribution of these areas is crucial in order to manage them carefully and to avoid their destruction with the concomitant loss of endemic species and ecosystem services.

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References

Acuña FH, Griffiths CL (2004) Species richness, endemicity and distribution patterns of South African sea anemones (Cnidaria: Actiniaria and Corallimorpharia). Afr Zool 39 (2):193–200

Anderson RJ, Bolton JJ, Stegenga H (2009) Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa. Biodivers Res 15:1017–1027

Anderson TJ, Morrison M, MacDiarmid A, Clark M, D'Archino R, Nelson W, Tracey D, Gordon D, Read G, Kettles H, Morrisey D, Wood A, Anderson O, Smith AM, Page M, Paul-Burke K, Schnabel K, Wadhwa S (2019) Review of New Zealand's key biogenic habitats. National Institute of Water and Atmospheric Research, Wellington

Atkinson (2010) Effects of demersal trawling on marine infaunal, epifaunal and fish assemblages: studies in the southern Benguela and Oslofjord. PhD thesis, University of Cape Town, p 141

Atkinson L, Sink K (2008) User profiles for the South African offshore environment. SANBI biodiversity series 10. South African National Biodiversity Institute, Pretoria, p 66. isbn:978-1-919976-46-4

Atkinson LJ, Sink KJ (eds) (2018) Field guide to the offshore marine invertebrates of South Africa. Malachite Marketing and Media, Pretoria, p 498. https://doi.org/10.15493/SAEON.PUB.10000001

Awad AA, Griffiths CL, Turpie JK (2002) Distribution of South African marine benthic invertebrates applied to the selection of primary conservation areas. Divers Distrib 8:129–145

Bastos AC, Moura RL, Moraes FC, Vieira LS, Braga JC, Ramalho LV, Amado-Filho GM, Magdalena UR, Webster JM (2018) Bryozoans are major modern builders of South Atlantic oddly shaped reefs. Sci Rep 8(1):9638

Bolton JJ, Anderson RJ (1990) Correlations between intertidal seaweed community composition and seawater temperature patterns on a geographical scale. Bot Mar 33:447–457

Bolton JJ, Anderson RJ (1997) Marine vegetation. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of southern Africa. Cambridge University Press, Oxford, pp 348–370

Bolton JJ, Stegenga H (2002) Seaweed biodiversity in South Africa. S Afr J Mar Sci 24:9–18

Bolton JJ, Leliaert F, DeClerck O, Stegenga ARJ, H. Engledow H.E. and Coppejans E. (2004) Where is the western limit of the tropical Indian Ocean seaweed flora? An analysis of intertidal seaweed biogeography on the east coast of South Africa. Mar Biol 144:51–59

Boonzaaier-Davids MK, Florence WK, Gibbons MJ (2020) Novel taxa of Cheilostomata Bryozoa discovered in the historical backlogs of the Iziko South African Museum. Zootaxa, 4820 (1):105–133

Branch GM, Branch ML (2018) Living shores: interacting with southern Africa's marine ecosystems. Struik Nature, Cape Town

Branch GM, Griffiths CL, Branch ML, Beckley LE (2016) Two oceans. A guide to the marine life of Southern Africa. Struik Nature, Cape Town

Brown DA (1952) The Tertiary cheilostomatous polyzoa of New Zealand. British Museum, London, 405 pp. https://doi.org/10.5962/bhl.title.118779

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50

Cairns SD (2001) A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). Smithsonian Contrib Zool 615:1–75. https://doi.org/10.5479/si.00810282.615

Cairns SD, Keller NB (1993) New taxa and distributional records of azooxanthellate scleractinia (Cnidaria, Anthozoa) from the tropical South-west Indian Ocean, with comments on their zoogeography and ecology. Ann S Afr Mus 103(5):213–292

Cairns SD, Kitahara MV (2012) An illustrated key to the genera and subgenera of the recent azooxanthellate Scleractinia (Cnidaria, Anthozoa), with an attached glossary. ZooKeys 227:1–47. https://doi.org/10.3897/zookeys.227.3612

Cairns SD, Zibrowius H (2013) Stylasteridae (Cnidaria, Hydrozoa, Filifera) from South Africa. Zootaxa 3691(1):1–57

Clark MR, Althaus F, Schlacher TA, Williams A, Bowden DA, Rowden AA (2015) The impacts of deep-sea fisheries on benthic communities: a review. ICES J Mar Sci 73(Suppl 1):i, 51–69

Cook PL (1968) Bryozoa (Polyzoa) from the coast of tropical West Africa. Atlantide Rep 10:115–262

Cordes EE, Jones DOB, Schlacher TA, Amon DJ, Bernardino AF, Brooke S, Carney R, DeLeo DM, Dunlop KM, Escobar-Briones EG, Gates AR, Génio L, Gobin J, Henry LA, Herrera S, Hoyt S, Joye M, Kark S, Mestre NC, Metaxas A, Pfeifer S, Sink K, Sweetman AK, Witte U (2016) Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. Front Environ Sci 4:58. https://doi.org/10.3389/fenvs.2016.00058

Durholtz MD, Singh L, Fairweather TP, Leslie RW, van der Lingen CD, Bross CA, Hutchings L, Rademeyer RA, Butterworth DS, Payne AI, Yáñez-Arancibа H (2015) Fisheries, ecology and markets of South African hake. Hakes: Biol Exploitation 38–69

FAO (Fisheries and Agriculture Organization) (2008) International guidelines for the management of deep-sea fisheries in the high seas. FAO Technical Consultation Document. FAO, Rome

Florence WK (2016) Some deep-water cheilostome Bryozoa from the south coast of South Africa. Afr Nat Hist 12:05–11

Florence WK, Atkinson LJ (2018) Phylum Bryozoa. In: Atkinson LJ, Sink KJ (eds) Field guide to the offshore marine invertebrates of South Africa. Malachite Marketing and Media, Pretoria, pp 227–243

Florence WK, Hayward PJ, Gibbons MJ (2007) Taxonomy of shallow-water Bryozoa from the west coast of South Africa. Afr Nat Hist 3:1–58

Freiwald A, Fosså JH, Grehan A, Koslow T, Roberts JM (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge

Gibbons MJ, Barange M, Hutchings L (1995) Zoogeography and diversity of euphausiids around southern Africa. Mar Biol 123:257–268

Gibbons MJ, Abiahy BB, Angel M, Assuncao CML, Bartsch I, Best P, Biseswar R, Bouillon J, Bradford-Grieve JM, Branch W, Burreson E, Cannon L, Casanova J-P, Channing A, Child CA, Compagno L, Cornelius PFS, Dadon JR, David JHM, Day J, Della Croce N, Emschermann P, Erseus C, Esnal G, Gibson R, Griffiths CL, Hay-ward PJ, Heard R, Heemstra P, Herbert D, Hessler R, Higgins R, Hiller N, Hirano YM, Kensley B, Kilburn R, Kornicker L, Lambshead J, Manning R, Marshall D, Mianzan H, Monniot C, Monniot F, Newman W, Nielsen C, Patterson G, Pugh P, Roeleveld M, Ross A, Ryan P, Ryland JS, Samaai T, Schleyer M, Schockaert E, Seapy R, Shiel R, Sluys R, Southward EC, Sulaiman A, Thandar A, van der Land J, van der Spoel S, van Soest R, Vetter E, Vinogradov G, Williams G, Wooldridge T (1999) The taxonomic richness of South Africa's marine fauna: crisis at hand. S Afr J Sci 95:8–12

Grieve C, Brady DC, Polet H (2015) Best practices for managing, measuring and mitigating the benthic impacts of fishing. Mar Stewardship Council Sci Ser 3:81–120

Griffiths CL, Robinson TB, Lange L, Mead A (2010) Marine biodiversity in South Africa: an evaluation of current states of knowledge. PLoS One 5(8):e12008. https://doi.org/10.1371/journal.pone.0012008

Hayward PJ, Cook PL (1979) The South African museum's Meiring Naudé cruises. Part 9, Bryozoa. Ann S Afr Mus 79:43–130

Hayward PJ, Cook PL (1983) The South African Museum's Meiring Naudé cruises. Part 13, Bryozoa II. Ann S Afr Mus 91:1–161

Hayward PJ, Ryland JS (1999) Cheilostomatous Bryozoa, Part 2, Hippothooidea – Celleporoidea. Issue 14 (2nd edn). Field Studies Council for the Linnean Society of London and The Estuarine and Coastal Science Association, Shrewsbury

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc Natl Acad Sci 114 (31):8301–8306

Hooper JNA, Kennedy JA (2002) Small-scale patterns of sponge biodiversity (Porifera) on sunshine coast reefs, eastern Australia. Invertebr Syst 16:637–653

Hooper JNA, Van Soest RWM (eds) (2002) Systema Porifera: a guide to the classification of sponges. 2 volumes. Kluwer Academic/Plenum, New York, 1718 p

Hughes KM, Kaiser MJ, Jennings S, McConnaughey RA, Pitcher R, Hilborn R, Amoroso RO, Collie J, Hiddink JG, Parma AM, Rijnsdorp A (2014) Investigating the effects of mobile bottom fishing on benthic biota: a systematic review protocol. Environ Evid 3(1):23

Joseph B, Sujatha S (2011) Pharmacologically important natural products from marine sponges. J Nat Prod 4:5–12

Kaiser MJ, Hilborn R, Jennings S, Amaroso R, Andersen M, Balliet K, Barratt E, Bergstad OA, Bishop S, Bostrom JL, Boyd C (2016) Prioritization of knowledge needs to achieve best practices for bottom trawling in relation to seabed habitats. Fish Fish 17(3):637–663

Laird MC (2014) Taxonomy, systematics and biogeography of South African Actiniaria and Corallimorpharia. PhD Thesis. University of Cape Town, p 368

Laird MC, Griffiths CL (2016) Additions to the South African sea anemone (Cnidaria, Actiniaria) fauna, with expanded distributional ranges for known species. African Invertebr 57(1):15–37. https://doi.org/10.3897/afrinvertebr.57.8459

Lallemand P, Bergh M, Hansen M, Purves M (2016) Estimating the economic benefits of MSC certification for the South African hake trawl fishery. Fish Res 182:98–115

Lartaud F, Galli G, Raza A, Priori C, Benedetti MC, Cau A, Santangelo G, Iannelli M, Solidoro C, Bramanti L (2017) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forest, the ecology of benthic biodiversity hotspots. Springer International, Cham

Lombard AT, Strauss T, Harris J, Sink K, Attwood C, Hutchings L (2004) South African National spatial biodiversity assessment 2004. S Afr J Mar Sci 25:131–157

Lutjeharms JRE (2006) The Agulhas current. Springer, New York, xiii, 329 pp

Majiedt P, Holness S, Sink K, Oosthuizen A, Chadwick P (2013) Systematic marine biodiversity plan for the west coast of South Africa. South African National Biodiversity Institute, Cape Town, p 46

Makwela MS, Kerwath SE, Götz A, Sink K, Samaai T, Wilke CG (2016) Notes on a remotely operated vehicle survey to describe reef ichthyofauna and habitats – Agulhas Bank, South Africa. Bothalia 46(1):a2108. https://doi.org/10.4102/abc.v46i1.2108

Martin SM, Cambridge TA, Grieve C, Nimmo FM, Agnew DJ (2012) An evaluation of environmental changes within fisheries involved in the marine stewardship council certification scheme. Rev Fish Sci 202:61–69. https://doi.org/10.1080/10641262.2011.654287

Matcher GF, Waterworth SC, Walmsley TA, Matsatsa T, Parker-Nance S, Davies-Coleman MT et al (2017) Keeping it in the family: coevolution of latrunculid sponges and their dominant bacterial symbionts. Microbiol Open 6:1–13. https://doi.org/10.1002/mbo3.417

Miller KA, Thompson KF, Johnston P, Santillo D (2018) An overview of seabed mining including the current state of development, environmental impacts, and knowledge gaps. Front Mar Sci 4:418. https://doi.org/10.3389/fmars.2017.00418

Monniot C, Monniot F, Griffiths CL, Schleyer M (2001) South African ascidians. Ann S Afr Mus 108:1–141

Moyano HI (1979) Bryozoa from Antarctic bays: some ecological aspects. In: Larwood GP, Abbott MB (eds) Advances in bryozoology. Academic, London, pp 383–402

Parker-Nance S, Atkinson LJ (2018) Phylum chordata. In: Atkinson LJ, Sink KJ (eds) Field guide to the offshore marine invertebrates of South Africa. Malachite Marketing and Media, Pretoria, pp 477–490

Payne AI (1989) Cape hakes. In: Payne AI, Crawford RJ, Van Dalsen AP (eds) Oceans of life off southern Africa. Vlaeberg, pp 136–147

Porter S, Schleyer MH (2017) Long-term dynamics of a high-latitude coral reef community at Sodwana Bay, South Africa. Coral Reefs 36:369–382. https://doi.org/10.1007/s00338-016-1531-z

Proches S, Marshall DJ (2002) Diversity and biogeography of southern African intertidal *Acari*. J Biogeogr 29:1201–1215

Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Rossi S, Bramanti L, Gori A, Orejas Saco del Valle C (2017) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Berlin

Samaai T (2002) Systematics of the family Latrunculiidae Topsent (Porifera: Demospongiae) and consideration of the diversity and biogeography of shallow-water sponges of western South Africa. Volumes 1 & 2. Ph.D Thesis, University of the Western Cape, Unpublished

Samaai T (2005) Biodiversity “hotspots”, patterns of richness and endemism, and distribution of marine sponges in South Africa based on actual and interpolation data: a comparative approach. Zootaxa 1358:1–37

Samaai T, Kelly M (2002) Family Latrunculiidae. In: Hooper JNA, Soest Van RWM (eds) Systema Porifera. Guide to the supraspecific classification of sponges and Spongiomorphs (Porifera). Plenum, New York, pp 709–719

Samaai T, Gibbons MJ, Kerwath S, Yemane D, Sink K (2010) Sponge richness along a bathymetric gradient within the iSimangaliso Wetland Park, South Africa. Mar Biodivers 40:205–217

Samaai T, Maduray S, Janson L, Gibbons M, Ngwakum B, Teske P (2017) A new species of habitat-forming *Suberites* (Porifera, Demospongiae, Suberitida) in the Benguela upwelling region (South Africa). Zootaxa 4254:49–81

Santagata S, Ade V, Mahon AR, Wisocki PA, Halanych KM (2018) Compositional differences in the habitat-forming bryozoan communities of the Antarctic shelf. Front Ecol Evol 6:116

Schleyer MH (1999) South African coral communities. In: McClanahan T, Sheppard C, Obura D (eds) Coral reefs of the Indian Ocean: their ecology and conservation. Oxford University Press, New York, pp 83–105

Schleyer MH, Celliers L (2003a) Coral dominance at the reef-sediment interface in marginal coral communities at Sodwana Bay, South Africa. Mar Freshwater Res 54:967–972. https://doi.org/10.1071/MF02049

Schleyer MH, Celliers L (2003b) Biodiversity on the marginal coral reefs of South Africa: what does the future hold? Zool Verhandelingen 345:387–400

Schleyer MH, Celliers L (2005) Modelling reef zonation in the Greater St Lucia Wetland Park, South Africa. Estuarine, Coastal Shelf Sci 63(3):373–384. https://doi.org/10.1016/j.ecss.2004.12.003

Shannon LV (1985) The Benguela ecosystem 1. Evolution of the Benguela, physical features and processes. Oceanogr Mar Biol Annu Rev 23:105–182

Sharma R (2017) Deep-sea mining: current status and future considerations. In: Deep-sea mining 2017. Springer, Cham, pp 3–21. https://doi.org/10.1007/978-3-319-52557-0_1

Shenkar N, Swalla BJ (2011) Global diversity of Ascidiacea. PLoS One 6(6):e20657. https://doi.org/10.1371/journal.pone.0020657

Sink K (2016) Operation Phakisa African coelacanth ecosystem Programme (ACEP) deep secrets cruise: the outer shelf and slope ecosystems of South Africa – RV Algoa Voyage 230, p 77

Sink K, Samaai T (2009) Identifying potential vulnerable marine ecosystems in the offshore environment of South Africa. Technical report. South African National Biodiversity Institute, Cape Town, p 21

Sink KJ, Boshoff W, Samaai T, Timm PG, Kerwath SE (2006) Observations of the habitats and biodiversity of the submarine canyons at Sodwana Bay. S Afr J Sci 102(9):466–474

Sink KJ, Atkinson LJ, Kerwath S, Samaai T (2010) Assessment of offshore benthic biodiversity on the Agulhas Bank and the potential role of petroleum infrastructure in offshore spatial management. Report prepared for WWF South Africa and PetroSA through a SANBI initiative. South African National Biodiversity Institute, Cape Town, p 78

Sink KJ, Attwood CG, Lombard AT, Grantham H, Leslie R, Samaai T, Kerwath S, Majiedt P, Fairweather T, Hutchings L, van der Lingen C, Atkinson LJ, Wilkinson S, Holness S, Wolf T (2011) Spatial planning to identify focus areas for offshore biodiversity protection in South Africa. Final Report for the Offshore Marine Protected Area Project. South African National Biodiversity Institute, Cape Town

Sink K, Holness S, Harris L, Majiedt P, Atkinson L, Robinson T, Kirkman S, Hutchings L, Leslie R, Lamberth S, Kerwath S, von der Heyden S, Lombard A, Attwood C, Branch G, Fairweather T, Taljaard S, Weerts S, Cowley P, Awad A, Halpern B, Grantham H, Wolf T (2012a) National biodiversity assessment 2011: technical report. Marine and coastal component, vol 4. South African National Biodiversity Institute, Pretoria, p 325

Sink KJ, Wilkinson S, Atkinson LJ, Sims PF, Leslie RW, Attwood CG (2012b) The potential impacts of South Africa's demersal hake trawl fishery on benthic habitats: historical perspectives, spatial analyses, current review, and potential management actions. Unpublished report, South African National Biodiversity Institute, p 75

Sink KJ, Gibbons MJ, Laird MC, Atkinson LJ (2018) Phylum Cnidaria. In: Atkinson LJ, Sink KJ (eds) Field guide to the offshore marine invertebrates of South Africa. Malachite Marketing and Media, Pretoria, pp 65–115

Sink KJ, Sibanda SM, Fielding P, Skowno AL, Franken M, Harris LR, Adams R, Baleta T (2019) Ecosystem protection level. In: Sink KJ, van der Bank MG, Majiedt PA, Harris LR, Atkinson LJ, Kirkman SP, Karenyi N (eds) South African National Biodiversity assessment 2018 technical report. Marine Realm, vol 4. South African National Biodiversity Institute, Pretoria. http://hdl.handle.net/20.500.12143/6372

Smith AM, Gordon DP (2011) Bryozoans of Southern New Zealand: a field identification guide. In: New Zealand aquatic environment and biodiversity report no. 75. Ministry of Fisheries, Wellington, p 65

Stach LW (1936) Correlation of zoarial form with habitat. J Geol 44:60–65

Sweetman AK, Thurber AR, Levin LA, Smith CR, Levin LA, Moral C, Wei CL, Gooday AJ, Jones DOB, Rex M, Yasuhara M, Ingels J, Ruhl HA, Fieder CA, Danovaro R, Würzberg L, Baco A, Grupe BM, Pasulka A, Meyer KS, Dunlop KM, Henry LA, Roberts MJ (2017) Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anthropocene 5:4. https://doi.org/10.1525/elementa.203

Turpie JK, Beckley LE, Katua SM (2000) Biogeography and the selection of priority areas for conservation of South African coastal fishes. Biol Conserv 92:59–72

Uriz M (1988) Deep-water sponges from the continental shelf and slope off Namibia (south-west Africa): classes Hexactinellida and Demospongiae. Monografías Zool Marina 3:9–157

Van Dover CL, Ardron JA, Escobar E, Gianni M, Gjerde KM, Jaeckel A, Jones DO, Levin LA, Niner HJ, Pendleton L, Smith CR (2017) Biodiversity loss from deep-sea mining. Nat Geosci 10 (7):464. https://doi.org/10.1038/ngeo2983

Van Soest RWM, Boury-Esnault N, Vacelet J, Dohrmann M, Erpenbeck D et al (2012) Global diversity of sponges (Porifera). PLoS One 7(4):e35105. https://doi.org/10.1371/journal.pone.0035105

Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, de Voogd NJ, Alvarez B, Hajdu E, Pisera AB, Manconi R, Schönberg C, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Díaz M-C, Cárdenas P, Carballo JL, Ríos P, Downey R (2019) World Porifera database. https://doi.org/10.14284/359. http://www.marinespecies.org/porifera. Accessed 11 July 2019

Wood ACL, Probert PK, Rowden AA, Smith AM (2012) Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. Aquat Conserv Mar Freshwat Ecosyst 22:547–563

Wood ACL, Rowden AA, Compton TJ, Gordon DP, Probert PK (2013) Habitat-forming bryozoans in New Zealand: their known and predicted distribution in relation to broad-scale environmental variables and fishing effort. PLoS One 8:1–31

Zibrowius H, Gili J (1990) Deep-water scleractinia (Cnidaria: Anthozoa) from Namibia, South Africa, and Walvis Ridge, southeastern Atlantic. Sci Mar 54(1):19–46

Coral and Reef Fish Communities in the Thermally Extreme Persian/Arabian Gulf: Insights into Potential Climate Change Effects

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Abstract Coral reefs are facing global challenges, with climate change causing recurrent coral bleaching events at a faster rate than corals may be able to recover from, and leading to an overall decline of coral cover and shifts in communities across the tropics. Scleractinian corals are ecosystem builders that provide a habitat for numerous marine species, and their loss is disrupting a range of ecosystem functions and services that reefs normally provide. Climate change will continue to warm the world's oceans, leading to thermal conditions similar to those already existing in the Persian/Arabian Gulf (hereafter termed "the Gulf"). Indeed, the Gulf is in the summer the world's hottest sea (SST > 36 °C) and thus represents a "natural laboratory" in which to understand how reefs in other regions might respond under

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increasing temperatures. Recent research has shown that physiological thresholds of Persian/Arabian Gulf corals are higher than elsewhere, allowing them to survive in the Gulf's extreme temperatures. However, these marginal conditions result in coral communities that are low in diversity and comprised mainly of stress-tolerant species that provide limited three-dimensional structure. This low complexity habitat and the environmental extremes are associated with reef fish communities that have lower diversity, abundance, biomass, and size at maturity compared with conspecifics outside of the Gulf, and these fish communities have been shown to function quite differently. As climate change continues, coral reef ecosystems around the world are expected to gradually shift to thermal conditions similar to the present-day Gulf, and as such today's Gulf can provide insights into ecological patterns and processes we can expect in the tropics in the future. However, while Gulf fauna are adapted to extreme temperatures, they live very near their upper thermal threshold each summer. Recent climate change has resulted in recurrent mass bleaching events that have caused widespread loss of coral and knock-on effects on reef-dependent fishes. Thus, paradoxically, on the world's most robust reefs, we may be witnessing the world's first region-wide extirpation of reef fauna as a result of climate change.

Keywords Arabian Gulf · Climate change · Coral bleaching · Coral reef · Extreme environment · Persian Gulf · Scleractinian corals · Thermotolerance

1 Coral Reefs Around the Globe Are Facing Major Challenges in the Face of Climate Change, with Changing Environmental Conditions Progressively Reshaping Coral Reef Ecosystems

Coral reef ecosystems provide us each year with numerous ecosystem services (Moberg and Folke 1999), valued to 40 billion US dollars annually (Conservation International 2008). However, coral reefs around the world are now rapidly deteriorating from thermal stress, repeatedly exposed to ocean temperatures higher than they are able to handle for extensive periods (Burke et al. 2011). Since the development of the fossil fuel industry in the early nineteenth century, CO_2 levels in the atmosphere have risen from 280 ppm in the 1800s to over 410 ppm in 2019, heating both the atmosphere and the world's oceans (Cao and Caldeira 2008; Gruber et al. 2019). In this period, the highest ocean warming rates occurred in the past two decades, with accumulated heat reaching depths below 2000 m (Gleckler et al. 2016). Shallow tropical waters have also experienced numerous temperature anomalies in the recent decades, repeatedly reaching summer temperatures to which coral reefs are not acclimated (Heron et al. 2016; Lough et al. 2018).

Reef-building corals (order Scleractinia) acquire up to 95% of their metabolic needs from photosynthetic dinoflagellates that live within their host's tissue (Muscatine et al. 1983; Muscatine et al. 1984). In periods of thermal stress, the symbiosis between corals and their symbiotic dinoflagellates (family Symbiodiniaceae) is disrupted, and the symbionts are expelled, changing the colour of the coral host to a bright white colour (Weis 2008; Wooldridge 2013). Without symbionts to provide the food and energy it requires for survival, the bleached coral relies on stored reserves for recovery and survival and can die from starvation if new symbionts are not re-acquired in time (Rodrigues and Grottoli 2007).

Coral bleaching has now been reported in every region of the world that hosts coral reefs, and with the rapid recurrence of bleaching events, reefs are struggling to recover, leading to an overall decline in reef-building corals (Pandolfi et al. 2003; Heron et al. 2016; Hughes et al. 2018b). With species-specific susceptibility and resilience from coral bleaching, coral reef assemblages are also changing, shifting to coral assemblages with reduced three-dimensional structure, therefore decreasing the habitat of reef-associated fishes and other reef inhabitants (Hughes et al. 2018a; Darling et al. 2019; Fontoura et al. 2020). Further losses in coral cover and reef complexity will strongly affect ecosystem services that humanity currently benefits from. Recent estimates show that without reefs, annual flood damages would double and annual damage from storms would triple (Beck et al. 2018). With climate change, storms are expected to be stronger and more frequent, likely increasing annual coastal damage and potentially affecting a number of other ecosystem services (Beck et al. 2018; Woodhead et al. 2019). Additionally, the continuous loss and decline in the physical structure of reefs habitats will strongly affect coral reef fisheries (Pratchett et al. 2014), with an estimated loss of 5.4–8.4 billion US dollars per year by 2100, under a high-emission scenario (Speers et al. 2016). This economic loss from reef fishes is likely to have devastating consequences for the estimated billion people whose lives and livelihood rely on reef fish harvests (Speers et al. 2016).

The future of coral reefs is uncertain, but in some already warm regions—such as the Persian/Arabian Gulf (thereafter named “The Gulf”)—corals seem to be naturally adapted to higher temperatures, giving us insights into the processes and potential responses that are likely to occur in many other coral reefs around the globe in the coming decades (Burt et al. 2020).

2 The Gulf Is the World’s Hottest Sea Each Summer and Is, Thus, a Natural Laboratory to Understand How Climate Change Might Affect Reefs Elsewhere in the Future

The Gulf is a relatively young sea that was formed between 12,000 and 9000 years BP when the basin slowly flooded with rising sea levels after the Holocene glacial retreat (Purkis and Riegl 2012). However, its current sea level was only reached between 3000 and 6000 years BP, forming the modern Gulf and its current coastlines (Purkis and Riegl 2012). The Gulf is also relatively shallow, averaging 35 m depth, with a maximum depth of 100 m near its entrance at the Straits of Hormuz (Purser and Seibold 1973). It is characterised by some of the highest temperature, salinity,

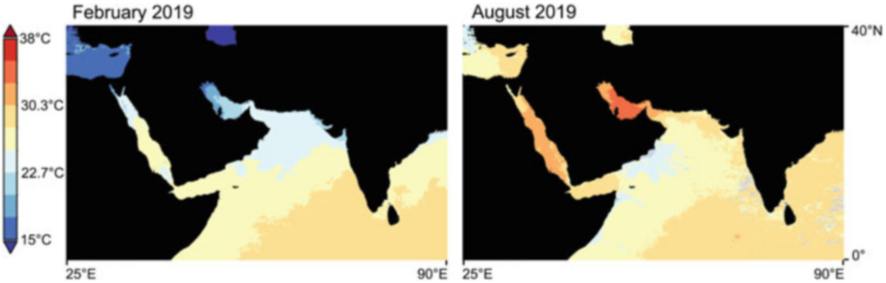

Fig. 1 The Gulf experiences some of the hottest water temperatures in the world in the summer, as well as major seasonal fluctuations in temperatures. In the winter (e.g. February 2019), water temperatures can fall down to 16 °C and less, and in the summer (e.g. August 2019), water temperatures reach 35 °C nearly every year, with shallow water bodies often warming further. The temperatures shown in the map are NASA Aqua/MODIS average monthly sea surface temperatures at 11 microns (Night). The map was produced with the Giovanni online data system, developed and maintained by the NASA GES DISC (available at giovanni.gsfc.nasa.gov)

and nutrient fluctuations encountered in marine ecosystems and represents one of the most extreme environments that scleractinian corals survive in (Riegl and Purkis 2012; Vaughan et al. 2019). Most of the shallow waters of the western and southern Gulf drop down to 16.5 °C in the winter and reach 35 °C in the summer (Fig. 1), with maxima found up to 40 °C in lagoons (Purser and Seibold 1973; John et al. 1990; Foster et al. 2012).

With summer temperatures reaching in excess of 35 °C every summer (Foster et al. 2012), coral bleaching thresholds in the Gulf are among the highest in the world, demonstrating how much corals have the capacity to acclimatise in a warming world (Riegl et al. 2012b). Studies in the SE Gulf have shown that even the more sensitive corals are able to withstand 35 °C temperatures for an average of 22 days before bleaching (Fig. 2) and an average of 27 days before dying (Riegl et al. 2012b). Gulf corals have acclimated to the region's extreme temperatures by adjusting both sides of the partnership: the coral host and the symbiotic dinoflagellates. Indeed, experiments on the brain coral *Platygyra daedalea* revealed that coral larvae from

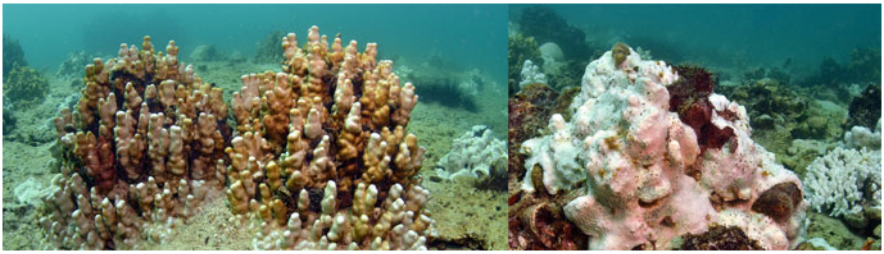

Fig. 2 Coral bleaching occurs regularly in the Gulf when summer temperatures are higher than usual for extended periods, although bleaching thresholds are some of the highest of the world. Left: bleached colony of *Porites harrisoni* showing partial mortality and partial algal overgrowth. Right: bleached colony of *Cyphastrea microphthalma*. Photos: J. Bouwmeester

the Gulf (which have not yet acquired their photosynthetic symbionts) have a higher tolerance to thermal stress than their counterparts outside of the Gulf and have shown to counteract thermal stress by increasing their antioxidant production (Howells et al. 2016a). Thermal tolerance heritability is indeed high for these larvae, which benefit from heat-tolerant gene sequences and gene expression that they acquired through their parental colonies (Kirk et al. 2018; Liew et al. 2020). Similarly, both *in situ* and extracted symbionts showed higher tolerance to thermal stress in populations from the Gulf, in comparison with populations outside the Gulf (Howells et al. 2016a). Recent research has also shown epigenetic changes related to thermal tolerance in the genome of these corals and that these epigenetic modifications are inherited from adults to sperm to larval offspring, providing a potentially much faster means for corals to acclimatise to increasing temperatures than through genetic changes alone (Liew et al. 2020). The symbiont community composition is an equally important factor in thermal tolerance, and studies have shown that most coral species in the environmentally extreme southern Gulf associate with the symbiont *Cladocopium thermophilum*, a species that is unusually tolerant of high temperatures and high salinities and that is prevalent across corals in the southern Gulf (Hume et al. 2013, 2015; D'Angelo et al. 2015; Smith et al. 2017; Howells et al. 2020b).

While Gulf corals exhibit considerable thermal tolerance, they are not immune to coral beaching (Fig. 2). The Gulf has experienced a number of temperature anomalies in recent decades, leading to major bleaching events that have strongly affected coral cover throughout the Gulf. Two back-to-back bleaching events in 1996 and 1998 wiped out large proportions of coral communities in the Gulf (Riegl 1999; Wilson et al. 2002; Rezai et al. 2004), following which recovery was slow in many areas as a result of add-on impacts from major coastal development projects in the region (Sale et al. 2011), although strong recovery was observed in some areas (e.g. Burt et al. 2008). Minor bleaching events returned in 2002 and 2007, followed by three consecutive years of bleaching in 2010, 2011, and 2012 (Riegl and Purkis 2015; Riegl et al. 2018; Burt et al. 2019). The last recorded bleaching event to date was in 2017, which was caused by one of the hottest summers recorded in the history of the region (Burt et al. 2019). In the UAE, corals spent nearly 2 months above bleaching thresholds and were exposed to temperatures above mortality thresholds for nearly 2 weeks, resulting in an overall loss of nearly three-quarters of the coral that year (Burt et al. 2019). Coral reefs often undergo a shift in coral communities following bleaching events (Furby et al. 2013; Hughes et al. 2018a). In the southern Gulf, the biggest shift in coral community occurred following the 1996 and 1998 bleaching events, when *Acropora* assemblages were wiped out at most shallow locations (Sheppard and Loughland 2002), with minimal recovery even 20 years later across much of the southern Gulf (Burt et al. 2011a, 2013a, 2016). While coral diversity was retained in deeper or offshore waters (Burt et al. 2016; Mateos-Molina et al. 2020), the shallow waters of the southern Gulf remain dominated by a low diversity assemblage of robust species, notably poritids and merulinids, which today characterise most southern Gulf coral assemblages (Riegl et al. 2018; Burt et al. 2019).

The Gulf represents one of the most extreme environments in the world where scleractinian corals exist, regularly reaching temperatures that would kill corals in other parts of the world. This acclimation to extreme thermal temperatures and high salinity occurred over a period of 9000–12,000 years, after the Gulf basin was last flooded following the last glaciations. The latest IPCC report predicts that ocean heatwaves are likely to increase 20-fold in frequency at 2 °C warming above pre-industrial levels and could reach a 50-fold increase in frequency if emissions continue to climb (Pörtner et al. 2019). While these changes risk happening at a much faster rate than corals are able to adapt, the Gulf is proof that adaptation is possible, albeit over thousands of years. While the possibility of the effects of climate change slowing down in the near future is highly unlikely, the Gulf offers an insight on how coral communities are likely to be shaped in the future and that thermal thresholds can increase with time under selective pressure. Overall, the Gulf is a unique "natural laboratory" for understanding how climate change might affect reefs elsewhere in the future.

3 The Cost of Surviving in an Extreme Environment Is Low Diversity and Limited Three-Dimensional Structure of Corals

The extreme environmental conditions encountered in the Gulf are selective for corals adapted to these extremes, with Gulf corals surviving in temperatures that would normally cause mortality in other areas (Coles 2003; Burt et al. 2008). As a result, out of the 401 scleractinian coral species that are present in waters surrounding the Arabian Peninsula, only 66 have been recorded in the Gulf (Riegl et al. 2012a; DiBattista et al. 2016; Berumen et al. 2019) although there is still some uncertainty regarding the validity of a few of these records (see Riegl et al. 2012a). However, many shallow coral assemblages in the Gulf have now shifted to a more stress-tolerant assemblage following repetitive bleaching events, with current assemblages mostly composed of sturdy poritids and merulinids (Burt et al. 2011a).

While comprehensive coral checklists exist for the Gulf (e.g. Riegl et al. 2012a; Berumen et al. 2019), they are not readily available for each country. Therefore, to be able to examine spatial patterns in scleractinian coral richness across the Gulf, records from the published literature were compiled for Iraq (Pohl et al. 2014), Kuwait (Downing and Roberts 1993; Hodgson and Carpenter 1995; Benzoni 2006; Benzoni et al. 2007; Riegl et al. 2012a), Saudi Arabia (Coles and Fadlallah 1991; Downing and Roberts 1993; Fadlallah 1996; Riegl et al. 2012a), Bahrain (Burt et al. 2013a), Qatar (Riegl et al. 2012a; Burt et al. 2016; Hoeksema et al. 2018), the UAE (Gulf only) (Riegl et al. 2012a), and Iran (Mostafavi et al. 2007; Samimi-Namin et al. 2009; Shahhosseiny et al. 2011; Riegl et al. 2012a; Rahmani and Rahimian 2013; Ghasemi et al. 2015; Mashini et al. 2015) and were supplemented with recent observations (2016–2018) from the authors in Qatar.

Historical coral richness, which includes every coral record published since the 1980s, varied between 5 species in Iraq and 42 species in Iran (Fig. 3a, Table 1). Qatar followed Iran closely with 38 species. Kuwait, Saudi Arabia, Bahrain, and the

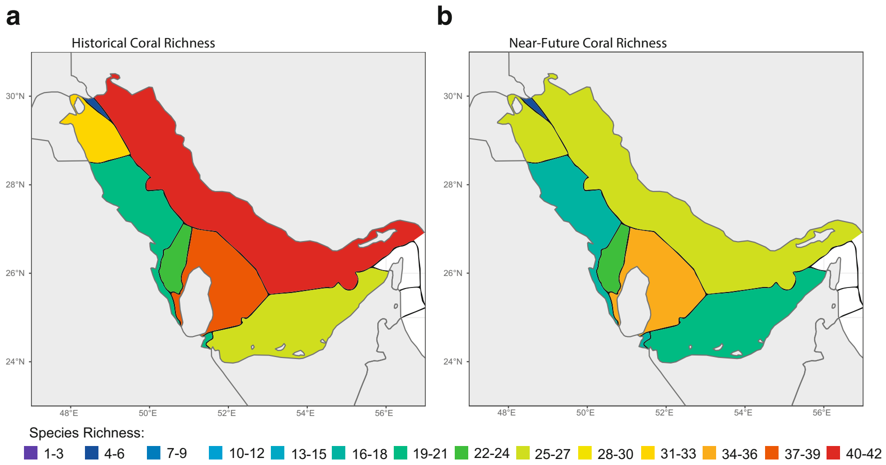

Fig. 3 Spatial patterns in coral richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. (**a**) Historical coral richness, which includes every verified coral species recorded in each country. (**b**) The near-future richness does not include species that have been extirpated from large areas of the Gulf in recent decades and are highly vulnerable to near-future climate change in their remaining Gulf distribution (see species marked with a star* in Table 1) and represents numbers closer to current or near-future coral richness in the Gulf

UAE had a species richness between 21 and 31 species. With a coral richness comparable to the one found in Iran, Qatar likely heavily benefits from natural larval dispersal from Iranian coral communities. Indeed, recent work revealed the presence of wind-driven large-scale eddies that are likely to carry coral larvae from the healthier and more speciose Iranian corals to the more degraded coral assemblages of Qatar and the UAE (Cavalcante et al. 2016). Nonetheless, some species have not recently been recorded in waters from Kuwait, Saudi Arabia, Bahrain, Qatar, and the UAE. These species are mostly branching Acroporidae and Pocilloporidae. Shallow populations of these more sensitive species may have been wiped out following the 1996 and 1998 bleaching events (Sheppard and Loughland 2002) or following the most recent bleaching in 2017 (Burt et al. 2019), potentially leaving the only surviving populations in deeper waters (Mateos-Molina et al. 2020). With populations that may now be restricted to locations further from the shore and potentially less regularly surveyed, current populations of sensitive species are mostly unknown in the western Gulf. Nonetheless, for these species to recover and thrive again throughout the Gulf, fresh larval supply is required. However, studies in the SE Gulf have shown that coral settlement numbers are low (Bento et al. 2017; Burt et al. 2019), with juvenile corals from the Acroporidae and Pocilloporidae families mostly absent, limiting options for the recovery of these populations (Pratchett et al. 2017; Burt and Bauman 2019). Therefore, a second coral richness map was made, excluding those species that are sensitive to thermal stress and that may disappear in the near future in many areas around the Gulf. In the second coral

Table 1 Checklist of zooxanthellate scleractinian corals, in each country that borders the Gulf

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Dendrophylliidae							
Turbinara reniformis		X			x	x	
Turbinaria cf. *patula*					x		
Turbinaria peltata		X	X		x	x	
Turbinaria reniformis		X	X	X	x		x
Poritidae							
Goniopora lobata		X			x		x
Porites harrisoni	x	X	X	X	x	x	x
Porites lobata				X		x	x
Porites lutea		X	X	X	x	x	
Porites cf. *nodifera*						x	
Acroporidae							
*Acropora arabensis**		X	X			x	x
*Acropora clathrata**		X	X	X		x	x
*Acropora downingi**		X	X		x	x	x
Acropora cf. *gemmifera**							x
*Acropora horrida**							x
*Acropora mossambica**							x
*Acropora muricata**							x
*Acropora nasuta**							x
*Acropora pharaonis**						x	x
*Acropora tortuosa**					x		x
Acropora cf. *valida**							x
Alveopora tizardi					x		
*Montipora aequituberculata**		X			x		x
*Montipora danae**							x
*Montipora informis**							x
*Montipora spongiosa**							x
Agariciidae							
Pavona cf. *explanulata*		X			x		
Pavona decussata		X		X	x	x	x
Pavona varians			X				
Siderastreidae							
Siderastrea savignyana		X		X	x	x	x
Pocilloporidae							
Madracis kirbyi		X		X			
*Pocillopora damicornis**			X				x
*Stylophora pistillata**		X	X			x	x
Coscinareidae							
Anomastraea irregularis		X	X	X	x		x
Coscinaraea monile	x	X	X		x	x	x
Fungiidae							
Cycloseris costulata					x		

(continued)

Table 1 (continued)

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Cycloseris curvata		X			x		x
Cycloseris fragilis					x		
Psammocoridae							
Psammocora albopicta		X	X		x		
Psammocora profundacella					x		x
Psammocora stellata		x	X	X	x	x	x
Incertae sedis							
Leptastrea purpurea	x			X	x	x	
Leptastrea transversa		x	X	X	x		x
Plesiastreidae							
Plesiastrea versipora		x		X	x	x	
Merulinidae							
Cyphastrea microphthalma		x	X	X	x	x	x
Cyphastrea serailia		x		X	x		x
Dipsastraea favus	x		X	X	x	x	x
Dipsastraea pallida		x	X	X	x	x	x
Dipsastraea speciosa			X	X	x	x	x
Echinopora hirsutissima							x
Favites abdita				X			
Favites acuticolis	x	x		X	x		
Favites pentagona		x	X	X	x		x
Hydnophora pilosa		x			x		x
Platygyra daedalea		x	X	X	x	x	x
Platygyra lamellina				X	x	x	
Lobophylliidae							
Echinophyllia aspera					x		x
Sclerophyllia maxima		x			x	x	x
Symphyllia radians							x
Acanthastrea echinata		x		X	x	x	x

The species listed abovereflects recent taxonomic changes. Species marked with an * represent corals that are highly sensitive to bleaching and have disappeared from large areas of the Gulf following recent bleaching events, or are likely to do so in the near future

richness map (Fig. 3b), patterns have changed with numbers likely closer to ones that exist today in the southern Gulf and that might exist soon in the remaining Gulf. In this latter scenario, a drop in species is most noticeable in Iran and in Kuwait. Therefore, coral communities in these regions, which still harbour high richness, need to be monitored and regularly assessed, which is frequently not the case (e.g., Kuwait, Alhazeem et al. 2017). Without regular quantitative surveys and bleaching assessments, it is not possible to accurately determine which populations are healthy and which are threatened.

Extreme temperatures clearly play a major role in shaping Gulf coral populations through mortality, but other life-history processes are affected as well. The recurrent bleaching events have been implicated in the reduction in lifespans of corals, preventing many species from reaching the large colony size that they would if left undisturbed (Bauman et al. 2013). Additionally, corals grow slower in the Gulf compared with their counterparts in less extreme environments (Bauman et al. 2013), but contrasting growth trends are found across species. Indeed, in the southern Gulf, calcification in *Cyphastrea microphthalma* is constrained by high temperature maxima and low light, while calcification in *Platygyra daedalea* is limited by low temperature minima (Howells et al. 2018). They are also subject to high prevalence of disease, which is tied to extreme summer temperatures and proximity to population-related pressures (Aeby et al. 2020; Howells et al. 2020a). Finally, the maintenance and post-disturbance recovery of coral populations are highly dependent on a regular supply of coral recruits, produced locally (self-recruitment) or acquired through larval dispersal from further populations (connectivity) (Jones et al. 2009). Corals spawn in April–May in the southern and western Gulf, in May–June in the NW Gulf, and in June and August in Iran, close to the Straits of Hormuz (Howells et al. 2014). In the southern Gulf, their reproductive output is lower than their counterparts outside the Gulf, in at least two species (Howells et al. 2016b), and settlement numbers are drastically lower than in other regions of the world, revealing limited larval supply (Bauman et al. 2014; Bento et al. 2017; Burt and Bauman 2019).

With restricted larval supply, limited coral growth, coral bleaching, and mass mortality being recurrent processes in the Gulf, coral populations in the Gulf have limited opportunities to form the intricate three-dimensional reef framework that can be found in other regions of the world, particularly in the more environmentally extreme southern Gulf. Furthermore, the already low rates of reef accretion may be further diminished by the high bioerosion rates found in some parts of the Gulf (Al-Mansoori et al. 2019). As a result, the Gulf has few true reef frameworks, with coral assemblages often forming coral carpets instead (Fig. 4) (Riegl 1999; Sale et al. 2011), although true reefs exist in the fossil records (Bruthans et al. 2006; Samimi-Namin and Riegl 2012).

Fig. 4 Examples of coral framework in the Gulf. Left: shallow reef dominated by colonies of *Porites harrisoni*. Centre: coral carpets in deeper (18 m depth) waters, dominated by merulinids. Right: *Acropora downingi* populations have survived in deep coral assemblages exposed to less thermal stress. Photos: J. Bouwmeester

4 With a Limited Reef Framework Comes Low Diversity, Abundance, Biomass, Size at Maturity of Fishes, and Different Functional Roles

Fishes of the Gulf are adapted to the region's extreme environment and are capable of withstanding the stress of osmotic and temperature extremes (Coles and Tarr 1990). In addition to environmental pressures, fish communities are restricted by the natural lack of reef complexity in the Gulf and the high turnover in coral communities following regular bleaching events (Paparella et al. 2019). Around 53% of known fish species in the Gulf are coral-associated, and 5% are coral-dependent (Buchanan et al. 2016); therefore, fish communities in the Gulf are impacted by coral mortality events, together with human-driven perturbations such as fishing, pollution, and coastal development (Burt 2014; Buchanan et al. 2016). After two heavy coral mortality events in the southern Gulf in 1996 and 1988, overall fish richness decreased, and there was a functional shift towards more herbivores, reflecting the change of substrate from coral to algae-dominated (Riegl 2002). In fact, an unusual dominance by herbivores is a common feature of reef fish communities in the southern Gulf, suggesting that recurrent disturbance and extreme conditions are having community-wide influence on fishes (Feary et al. 2010; Burt et al. 2011b). In comparison with other regions of the Indo-Pacific, the Gulf is relatively depauperate in fish species due to the Gulf's extreme environmental constraints on adult fishes and the larval supply (Coles 2003; Feary et al. 2010). Fishes in the Gulf add up to a total of 744 recorded species (Eagderi et al. 2019), representing 43% of the total fishes found throughout the Arabian Peninsula (DiBattista et al. 2016). In coral habitats, total fish richness is highest in offshore coral assemblages, but coral-dependent fish richness is highest on inshore coral reefs which are typically more widespread (Coles and Tarr 1990; Buchanan et al. 2016). However, due to the extensive loss of reefs in coastal areas of the Gulf, particularly in the southwest (i.e. Bahrain, Qatar, and the UAE), an impoverishment of fish assemblages on coastal coral assemblages has been recently observed, with concerns for their conservation (Buchanan et al. 2019). The pervasive extreme environmental stress of the southern Gulf has also been shown to reduce the diversity and productivity of cryptic reef fish species, which has important knock-on implications for the wider fish community as cryptic fish species serve as a primary food source for many larger species on reefs (Brandl et al. 2020).

Comprehensive species lists at the country level are not available for all countries surrounding the Gulf. Therefore, to examine spatial patterns in fish richness across the region, six ecologically important fish families that were more likely to have observation records in the literature than other groups were selected, for which we compiled a species list from the published literature, supplemented with recent observations (2016–2018) from the authors in Qatar. We chose two reef-dependent herbivore families, surgeonfishes (Acanthuridae) and parrotfishes (Scaridae); one corallivore family, butterflyfishes (Chaetodontidae); and three predator families, snappers (Lutjanidae), sea breams (Sparidae), and groupers (Serranidae), and compiled species data from Iraq (Hussain et al. 1988; Jawad et al. 2018; Mhaisen et al. 2018), Kuwait (Downing 1985; Bishop 2003), Saudi Arabia (Krupp and Almarri 1996), Bahrain (Smith and Saleh 1987), Qatar (Sivasubramaniam and Ibrahim 1982; Al-Ansi et al. 2002), the UAE (Gulf only) (Burt et al. 2009; Feary et al. 2010; Burt et al. 2011b, 2013b; Grandcourt et al. 2011), and Iran (Sahafi 2000; Rezai and Savari 2004; Shokri et al. 2005; Raeisi et al. 2011; Khatami et al. 2014; Esmaeili et al. 2015; Tavakoli-Kolour et al. 2015).

Overall, Kuwait, Saudi Arabia, and Iran had the highest fish richness, when only considering the six families, followed by Qatar, Iraq, Bahrain, and the UAE (Fig. 5, Table 2). The northwestern (Saudi Arabia, Kuwait, Iraq) and northeastern Gulf (Iran) experience less extreme environmental conditions than the southern Gulf (Fig. 1, Moradi and Kabiri 2015), which explains why fish richness is higher in these regions, such as within the Lutjanidae and Serranidae families. Saudi Arabian waters also host some of the few complex reef structures that exist in the region (Downing 1985; Coles and Tarr 1990), offering a higher diversity of habitats to fishes and invertebrates. This is here mostly reflected in the snappers (Lutjanidae), groupers (Serranidae), and seabreams (Sparidae), which are some of the larger fishes also commercially targeted by artisanal fisheries (Siddeek et al. 1999). Kuwait showed similar patterns, and Iraq had overall healthy numbers (particularly in the speciose Lutjanidae and Sparidae families) given its smaller surface and given that the presence of coral communities was only recently discovered within its jurisdictional waters (Pohl et al. 2014). Iran showed the highest fish richness for butterflyfishes, parrotfishes, snappers, and groupers, particularly in the latter two families. These fishes are mostly reef-dependent, and their higher richness likely reflects on the higher coral diversity present in Iran, where waters are deeper and cooler than elsewhere in the Gulf (Grandcourt 2012). Bahrain has a lower richness than its neighbour countries in all families, but the country expands over a smaller surface and is mostly surrounded by shallow waters, limiting both coral and fish communities to only the tougher ones that are adapted to the extreme shallow conditions (Smith and Saleh 1987). In contrast, Qatar has access to much deeper waters, where the less extreme conditions leave room for higher diversity (Walton et al. 2018). The UAE, in the southern Gulf, likely has some of the most challenging conditions for corals and fishes, which is reflected in its low fish richness in all families (Finucci et al. 2019).

A particular characteristic of Gulf fishes that is not found elsewhere is the strong seasonal fluctuation in species richness and abundance (Coles and Tarr 1990; Burt et al. 2009). In the southern Gulf, for example, total commercial fish biomass is the highest in the mid-winter and lowest in the hot mid-summer months, although different patterns emerge when considering individual species (Grandcourt 2012). Indeed, while most species are overall more abundant in the winter, a small group of fishes show the opposite pattern with the highest abundance in the summer, and some fishes show no seasonal change (Grandcourt 2012). While no direct evidence exists from tagging studies, it is assumed that the seasonal fluctuations in abundance result from movement of fishes between shallower and deeper waters (Coles and Tarr 1990; Grandcourt 2012). In addition to seasonal movements, some fishes have

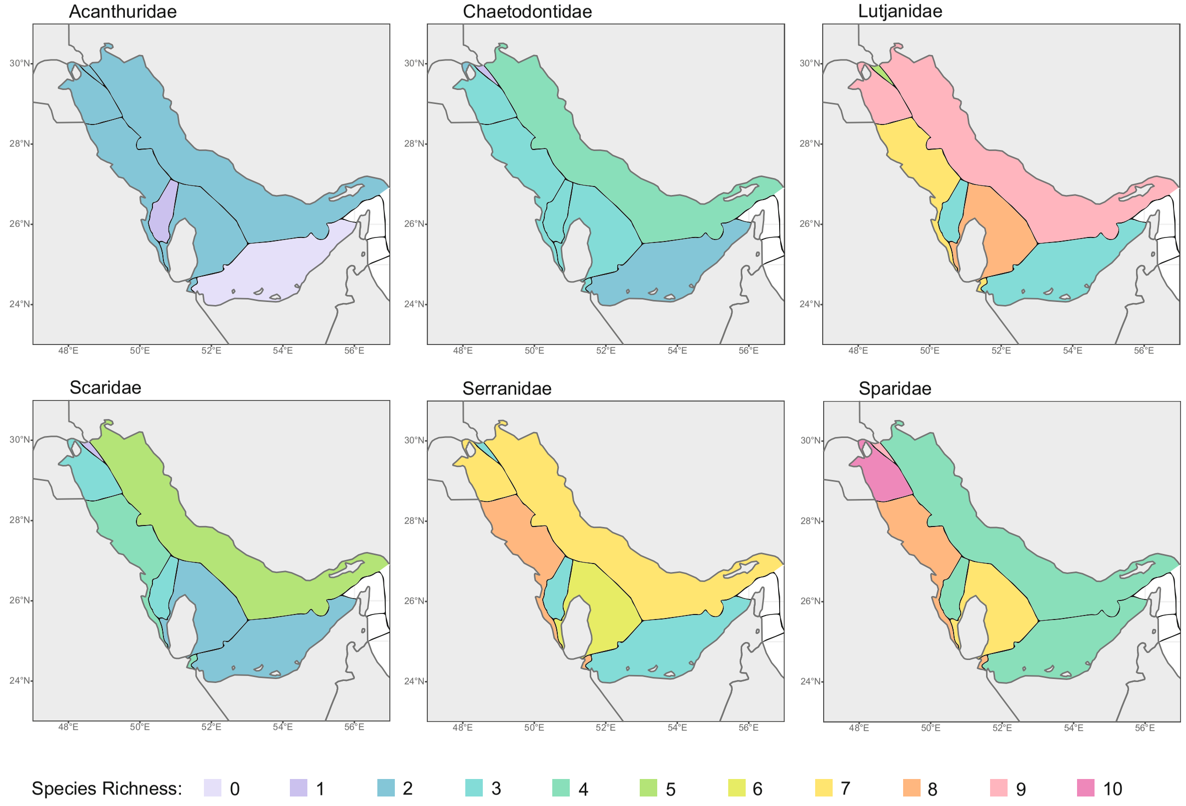

Fig. 5 Spatial patterns in fish richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. The families represented are the surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), snappers (Lutjanidae), parrotfishes (Scaridae), groupers (Serranidae), and seabreams (Sparidae)

Table 2 Species checklist for each of the six families studied, in each country that borders the Gulf

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Acanthuridae							
Acanthurus sohal	x	x	x		x		x
Zebrasoma xanthurum	x	x	x	x	x		x
Chaetodontidae							
Chaetodon melapterus		x	x	x	x	x	x
Chaetodon nigropunctatus		x	x	x	x	x	x
Chaetodon vagabundus							x
Heniochus acuminatus	x	x	x	x	x		x
Lutjanidae							
Lutjanus argentimaculatus		x	x	x		x	x
Lutjanus ehrenbergii		x	x	x	x	x	x
Lutjanus fulviflamma	x	x	x	x	x	x	x
Lutjanus johnii	x	x			x		x
Lutjanus kasmira					x		
Lutjanus lutjanus		x	x				x
Lutjanus malabaricus		x			x		x
Lutjanus quinquelineatus		x	x				x
Lutjanus rivulatus	x						
Lutjanus russellii	x	x	x		x		x
Lutjanus sanguineus					x		
Pinjalo pinjalo	x	x	x		x		x
Scaridae							
Chlorurus sordidus		x	x	x			x
Scarus ferrugineus			x				x
Scarus ghobban	x	x	x	x	x	x	x
Scarus persicus		x	x	x	x	x	x
Scarus psittacus							x
Serranidae							
Aethaloperca rogaa			x		x		
Cephalopholis formosa							x
Cephalopholis hemistiktos		x	x	x	x	x	x
Epinephelus areolatus	x	x	x		x		x
Epinephelus bleekeri	x		x				x
Epinephelus coeruleopunctatus		x	x	x			
Epinephelus chlorostigma					x		x
Epinephelus coioides	x	x	x	x	x	x	x
Epinephelus latifasciatus		x					
Epinephelus multinotatus		x	x				
Epinephelus polylepis		x					
Epinephelus stoliczkae					x	x	x
Pseudanthias townsendi			x				

(continued)

Table 2 (continued)

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Sparidae							
Acanthopagrus arabicus	x	x			x	x	x
Acanthopagrus berda	x	x	x	x			
Acanthopagrus bifasciatus	x	x	x	x	x	x	x
Argyrops spinifer	x	x	x		x		x
Cheimerius nufar		x	x				
Crenidens crenidens	x	x	x		x		
Diplodus kotschyi	x	x	x	x	x	x	x
Pagellus affinis					x		
Rhabdosargus haffara	x	x	x				
Rhabdosargus sarba	x	x			x	x	
Sparidentex hasta	x	x	x	x			

The species names listed above reflect recent taxonomic changes

adapted to the Gulf's extreme environmental conditions by altering their diets. Indeed, in a seasonal study conducted in the SE Gulf, three fish species, which outside of the Gulf feed predominantly on algae, sponges, or plankton, were found to have coral-dominated diets, with diets even more dominated by coral in the hotter summer months, potentially to meet their energy budgets when thermal stress is at its highest (Shraim et al. 2017). These observations are supported by a recent field and lab study which showed susbtantial changes in feeding behavior of the damselfish P*omacentrus trichrourus* across seasons, with feeding capacity apparently constrained by both extreme heat and cold across seasons (D'Agostino et al. 2020).

The pervasive loss of coastal coral assemblages in the Gulf has triggered a shift in coral-associated fish assemblages (Feary et al. 2013). Hence, with the absence of true reef frameworks throughout the Gulf, submerged artificial structures play an important ecological role in the region, potentially serving as stepping stones between natural habitats (Burt et al. 2009, 2012). They have inadvertently become major artificial reefs, attracting fishes through the complex three-dimensional framework that they offer (Burt et al. 2012). Many of these structures are extensively spread throughout the Gulf, mainly in coastal areas (e.g. breakwaters, groynes, jetties, and seawalls) (Burt et al. 2012), but also offshore, with almost 900 oil and gas platforms and related-submerged infrastructures (Sheppard et al. 2010). The platforms are each surrounded by a strict 500 m no-entrance policy, and permits are required to approach platforms within 5 km. Therefore, fishing activities are exceptionally well-controlled in these areas, which act as protected areas for corals and associated communities such as fishes. In Qatari jurisdictional waters, the largest concentration of oil and gas platforms is located in the Al Shaheen Oil Field, *ca*. 100 km offshore. A high fish diversity (83 species) was reported around surveyed platforms (Torquato et al. 2017), including large aggregations of the whale shark *Rhincodon typus* (Fig. 6) found to feed on high amounts of nutritious food, i.e. mackerel tuna

Fig. 6 Offshore oil and gas platforms are natural preserves for Gulf fishes, including the whale shark *Rhincodon typus*. Photographs: J. Bouwmeester

(*Euthynnus affinis*) eggs, in that area (Robinson et al. 2013). Further work still needs to be conducted since these offshore assemblages are understudied and their role as potential stepping stones among natural reefs is still poorly understood.

Despite the rapid growth of reef science in the Arabian region in the past decade (Burt 2013; Vaughan and Burt 2016), substantial baseline knowledge gaps remain in the region (Feary et al. 2013). Annotated fish checklists have not been conducted in every country, and limited fish surveys are available to compare abundance and biomass patterns across the Gulf (Eagderi et al. 2019). Additionally, coral research is limited in Iran due to restricted access and remote sites, limiting research opportunities in the country that has the longest coastline in the Gulf. Nevertheless, the Gulf is showing that many fishes are capable of adapting to its extreme conditions, at the cost of limited diversity, abundance, biomass, and functional roles. Modelling environmental scenarios is crucial to describe plausible trajectories of the different aspects of the future of the Gulf in general and the fish assemblages in particular.

5 Today's Gulf Coral Communities Can Offer Insights into What Other Reefs Around the Globe May Look Like in the Future

Coral reefs around the world are deteriorating because of climate change (Hughes et al. 2017). Warming waters are affecting the partnership between corals and their symbiotic algae resulting in bleaching events that are now happening at a faster rate than coral communities are able to recover from. Coral assemblages around the world will change, and the Gulf can offer strong insights into how reef fauna will cope with and respond to increasing temperatures (Burt et al. 2020). A loss of diversity, coral cover, and reef complexity are expected, which will have important consequences on reef-dependent fauna, while those corals that acclimate or adapt will need to undergo major physiological changes. Gulf corals provide an opportunity to understand and study adaptations to climate change at the physiological, genetic, and ecological level. Research from the Gulf may help identify corals that are likely to adapt and help direct research and conservation efforts towards those species.

Nonetheless, the Gulf is facing challenges in the future with water temperatures starting to rise above the corals' already high thresholds of bleaching and mortality. While the Gulf's coral communities and associated fish fauna represent a valuable asset for climate science (Burt et al. 2014), even these hardy fauna are under threat. While these are the most thermally tolerant reef species on the planet, they live within a degree of their upper thermal limits each summer. Therefore, as climate change ramps up ocean temperatures globally, the Gulf is likely to be among the first to experience the push across their upper thermal threshold. The increasing magnitude and frequency of bleaching events in the Gulf in recent years suggest that this process may occur sooner rather than later and that the region is at real risk of losing one of its most economically important and biodiverse ecosystems in the coming decades.

References

Al-Ansi M, Abdel-Moati M, Al-Ansari I (2002) Causes of fish mortality along the Qatari waters (Arabian Gulf). Int J Environ Stud 59:59–71

Alhazeem S, Burt J, Alsaffar A, Chen W, Al-Kandari M (2017) Long-term coral community stability in a disturbed marginal reef in Kuwait. J Water Res Ocean Sci 6:85–89. https://doi.org/10.11648/j.wros.20170606.12

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA (2020) Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39:829–846. https://doi.org/10.1007/s00338-020-01928-4

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA (2020) Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39:829-846 https://doi.org/10.1007/s00338-020-01928-4

Bauman AG, Pratchett MS, Baird AH, Riegl B, Heron SF, Feary DA (2013) Variation in the size structure of corals is related to environmental extremes in the Persian Gulf. Mar Environ Res 84:43–50

Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (2014) Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). Mar Ecol Prog Ser 499:115–126

Beck MW, Losada IJ, Menéndez P, Reguero BG, Díaz-Simal P, Fernández F (2018) The global flood protection savings provided by coral reefs. Nat Commun 9:2186

Bento R, Feary DA, Hoey AS, Burt JA (2017) Settlement patterns of corals and other benthos on reefs with divergent environments and disturbances histories around the northeastern Arabian peninsula. Front Mar Sci 4:305

Benzoni F (2006) *Psammocora albopicta* sp. nov., a new species of Scleractinian coral from the Indo-West Pacific (Scleractinia; Siderastreidae). Zootaxa 1358:49–57

Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P (2007) Debating phylogenetic relationships of the scleractinian Psammocora: molecular and morphological evidences. Contrib Zool 76:35–54

Berumen ML, Arrigoni R, Bouwmeester J, Terraneo TI, Benzoni F (2019) Corals of the Red Sea. In: Voolstra CR, Berumen ML (eds) Coral reefs of the Red Sea. Springer, Cham, pp 123–155

Bishop J (2003) History and current checklist of Kuwait's ichthyofauna. J Arid Environ 54:237–256

Brandl SJ, Johansen JL, Casey JM, Tornabene L, Morais RA, Burt JA (2020) Extreme environmental conditions reduce coral reef fish biodiversity and productivity. Nat Commun 11:3832. https://doi.org/10.1038/s41467-020-17731-2

Bruthans J, Filippi M, Geršl M, Zare M, Melková J, Pazdur A, Bosák P (2006) Holocene marine terraces on two salt diapirs in the Persian Gulf, Iran: age, depositional history and uplift rates. J Quat Sci 21:843–857

Buchanan JR, Krupp F, Burt JA, Feary DA, Ralph GM, Carpenter KE (2016) Living on the edge: vulnerability of coral-dependent fishes in the Gulf. Mar Pollut Bull 105:480–488

Buchanan JR, Ralph GM, Krupp F, Harwell H, Abdallah M, Abdulqader E, Al-Husaini M, Bishop JM, Burt JA, Choat JH (2019) Regional extinction risks for marine bony fishes occurring in the Persian/Arabian Gulf. Biol Conserv 230:10–19

Burke LM, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, DC

Burt JA (2014) The environmental costs of coastal urbanization in the Arabian Gulf. City 18:760–770

Burt JA, Bauman AG (2019) Suppressed coral settlement following mass bleaching in the southern Persian/Arabian Gulf. Aquat Ecosyst Health Manage. https://doi.org/10.1080/14634988.2019.1676024

Burt JA, Bartholomew A, Usseglio P (2008) Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. Mar Biol 154:27–36

Burt JA, Bartholomew A, Usseglio P, Bauman A, Sale P (2009) Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? Coral Reefs 28:663–675

Burt JA, Al-Harthi S, Al-Cibahy A (2011a) Long-term impacts of coral bleaching events on the world's warmest reefs. Mar Environ Res 72:225–229

Burt JA, Feary DA, Bauman AG, Usseglio P, Cavalcante GH, Sale PF (2011b) Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. ICES J Mar Sci 68:1875–1883

Burt JA, Bartholomew A, Feary DA (2012) Man-made structures as artificial reefs in the Gulf coral reefs of the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 171–186

Burt J (2013) The growth of coral reef science in the Gulf: a historical perspective. Mar Pollut Bull 72:289–301. https://doi.org/10.1016/j.marpolbul.2013.05.016

Burt JA, Al-Khalifa K, Khalaf E, AlShuwaikh B, Abdulwahab A (2013a) The continuing decline of coral reefs in Bahrain. Mar Pollut Bull 72:357–363

Burt JA, Feary DA, Cavalcante G, Bauman AG, Usseglio P (2013b) Urban breakwaters as reef fish habitat in the Persian Gulf. Mar Pollut Bull 72:342–350

Burt JA, van Lavieren H, Feary D (2014) Persian Gulf reefs: an important asset for climate science in urgent need of protection. Ocean Challenge 20:49–56

Burt JA, Smith EG, Warren C, Dupont J (2016) An assessment of Qatar's coral communities in a regional context. Mar Pollut Bull 105:473–479

Burt JA, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. Coral Reefs 38:567–589

Burt JA, Camp EF, Enochs IC, Johansen JL, Morgan KM, Riegl B, Hoey AS (2020) Insights from extreme coral reefs in a changing world. Coral Reefs 39:495–507. https://doi.org/10.1007/s00338-020-01966-y

Cao L, Caldeira K (2008) Atmospheric CO_2 stabilization and ocean acidification. Geophys Res Lett 35:L19609

Cavalcante GH, Feary DA, Burt JA (2016) The influence of extreme winds on coastal oceanography and its implications for coral population connectivity in the southern Arabian Gulf. Mar Pollut Bull 105:489–497

Coles SL (2003) Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific region. Atoll Res Bull 507:1–19

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. Coral Reefs 9:231–237

Coles SL, Tarr BA (1990) Reef fish assemblages in the western Arabian Gulf: a geographically isolated population in an extreme environment. Bull Mar Sci 47:696–720

Conservation International (2008) Economic values of coral reefs, mangroves, and seagrasses: a global compilation. Center for Applied Biodiversity Science, Arlington

D'Angelo C, Hume BCC, Burt J, Smith EG, Achterberg EP, Wiedenmann J (2015) Local adaptation constrains the distribution potential of heat-tolerant *Symbiodinium* from the Persian/Arabian Gulf. ISME J 9:2551

D'Agostino D, Burt JA, Reader T, Vaughan GO, Chapman BB, Santinelli V, Cavalcante GH, Feary DA (2020) The influence of thermal extremes on coral reef fish behaviour in the Arabian/Persian Gulf. Coral Reefs 39:733–744. https://doi.org/10.1007/s00338-019-01847-z

Darling ES, McClanahan TR, Maina J, Gurney GG, Graham NAJ, Januchowski-Hartley F, Cinner JE, Mora C, Hicks CC, Maire E, Puotinen M, Skirving WJ, Adjeroud M, Ahmadia G, Arthur R, Bauman AG, Beger M, Berumen ML, Bigot L, Bouwmeester J, Brenier A, Bridge TCL, Brown E, Campbell SJ, Cannon S, Cauvin B, Chen CA, Claudet J, Denis V, Donner S, Estradivari FN, Feary DA, Fenner D, Fox H, Franklin EC, Friedlander A, Gilmour J, Goiran C, Guest J, Hobbs J-PA, Hoey AS, Houk P, Johnson S, Jupiter SD, Kayal M, C-y K, Lamb J, Lee MAC, Low J, Muthiga N, Muttaqin E, Nand Y, Nash KL, Nedlic O, Pandolfi JM, Pardede S, Patankar V, Penin L, Ribas-Deulofeu L, Richards Z, Roberts TE, Rodgers KS, Safuan CDM, Sala E, Shedrawi G, Sin TM, Smallhorn-West P, Smith JE, Sommer B, Steinberg PD, Sutthacheep M, Tan CHJ, Williams GJ, Wilson S, Yeemin T, Bruno JF, Fortin M-J, Krkosek M, Mouillot D (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nat Ecol Evol 3:1341–1350

DiBattista JD, Roberts MB, Bouwmeester J, Bowen BW, Coker DJ, Lozano-Cortés DF, Howard Choat J, Gaither MR, Hobbs J-PA, Khalil MT, Kochzius M, Myers RF, Paulay G, Robitzch VSN, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toonen RJ, Westneat MW, Williams ST, Berumen ML (2016) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. J Biogeogr 43:423–439

Downing N (1985) Coral reef communities in an extreme environment: the northwestern Arabian Gulf. In: Proceedings of 5th international coral reef congress, vol 6, pp 343–348

Downing N, Roberts C (1993) Has the Gulf War affected coral reefs of the northwestern Gulf? Mar Pollut Bull 27:149–156

Eagderi S, Fricke R, Esmaeili HR, Jalili P (2019) Annotated checklist of the fishes of the Persian Gulf: diversity and conservation status. Iran J Ichthyol 6:1–171

Esmaeili HR, Masoudi M, Mehraban HR (2015) Assignment of Acanthopagrus populations in the Persian Gulf drainage system of Iran to *Acanthopagrus arabicus* Iwatsuki, 2013 (Perciformes: Sparidae). Iran J Ichthyol 1:23–28

Fadlallah YH (1996) Synchronous spawning of *Acropora clathrata* coral colonies from the western Arabian Gulf (Saudi Arabia). Bull Mar Sci 59:209–216

Feary D, Burt J, Bauman A, Usseglio P, Sale P, Cavalcante G (2010) Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? J Fish Biol 77:1931–1947

Feary DA, Burt JA, Bauman AG, Al Hazeem S, Abdel-Moati MA, Al-Khalifa KA, Anderson DM, Amos C, Baker A, Bartholomew A (2013) Critical research needs for identifying future changes in Gulf coral reef ecosystems. Mar Pollut Bull 72:406–416

Finucci B, Hurst R, Bagley N, Al Dhaheri S, Grandcourt E (2019) Diversity, abundance, behaviour, and catchability of fishes from trap catch and underwater video in the Arabian Gulf. Fish Res 220:105342

Fontoura L, Zawada KJ, D'agata S, Álvarez-Noriega M, Baird AH, Boutros N, Dornelas M, Luiz OJ, Madin JS, Maina JM (2020) Climate-driven shift in coral morphological structure predicts decline of juvenile reef fishes. Glob Chang Biol 26:557–567

Foster K, Foster G, Al-Cibahy AS, Al-Harthi S, Purkis SJ, Riegl BM (2012) Environmental setting and temporal trends in southeastern Gulf coral communities. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 51–70

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of Central Red Sea corals during a major bleaching event. Coral Reefs 32:505–513

Ghasemi S, Mola N, Hoseinpour M, Hosseini-Tayefeh F, Naji A, Pakravan J (2015) Coral diversity of Hengam Island, Persian Gulf, Iran. J Appl Environ Biol Sci 5:43–52

Gleckler PJ, Durack PJ, Stouffer RJ, Johnson GC, Forest CE (2016) Industrial-era global ocean heat uptake doubles in recent decades. Nat Clim Chang 6:394–398

Grandcourt E (2012) Reef fish and fisheries in the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 127–161

Grandcourt E, Al Abdessalaam T, Francis F, Al Shamsi A (2011) Demographic parameters and status assessments of *Lutjanus ehrenbergii*, *Lethrinus lentjan*, *Plectorhinchus sordidus* and *Rhabdosargus sarba* in the southern Arabian Gulf. J Appl Ichthyol 27:1203–1211

Gruber N, Clement D, Carter BR, Feely RA, Van Heuven S, Hoppema M, Ishii M, Key RM, Kozyr A, Lauvset SK (2019) The oceanic sink for anthropogenic CO_2 from 1994 to 2007. Science 363:1193–1199

Heron SF, Maynard JA, Van Hooidonk R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985–2012. Sci Rep 6:38402

Hodgson G, Carpenter KE (1995) Scleractinian corals of Kuwait. Pac Sci 49:227–246

Hoeksema BW, Bouwmeester J, Range P, Ben-Hamadou R (2018) A large aggregation of self-fragmenting mushroom corals in the Arabian/Persian Gulf. Ecology 99:1236–1238

Howells E, Abrego D, Vaughan G, Burt J (2014) Coral spawning in the Gulf of Oman and relationship to latitudinal variation in spawning season in the northwest Indian Ocean. Sci Rep 4:7484

Howells EJ, Abrego D, Meyer E, Kirk NL, Burt JA (2016a) Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. Glob Chang Biol 22:2702–2714

Howells EJ, Ketchum RN, Bauman AG, Mustafa Y, Watkins KD, Burt JA (2016b) Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. Mar Pollut Bull 105:532–539

Howells EJ, Dunshea G, McParland D, Vaughan GO, Heron SF, Pratchett MS, Burt JA, Bauman AG (2018) Species-specific coral calcification responses to the extreme environment of the southern Persian Gulf. Front Mar Sci 5:56

Howells E, Vaughan G, Work T, Burt J, Abrego D (2020a) Annual outbreaks of coral disease coincide with extreme seasonal warming. Coral Reefs 39:771–781. https://doi.org/10.1007/s00338-020-01946-2

Howells EJ, Bauman AG, Vaughan GO, Hume BCC, Voolstra CR, Burt JA (2020b) Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility. Mol Ecol 29:899. https://doi.org/10.1111/mec.15372

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G (2018a) Global warming transforms coral reef assemblages. Nature 556:492–496

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC (2018b) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hume B, D'angelo C, Burt J, Baker AC, Riegl B, Wiedenmann J (2013) Corals from the Persian/Arabian Gulf as models for thermotolerant reef-builders: prevalence of clade C3 *Symbiodinium*, host fluorescence and ex situ temperature tolerance. Mar Pollut Bull 72:313–322

Hume BC, D'Angelo C, Smith EG, Stevens JR, Burt J, Wiedenmann J (2015) *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. Sci Rep 5:8562

Hussain N, Naiama A, Al-Hassan L (1988) Annotated check list of the fish fauna of Khor Al-Zubair, north west of the Arabian Gulf, Iraq. Acta Ichthyol Piscat 8:17–24

Jawad LA, Faddagh Ziyadi M, Näslund J, Pohl T, Al-Mukhtar MA (2018) Checklist of the fishes of the newly discovered coral reef in Iraq, north-west Arabian Gulf, with 10 new records to the Arabian Gulf. Aqua, J Ichthyol Aquat Biol 24:89–138

John V, Coles S, Abozed A (1990) Seasonal cycles of temperature, salinity and water masses of the western Arabian Gulf. Oceanol Acta 13:273–281

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325

Khatami S, Valinassab T, Tavakoli-Kolour P (2014) Identification and assess anthropogenic impacts on species richness of coral reef fishes in Larak Island, Persian Gulf. Int J Mar Sci 4:1–5

Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E (2018) Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf. Mol Ecol 27:5180–5194

Krupp F, Almarri MA (1996) Fishes and fish assemblages of the Jubail Marine Wildlife Sanctuary. In: Krupp F, Abuzinada AH, Nader LA (eds) A Marine Wildlife Sanctuary for the Arabian Gulf environmental research and conservation following the 1991 Gulf War oil spill NCWCD. Riyadh and Senckenberg Research Institute, Frankfurt a.M., pp 339–350

Liew YJ, Howells EJ, Wang X, Michell CT, Burt JA, Idaghdour Y, Aranda M (2020) Intergenerational epigenetic inheritance in reef-building corals. Nat Clim Chang 10:254. https://doi.org/10.1038/s41558-019-0687-2

Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. Sci Rep 8:6079

Mashini AG, Parsa S, Mostafavi PG (2015) Comparison of *Symbiodinium* populations in corals from subtidal region and tidal pools of northern coasts of Hengam Island, Iran. J Exp Mar Biol Ecol 473:202–206

Mateos-Molina D, Antonopoulou M, Baldwin R, Bejarano I, Burt JA, Garcia-Charton JA, Al-Ghais SM, Walgamage J, Taylor OJS (2020) Applying an integrated approach to coastal marine habitat mapping in the north-western United Arab Emirates. Mar Environ Res 161:105095. https://doi.org/10.1016/j.marenvres.2020.105095

Mhaisen FT, Ali AH, Khamees NR (2018) Marine fish parasitology of Iraq: a review and checklists. Biol Appl Environ Res 2:231–297

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233

Moradi M, Kabiri K (2015) Spatio-temporal variability of SST and chlorophyll-a from MODIS data in the Persian Gulf. Mar Pollut Bull 98:14–25

Mostafavi PG, Fatemi SMR, Shahhosseiny MH, Hoegh-Guldberg O, Loh WKW (2007) Predominance of clade D Symbiodinium in shallow-water reef-building corals off Kish and Larak Islands (Persian Gulf, Iran). Mar Biol 153:25–34

Muscatine L, Falkowski P, Dubinsky Z (1983) Carbon budgets in symbiotic associations. In: Schwemmler W, Schenk H (eds) Endocytobiology II. Walter de Gruyter, Berlin, pp 649–658

Muscatine L, Falkowski P, Porter J, Dubinsky Z (1984) Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proc R Soc Lond Ser B Biol Sci 222:181–202

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJ, Paredes G (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Paparella F, Xu C, Vaughan GO, Burt JA (2019) Coral bleaching in the Persian/Arabian Gulf is modulated by summer winds. Front Mar Sci 6:205

Pohl T, Al-Muqdadi SW, Ali MH, Fawzi NA-M, Ehrlich H, Merkel B (2014) Discovery of a living coral reef in the coastal waters of Iraq. Sci Rep 4:4250

Pörtner H, Roberts D, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Nicolai M, Okem A, Petzold J (2019) IPCC special report on the ocean and cryosphere in a changing climate. IPCC Intergovernmental Panel on Climate Change, Geneva

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain 7:37–43

Pratchett MS, Baird AH, Bauman AG, Burt JA (2017) Abundance and composition of juvenile corals reveals divergent trajectories for coral assemblages across the United Arab Emirates. Mar Pollut Bull 114:1031–1035

Purkis SJ, Riegl BM (2012) Geomorphology and reef building in the SE Gulf coral reefs of the Gulf. Springer, Dordrecht, pp 33–50

Purser B, Seibold E (1973) The principal environmental factors influencing Holocene sedimentation and diagenesis in the Persian Gulf. In: Purser BH (ed) The Persian Gulf. Springer, Heidelberg, pp 1–9

Raeisi H, Daliri M, Paighambari SY, Shabani MJ, Bibak M, Davoodi R (2011) Length-weight relationships, condition factors and relative weight of five fish species of Bushehr waters, Northern Persian Gulf. Afr J Biotechnol 10:19181–19186

Rahmani M, Rahimian H (2013) Preliminary study on *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) of the Persian Gulf, with emphasis on the north and northeastern areas. Turk J Zool 37:308–320

Rezai H, Savari A (2004) Observation on reef fishes in the coastal waters off some Iranian Islands in the Persian Gulf. Zool Middle East 31:67–76

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson C (ed) Status of coral reefs of the world, vol 1. Australian Institute of Marine Science, Townsville, pp 155–170

Riegl B (1999) Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. Coral Reefs 18:63–73

Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Mar Biol 140:29–40

Riegl BM, Purkis SJ (2012) Environmental constraints for reef building in the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf. Springer, New York, pp5–32

Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. Glob Chang Biol 21:3995–4005

Riegl BM, Benzoni F, Samimi-Namin K, Sheppard C (2012a) The Hermatypic Scleractinian (hard) coral fauna of the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp187–224

Riegl BM, Purkis SJ, Al-Cibahy AS, Al-Harthi S, Grandcourt E, Al-Sulaiti K, Baldwin J, Abdel-Moati AM (2012b) Coral bleaching and mortality thresholds in the SE Gulf: highest in the world. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp95–105

Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SC, Sheppard CR, Bauman A (2018) Population collapse dynamics in Acropora downingi, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. Glob Chang Biol 24:2447–2462

Robinson DP, Jaidah MY, Jabado RW, Lee-Brooks K, El-Din NMN, Malki AAA, Elmeer K, McCormick PA, Henderson AC, Pierce SJ (2013) Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. PLoS One 8:e58255

Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52:1874–1882

Sahafi HH (2000) Identification of marine ornamental fishes in northern part of the Persian Gulf, Iran. Iran J Fish Sci 2:21–36

Sale PF, Feary DA, Burt JA, Bauman AG, Cavalcante GH, Drouillard KG, Kjerfve B, Marquis E, Trick CG, Usseglio P (2011) The growing need for sustainable ecological management of marine communities of the Persian Gulf. Ambio 40:4–17

Samimi-Namin K, Riegl B (2012) Raised reef on Larak suggests *Acropora* dominance on the Persian Gulf coral reefs since the Pleistocene. Coral Reefs 31:763–763

Samimi-Namin K, Rezai H, Kabiri K, Zohari Z (2009) Unique coral community in the Persian Gulf. Coral Reefs 28:27–27

Shahhosseiny MH, Mostafavi PG, Fatemi SMR, Karimi E (2011) Clade identification of symbiotic zooxanthellae of dominant sclerectinian coral species of intertidal pools in Hengam Island. Afr J Biotechnol 10:1502–1506

Sheppard C, Loughland R (2002) Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. Aquat Ecosyst Health Manage 5:395–402

Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J, Benzoni F, Dutrieux E, Dulvy NK, Durvasula SRV, Jones DA, Loughland R, Medio D, Nithyanandan M, Pilling GM, Polikarpov I, Price ARG, Purkis S, Riegl B, Saburova M, Samimi-Namin K, Taylor O, Wilson S, Zainal K (2010) The Gulf: a young sea in decline. Mar Pollut Bull 60:13–38

Shokri MR, Fatemi SMR, Crosby MP (2005) The status of butterflyfishes (Chaetodontidae) in the northern Persian Gulf, IR Iran. Aquat Conserv Mar Freshwat Ecosyst 15:S91–S99

Shraim R, Dieng MM, Vinu M, Vaughan G, McParland D, Idaghdour Y, Burt JA (2017) Environmental extremes are associated with dietary patterns in Arabian Gulf reef fishes. Front Mar Sci 4:285

Siddeek M, Fouda M, Hermosa G Jr (1999) Demersal fisheries of the Arabian Sea, the Gulf of Oman and the Arabian Gulf. Estuar Coast Shelf Sci 49:87–97

Sivasubramaniam K, Ibrahim MA (1982) Demersal fish resources around Qatar. Qatar Univ Sci Bull 2:305–351

Smith GB, Saleh MA (1987) Abundance and bathymetric distribution of Bahrain (Arabian Gulf) reef ichthyofaunas. Estuar Coast Shelf Sci 24:425–431

Smith EG, Hume BC, Delaney P, Wiedenmann J, Burt JA (2017) Genetic structure of coral-*Symbiodinium* symbioses on the world's warmest reefs. PLoS One 12:e0180169

Speers AE, Besedin EY, Palardy JE, Moore C (2016) Impacts of climate change and ocean acidification on coral reef fisheries: an integrated ecological–economic model. Ecol Econ 128:33–43

Tavakoli-Kolour P, Khatami S, Barkhordari A, Farhadi A (2015) Short communication first record of *Cephalopholis formosa* (Shaw, 1812) (Perciformes: Serranidae) in the Persian Gulf. J Appl Ichthyol 31:197–198

Torquato F, Jensen HM, Range P, Bach SS, Ben-Hamadou R, Sigsgaard EE, Thomsen PF, Møller PR, Riera R (2017) Vertical zonation and functional diversity of fish assemblages revealed by ROV videos at oil platforms in the Gulf. J Fish Biol 91:947–967

Vaughan GO, Burt JA (2016) The changing dynamics of coral reef science in Arabia. Mar Pollut Bull 105:441–458. https://doi.org/10.1016/j.marpolbul.2015.10.052

Vaughan G, Al-Mansoori N, Burt J (2019) The Arabian Gulf. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd edn. Elsevier Science, Amsterdam, NL, pp 1–23

Walton ME, Hayes J, Al-Ansi M, Abdallah M, Al Maslamani I, Al-Mohannadi M, Al-Shaikh I, D'Urban Jackson T, Szostek C, Egerton J (2018) Towards spatial management of fisheries in the Gulf: benthic diversity, habitat and fish distributions from Qatari waters. ICES J Mar Sci 75:178–189

Weis VM (2008) Cellular mechanisms of cnidarian bleaching: stress causes the collapse of symbiosis. J Exp Biol 211:3059–3066

Wilson S, Fatemi SMR, Shokri MR, Claereboudt M (2002) Status of coral reefs of the Persian/Arabian Gulf and Arabian Sea region. In: Wilkinson CR (ed) Status of coral reefs of the world, pp 53–62

Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NA (2019) Coral reef ecosystem services in the Anthropocene. Funct Ecol 33:1023–1034

Wooldridge SA (2013) Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae. Biogeosciences 10:1647–1658

Marginal Reefs in the Anthropocene: They Are Not Noah's Ark

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Abstract In this book chapter, we review and discuss the resistance of marginal reefs and their potential as refugia. Marginal reefs (MRs) greatly differ from each other owing to their diverse biogeographic conditions and the different environmental parameters under suboptimal conditions to which they are subjected (e.g., temperature, depth, extreme pH, siltation, nutrients, and turbidity). The bulk of suboptimal conditions represent unsuitable environments for most species, which

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are filtered out by natural selection, resulting in two conspicuous characteristics of marginal reefs: low biological richness and dominance of stress-tolerant species. Moreover, this low diversity could result in a low ecological redundancy in several functions, which would lead these functions to a status close to collapse when faced with the loss of one or more of their species. Thus, the loss of one or more functions could result in a persistent phase shift. In contrast, tolerant species have high environmental plasticity and can live in a wide range of one parameter. In other words, although these reefs have a lower functional redundancy, their species are usually more resistant to one or even several environmental parameters under suboptimal conditions (e.g., heatwaves and/or moderate turbidity). In this scenario, a plethora of different MR conformations (e.g., turbid-zone, high-latitude and high-temperature reefs, and mesophotic coral ecosystems) is presented, some of which are considered as potential short-term refuge, but restricted to adapted species. In parallel, other MRs could also take some climatic refugees by shifts in species distribution in the Anthropocene. Nevertheless, most MRs are threatened by multiple chronic and acute stressors, including long-term warming, invasive species, heatwaves, overfishing, acidification, bottom trawling, weakening of benthic-pelagic coupling, plastic and organic pollution, oil spills, sea-level rise, and increased siltation. Therefore, the resistance and refugia potential of MRs will be lower than expected because they are under severe anthropogenic pressure and are ecologically distinct ecosystems from the shallow-water coral reefs under optimal conditions. Thus, the heterogeneous set of MRs actually represents limited long-term refugia, and their resistance and recovery potential will be lost if resilience-based management actions at the local and global scale are not urgently adopted. We highlight the importance of maintaining pathways of connectivity, reducing reef stressors, and also protecting the endemism hotspots, unique diversity of marginal reefs, and their few functional groups.

Keywords Coral reef · Turbid-zone reef · Refugia · Mesophotic coral ecosystem · High-latitude reef · High-temperature reef · Global warming · Ocean acidification · Pollution · Heatwaves · Coral bleaching · Climate change

1 Introduction

The concept that tropical coral reefs only occur and thrive in clear, shallow, and oligotrophic waters with a narrow temperature range (around 20–30 °C) has long been a paradigm in the literature (Dubinsky and Stambler 2011). This paradigm arose because most of our knowledge was based on the structure and functioning of reefs in shallow seascapes from the Caribbean Sea and Australia (Mumby 2009; Hughes et al. 2018). In these areas, marine animal forests (sensu Rossi et al. 2017) occur with high coverage and richness of reef-building corals, such as the Coral Triangle and Great Barrier Reef.

For these biogenic constructions, optimal conditions, such as low nutrient and adequate pH levels, water transparency, and narrow sea temperature variability, should enhance carbonate production and the persistence of marine forests with high benthic productivity and biodiversity (Hoegh-Guldberg et al. 2017; Hughes et al. 2018; Perry and Alvarez-Filip 2019). Moreover, these environmental conditions support the coral reef maintenance and their high-value ecosystem services (Costanza et al. 2014), such as tourism (Spalding et al. 2017), flood control (Beck et al. 2018), shoreline protection (Elliff and Silva 2017), sediment generation (Perry and Alvarez-Filip 2019), or nursery habitat and provision of renewable resources (e.g., fisheries) (Cruz-Trinidad et al. 2014).

However, growing research has focused on the Caribbean Sea, Coral Triangle and Australia (Smithers and Larcombe 2003; Lybolt et al. 2010; Guest et al. 2016; Pizarro et al. 2017; Enochs et al. 2020), and in other seas worldwide (e.g., in the South Atlantic Ocean, Red Sea, NW Pacific, Kuroshio region, Mozambique, and Persian/Arabian Gulf) (Perry 2003; Nakajima et al. 2012; Hume et al. 2015; Suzuki et al. 2016; Porter and Schleyer 2017; Cruz et al. 2018; Kurihara et al. 2019); the results showed that reef ecosystems also occur under marginal or suboptimal conditions (Perry and Larcombe 2003; Burt et al. 2020; Soares 2020). These marginal reefs (MRs) have broadened our knowledge of the structure, functioning, resistance, and refugia potential of marine forests, and they represent a significant, peculiar, and overlooked portion of reef biodiversity overseas.

Studying present-day MRs is crucial to further understand coral reef diversity, endemism, ecosystem goods and services, and calcium carbonate production (Hennige et al. 2010; Pinheiro et al. 2017). As global environmental change alters energy fluxes and seascapes in marine forests worldwide (Rossi et al. 2019), research into populations thriving within MRs becomes extremely relevant, as it can provide useful insights into the future scenarios of coral reefs currently under optimal conditions (Camp et al. 2018).

Herein, we discuss the resistance and potential as refugia of the heterogeneous set of MRs (e.g., turbid-zone, high-latitude, high-temperature reefs, and mesophotic coral ecosystems) (Fig.1) using consolidated scientific concepts (Table 1) and empirical evidence from the literature. In this scenario, a plethora of different MR conformations are presented (Sect. 2), some of which appeared as potential short-term refuge, but restricted to adapted species, while others could also take some climatic refugees by shifts in species distribution. We also point out that MRs are under severe human pressure and need conservation actions at local and global scales. To understand these important and controversial aspects, we will discuss how the environmental and ecological characteristics of MRs shape their stability (Sect. 3) and potential refugia (Sect. 4). Finally, we will discuss the management for MR persistence (Sect. 5), considering that they are subjected to increasing human pressures worldwide.

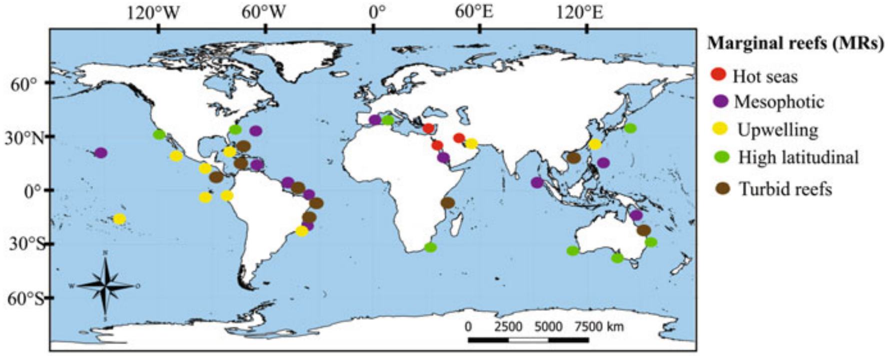


Fig. 1 Map highlighting some marginal reefs and their extensive distribution around the planet. Modified from Camp et al. (2018) and Soares et al. (2020a)

Table 1 Key concepts and their definitions

Concept	Definition
Marginal reefs (MRs)	Marine communities developed in hard-bottoms that survive under marginal or suboptimal conditions. These conditions include, among others, elevated siliciclastic sedimentation rates, turbid waters, high depths, high nutrient levels, extreme pH fluctuations, increased primary productivity, and/or highly variable temperatures
Marine animal forest	Benthic communities dominated by sessile suspension feeder organisms (e.g., sponges, corals, gorgonians, bivalves) that generate three-dimensional structures, as trees in the terrestrial forest
Ecological redundancy	Ecological phenomenon in which multiple species representing a variety of taxonomic groups can play similar, if not identical, roles in ecosystem functionality. Conservation efforts are especially important where redundancy is minimal
Refuge sites	Areas that maintain short-term (e.g., days or years) suitable conditions previously lost in other places
Refugia	Areas that components of biodiversity retreat to, persist in, and can potentially expand from under changing environmental conditions for a long term (centuries to millennia). Defined considering species-range dynamics, several generations, and climate change in the Anthropocene
Resistance	Capacity of a reef to absorb pressure or disturbance (e.g., nutrient pollution or heatwaves) without shifting its community (e.g., phase shift from scleractinian coral to algae, zoanthids, sponges, or gorgonians)
Resilience	Capacity of a reef ecosystem to recover itself from a pressure that breaks its resistance
Pressure	Result of a driver-initiated mechanism (human activity or natural process) causing an effect on any part of a reef ecosystem that may alter the environmental state
Impact	Consequences of reef state change in terms of substantial environmental and/or socioeconomic effects (e.g., loss of richness, loss of fish biomass, and permanent phase shift)

2 Marginal Reefs (MRs)

Environmental conditions are the core of the MR concept, being suboptimal or unsuitable conditions for most species of "traditional" reefs, i.e., shallow-water coral reefs developed under optimal conditions. Similar foundations have been applied to terrestrial ecosystems. In tropical forests, for instance, rainfall determines water availability for plants, a basic condition for plant growth and reproduction (Lawler and Cornic 2002). As rainfall distribution is not homogeneous in space and time, dry forests establish in the dry regions, while rain forests grow under wet conditions (Gentry 1988). Both systems have their own biogeographic history, and the balance between extinction and speciation over million years has resulted in the plant communities we observe today. In both cases, the level of unsuitability depends on the species' life history and ultimately determines ecosystem resistance and resilience. As you will see in this chapter, MRs worldwide comprise conditions that deviate substantially from those optimal for most species that constitute the "traditional" reefs.

MRs can be defined as marine communities developed in hard-bottoms that survive under marginal or suboptimal conditions (Table 1). These carbonate bioconstructions are built by a mix of organisms such as hydrozoans, bryozoans, hydrocorals, calcareous algae, and stress-tolerant scleractinian corals even under suboptimal conditions. These conditions include, among others, elevated siliciclastic sedimentation rates, turbid waters, mesophotic depths (~30–150 m), high nutrient content (such as phosphorus and nitrogen), extreme pH fluctuations, increased primary productivity (mesotrophic or eutrophic waters), and/or highly variable temperatures (Kleypas et al. 1999; Perry and Larcombe 2003; Halfar et al. 2005; Schoepf et al. 2015; Chow et al. 2019; Enochs et al. 2020).

Marginal communities may also thrive on hard substrates, such as intertidal or subtidal rocky reefs, estuarine habitats, and rhodolith beds (Soares et al. 2017; Francini-Filho et al. 2018). Thus, different types of MRs are identified worldwide where reef communities survive, including turbid-zone and high-temperature areas, macro-tidal reefs, tide pools, volcanic CO_2 vents, *ojos* (low pH springs), marine areas with submarine groundwater discharge, mangrove systems, upwelling areas, temperate mesophotic ecosystems, mesophotic coral ecosystems, and cold-water coral ecosystems (Camp et al. 2018; Enochs et al. 2020) (Fig. 2).

In MRs, some species are actually marginal reef specialists, most are stress-tolerant species, and the diversity of such marine forests may be very dissimilar to that of non-marginal coral reefs owing to differences in richness, endemism, and composition (Burt et al. 2020; Soares 2020) (Fig. 3). MRs are very different from each other owing to the diverse biogeographic conditions they occupy as well as to their different environmental conditions (Kleypas et al. 1999; e.g., turbid water, temperature, high nutrient content, extreme pH fluctuations, and others). The bulk of suboptimal conditions represent unsuitable environments for most reef species, which are filtered out by natural selection, resulting in two conspicuous ecological characteristics of MRs: lower species richness than that of reefs under optimal

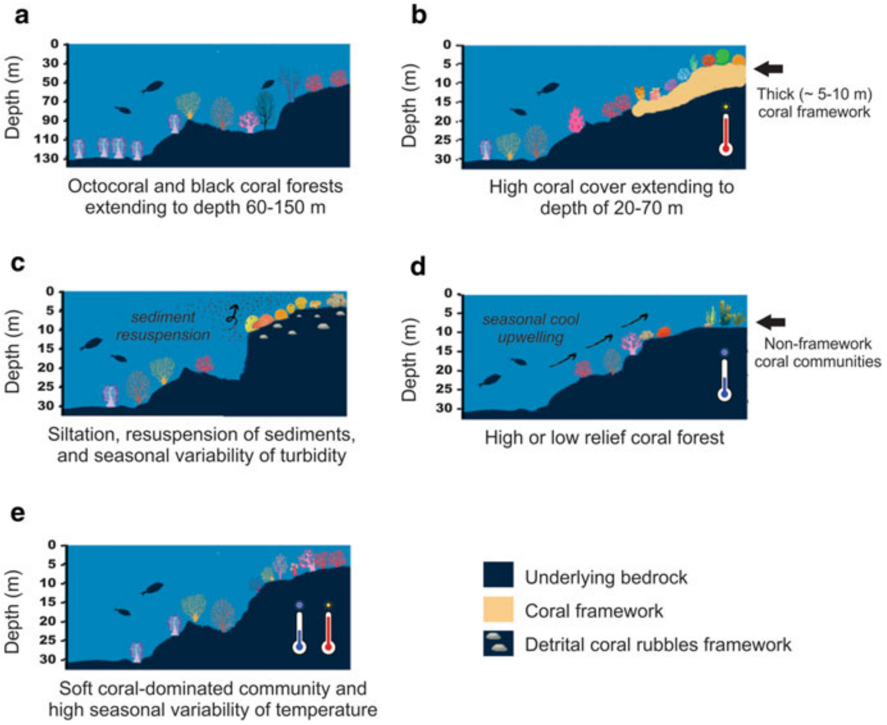


Fig. 2 Schematic diagram illustrating some of the marginal marine forests developed under suboptimal conditions discussed in this book chapter. (**a**) Mesophotic depth, (**b**) high-temperature, (**c**) turbid, (**d**) upwelling, and (**e**) high-latitude settings. Modified from Perry and Larcombe (2003). The red and blue thermometers represent high and low temperatures, respectively

conditions (Kleypas et al. 1999; Bak and Meesters 2000; Perry 2003) and dominance of stress-tolerant species (Harriott and Banks 2002; Bennett et al. 2010; Lybolt et al. 2010; Narayan et al. 2015; Bento et al. 2016; Browne et al. 2019). These patterns of unique diversity, endemism, and high turnover of species provide evidence that MRs such as turbid-zone, mesophotic coral ecosystems (MCEs), and high-temperature and high-latitude reefs are ecologically distinct from the reefs under optimal conditions (Beger et al. 2014; Camp et al. 2018; Rocha et al. 2018; Soares 2020).

These ecological characteristics shape important aspects of the resistance of MRs. Stress-tolerant species have high environmental plasticity and can live and flourish in a wide range of one or more specific suboptimal parameters. For example, the Atlantic coral *Montastraea cavernosa* flourishes in turbid-zone reefs (Leão et al. 2016), mesophotic depths (Soares et al. 2019a) (Fig. 4), and even in areas that periodically experience vent-associated acidification (Enochs et al. 2020). The occurrence of these tolerant species could confer MRs their large resistance and capacity to recover from some disturbance (Glynn 1996; Riegl and Piller 2003; Guest et al. 2016; Sully and Woesik 2020). In other words, although these reefs have

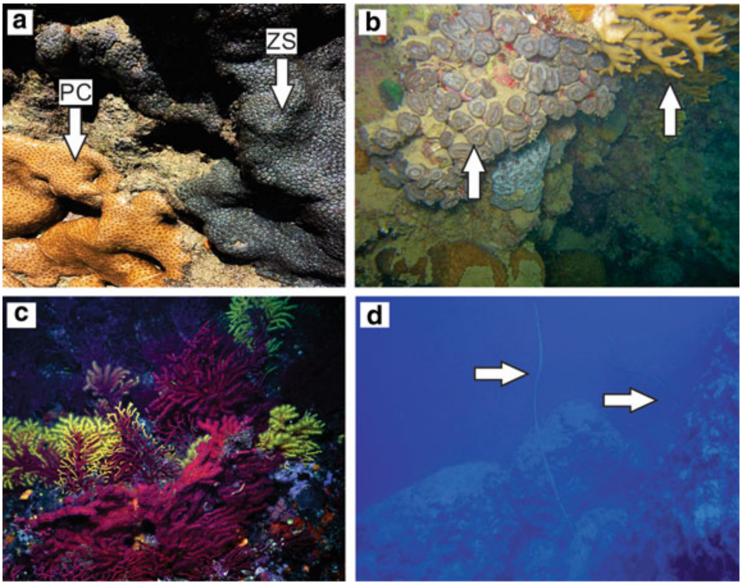


Fig. 3 Marginal communities under suboptimal conditions: (**a**) Tide pools in intertidal sandstone reefs (northeastern Brazil), where the stress-tolerant zoanthids *Palythoa caribaeorum* (left-side arrow—PC) and *Zoanthus sociatus* (right-side arrow—ZS) live and thrive in temperatures sometimes above 35 °C during the low tides; (**b**) nearshore turbid-zone reef in the Abrolhos Bank (the richest coral reef complex in Western South Atlantic) with hydrocoral *Millepora* sp. (right side arrow) and the stress-tolerant and endemic coral *Mussismilia harttii* (left side arrow); (**c**) temperate mesophotic ecosystem in the Mediterranean Sea with high-canopy gorgonian (*Paramuricea clavata*) forests; (**d**) mesophotic coral ecosystem with a black coral *Cirrhipathes* sp. (51 m depth) in the Western South Atlantic (photos from A.L.A. Gurgel, I.C.S. Cruz, B. Santos, O.A. Silva, S. Rossi)

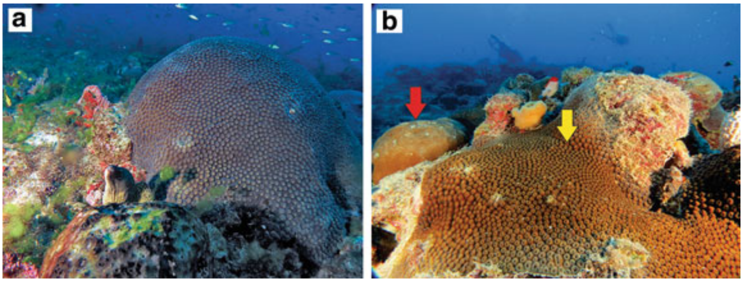


Fig. 4 Stress-tolerant species have a large environmental plasticity, *Montastraea cavernosa*, a cosmopolitan Atlantic coral species, which occurs in a wide range of depth, extreme pH, turbidity, and temperature (Lesser et al. 2010; Budd et al. 2012; Studivan et al. 2019; Soares et al. 2019a; Enochs et al. 2020), such as (**a**) shallow-water turbid-zone reef at 15 m depth with dominance of *M. cavernosa* and massive sponges and (**b**) mesophotic coral ecosystem (MCE) at 38 m depth with dominance of stress-tolerant corals *M. cavernosa* (yellow arrow) and *Siderastrea stellata* (red arrow) (photos from M. Davis, A.L.A. Gurgel, M.O. Soares)

a lower species richness, their species are usually more resistant, at least to environmental parameters under suboptimal conditions (e.g., turbidity, extreme pH values, or variable temperature). However, a large resistance to all types of natural disturbances and human pressures is not expected in MRs (Soares 2020).

Furthermore, MRs with low species richness could exhibit low ecological redundancy (Table 1), i.e., species playing the same or similar roles for the ecosystem functioning (c.f. Norström 2006; Bellwood et al. 2003). This may result in reef functional collapse if species are lost (Denis et al. 2013) and in a persistent phase shift (Bellwood et al. 2004), which means a significant impact. Moreover, species plasticity has been shaped by natural selection at rates much lower than those involved in the adaptation to recent growing pressures in the Anthropocene. In this context, pressure can be formally described as a result of a driver-initiated mechanism (human activity/natural process) causing an effect on any part of a reef ecosystem that may alter the environmental state, while impacts can be defined as the consequences of reef state change in terms of substantial environmental and/or socioeconomic effects (Oesterwind et al. 2016) (Table 1).

MRs recently came under the spotlight owing to the resistance to marine heatwaves recorded on reefs that live under particularly turbid conditions (Guest et al. 2016; Mies et al. 2020; Sully and Woesik 2020). This agreed with previous studies, which found resistance to heatwaves in MRs at mesophotic depths and in upwelling areas (Glynn 1996; Perry and Larcombe 2003; Riegl and Piller 2003, Muir et al. 2017; Frade et al. 2018). Owing to such resistance, species distribution models projected over future climate change scenarios corroborate that some MRs at mesophotic depths, upwelling areas, or where there was a strong coupling between turbidity and tidal fluctuations could work as refugia (Cacciapaglia and Woesik 2016). Hence, the hypothesized regional-scale refugia against increasing sea temperatures comprise areas with naturally low thermal stress (Chollett and Mumby 2013), such as deep areas, areas of high currents, turbid-zones, high-latitude areas, and where cooler waters occur seasonally. Although they differ under their suboptimal conditions, the assumption is that reefs under any marginal condition are potential refugia (Table 1) for species, which may not be true.

3 Stability of Marginal Reefs

3.1 Resistance and Resilience: Core Concepts of Reef Systems

The stability of coral reefs is defined according to their resistance and resilience (Dudgeon et al. 2010). Resistance is defined as the capacity of a reef to absorb pressure or disturbance (e.g., nutrient pollution or thermal stress) without shifting their community (e.g., phase shift from scleractinian coral to algae, zoanthids, sponges, or gorgonians c.f. Cruz et al. 2018; Norström et al. 2009; Rossi et al. 2018, 2020) (Table 1). The loss of coral reef resistance is known as phase shift or regime shift (Done 1992). A phase or regime shift starts an alternative state that may be stable or unstable and settles in when the resistance is broken. Overall, the loss of coral reef resistance has led to a decrease in high-value goods and services (Costanza et al. 2014; Perry and Alvarez-Filip 2019), and precipitated phase shifts to benthic communities dominated by macroalgae or other non-coral taxa (Dudgeon et al. 2010).

Resilience is the capacity of an ecosystem to recover itself from a pressure that breaks its resistance (Table 1). In this sense, the resilience of coral reefs can be eroded to an extent that they are unable to recover after recurrent disturbances (Hughes et al. 2010). However, resilience is more complex to determine because it is related to the persistence of the phenomenon. This means that an alternative stable state can be reached as a result of loss of resilience or by a chronic pressure, such as sewage discharge, which maintains a persistent alternative state as long as it persists. This second condition (persistence of chronic impact) was well documented in Kane'Ohe Bay, Hawaii, where the coral-dominated state was restored from the phase shift to macroalgae dominance after eliminating all disturbances (Stimson 2018).

In one of the best-studied coral reef areas (Caribbean Sea), the overall trend of non-marginal reef assemblages is the loss of scleractinian species with stress-sensitive life histories and increased dominance of stress-tolerant and opportunistic species that rapidly colonize following a disturbance (Bozec and Mumby 2015; Cramer et al. 2020). In this context, sponges (Bell et al. 2013), zoanthids (Cruz et al. 2018), mixotrophic or heterotrophic corals (Conti-Jerpe et al. 2020), and gorgonians (Lenz et al. 2015; Lasker et al. 2020) (Fig. 5) become prominent in the marine animal forest (Table 1), substituting the autotrophic scleractinian corals, probably because of a better adaptive physiology, resistance to disturbances, and plasticity in their trophic ecology.

Moreover, the fast macroalgal growth rates, high algal recruitment rates, low herbivore biomass, historical and current human pressures, and missing key groups of herbivores predispose Caribbean non-marginal reefs to the loss of resistance (Mumby 2009; Cramer et al. 2020) and phase shifts to an algae-dominated state.

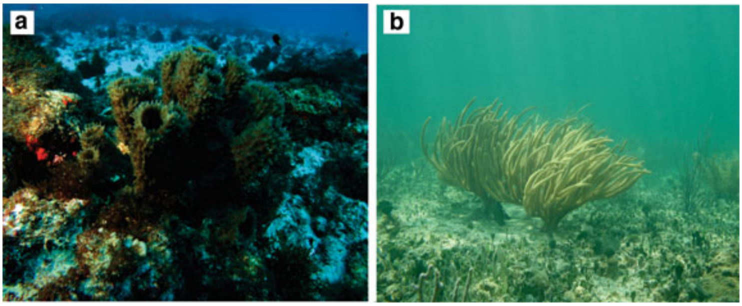


Fig. 5 Marginal reefs: Benthic suspension feeders and mixotrophic stress-tolerant habitat-forming species such as Southwestern Atlantic sponges [*Callyspongia (Chadochalina) aculeata*] (**a**) and Caribbean gorgonians (**b**) become dominant in marine animal forests under current or future suboptimal conditions (Photos from A.L.A. Gurgel, M. Davis, S. Rossi)

In contrast, some reefs from the Indo-Pacific are considered to have greater resistance than those of the Caribbean, which indicates a disparity in reef resistance and urges caution when dealing with concepts of transferability (Roff and Mumby 2012). Accordingly, the knowledge about reef resistance stems mainly from scientific studies conducted in two regions, i.e., the non-marginal coral reefs under optimal conditions of the Caribbean Sea and Indo-Pacific region (Roff and Mumby 2012; Hughes et al. 2018; Morais et al. 2018).

Turbid-zone (Guest et al. 2016; Porter and Schleyer 2017; Teixeira et al. 2019; Mies et al. 2020), volcanically acidified (Enochs et al. 2020), and high-temperature reefs (Bento et al. 2016; Burt et al. 2019), as well as MCEs (Muir et al. 2017; Frade et al. 2018; Soares et al. 2019a, 2020a) have recently been investigated owing to their resistance and persistence against growing pressures and have been shown to be more resistant to heatwaves (acute stress) than reefs that occur under optimal conditions. MCEs and turbid-zone and high-temperature reefs have undergone lower rates of bleaching and/or had a higher resistance, with lower coral mortality rates after thermal stress events, such as heatwaves or cold spells, than those of non-marginal reefs (Fig. 6).

Together with long-term persistent warming (chronic stress), discrete periods of extreme regional ocean warming by heatwaves have increased in frequency (Smale et al. 2019), causing acute stress to coral reefs. However, marginal coral populations have different responses worldwide to this suboptimal temperature condition, which clearly suggests a global heterogeneity on their stability. MRs comprise a large and heterogeneous set of marine forests with, consequently, different resistance and resilience according to the suboptimal condition (e.g., heat stress, cooler waters, extreme pH, depth) and regional atmospheric and oceanographic conditions (e.g., resuspension of sediments, cold spells, cyclonic eddies, thermocline, and warm current advections).

The resilience of some marginal coral populations against acute pressures (e.g., heatwaves) can be explained by several environmental conditions and/or biological adaptations, such as ability to cope with oxidative stress (Camp et al. 2018) and extreme pH values (Enochs et al. 2020), multitude of host-microorganism associations (Symbiodinaceae and bacteria) (Camp et al. 2020; Roitman et al. 2020), protection against light/heat stress by turbidity/shading (Cacciapaglia and Woesik 2016; Sully and Woesik 2020), and buffering by depth (Muir et al. 2017) or cooler waters in upwelling systems (Frade et al. 2018). Moreover, in some MRs, holobiont responses to variable temperatures (Lien et al. 2007; Hume et al. 2015; Ng and Ang 2016), such as symbionts of high heat-tolerant and/or transcription of heat-responsive genes and alleles pre-adapted to thermal stress in the coral host, may be important local adaptations. Finally, significant heterotrophic rates that temporarily compensate for the trophic loss of endosymbionts during severe coral bleaching (Mies et al. 2018; Conti-Jerpe et al. 2020) can also help to understand resilience under severe stress. In MRs, the balance of energy acquisition between autotrophic, mixotrophic, and heterotrophic organisms can play an important role in coral adaptation against pressures.

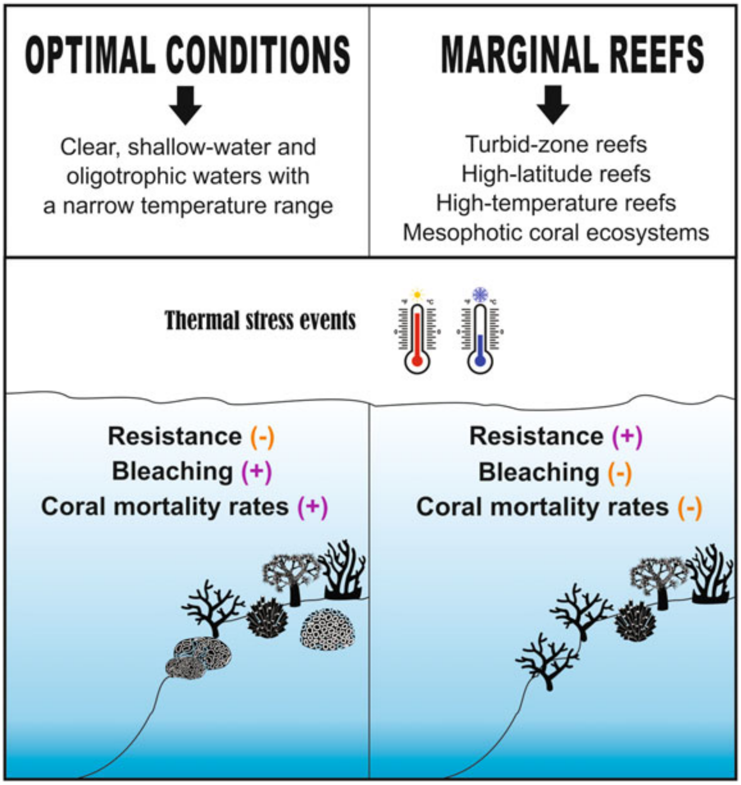


Fig. 6 Schematic and hypothetic diagram to highlight the bleaching, resistance, and coral mortality rates in reefs under current optimal and marginal conditions. Temperature stress is shown by a thermometer suggesting that it may be by high (e.g., heatwaves), with extreme intra-annual variability, or low (e.g., cold spells or upwelling) sea temperatures

In this way, corals more reliant on autotrophy will lose their competitive advantage in fast changing environments and are likely to be the first to disappear from reefs in the ongoing Anthropocene (Conti-Jerpe et al. 2020). Heterotrophic or mixotrophic trophic strategies are key to understand the energy budget of corals (Crandall et al. 2016; Gori et al. 2018) and to sustain their health (Lim et al. 2017) under stressful conditions, when photosynthesis and autotrophic inputs are not entirely possible. Heterotrophy has been regarded as an indicator of resilience to bleaching stress (Baumann et al. 2014; Connolly et al. 2012; Ezzat et al. 2016; Mies et al. 2018), when the increased heterotrophic feeding was a good predictor of survival and reduced mortality risk during a bleaching event such as under severe heatwaves. Furthermore, zooplankton has been reported as an important food source for corals (Hinrichs et al. 2013; Gori et al. 2015; Rossi et al. 2020), especially copepods (Servetto et al. 2017).

Adaptive traits expressed by corals within the MRs in intertidal and subtidal waters include plasticity, conservation of energy fluxes (e.g., enhanced heterotrophy), flexible symbiotic associations, and endosymbiont and genetic diversity (Camp et al. 2018; Mies et al. 2020; Soares 2020). MRs generally comprise and are dominated by adapted coral species, algae, and other stress-tolerant benthic suspension feeders (e.g., sponges, zoanthids, octocorals, and bryozoans), which increase the ability of a reef ecosystem to resist pressures (Côté and Darling 2010). Moreover, it is well-known that massive coral species may be dominant in MRs and they are typically more tolerant to light and heat stress (Camp et al. 2018). All these ecophysiological characteristics shaped by the host-microorganism association and functional coral traits suggest that some MRs are more stable than their tropical counterparts under optimal conditions, at least to one suboptimal condition. However, the limits of such stability in the understudied MRs are largely unknown. Moreover, MRs suffer species-specific impacts, and their resistance thresholds may be narrower than expected.

3.2 Lower than Expected: Vulnerability to Pressures and Thresholds of Resistance of Marginal Reefs

The thresholds of MR resistance against pressures (e.g., heatwaves) vary according to the biogeographic region (Burt et al. 2011; Guest et al. 2016; Fine et al. 2019), historical temperature stress (Skirving et al. 2019), reef community composition (Cruz et al. 2018), magnitude of non-climatic disturbances (Cruz et al. 2018; Fisher et al. 2019), and oceanographic and atmospheric conditions during acute stress (Celliers and Schleyer 2002; Soares et al. 2019b), indicating a great heterogeneity of resistance thresholds between the different types of MR.

The limited resistance of MRs is shown by their high susceptibility to human activities and phase shift frequency. For example, the high frequency of phase-shifting Brazilian turbid-zone reefs suggests greater degradation than that reported for Caribbean reefs, indicating that some MRs do not have high natural resistance (Cruz et al. 2018). In this case the macroalgal shifts positively correlated to ports and urbanized surfaces, high latitudes, and shore proximity, which indicate a possible link to nutrient runoff (Cruz et al. 2018).

Highlighting this, Lybolt et al. (2010) indicated that natural historical instability, coupled with non-climate pressures since the European colonization in Australia, severely impacted some MRs, and they thus offer limited potential refuge habitats for reef species. MRs are not immune to local and regional human pressures, such as eutrophication-related ones. Hence, urbanization (Burt et al. 2013; Portugal et al. 2016; Cruz et al. 2018), fisheries (Floros et al. 2013), invasive species (Creed et al. 2017), contamination (Cruz et al. 2018), derelict fishing gears (Figueroa-Pico et al. 2020), and dredging (Fisher et al. 2019) may drive the loss of resistance in MRs.

MR vulnerability to human pressures is partly explained by their unique ecological dynamics such as low richness. However, they exhibit high rates of endemism and the presence of stress-tolerant species. The combination of features such as few

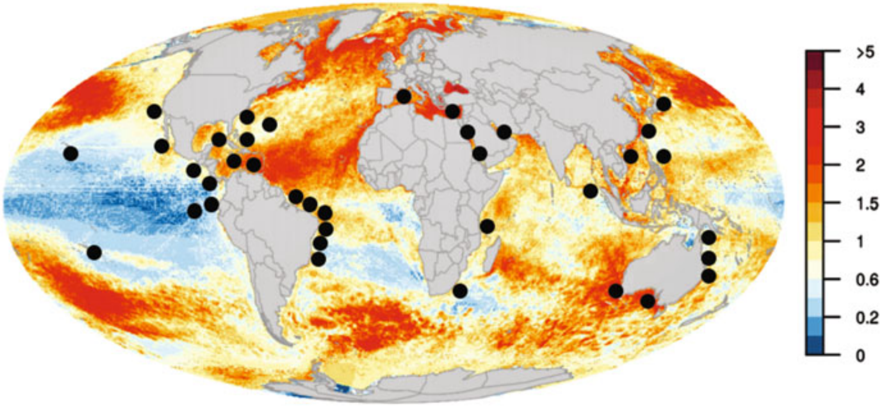


Fig. 7 Global pattern of cumulative human impact in the ocean (Halpern et al. 2019) and the location of some marginal reefs (black spots). Yellow, orange, and red represent increasing human impact. Blue colors represent the lowest cumulative human impact. To see the marginal reef types please see the Fig. 1

key species, endemism, low vagility, small population sizes, geographic isolation, and/or low functional redundancy may occur in MRs. If all of these features occur, MRs may result particularly vulnerable to human activities. Non-climate pressures that harm these key species (such as fishing or pollution) may lead to the loss of resistance and severe impacts such as phase shifts (Cruz et al. 2018), high bioerosion rates in coral species (Browne et al. 2019), loss of habitat-forming species (Portugal et al. 2016), and/or reduction of fish biomass (Morais et al. 2017).

These local and regional pressures also interact with the global-scale stressors (Fig. 7) to undermine the resistance of MRs, causing loss of reef framework production and/or forest structural complexity. Most of the ocean (59%) (Fig. 7) is experiencing significantly increasing cumulative impacts, in particular owing to climate change but also from fishing, land-based pollution, and shipping (Halpern et al. 2019). For example, strong thermal anomalies, sediment-related stress, large-scale algal blooms, and local nutrient pollution (e.g., nitrogen and phosphorus) both interact and act independently to alter health in several ways that finally contribute to significant impacts such as disease, bioerosion, bleaching, and mortality of reef-building corals (Wang et al. 2018; Al-Monsoori et al. 2019; Fisher et al. 2019). Accordingly, Camp et al. (2018) suggested that understanding the interaction of multiple pressures (Halpern et al. 2019) across varying temporal scales is an important research priority to improve the conservation and management of MRs.

MRs are commonly dominated by benthic suspension feeders that provide structural complexity (Rossi et al. 2017). These marginal forests and their habitat-forming species depend on energy availability mainly provided by the water column productivity and benthic-pelagic coupling (Rossi et al. 2019). However, climate change will intensify the stratification of marine waters (0–200 m) and, consequently, decrease nutrient availability and primary and secondary productivity delivered to these seafloor forests. This change will have severe impacts on multiple trophic levels and the energy budgets of active and passive suspension feeding organisms (e.g., sponges, bryozoans, hydrozoans, corals, ascidians), as well as on their abundance, phenology, larval nutritional condition, and population viability (Rossi et al. 2019; Lesser and Slattery 2020).

The literature reviewed in this chapter indicates that we need to exercise caution about overstatements concerning the resistance and refugia potential (Table 1) of the distinct MR types, such as MCEs, temperate mesophotic ecosystems, cold-water coral ecosystems, and high-latitude, high-temperature, and turbid-zone reefs.

3.2.1 Turbid-Zone Reefs

Turbid-zone reefs (Figs. 1 and 2c) are one of the most studied MRs concerning the resilience potential of coral populations in the face of global warming and heatwaves. Moderate turbidity is one of the factors that can protect corals by shading from sea surface temperature anomalies and high irradiance. Consequently, it is considered one of the factors that led to the hypothesis that these MRs represent climate change refugia. Cacciapaglia and Woesik (2016) identified turbid nearshore refuges for corals between latitudes 20–30° N and 15–25° S, where there was a significant coupling between turbid waters and tidal oscillations. Their model also suggests that turbidity will mitigate high thermal stress bleaching for 9% of shallow reef habitats (0–30 m depth). Moreover, Sully and Woesik (2020) suggested that approximately 12% of reefs worldwide exist within the “moderating turbidity” range (K_d490, a measurement positively related to turbidity, between 0.080 and 0.127), 30% of which are in the Coral Triangle. They also indicated that these turbid-zone reefs may provide some refuge through climate change but will need high conservation status (Sully and Woesik 2020).

Accordingly, higher bleaching resistance was found in nearshore turbid-zone corals in Australia (Morgan et al. 2017) and Brazil (Teixeira et al. 2019) following the global mass coral bleaching event in 2015–2016. Only 1.5% of the studied coral colonies in Australia demonstrated partial bleaching, and coral cover after the onset of temperature stress remained unchanged from pre-event measures. The Brazilian nearshore MRs have grown under suboptimal turbidity conditions (Suggett et al. 2012; Loiola et al. 2019) and have been tolerant to heatwaves for the last two decades (Leão et al. 2010; Miranda et al. 2013). In these MRs, bleaching events affected ~ 26 species of scleractinians, hydrocorals, octocorals, and zoanthids over the last 25 years (1994–2019). Moreover, nine scleractinian species are endemic to Brazilian MRs and suffered bleaching during these last two decades (Soares 2020). Despite the high rates of coral bleaching (e.g., up to >60%), these reefs have not exhibited mass mortalities following bleaching events until 2019 (Leão et al. 2016; Teixeira et al. 2019). In Brazil, the overall mortality of reef-building corals, after an intense heatwave and severe bleaching in 2016–2017, was very low (~2%) (Teixeira et al. 2019). Some of these corals in turbid-zone MRs can increase their proportion of carbon incorporated via heterotrophy when more food is available and under conditions such as high turbidity (Mies et al. 2018). Heterotrophy can play an important role in corals during episodes of stress (e.g., heatwaves) and to improve the coral health (Conti-Jerpe et al. 2020) mainly under certain conditions, when photosynthesis is not satisfactorily accomplished in turbid waters and/or intense bleaching events.

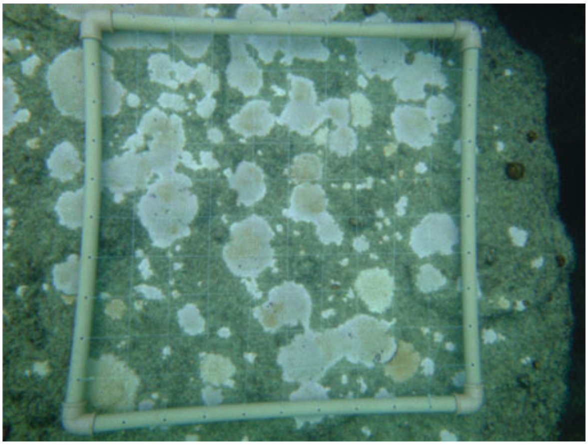
However, in 2019, several Brazilian turbid-zone MRs (e.g., the Abrolhos bank, Brazil) suffered an intense heatwave with the first ever recorded post-bleaching mass mortality in one hydrocoral (i.e., *Millepora alcicornis*), while other stress-tolerant corals resisted despite severe bleaching (Duarte et al. 2020; Soares 2020). To explain the previous absence of mass coral mortality in turbid-zone reefs in the SW Atlantic, other hypothesis may be the lack of severe and prolonged heatwaves in the past owing to lower historical stress (Skirving et al. 2019), deeper bathymetric distribution of corals, dominance of massive corals, higher tolerance to nutrient enrichment (Mies et al. 2020), and higher bleaching threshold (Duarte et al. 2020). Furthermore, considering the projected ocean-climate change in IPCC (Intergovernmental Panel on Climate Change) scenarios, Mazzuco et al. (2019) suggested that recruitment of some marine populations in these turbid-zone MRs could be highly sensitive to climate change. These species-specific results indicate that the resistance potential of some turbid-zone MRs is extremely limited and may promote reef community changes in the ongoing Anthropocene, owing to the multiple and growing human activities (Halpern et al. 2019) and resilience heterogeneity of their habitat-forming species.

Moreover, even if moderate turbidity may decrease coral bleaching during temperature stress (Cacciapaglia and Woesik 2016; Sully and Woesik 2020), such shading conditions are highly variable. Oceanographic and atmospheric seasonal conditions that combine high temperatures during extended periods, low wind speeds, reduced sediment supply to the coast (e.g., during droughts or multiple dams on rivers), and reduced water turbulence may decrease the water turbidity during thermal stress events (Soares et al. 2019b; Teixeira et al. 2019). Although occurring in moderate turbid waters, this combination of conditions over the course of a few months coincident with severe heatwaves and local human pressures may expose stress-tolerant corals in these "havens" to intense mass bleaching events (Fig. 8).

Other recent evidence regarding the resistance threshold of turbid-zone MRs is the assumption that there is a limit to the protective function of turbidity against high light conditions (Fisher et al. 2019; Sully and Woesik 2020) and, consequently, to the capacity of turbid-zone MRs to act as long-term refugia (Table 1). Low-to-moderate decreases in light conferred by suspended sediments can reduce the frequency of coral bleaching and may reduce mortality, especially for branching corals (Fisher et al. 2019). However, Fisher et al. (2019) found that when sediment loads are high, any reduction in bleaching frequency is overwhelmed by increased mortality associated with severe low light periods and high levels of sediment deposition, which affects the polyp function of corals.

Therefore, with low sediment inputs, the cumulative impact of suspended sediments and temperature stress may be less than expected (antagonistic), whereas with

Fig. 8 Severe bleaching in a monotypic population of the stress-tolerant and encrusting coral *Siderastrea* spp. in turbid waters off the Western Atlantic coast (~6 m depth)



high sediment inputs, the aggregate impact is greater than that when these stressors occur in isolation (synergistic) (Fisher et al. 2019). In this way, Freitas et al. (2019) also highlighted the deleterious effect of increased turbidity (e.g., owing to deforestation) in bioconstruction even for Brazilian turbid-zone MRs. The results of Fisher et al. (2019) and Freitas et al. (2019) in Australia and Brazil, respectively, emphasized that mismanagement of local pressures (e.g., runoff and dredging) may, in some cases, have the capacity to modify their overall impact (including that from temperature stress) and undermine the competence of MRs to provide long-term refugia (Table 1).

This clearly indicates that those human activities increasing sediment runoff and suspended sediments above the threshold of turbid-zone MRs are an immediate local pressure and must be controlled by society. As the increase in suspended sediment concentrations through urban, agricultural, and industrial runoff, as well as deforestation, resuspension, and dredging activities is an important local driver of resistance loss and impacts in turbid-zone MRs (Fisher et al. 2019; Freitas et al. 2019), the synergistic interaction between non-climate and large-scale chronic (prolonged warming) and acute (heatwaves) pressures threatens turbid-zone MRs and may decrease their overall resistance.

3.2.2 High-Temperature and High-Latitude Reefs

High-temperature and high-latitude reefs (i.e., subtropical or temperate regions) are important MRs that occur in several coasts (Figs. 1 and 2b, e). These MRs provide a unique opportunity to understand the responses of reef communities to highly variable and/or high values of some suboptimal environmental conditions (e.g., temperature and salinity). The Persian/Arabian Gulf (PAG) is one of the best-known regions to understand the responses of high-temperature MRs. This region experiences the highest water temperatures (<35 °C in summer) and also has high salinity (>40) owing to its high evaporation rates (Burt et al. 2019). However, even under these stressful conditions, these MRs house a significant number of coral reef species (55–60) (Camp et al. 2018).

These MRs are composed by naturally heat-resistant populations with the highest upper temperature thresholds for coral bleaching (Coles and Riegl 2013), being composed and dominated by massive stress-tolerant corals, such as Poritidae and Faviidae adapted to high temperatures. Heat resistance can also be explained by the contributions of both partners (coral and symbionts) that are characterized by a genetic divergence of the coral population to an extreme marginal environment (southern PAG) and the presence of a rare and thermally tolerant symbiont *Symbiodinium thermophilum* (Hume et al. 2015). However, while limited gene flow has driven a role in adaptation within these MRs, it also indicates the limited potential for natural export of suboptimal tolerance traits to non-marginal reefs elsewhere in the same ocean basin (Smith et al. 2017).

To explain thermal tolerance in stress-tolerant corals, the maintenance of energy reserves and heterotrophic feeding of the coral holobiont in the northern Red Sea appear to be important functional traits (Grottoli et al. 2017). In addition, Fine et al. (2019) argued that despite the past bleaching events and higher temperatures, MRs in northern sections of the Red Sea are considered reef refugia from global warming and acidification, at least for the coming decades. In other words, these MRs may represent a short-term refuge by the definition adopted in this book (Table 1). Kleinhaus et al. (2020) may support this as they indicate that MRs in the Gulf of Aqaba will only survive and flourish in the ongoing Anthropocene if serious regional environmental challenges such as severe coastal urbanization are addressed. Thus, localized human activities compound the effects of warming seawater to damage corals and should be mitigated immediately in this portion of the Red Sea.

In the Persian Gulf coast, MRs appear to be resistant to the ongoing temperature stress (Bento et al. 2016). In contrast, Burt et al. (2019) recently found severe impacts on coral communities in this region. The already rare coral *Acropora* was locally extirpated in summer 2017 owing to the longest and most severe heatwave ever recorded, and Burt et al. (2019) showed that, compared with non-bleaching years (2013–2016), MRs in this coast were characterized by an extended period of mid-summer calm in 2017, when winds rarely exceeded breeze conditions, reducing evaporative heat loss and inducing dramatic warming and mass mortality. Monroe et al. (2018) also showed that, during the 2015/2016 global coral bleaching event, the extreme heat stress in Saudi Arabian Red Sea led to decreased species richness.

Moreover, several MRs (Burt et al. 2011, 2013, 2019) in this region clearly show continuous decline owing to large-scale coastal development and elevated sea surface temperature anomalies. In Bahrain, all MRs having a recent and historical data set available show continued reef degradation and loss of recovery potential (Burt et al. 2013). Accordingly, species-specific outbreaks of coral diseases were associated with the extreme temperature range combined with organic pollution and proximity to shore in high-temperature MRs (Aeby et al. 2020). Consequently, these results indicate that even the short refuge against thermal stress provided by high-temperature MRs is not universal and impervious to impacts. Furthermore, Eakin et al. (2016) suggested that it is currently unclear whether even heat-resistant corals can continue to improve their tolerance fast enough to keep up with global warming, with locations across hot-seas MRs (Fig. 1) recently suffering intense bleaching and mortality of reef-building species.

High-latitude reefs are also important MRs (Fig. 2e), where temperatures are highly variable among seasons. These MRs differ considerably from their tropical counterparts in several ecological aspects (Beger et al. 2014; Camp et al. 2018). High-latitude corals may tolerate short-term stress even under severe marine cold spells (Tuckett and Wernberg 2018). However, some high-latitude MRs and their coral communities are particularly susceptible to long-term climate change especially heatwaves, tropicalisation, acidification, and global warming (Schleyer et al. 2018; Jones et al. 2020). This is mainly caused by the latitudinal light attenuation, geographic isolation, small population sizes, greater predicted ocean warming, and lower Ω_{arag} (aragonite saturation state) of cooler waters (Beger et al. 2014). Accordingly, Camp et al. (2018) also suggested that, to date, it is unclear whether and to what extent high-latitude MRs can in fact serve as long-term refugia (Table 1) from continued climate change, despite evidence of some adaptations to their marginal environmental conditions such as short-term cold spells and heatwaves.

High-latitude MRs also present heterogeneity of coral bleaching responses according to their atmospheric and oceanographic conditions. In this context, spatial and temporal differences in bleaching prevalence were found in subtropical MRs (Hawaii) owing to the heterogeneity of local irradiance incidence, rainfall patterns, and turbidity levels (Bahr et al. 2017). The distance to the coast and the presence of non-climate human impacts (more common on nearshore reefs) also affect the resilience of corals in high-latitude MRs. Pollution and siltation are more common in coastal sites and may amplify the light/heat stress in these reefs (Jones et al. 2020). Accordingly, Banha et al. (2019) recently found record values of thermal stress for coastal and insular high-latitude MRs, which had the highest temperatures ever documented for a subtropical reef in the South Atlantic. Bleaching levels in a coastal reef were higher than those in an insular reef (80% and 20%, respectively) on the stress-tolerant *Mussismilia hispida*. However, mortality (2%) was far lower than that of similar magnitude episodes in other regions during the global episode of 2015–2016, particularly in the Indo-Pacific, suggesting a local adaptation to short-term heatwave on this high-latitude MR. Moreover, Jones et al. (2020) conducted an ecological long-term (2007–2016) assessment of changes to high-latitude reef benthic communities in relation to thermal stress duration on the Florida Reef Tract. They found that coral and octocoral cover decreased within four of six sub-regions, sponge cover increased in half of the sub-regions, and algae cover increased in four sub-regions consequently increasing the risk of inhibition of reef recovery in the next years.

3.2.3 Mesophotic Coral Ecosystems

Mesophotic Coral Ecosystems (MCEs) (~30–150 m depth) are marginal marine forests in tropical and subtropical ecoregions (Figs. 1 and 2a). These ecosystems comprise distinct seascapes and may be dominated by sponge gardens, black coral and octocoral forests, rhodolith beds, macroalgae, and/or depth-specialist corals that thrive using autotrophic and/or heterotrophic strategies (Soares et al. 2020a). They are different from shallow-water tropical reefs (Rocha et al. 2018; Soares et al. 2019a), particularly their deepest portion (i.e., 70–150 m), owing to their unique diversity (Soares et al. 2020a).

Recently, some studies proposed that reef-building corals living in these forests may escape heat-light stress and other human pressures (e.g., contamination) experienced by shallow-water corals, which suggests their potential as refugia. This idea is called the deep reef refugia hypothesis (DRRH). DRRH indicates that the incidence and frequency of bleaching, occurrence of coral diseases, and incidence of natural disturbances (e.g., storms and hurricanes) in these MRs are lower than those in shallow-water reefs (Loya et al. 2016). Moreover, these forests may also act as a limited source of propagules to recolonize affected areas (e.g., recovery of tropical shallow-water reefs) (Rocha et al. 2018; Bongaerts and Smith 2019).

The offshore location of MCEs sometimes leads to low human pressure such as pollution from coastal zones, overfishing, and high loads of sediments by continental runoff. However, it is possible that MCE resistance to certain environmental changes, such as temperature and pH, is narrower than that of shallow-water coral reefs owing to their low exposure history (Shlesinger et al. 2018). Moreover, they may be located (e.g., shallower shelves and insular countries) near human populations, which increases their susceptibility to non-climate pressures (Soares et al. 2020a). DRRH is highly debated on the literature especially owing to miscommunication and poor conceptual delineation (Bongaerts and Smith 2019).

To solve this problem, Bongaerts and Smith (2019) recently proposed three definitions of depth areas protected from pressures and their functional roles. First, "depth refuges" comprise a depth range that provides short-term buffering or shelter (i.e., avoidance) for one or multiple species or a biological community against a particular disturbance episode. Second, a "depth refugium" is a depth range that provides a long-term buffering or shelter (i.e., avoidance) for one or multiple species or a biological community against a particular or multiple disturbances types. Finally, a "depth resilience area" is a depth range that harbors one or multiple species or a biological community that is/are resilient (owing to resistance or rapid recovery, not avoidance) over the long term to a particular or multiple disturbance type(s). Moreover, these definitions do not require a demonstrated functional role with regard to the ability to act as a source of replenishment (Bongaerts and Smith 2019).

Bleaching reports that assessed tropical corals along a shallow-mesophotic gradient suggested that bleaching incidence decreases with depth (Muir et al. 2017), indicating the short-term refuge potential against temperature anomalies. In contrast, some MCEs demonstrate susceptibility to sea surface temperature (SST) anomalies (Bongaerts and Smith 2019), owing to their low bleaching thresholds and lower historical exposure to higher temperatures. Accordingly, Frade et al. (2018) found that cooler waters from upwelling initially provided thermal relief at upper mesophotic depths (40 m) in the Great Barrier Reef, which then subsided, resulting in anomalously higher temperatures even at high depths.

Projected warming rates and the existing "community thermal safety margin" (the inherent buffer against temperature anomalies based on thermal sensitivity of constituent species) (Bruno et al. 2018) may vary with latitude among marine ecoregions and MCEs (Soares et al. 2020a). Nevertheless, MCE safe thermal range is poorly known and may be lower than that for shallow-water coral reefs, especially in regions with a unithermal water column (i.e., the same temperature from the surface to the sea floor at mesophotic depths) (Soares et al. 2020a). Additionally, Venegas et al. (2019) analyzed 457 reef sites in the western and central Pacific Ocean and found no meaningful depth refuge from heat stress down to 38 m and no significant association between depth and subsurface heat stress.

Natural disturbances (i.e., storms and hurricanes) and human impacts (i.e., fishing activities and plastic debris) threaten MCEs in the Indo-Pacific and Caribbean Sea (Rocha et al. 2018) and the South Atlantic Ocean (Soares et al. 2019a) and, consequently, undermine their capacity to act as *depth refugium* or *depth resilience areas* (Soares et al. 2020a). Furthermore, MCEs are also susceptible to other human disturbances, such as ocean acidification (Couce et al. 2013), invasive species (Soares et al. 2019a), pollution (Soares et al. 2020b), environmental disasters (Silva et al. 2016), and thermal stress (Frade et al. 2018). Although there is evidence for depth refuges from storms and thermal anomalies, the impacts are case- and species-specific. Moreover, there is little evidence to support the idea that MCEs may provide long-term (*depth refugium* or *depth resilience areas*) over multiple disturbances (Bongaerts and Smith 2019). Accordingly, the current evidence does not indicate that MCEs represent a long-term refugia for corals in the ongoing Anthropocene (Soares et al. 2020a) unless important management actions at local and global scale are urgently implemented.

4 Refugia Potential of Marginal Reefs

The degradation of coral reefs has led to a growing interest in identifying areas that can offer long-term refugia against adverse conditions (Keppel et al. 2012; Soares 2020) such as warmer and acid seas in the Anthropocene. Research analyzing stable populations that already thrive under naturally occurring marginal conditions have, therefore, become increasingly popular to advance ecosystem scale predictions. However, no single site provides a perfect future analog to tropical coral reefs (Camp et al. 2018; Enochs et al. 2020). The occurrence of MRs under extreme and different from optimal conditions makes it possible to test hypotheses about short-term refuge or long-term refugia potential (Table 1) under the ongoing global environmental changes (Woesik et al. 2011; Morgan et al. 2016; Soares 2020).

MRs have been hypothesized to provide refuge from natural and human pressures (Glynn 1996; Riegl and Piller 2003; Cacciapaglia and Woesik 2016; Guest et al. 2016; Soares 2020; Sully and Woesik 2020). Marginal coral communities predisposed to environmental plasticity have been suggested as potential refuges for their resident populations or immigrant species (refugees) in a future of warming seas, frequent heatwaves, and ocean acidification (Glynn 1996; Riegl and Piller 2003; Enochs et al. 2020). Accordingly, a recent global analysis (Sully et al. 2019) of coral bleaching during the last two decades indicated that the onset of coral bleaching on the last decade (2007–2017) has occurred at significantly higher SST (~0.5 °C) than that in the previous decade (1998–2006). This suggests that thermally susceptible genotypes may have declined and/or adapted so that the remaining coral populations now have a higher thermal threshold for bleaching (Sully et al. 2019), which may also be attributed to some refuge areas overseas with stress-tolerant coral communities already adapted to one suboptimal condition (e.g., higher temperatures).

Similarly, MRs in naturally acidified environments (volcanic CO_2 vents) may provide insights into the mechanisms of resistance and resilience on coral reefs (Camp et al. 2018). Despite localized CO_2 enrichment and gas venting, MRs in the Caribbean Sea have high hard and soft coral cover, as well as extensive carbonate frameworks (Enochs et al. 2020). This persistence, despite the periodic ocean acidification, suggests a potential to act as a refuge, considering some adapted species to this suboptimal condition.

However, current information on refuge environments in MRs is still highly debated (Camp et al. 2018). Moreover, various concepts and hypotheses regarding the role of MRs and their subsequent persistence remain poorly discussed or misunderstood in the literature such as their refuge or refugia potential (Table 1). The empirical evidence from the literature discussed in Sect. 3 is not sufficient to support the hypothesis that MRs represent long-term refugia. In this Sect. 4, we clarify some core concepts and applications of these hypotheses.

4.1 Refugia: Right Concepts to Solve the Misunderstanding

Refuge sites are areas that maintain suitable conditions previously lost in other places (Kavousi and Keppel 2018). Identifying and protecting refugia are a priority for reef conservation under ongoing global environmental change, owing to their demonstrated ability to facilitate the survival of biota under adverse conditions. Refugia (Table 1) are also areas that "components of biodiversity retreat to, persist in, and can potentially expand from under changing environmental conditions" (Keppel et al. 2012). These could vary across temporal scales, with some environments providing *short-term* refuge against acute pressure (e.g., turbid-zone nearshore reefs reducing irradiance during a bleaching event) and others acting against

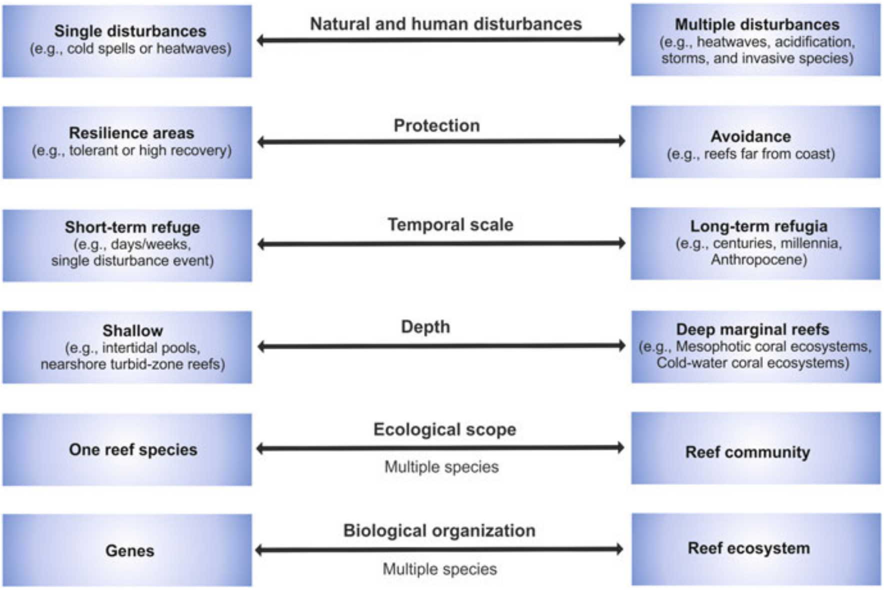


Fig. 9 Indicators to characterize refugia potential of marginal reefs. Modified from Bongaerts and Smith (2019)

long-term chronic changes (e.g., MRs that provide refugia under extreme environmental changes along geological history) (Camp et al. 2018; Brown et al. 2020) (Table 1 and Fig. 9).

Acting as a short-term refuge or long-term refugia (Table 1) involves MR patterns and processes that operate at different spatial and temporal scales. Accordingly, the refugia potential involves at least six different criteria (Fig. 9) including a number of disturbances, degree of protection against pressures, depth, temporal scale, ecological scope, and biological organization (Fig. 9). In this way, MRs that provide long-term protection for multiple reef species against multiple disturbances need to be given maximum priority in conservation actions (Fig. 9).

Considering an evolutionary time scale (thousands of years), a given marginal reef may have served as refugia for its ecoregion during past environmental conditions (Lybolt et al. 2010). For example, Potts and Jacobs (2000) suggested that turbid-zone coastal areas have provided ecological and evolutionary continuity as well as long-term refugia for corals during non-reefal periods, when physicochemical conditions were too extreme for coral reef growth. An interesting example is the case of the coral *Mussismilia*, which is widely distributed in the Atlantic Ocean before the Pleistocene and is currently a paleoendemic genus restricted to the Brazilian coast, probably owing to a long-term refugia in this marginal turbid-zone region (Peluso et al. 2018; Laborel-Deguen et al. 2019, Menezes et al. 2020). Moreover, MRs in seamounts and oceanic islands have an important role as refugia for diversification and maintenance of marine biodiversity throughout geological time (Pinheiro et al. 2017). In this way, Pleistocene sea-level fluctuations seem to have boosted the dispersal of weak colonizers by exposing seamounts as stepping stones and consequently created additional opportunities for vicariance (Pinheiro et al. 2017).

Nevertheless, considering an ecological time scale (decades), the same MR may be unable to reseed or recover some degraded reefs located under optimal conditions owing to species demographic constraints that reduce recruitment, dispersal, and reproduction. Most research reviewed in this book chapter (especially on Sect. 3) suggests a short-term (i.e., days or weeks) or mid-term (i.e., years or decades) refuge ability for the corresponding region/reef and also for some adapted species (Fig. 9). Moreover, the reviewed literature on turbid-zone, high-temperature and high-latitude reefs, and MCEs indicates that they act as a short-term refuge against single disturbances (e.g., heatwaves). However, this does not mean that a marginal reef could act as a long-term refugia for their own diversity and also to other reef ecosystems against multiple disturbances (Fig. 9 and Table 1). Although difficult to quantify, the concept of refuges is based on shorter ecological time scales of days to years, while refugia operate over longer evolutionary time scales of millennia (Fig. 9).

Moreover, the high phenotypic plasticity of some MR species and their adaptations to short-term environmental fluctuations (reviewed along this book chapter) do not imply that these species will be successful under ongoing long-term climate change. Seasonally plastic species may be especially vulnerable to climate change owing to genetic limitations for evolutionary responses (Oostra et al. 2018).

Finally, the refugia potential also involves different levels of biological organization, from genes to reef ecosystems (Fig. 9). Even if one species occurs in an extensive reef area spreading through optimal and marginal conditions, this does not support the hypothesis that the marginal portion is acting as a refugia for the entire reef area or multiple species, including sectors located under optimal conditions. To avoid confusion, Keppel et al. (2012) suggested using the term refugia when considering a species-range dynamics and climate change.

In this way, Kavousi and Keppel (2018) identified misunderstanding of concepts, such as climate change refugia for coral reefs, which is commonly applied to different phenomena. The term has been used to refer to pristine areas, i.e., large reserves or very preserved areas, reefs with high resistance to environmental stress; "short-term refuges," i.e., areas that provide short-term spatial and/or temporal shelter from pressures or advantages in biotic interactions; and "long-term refugia," i.e., areas that facilitate species persistence over several generations. The authors defend that climate change refugia are a kind of "long-term refugia" and indicate criteria to define them, such as areas with long-term buffering, protection from multiple climatic stressors, accessibility to migrants (refugees), high microclimatic heterogeneity, minimal size for populations persistence, and low exposure to non-climate disturbances (Fig. 10). Although past examples (Sect. 3) have confirmed the role of MRs as short-term ecological refuge, there is not enough evidence

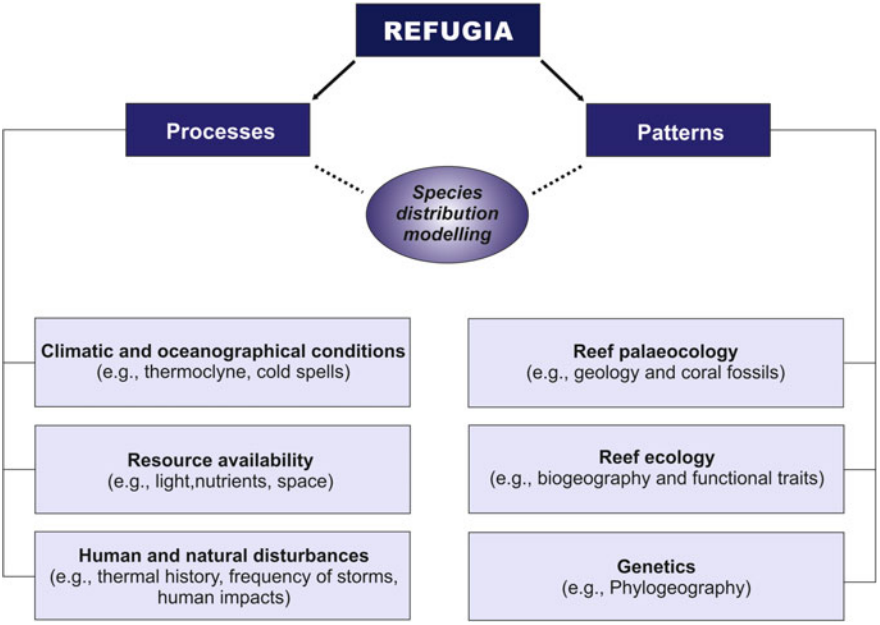


Fig. 10 Summary of the refugia potential of marginal reefs. Modified from Keppel et al. (2012)

supporting that they are long-term refugia and/or could be climate change refugia in oceans worldwide during the ongoing Anthropocene.

Moreover, niche modeling using future IPCC projections (Collins et al. 2013; Cacciapaglia and Woesik 2016) has indicated long-term refugia in some reef areas worldwide. This kind of methodology (Fig. 9) has been supported by studies that indicate past climate refugia associated to paleontological, ecological, environmental, and genetic data and has been used to explain current biodiversity in marine and terrestrial environments (Leão et al. 2003; Carnaval et al. 2009; Pellissier et al. 2014; Gavin et al. 2014; Menezes et al. 2020).

Model predictions based on IPCC projections suggest that optimal conditions for reef diversity will become more peripheral (in the edge of reef distribution), reaching higher latitudes (Guinotte et al. 2003; Couce et al. 2013; Cacciapaglia and Woesik 2016; Freeman 2015; Rodriguez et al. 2019). These studies indicate that peripheral regions will be climatically more favorable to some reef species, maybe owing to a shift to an optimal condition, and will probably shelter the major part of coral species for several generations. However, concluding that coral reefs will migrate to higher latitudes as they warm would be unfounded, because the observations of tropical species appearing at high latitudes do not provide evidence of the entire coral reef ecosystem shifting poleward (Hoegh-Guldberg et al. 2017). This aspect is extremely important and arises from misunderstandings about the biological levels of refugia potential (Fig. 9) and dimensions of reef biodiversity that need further investigation.

4.2 Refugia for Whom? Dimensions of Reef Biodiversity

As biodiversity analyses surpass counting species and individuals at multiple sites, defining the dimension of reef biodiversity is critical when analyzing MRs and their potential as refugia (Cavender-Bares et al. 2009; Keppel et al. 2012; Brown et al. 2020). The functional profile may vary greatly between reef communities with the same number of species, individuals, and evenness (Fig. 9). This underlies patterns of functional redundancy and should be better understood to identify the ecological role of MRs, because, if functions are lost from the supposed marginal reef, its ability to safeguard the biodiversity of refugees and/or provide long-term refugia for its own biodiversity would not be fully achieved.

Similarly, the phylogenetic diversity of evolutionary lineages should be taken into account, as changes in phylogenetic richness, divergence, and regularity are directly associated to the recovery ability from human or natural pressures (Tucker et al. 2017). In this way, it is imperative to analyze the multiple dimensions of reef biodiversity to understand MRs as potential refugia, as a particular MR may act as a short-term refuge for a particular adapted reef species but not necessarily for most reef species in the Anthropocene.

The taxonomic, functional, and phylogenetic dimensions of biodiversity are not equally distributed across all reef types. This adds another component to the study of MR diversity: the beta diversity. Alpha-diversity (α-diversity) is the mean species diversity within sites or habitats at a local scale (Whittaker 1972). Moreover, the total species diversity in a reef seascape (gamma diversity) is determined by two different things, α-diversity and the differentiation among reef habitats (β-diversity) (Whittaker 1972).

There are several ways to estimate β-diversity, sharing the same goal of describing dissimilarity or similarity among reef communities. β-diversity analyses have been increasingly used to identify the extent of biotic homogenization and differentiation driven by human pressures. One promising approach is Jost's multiplicative partition of gamma diversity into independent α and β components (Jost 2007, 2010), which is based on multiplicative diversity decompositions of effective number of species (so-called Hill numbers) and corrects several mathematical biases inherent to the traditional metrics of diversity, such as Shannon entropy, Gini-Simpson, Jaccard, Sorensen, and Morisita-Horn indices. In practical terms, Jost's β-diversity measures the "effective number of completely distinct communities" that compose a given reef region.

If all species of N local communities are everywhere in the region, the mean α-diversity is equal to gamma diversity, and, therefore, β-diversity represents only one completely different community, indicating maximum biotic homogenization. Conversely, if no reef species are shared among the local communities, β-diversity reaches N completely distinct communities, denoting maximum differentiation. This portioning can be calculated for species, functions, and lineages (Chao et al. 2014), providing a comprehensive picture of the MRs potential as refuges and/or refugia (Table 1). Another promising method to measure β-diversity, which complements that of Jost, is Baselga's additive partition of β-diversity into nestedness and turnover components (Baselga 2010; see Cardoso et al. (2020), e.g., of the use of both approaches). Baselga's methodology solves the issue of similar β-diversity values arising from differences in species richness between communities as well as from differences in species composition per se.

When turnover is high, all reef communities show similar levels of α-diversity (i.e., local richness) but share a few species, functions, or lineages, possibly because there are well-defined spatial niches within which species are sorted. This mechanism has been described as species sorting in structuring metacommunities (Leibold et al. 2004). When nestedness is high, some reef communities are richer, and poorer communities are nested within the richest, indicating species loss over the space and undefined spatial niches (mass effect sensu Leibold et al. 2004). For example, for MCEs to act as refuges from shallow communities, shallow communities should be nested within mesophotic communities. The same approach can be used to determine if the turbid-zone or high-latitude MRs are nested within tropical reefs under optimal conditions along a regional ocean basin scale.

Regardless of the temporal and spatial scale of protection provided by MRs, the level of biological organization (Fig. 9) should be clear to avoid overstatements concerning their potential as refugia (Fig. 10). For instance, vertical connectivity between shallow reefs and MCEs has been used to state that MCEs may act as refuge for shallow reefs. However, if the study was conducted on a single species, the correct conclusion would be that MCE may act as refuge for that species, not for non-studied co-occurring species that might be genetically isolated across the depth gradient (Bongaerts et al. 2017).

Scaling up this rationale to the community level (Fig. 9), the presence of a given species at both MCE and shallow reefs (i.e., depth generalist) is not sufficient to support the refuge reseeding hypothesis at MCEs. For this, most species, or at least those more dominant in shallow communities, should be depth generalists. If they are shallow specialists, there will be no conspecific at deep areas to recover their populations at shallow reefs (Morais and Santos 2018). Morais and Santos (2018) showed that only three of 17 species occurred throughout the gradient (3–61 m depth) between shallow-water reefs and MCEs in Western South Atlantic. Moreover, the authors reported that MCEs may be refuge for only two stress-tolerant corals (*Siderastrea stellata* and *M. cavernosa*).

Another evidence of the partition and multiple dimensions of reef diversity was provided within an Indonesian shallow-water reef (Hennige et al. 2010). Along a gradient (e.g., light quality, temperature, and turbidity) that included optimal, intermediate, and marginal environmental conditions, coral forest assemblages changed from dominance of diverse and mixed growth forms to dominance of specialized and massive growth forms, with branching species *Acropora formosa* and *Porites cylindrica* only being identified at optimal sites. Furthermore, only one species (the massive coral *Goniastrea aspera*) was identified at the most marginal and optimal sites, suggesting a refuge only for this particular species and not at the community level (Fig. 9), owing to the low overlap in species composition (Soares 2020). Moreover, even for this species, further analyses need to be conducted, such as validation of genetic connectivity and evaluation of reproductive strategies (e.g., fecundity).

Accordingly, Camp et al. (2018) suggested that knowledge about the connectivity of marginal coral populations relative to adjacent optimal reefs is a research priority. The refugia potential will also depend partly on the dispersal of adults, juveniles, and larvae (Chacon-Gomez et al. 2013), with sessile brooding species being more likely to exhibit survival and persistence to suboptimal environments over multiple generations than broadcast spawning species, which may recruit into the suboptimal environment as progeny from "parents" in less stressful reefs (Camp et al. 2018).

Other empirical evidence about the limitations to act as long-term refugia are supported by research conducted in high-latitude MRs. The unique diversity of these MRs is caused by the overlap of tropical and temperate species ranges, species that are rare or absent at lower latitudes (where tropical coral reefs are), strong seasonality in species composition, and a significant number of endemic species (e.g., nestedness) (Beger et al. 2014).

In high-latitude reefs, species temporal turnover can be high depending on larval supply and recruitment from lower latitudes and fluctuations under environmental conditions (Beger et al. 2014). Furthermore, high-latitude reefs are home to ecologically and functionally distinct communities such as MCEs, turbid-zone reefs, and other MRs cited along this book chapter. Camp et al. (2018) argued that the heterogeneous nature of reef systems (including marginal and optimal sites) challenges the ability of these environments to act as a refuge for multiple suboptimal conditions (Fig. 9). The same pattern of distinct and heterogeneous ecosystems was recently found between the shallow-water coral reefs and MCEs in the South Atlantic (Morais and Santos 2018; Soares et al. 2019a) and Caribbean/Indo-Pacific reefs (Rocha et al. 2018), indicating a limited short-term refuge potential of MRs for few reef species and not for reef communities or the entire ecosystem.

4.3 Finding Refugia Areas

Refugia areas constitute marginal regions in the ocean basins or biogeographical regions with naturally low stress, where some species may survive and flourish in the long term. For example, upwelling areas are short-term refuge against thermal stress within the Caribbean basin (Chollett and Mumby 2013). Moreover, Cacciapaglia and Woesik (2016) suggested that the turbid-zone coastal areas of the northwestern Hawaiian Islands, northern Philippines, Ryukyu Islands (Japan), eastern Vietnam, western and eastern Australia, New Caledonia, northern Red Sea, and Arabian Gulf may also be refugia areas and should become part of a global strategy for coral reef persistence under ongoing global environmental changes. Thus, these turbid-zone MRs and their marginal corals broaden the geographic scope and strengthen the network of locations that may act as critical refugia areas (Cacciapaglia and Woesik 2016).

Several studies have been conducted in the last decade to find refugia areas (Keppel et al. 2012; Kavousi and Keppel 2018) using methods to analyze the processes and patterns of reef ecosystems (Fig. 10), especially species distribution modeling. However, many studies published worldwide are based on intrinsic characteristics of MRs and do not consider that the vast majority of reef species under optimal conditions cannot survive under present-day marginal conditions. MRs, usually with high turbid, deep, or cold waters, are characterized by suboptimal environmental conditions compared to those of reef diversity centers (Table 1). Thus, the high capacity to tolerate environmental changes and recover afterwards is a specific trait of these reef communities and indicates that plastic and species adapted to marginal conditions could probably thrive under new conditions (Kawecki 2008). However, these intrinsic traits cannot be considered as parameters to indicate that current MRs will be long-term refugia to most refugees.

To help finding refugia areas, the "tropicalization" phenomenon has also been considered (Tuckett et al. 2017; Figueira and Booth 2010). "Tropicalization" forecasts that with temperature increases, high-latitude MRs, such as subtropical and temperate systems usually dominated by algae, will become dominated by tropical warm taxa, such as zoanthids (González-Delgado et al. 2018) and scleractinian corals. Hence, MRs will no longer be marginal and, certainly, will be able to receive common species (refugees) from reefs under optimal conditions. Some evidence of this process has already been recorded in Western Australia (Steneck et al. 2017) and the Mediterranean Sea (Bianchi 2007). However, despite the evidence for some species, this phenomenon is mainly based on niche modeling that uses climate variables. However, other non-climate variables should be included in these projections (Fig. 10).

The most important factors usually not considered in these projections to find refugia areas are the non-climate disturbances, such as local and regional-scale pressures (Fig. 10). MRs are usually extremely threatened by local and regional human activities, such as domestic sewage, agricultural and industrial runoff, overfishing, tourism, and oil spill, which could be seen in shallow-water reefs from Brazil and Florida (Bruno et al. 2009; Cruz et al. 2018; Soares et al. 2020b). Even MCEs are also threatened worldwide (Rocha et al. 2018; Soares et al. 2019a) and not yet protected by fishery regulations, marine protected areas (MPAs), or marine spatial planning, which undermine their capacity to act as a refugia (Soares et al. 2020a). Even though they are potential refugia with high intrinsic capacity to persist under new conditions, they are not immune or more tolerant. Overfishing, nonregulated tourism, and pollution may impose serious risks to MRs at a local scale (Morais et al. 2018), possibly making them as sensible to human pressures as tropical reefs under optimal conditions.

The degradation of MRs owing to the coupling between climate change and non-climate pressures undermines their potential to act as long-term refugia during the ongoing Anthropocene. The changes from stable to unstable temperatures projected for most biodiverse regions threaten to reduce the size and extent of important climatic safe havens for diversity (Skirving et al. 2019). Moreover, the temperatures in these refuge sites at the end of this century are likely to exceed the acclimation capacity for many key species, making them short-term hospices for some species at best (Brown et al. 2020).

Moreover, the criteria established by Kavousi and Keppel (2018) to determine the capacity of refuges to facilitate the persistence of species on reefs (i.e., long-term buffer, protection against multiple climatic stressors, accessibility, microclimate heterogeneity, size, and low exposure to non-climatic disturbances) are not found in several MRs in shallow, mesophotic, and deep-sea waters. Unfortunately, several MRs are threatened in the long term owing to climate change (e.g., rising sea levels, storms, floods and droughts, ocean acidification, heatwaves) and local human pressures such as urbanization, increased suspended sediments, and excessive pollution and fishing, as revised throughout this chapter.

5 Management for Marginal Reef Persistence

The vulnerability of MRs to pressures, which undermines their limited refugia potential, has been addressed in the literature and discussed along this book chapter. However, one question needs to be considered: How can we manage these MRs to maintain and/or improve their natural resistance and resilience? Côté and Darling (2010) indicated that management of local human activities to reverse degradation and recover original reef species assemblages will actually increase the proportion of sensitive taxa within the community and may decrease ecosystem resistance to climate change. This may be true for some tropical coral reefs under optimal conditions that are dominated by stress-sensitive species (e.g., Caribbean Sea). Contrastingly, MRs are distinct ecological ecosystems, with different responses to those of coral reefs under optimal conditions. In other words, MRs have communities that derived and naturally contain stress-tolerant habitat-forming species that dominate the reef structure.

MRs in shallow, mesophotic, and deep waters have a higher susceptibility, notably if pressures eliminate their functionally irreplaceable species, driving the assemblage to biological impoverishment. Human activities that impact sensitive life history stages, decreasing reproductive effort and the supply of juveniles essential for reef recovery, need to be avoided using the greatest conservation actions. Thus, as niche specialization or temporal and spatial segregation make each species unique, MRs can be highly susceptible to the decline of their few habitat-forming species (i.e., low redundancy). This hypothesis was proposed by Mora et al. (2016), and, considering their lower functional diversity, it is even more important for MRs than for coral reefs under optimal conditions. This hypothesis also implies that important functions in MRs can be lost (Table 1) owing to impacts such as bottom trawling, invasive species, and/or eutrophication.

In fact, various publications emphasize the need to protect MRs from several human activities such as pollution in South China (Chen et al. 2013), contamination in South Atlantic reefs (Portugal et al. 2016), derelict fishing gears in Ecuador (Figueroa-Pico et al. 2020), and urban development and eutrophication in Borneo

(Browne et al. 2019), Bahrain (Burt et al. 2013), Arabian (Aedy et al. 2020) and the Red Sea (Fine et al. 2019). For example, Fine et al. (2019) and Kleinhaus et al. (2020) highlighted the urgent action to conserve northern sections of the Red Sea (including Gulf of Aqaba) as a climate change refugia by management and removal of local human pressures. Moreover, Sully and Woesik (2020) suggested that turbid-zone MRs need high conservation status to keep them close to dense human populations.

Despite awareness gaps, MRs may have an overlooked high conservation value, owing to the phenotypic plasticity of habitat-forming species adapted to marginal conditions (Camp et al. 2018; Schoepf et al. 2019). Moreover, MRs may have significant endemism rates (Pinheiro et al. 2017) and offer genetic rescue (e.g., heat-tolerant genotypes across latitudes), which would give them a high research and conservation value (Coles and Riegl 2013; Camp et al. 2018). Governance options include management strategies, such as the establishment of sewage systems in urbanized areas, urgent control of continental runoff and siltation by deforestation, as well as MPAs that aim to minimize pressures under a context of resilient-based management actions (McLeod et al. 2019). Therefore, building adequate no-take MPAs in suitable MCEs (Soares et al. 2019a, 2020a), high-latitude (Beger et al. 2014), high-temperature (Cavalcante et al. 2016), and turbid-zone reefs (Endo et al. 2019) to enhance genetic and ecological connectivity along dispersal routes and maintain ecosystem resilience through reduced human activities may be an important strategy.

Finally, it is important to design conservation and scientific outreach strategies for MRs worldwide, including (1) an efficient and permanent environmental education policy, (2) promoting research and scientific outreach to show the importance of decreasing the human pressures to governments and the private sector, (3) the creation and effectiveness of MPAs, (4) closure of sensitive areas in MRs to fisheries and mass tourism, (5) encouragement of ecotourism, (6) restoration of MRs, and (7) community participation and co-management in conservation projects.

6 Concluding Thoughts

In conclusion, we discussed in this book chapter that MRs comprise a heterogeneous and important set of seascapes in the world's oceans. The patterns of unique diversity and high turnover of species provide evidence that reefs in optimal sites are ecologically distinct from MRs, such as turbid-zone, high-temperature and high-latitude reefs, and MCEs. Moreover, they are understudied and represent limited long-term refugia. We also argue that MRs are under severe pressure owing to a plethora of human and natural pressures and in as much need of management actions as coral reefs developed under optimal conditions. Thus, their resistance and recovery potential will be lost if management actions are not urgently adopted (Mcleod et al. 2019). We especially highlight the importance of maintaining pathways of connectivity, reducing reef stressors, and protecting the unique diversity of MRs including the endemism hotspots and the few functional groups.

In MRs, non-climate pressures (dredging, bottom trawling, oil spills, silting, fisheries, marine pollution, tourism) (Soares 2020) interact with global pressures (acidification, sea-level rise, heatwaves, and warming) (Guinotte et al. 2003; Morais et al. 2018; Kurihara et al. 2019), resulting in weakened resistance and limited potential to act as a long-term refugia in the ongoing Anthropocene. Moreover, MRs may only have resilience up to a point, as even thermal-, pH-, and turbid-tolerant species will have stress limits that may be exceeded by growing impacts in the next decades. In this regard, multiple MRs in the Pacific, Atlantic, and Indian Oceans are vulnerable to heatwave intensification owing to the co-occurrence of unique reef biodiversity, a prevalence of key species found at their warm range edge, and/or concurrent non-climate human pressures (Smale et al. 2019).

Another overlooked global pressure is the decrease in water productivity and, consequently, weakening of benthic-pelagic coupling and energy fluxes in MRs. Because primary and secondary productivity responds to different pressures, in particular to the rapid environmental changes driven by climate change, the benthic suspension feeders (Rossi et al. 2019; Lesser and Slattery 2020) that dominate and underpin marginal reef functioning in most parts of the oceans will be severely impacted. To preserve their unique biodiversity, ecosystem goods and services, and their limited refugia potential, it is necessary to ensure resilient-based management actions at local and regional scales (Mcleod et al. 2019) as well as to promote the urgent reduction of carbon emissions worldwide. Moreover, this will not be achieved without solid investments in research, conservation, and scientific outreach regarding MRs worldwide.

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References

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA (2020) Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39:829–846. https://doi.org/10.1007/s00338-020-01928-4

Al-Monsoori N, McParland D, Howells E, Bauman A, Burt JA (2019) Coral bioerosion on the marginal reefs of northeastern Arabia. Aquat Ecosyst Health Manage 1–9. https://doi.org/10.1080/14634988.2019.1677204

Bahr KD, Rodgers KS, Jokiel PL (2017) Impact of three bleaching events on the reef resilience of Kane'one Bay, Hawaii. Front Mar Sci 4:1–12. https://doi.org/10.3389/fmars.2017.00398

Bak RPM, Meesters EH (2000) Acclimatization/adaptation of coral reefs in a marginal environment. In: Proceedings 9th international coral reef symposium, Bali, Indonesia. http://coremap.or.id/downloads/ICRS9th-definitiefJPEGfigs.pdf

Banha TNS, Capel KCC, Kitahara MV, Francini-Filho RB, Francini CLB, Sumida PYG, Mies M (2019) Low coral mortality during the most intense bleaching event ever recorded in subtropical Southwestern Atlantic reefs. Coral Reefs 1–6. https://doi.org/10.1007/s00338-019-01856-y

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19(1):134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baumann J, Grottoli AG, Hughes AD, Matsui Y (2014) Photoautotrophic and heterotrophic carbon in bleached and non-bleached coral lipid acquisition and storage. J Exp Mar Biol Ecol 461:469–478. https://doi.org/10.1016/j.jembe.2014.09.017

Beck MW, Losada IJ, Menéndez P, Reguero BG, Díaz-Simal P, Fernández F (2018) The global flood protection savings provided by coral reefs. Nat Commun 9(1):1–7. https://doi.org/10.1038/s41467-018-04568-z

Beger M, Sommer B, Harrison PL, Smith SD, Pandolfi JM (2014) Conserving potential coral reef refuges at high latitudes. Divers Distrib 20(3):245–257. https://doi.org/10.1111/ddi.12140

Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? Glob Chang Biol 19(9):2613–2624. https://doi.org/10.1111/gcb.12212

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and function on coral reefs. Ecol Lett 6(4):281–285. https://doi.org/10.1046/j.1461-0248.2003.00432.x

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429(6994):827–833. https://doi.org/10.1038/nature02691

Bennett S, Vergés A, Bellwood DR (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. Coral Reefs 29(2):471–480. https://doi.org/10.1007/s00338-010-0594-5

Bento R, Hoey AS, Bauman AG, Feary DA, Burt JA (2016) The implications of recurrent disturbances within the world's hottest coral reef. Mar Pollut Bull 105(2):466–472. https://doi.org/10.1016/j.marpolbul.2015.10.006

Bianchi CN (2007) Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580:7. https://doi.org/10.1007/s10750-006-0469-5

Bongaerts P, Smith TB (2019) Beyond the "deep reef refuge" hypothesis: a conceptual framework to characterize persistence at depth. In: Loya Y, Puglise KA, Bridge TCL (eds) Mesophotic coral ecosystems. Springer, New York, pp 867–879. https://doi.org/10.1007/978-3-319-92735-0_45

Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-Guldberg O (2017) Deep reefs are not universal refuges: reseeding potential varies among coral species. Sci Adv 3(2): e1602373. https://doi.org/10.1126/sciadv.1602373

Bozec YM, Mumby PJ (2015) Synergistic impacts of global warming on coral reef resilience. Philos Trans R Soc B 370(1659):20130267. https://doi.org/10.1098/rstb.2013.0267

Brown SC, Wigley TML, Otto-Bliesner BL, Rahbek C, Fordham DA (2020) Persistent quaternary climate refugia are hospices for biodiversity in the Anthropocene. Nat Clim Chang 10:244–258. https://doi.org/10.1038/s41558-10-0682-7

Browne N, Braoun C, McIlwain J, Nagarajan R, Zinke J (2019) Borneo coral reefs subject to high sediment loads show evidence of resilience to various environmental stressors. PeerJ. 7:e7382. https://doi.org/10.7717/peerj.7382

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90(6):1478–1484. https://doi.org/10.1890/08-1781.1

Bruno JF, Bates AE, Cacciapaglia C, Pike EP, Amstrup SC, Hooidonk RV, Henson SA, Aronson RB (2018) Climate change threatens the world's marine protected areas. Nat Clim Chang 8 (6):499–503. https://doi.org/10.1038/s41558-018-0149-2

Budd FA, Nunes FLD, Weil E, Pandolfi JM (2012) Polymorphism in a common Atlantic reef coral (*Montastraea cavernosa*) and its long-term evolutionary implications. Evol Ecol 26:265–290. https://doi.org/10.1007/s10682-010-9460-8

Burt J, Al-Harthi S, Al-Cibahy A (2011) Long-term impacts of coral bleaching events on the world's warmest reefs. Mar Environ Res 72(4):225–229. https://doi.org/10.1016/j.marenvres.2011.08.005

Burt JA, Al-Khalifa K, Khalaf E, AlShuwaikh B, Abdulwahab A (2013) The continuing decline of coral reefs in Bahrain. Mar Pollut Bull 72(2):357–363. https://doi.org/10.1016/j.marpolbul.2012.08.022

Burt JA, Camp EF, Enochs IC, Johansen JL, Morgan KM, Riegl B, Hoey AS (2020) Insights from extreme coral reefs in a changing world. Coral Reefs 39:495–507. https://doi.org/10.1007/s00338-020-01966-y

Burt J, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. Coral Reefs 38 (4):567–589. https://doi.org/10.1007/s00338-019-01767-y

Cacciapaglia C, Woesik R (2016) Climate-change refugia: shading reef corals by turbidity. Glob Chang Biol 22(3):1145–1154. https://doi.org/10.1111/gcb.13166

Camp EF, Schoepf V, Mumby PJ, Hardtke LA, Rodolfo-Metalpa R, Smith DJ, Suggett DJ (2018) The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. Front Mar Sci 5(4):1–15. https://doi.org/10.3389/fmars.2018.00004

Camp EF, Suggett DJ, Pogoreutz C, Nitschke MR, Houlbreque F, Hume BCC, Gardner SG, Zampighi M, Rodolfo-Metalpa R, Voolstra CR (2020) Corals exhibit distinct patterns of microbial reorganisations to thrive in an extreme inshore environment. Coral Reefs 1–12. https://doi.org/10.1007/s00338-019-01889-3

Cardoso AP, Matos MR, Rosa RS, Alvarado F, Medeiros AP, Santos BA (2020) Increased fish diversity over day and night in structurally complex habitats of artificial reefs. J Exp Mar Biol Ecol 522:151244. https://doi.org/10.1016/j.jembe.2019.151244

Carnaval AC, Hickerson MJ, Haddad CF, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science 323(5915):785–789. https://doi.org/10.1126/science.1166955

Cavalcante GH, Feary DA, Burt JA (2016) The influence of extreme winds on coastal oceanography and its implications for coral population connectivity in the southern Arabian Gulf. Mar Pollut Bull 105(2):489–497. https://doi.org/10.1016/j.marpolbul.2015.10.031

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. Ecol Lett 12(7):693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Celliers L, Schleyer MH (2002) Coral bleaching on high-latitude marginal reefs at Sodwana Bay, South Africa. Mar Pollut Bull 44(12):1380–1387. https://doi.org/10.1016/S0025-326X(02)00302-8

Chacon-Gomez IC, Salas-Monreal D, Riveron-Enzastiga ML (2013) Current pattern and coral larval dispersion in a tropical coral reef system. Cont Shelf Res 68:23–32. https://doi.org/10.1016/j.csr.2013.08.014

Chao A, Chiu CH, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annu Rev Ecol Evol Syst 45:297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chen T, Li S, Yu K (2013) Macrobioerosion in Porites corals in subtropical northern South China Sea: a limiting factor for high-latitude reef framework development. Coral Reefs 32 (1):101–108. https://doi.org/10.1007/s00338-012-0946-4

Chollett I, Mumby PJ (2013) Reefs of the last resort: locating and assessing thermal refugia in the wider Caribbean. Biol Conserv 167:179–186. https://doi.org/10.1016/j.biocon.2013.08.010

Chow GSE, Chan YKS, Jain SS, Huang D (2019) Light limitation selects for depth generalists in urbanized reef coral communities. Mar Environ Res 147:101–112. https://doi.org/10.1016/j.marenvres.2019.04.010

Coles SL, Riegl BM (2013) Thermal tolerances of reef corals in the Gulf: a review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. Mar Pollut Bull 72(2):323–332. https://doi.org/10.1016/j.marpolbul.2012.09.006

Collins M, Knutti R, Arblaster J, Dufresne JL, Fichefet T, Friedlingstein P, Shongwe M (2013) Long-term climate change: projections, commitments and irreversibility. In: Climate change 2013-The physical science basis: contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, pp 1029–1136

Connolly SR, Lopez-Yglesias MA, Anthony KRN (2012) Food availability promotes rapid recovery from thermal stress in a scleractinian coral. Coral Reefs 31(4):951–960. https://doi.org/10.1007/s00338-012-0925-9

Conti-Jerpe I, Thompson PD, Wong CWM, Oliveira NL, Duprey NN, Moynihan MA, Baker DM (2020) Trophic strategies and bleaching resistance in reef-building corals. Sci Adv 6(15): eaaz5443. https://doi.org/10.1126/sciadv.aaz5443

Costanza R, de Groot R, Sutton P, der Ploeg SV, Anderson SJ, Kubiszewiski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. Glob Environ Chang 26:152–158. https://doi.org/10.1016/j.gloenvcha.2014.04.022

Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. PLoS Biol 8(7):e1000438. https://doi.org/10.1371/journal.pbio.1000438

Couce E, Ridgwell A, Hendy EJ (2013) Future habitat suitability for coral reef ecosystems under global warming and ocean acidification. Glob Change Biol 19(12):3592–3606. https://doi.org/10.1111/gcb.12335

Cramer KL, Jackson JBC, Donovan MK, Greenstein BJ, Korpanty CA, Cook GM, Pandolfi JM (2020) Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. Sci Adv 6(17):eaax9395. https://doi.org/10.1126/sciadv.aax9395

Crandall JB, Teece MA, Estes BA, Manfrino C, Ciesla JH (2016) Nutrient acquisition strategies in mesophotic hard corals using compound specific stable isotope analysis of sterols. J Exp Mar Biol Ecol 474:133–141. https://doi.org/10.1016/j.jembe.2015.10.010

Creed JC, Fenner D, Sammarco P, Cairns S, Capel K, Junqueira AOR, Cruz I, Miranda RJ, Carlos-Júnior L, Mantellato MC, Oigman-Pszczol S (2017) The invasion of the azooxanthellate coral Tubastraea (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors. Biol Invasions 19:283–305. https://doi.org/10.1007/s10530-016-1279-y

Cruz ICS, Waters LG, Kikuchi RKP, Leão ZMAN, Turra A (2018) Marginal coral reefs show high susceptibility to phase shift. Mar Pollut Bull 135:551–561. https://doi.org/10.1016/j.marpolbul.2018.07.043

Cruz-Trinidad A, Aliño PM, Geronimo RC, Cabral RB (2014) Linking food security with coral reefs and fisheries in the coral triangle. J Coastal Manage 42(2):160–182. https://doi.org/10.1080/08920753.2014.877761

Denis V, Mezaki T, Tanaka K, Kuo CY, Palmas SD, Keshavmurthy S, Chen CA (2013) Coverage, diversity, and functionality of a high-latitude Coral Community (Tatsukushi, Shikoku Island, Japan). PLoS One 8(1):e54330. https://doi.org/10.1371/journal.pone.0054330

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132. https://doi.org/10.1007/BF00008211

Duarte GAS, Villela HDM, Deocleciano M, Silva D, Barno A, Cardoso PM, Vilela CLS, Rosado P, Messias CSMA, Chacon MA, Santoro EP, Olmedo DB, Szpilman M, Rocha LA, Sweet M, Peixoto RS (2020) Heat waves are a major threat to turbid coral reefs in Brazil. Front Mar Sci. https://doi.org/10.3389/fmars.2020.00179

Dubinsky Z, Stambler N (2011) Coral reefs: an ecosystem in transition, vol 552. Springer, Cham. https://doi.org/10.1007/978-94-007-0114-4

Dudgeon SR, Aronson RB, Bruno JF, Precht WF (2010) Phase shifts and stable states on coral reefs. Mar Ecol Prog Ser 413:201–2016. https://doi.org/10.3354/meps08751

Eakin CM, Liu G, Gomez AM, De La Cour JL, Heron SF, Skirving WJ (2016) Global coral bleaching 2014–2017: status and an appeal for observations. Reef Encounter 31:20–26. https://coralreefwatch.noaa.gov/satellite/analyses_guidance/global_coral_bleaching_2014-17_status.php

Elliff CI, Silva IR (2017) Coral reefs as the first line of defense: shoreline protection in face of climate change. Mar Environ Change 127:148–154. https://doi.org/10.1016/j.marenvres.2017.03.007

Endo CAK, Gherardi DFM, Pezzi LP, Lima LN (2019) Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. Sci Rep 9 (1):1–9. https://doi.org/10.1038/s41598-019-45042-0

Enochs IC, Formel N, Manzello D, Morris J, Mayfield AB, Boyd A, Kolodziej G, Adams G, Hendee J (2020) Coral persistence despite extreme periodic pH fluctuations at a volcanically acidified Caribbean reef. Coral Reefs. https://doi.org/10.1007/s00338-020-01927-5

Ezzat L, Towle E, Irisson J-O, Langdon C, Ferrier-Pagès C (2016) The relationship between heterotrophic feeding and inorganic nutrient availability in the scleractinian coral *T. reniformis* under a short-term temperature increase. Limnol Oceanogr 61(1):89–102. https://doi.org/10.1002/lno.10200

Figueira WF, Booth DJ (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Glob Chang Biol 16(2):506–516. https://doi.org/10.1111/j.1365-2486.2009.01934.x

Figueroa-Pico J, Tortosa FS, Carpio AJ (2020) Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador. Coral Reefs. https://doi.org/10.1007/s00338-020-01926-6

Fine M, Cinar M, Voolstra CR, Safa A, Rinkevich B, Laffoley D, Hilmi N, Allemand D (2019) Coral reefs of the Red Sea – challenges and potential solutions. Reg Stud Mar Sci 25:100498. https://doi.org/10.1016/j.rsma.2018.100498

Fisher R, Bessell-Browne P, Jones R (2019) Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nat Commun 10:2346. https://doi.org/10.1038/s41467-019-10288-9

Floros C, Schleyer MH, Maggs JQ (2013) Fish as indicators of diving and fishing pressure on high-latitude coral reefs. Ocean Coastal Manage 84:130–139. https://doi.org/10.1016/j.ocecoaman.2013.08.005

Frade PR, Bongaerts P, Englebert N, Rogers A, Gonzalez-Rivero M, Hoegh-Guldberg O (2018) Deep reefs of the great barrier reef offer limited thermal refuge during mass coral bleaching. Nat Commun 9:3447. https://doi.org/10.1038/s41467-018-05741-0

Francini-Filho R, Asp NE, Siegle E, Hocevar J, Lowyck K, D'Avila N, Vasconcelos AA, Baitelo R, Rezende CE, Omachi CY, Thompson CC, Thompson FL (2018) Perspectives on the great Amazon reef: extension, biodiversity, and threats. Front Mar Sci. https://doi.org/10.3389/fmars.2018.00142

Freeman LA (2015) Robust performance of marginal Pacific coral reef habitats in future climate scenarios. PLoS One 10(6):e0128875. https://doi.org/10.1371/journal.pone.0128875

Freitas LM, Oliveira MDM, Leão ZMAN, Kikuchi RKP (2019) Effects of turbidity and depth on the bioconstruction of the Abrolhos reefs. Coral Reefs 38(2):241–253. https://doi.org/10.1007/s00338-019-01770-3

Gavin DG, Fitzpatrick MC, Gugger PF, Heath KD, Rodríguez-Sánchez F, Dobrowski SZ, Blois JL (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. New Phytol 204(1):37–54. https://doi.org/10.1111/nph.12929

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Bot Gard 75(1):1–34. https://doi.org/10.2307/2399464

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Glob Chang Biol 2:495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

González-Delgado S, López C, Brito A, Clemente S (2018) Marine community effects of two colonial zoanthids in intertidal habitats of the Canary Islands. Reg Stud Mar Sci 23:23–31. https://doi.org/10.1016/j.rsma.2018.03.006

Gori A, Reynaud S, Orejas C, Ferrier-Pagès C (2015) The influence of flow velocity and temperature on zooplankton capture rates by the cold-water coral *Dendrophyllia cornigera*. J Exp Mar Biol Ecol 466:92–97. https://doi.org/10.1016/j.jembe.2015.02.004

Gori A, Tolosa I, Orejas C, Rueda L, Viladrich N, Grinyó J, Flögel S, Grover R, Ferrier-Pagès C (2018) Biochemical composition of the cold-water coral *Dendrophyllia cornigera* under contrasting productivity regimes: insights from lipid biomarkers and compound-specific isotopes. Deep-Sea Res I Oceanogr Res Pap 141:106–117. https://doi.org/10.1016/j.dsr.2018.08.010

Grottoli AG, Tchernov D, Winters G (2017) Physiological and biogeochemical responses of super-corals to thermal stress from the Northern Gulf of Aqaba, Red Sea. Front Mar Sci 4:1–10. https://doi.org/10.3389/fmars.2017.00215

Guest JR, Tun K, Low J, Vergés A, Marzinelli EM, Campbell AH, Bauman AG, Feary DA, Chou LM, Steinberg PD (2016) 27 years of benthic and coral community dynamics on turbid, highly urbanized reefs off Singapore. Sci Rep 6:36260. https://doi.org/10.1038/srep36260

Guinotte JM, Buddemeier RW, Kleypas JA (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. Coral Reefs 22(4):551–558. https://doi.org/10.1007/s00338-003-0331-4

Halfar J, Godinez-Orta L, Riegl B, Valdez-Holguin JE, Borges JM (2005) Living on the edge: high-latitude *Porites* carbonate production under temperate eutrophic conditions. Coral Reefs 24(4):582–592. https://doi.org/10.1007/s00338-005-0029-x

Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. Sci Rep 9:11609. https://doi.org/10.1038/s41598-019-47201-9

Harriott VJ, Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. Coral Reefs 21:83–94. https://doi.org/10.1007/s00338-001-0201-x

Hennige SJ, Smith DJ, Walsh SJ, McGinley MP, Warner ME, Suggett DJ (2010) Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. J Exp Mar Biol Ecol 39(1–2):143–152. https://doi.org/10.1016/j.jembe.2010.06.019

Hinrichs S, Patten NL, Feng M, Strickland D, Waite AM (2013) Which environmental factors predict seasonal variation in the coral health of *Acropora digitifera* and *Acropora spicifera* at Ningaloo reef? PLoS One 8(4):e60830. https://doi.org/10.1371/journal.pone.0060830

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci. https://doi.org/10.3389/fmars.2017.00158

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25(11):633–642. https://doi.org/10.1016/j.tree.2010.07.011

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359(6371):80–83. https://doi.org/10.1126/science.aan8048

Hume BCC, D'Angelo C, Smith EG, Stevens SR, Burt J, Wiedenmann J (2015) *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. Sci Rep 5:8562. https://doi.org/10.1038/srep08562

Jones NP, Figueiredo J, Gilliam DS (2020) Thermal stress-related spatiotemporal variations in high-latitude coral reef benthic communities. Coral Reefs. https://doi.org/10.1007/s00338-020-01994-8

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439. https://doi.org/10.1890/06-1736.1

Jost L (2010) Independence of alpha and beta diversities. Ecology 91:1969–1974. https://doi.org/10.2307/25680448

Kavousi J, Keppel G (2018) Clarifying the concept of climate change refugia for coral reefs. ICES J Mar Sci 75(1):43–49. https://doi.org/10.1093/icesjms/fsx124

Kawecki TJ (2008) Adaptation to marginal habitats. Annu Rev Ecol Evol Syst 39:321–342. https://doi.org/10.1146/annurev.ecolsys.38.091206.095622

Keppel G, Niel KPV, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob Ecol Biogeogr 21(4):393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kleinhaus K, Al-Sawalmih A, Barshis DJ, Genin A, Grace LN, Hoegh-Guldberg O, Loya Y, Meibom A, Osman EO, Ruch JD, Shaked Y, Voolstra CR, Zvuloni A, Fine M (2020) Science, diplomacy, and the Red Sea's unique coral reef: It's time for action. Front Mar Sci 7(90):1–7. https://doi.org/10.3389/fmars.2020.00090

Kleypas JA, McManus JW, Menez LAB (1999) Environmental limits to coral reef development: where do we draw the line? Am Zool 39:146–159. https://doi.org/10.1093/icb/39.1.146

Kurihara H, Wouters J, Yasuda N (2019) Seasonal calcification of the coral *Acropora digitifera* from a subtropical marginal Okinawa reef under ocean acidification. Coral Reefs 38 (3):443–454. https://doi.org/10.1007/s00338-019-01794-9

Laborel-Deguen F, Castro CB, Nunes FLD, Pires DO (2019) Recifes do Brasil: O Legado de Laborel. Série livros do Museu Nacional, Rio de Janeiro

Lasker HR, Martínez-Quintana A, Bramanti L, Edmunds PJ (2020) Resilience of octocoral forests to catastrophic storms. Sci Rep 10:4286. https://doi.org/10.1038/s41598-020-61238-1

Lawler DW, Cornic G (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ 25(2):275–294. https://doi.org/10.1046/j.0016-8025.2001.00814.x

Leão ZMAN, Kikuchi R, Testa V (2003) Corals and coral reefs of Brazil. In: Cortés J (ed) Latin American coral reefs. Elsevier, Amsterdam, pp 9–52. https://doi.org/10.1016/B978-044451388-5/50003-5

Leão ZMAN, Kikuchi RKP, Oliveira MD, Vasconcellos V (2010) Status of Eastern Brazilian coral reefs in time of climate changes. Pan-Am J Aquat Sci 5(2):224–235. https://panamjas.org/pdf_artigos/PANAMJAS_5(2)_52-63.pdf

Leão ZMAN, Kikuchi RKP, Ferreira P, Neves EG, Sovieroski HH, Oliveira MD, Maida M, Correia MD, Johnsson R (2016) Brazilian coral reefs in a period of global change: a synthesis. Braz J Oceanogr 64(2):97–116. https://doi.org/10.1590/S1679-875920160916064sp2

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Loreau M (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7 (7):601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lenz AE, Bramanti L, Lasker RH, Edmunds JP (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34(4):1099–1109. https://doi.org/10.1007/s00338-015-1315-x

Lesser MP, Slattery M (2020) Will coral reef sponges be winners in the Anthropocene. Glob Chang Biol. https://doi.org/10.1111/gcb.15039

Lesser MP, Slattery M, Stat M, Ojimi M, Gates RD, Grottoli A (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. Ecology 91:990–1003. https://doi.org/10.1890/09-0313.1

Lien YT, Nakano Y, Plathong S, Fukami H, Wang JT, Chen CA (2007) Occurrence of the putatively heat-tolerant Symbiodinium phylotype D in high-latitudinal outlying coral communities. Coral Reefs 26(1):35–44. https://doi.org/10.1007/s00338-006-0185-7

Lim C-S, Bachok Z, Hii Y-S (2017) Effects of supplementary polyunsaturated fatty acids on the health of the scleractinian coral *Galaxea fascicularis* (Linnaeus, 1767). J Exp Mar Biol Ecol 491:1–8. https://doi.org/10.1016/j.jembe.2017.02.009

Loiola M, Cruz ICS, Lisboa DS, Mariano-Neto E, Leão ZMAN, Oliveira MDM, Kikuchi RKP (2019) Structure of marginal coral reef assemblages under different turbidity regime. Mar Environ Res 147:138–148. https://doi.org/10.1016/j.marenvres.2019.03.013

Loya Y, Eyal G, Treibitz T, Lesser MP, Appeldoorn R (2016) Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9. https://doi.org/10.1007/s00338-016-1410-7

Lybolt M, Neil D, Zhao J, Feng Y, Yu KF, Pandolfi J (2010) Instability in a marginal coral reef: the shift from natural variability to a human-dominated seascape. Front Ecol Environ 9(3):154–160. https://doi.org/10.1890/090176

Mazzuco ACA, Stelzer PS, Donadia G, Bernardino JV, Joyeux JC, Bernardino AF (2019) Lower diversity of recruits in coastal reef assemblages are associated with higher sea temperatures in the tropical South Atlantic. Mar Environ Res 148:87–98. https://doi.org/10.1016/j.marenvres.2019.05.008

Mcleod E, Anthony KRN, Mumby PJ, Maynard J, Beeden R, Graham NAJ, Heron SF, Hoegh-Guldberg O, Jupiter S, MacGowan P, Mangubhai S, Marshall PA, McClanahan TR, Mcleod K, Nystrom M, Obura D, Parker B, Possingham HP, Salm RV, Tamelander J (2019) The future of resilience-based management in coral reef ecosystems. J Environ Manag 233:291–301. https://doi.org/10.1016/j.jenvman.2018.11.034

Menezes N, Sobrau-Souza T, Silva M, Solferini VN (2020) Paleoclimatic distribution and phylogeography of *Mussismilia braziliensis* (Anthozoa; Scleractinia), an endemic Brazilan reef coral. Mar Biodivers 50

Mies M, Güth AZ, Tenório AA, Banha TNS, Waters LG, Polito PS, Taniguchi S, Bícego MC, Sumida PYG (2018) In situ shifts of predominance between autotrophic and heterotrophic feeding in the reef-building coral *Mussismilia hispida*: an approach using fatty acid trophic markers. Coral Reefs 37(6):677–689. https://doi.org/10.1007/s00338-018-1692-z

Mies M, Francini-Filho RB, Zilberberg C, Garrido AG, Longo GO, Laurentino E, Güth AZ, Sumida PYG, Banha TNS (2020) South Atlantic coral reefs are major global warming refugia and less susceptible to bleaching. Front Mar Sci 7:514. https://doi.org/10.3389/fmars.2020.00514

Miranda RJ, Cruz ICS, Leão ZMAN (2013) Coral bleaching in the Caramuanas reef (Todos os Santos Bay, Brazil) during the 2010 El Niño event. Lat Am J Aquat Res 41(2):351–360. https://doi.org/10.3856/vol41-issue2-fulltext-14

Monroe AA, Ziegler M, Roik A, Rothig T, Hardenstine RS, Emms MA, Jensen T, Voolstra CR, Berumen ML (2018) In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. PLoS One 13(4):e0195814. https://doi.org/10.1371/journal.pone.0195814

Mora C, Graham NAJ, Nystrom M (2016) Ecological limitations to the resilience of coral reefs. Coral Reefs 35(4):1271–1280. https://doi.org/10.1007/s00338-016-1479-z

Morais J, Santos BA (2018) Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. Ecosphere 9(7):e02281. https://doi.org/10.1002/ecs2.2281

Morais RA, Ferreira CEL, Floeter SR (2017) Spatial patterns of fish standing biomass across Brazilian reefs. J Fish Biol 91(6):1642–1667. https://doi.org/10.1111/jfb.13482

Morais J, Medeiros AP, Santos BA (2018) Research gaps of coral ecology in a changing world. Mar Environ Res 140:243–250. https://doi.org/10.1016/j.marenvres.2018.06.021

Morgan KM, Perry CT, Smithers SG, Johnson JA, Daniell JJ (2016) Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. Sci Rep 6(1):29616. https://doi.org/10.1038/srep29616

Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore turbid-zone corals exhibit high bleaching tolerance on the great barrier reef following the 2016 ocean warming event. Front Mar Sci 4:224. https://doi.org/10.3389/fmars.2017.00224

Muir PR, Marshall PA, Abdulla A, Aguirre JD (2017) Species identity and depth predict bleaching severity in reef-building corals: shall the deep inherit the reef? Proc R Soc B Biol Sci 284 (1864):20171551. https://doi.org/10.1098/rspb.2017.1551

Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs 28(3):761–773. https://doi.org/10.1007/s00338-009-0506-8

Nakajima Y, Nishikawa A, Iguchi A, Sakai K (2012) Regional genetic differentiation among northern high-latitude island populations of a broadcast-spawning coral. Coral Reefs 31 (4):1125–1133. https://doi.org/10.1007/s00338-012-0932-x

Narayan YR, Lybolt M, Zhao JX, Feng Y, Pandolf JM (2015) Holocene benthic foraminiferal assemblages indicate long-term marginality of reef habitats from Moreton Bay, Australia. Palaeogeogr Palaeoclimatol Palaeoecogol 420:49–64. https://doi.org/10.1016/j.palaeo.2014.12.010

Ng TY, Ang P Jr (2016) Low symbiont diversity as a potential adaptive strategy in a marginal non-reefal environment: a case study of corals in Hong Kong. Coral Reefs 35(3):941–957. https://doi.org/10.1007/s00338-016-1458-4

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306. https://doi.org/10.3354/meps07815

Norström M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. AMBIO J Hum Environ 35(1):30–35. https://doi.org/10.1579/0044-7447-35.1.30

Oesterwind D, Rau A, Zaiko A (2016) Drivers and pressures – untangling the terms commonly used in marine science and policy. J Environ Manag 181:8–15. https://doi.org/10.1016/j.jenvman.2016.05.058

Oostra V, Saastamoinen M, Zwaan BJ, Wheat CW (2018) Strong phenotypic plasticity limits potential for evolutionary responses to climate change. Nat Commun 9:1005. https://doi.org/10.1038/s41467-018-03384-9

Pellissier L, Leprieur F, Parravicini V, Cowman PF, Kulbicki M, Litsios G, Mouillot D (2014) Quaternary coral reef refugia preserved fish diversity. Science 344(6187):1016–1019. https://doi.org/10.1126/science.1249853

Peluso L, Tascheri V, Nunes FLD, Castro CB, Pires DO, Zilberberg C (2018) Contemporary and historical oceanographic processes explain genetic connectivity in a Southwestern Atlantic coral. Sci Rep 8:2684. https://doi.org/10.1038/s41598-018-21010-y

Perry CT (2003) Reef development at Inhaca Island, Mozambique: coral communities and impacts of the 1999/2000 southern Africa floods. Ambio 32:133–139. https://doi.org/10.1579/0044-7447-32.2.134

Perry CT, Alvarez-Filip L (2019) Changing geo-ecological functions of coral reefs in the Anthropocene. Funct Ecol 33(6):976–988. https://doi.org/10.1111/1365-2435.13247

Perry CT, Larcombe P (2003) Marginal and non-reef-building coral environments. Coral Reefs 22 (4):427–432. https://doi.org/10.1007/s00338-003-0330-5

Pinheiro HT, Bernardi G, Simon T, Joyeux JC, Macieira RM, Gasparini JL, Rocha C, Rocha LA (2017) Island biogeography of marine organisms. Nature 549:82–85. https://doi.org/10.1038/nature23680

Pizarro V, Rodríguez SC, López-Victoria M, Zapata FA, Zea S, Galindo-Martínez CT, Iglesias-Prieto R, Pollock J, Medina M (2017) Unraveling the structure and composition of Varadero reef, an improbable and imperiled coral reef in the Colombian Caribbean. PeerJ 5:e4119. https://doi.org/10.7717/peerj.4119

Porter SN, Schleyer MH (2017) Long-term dynamics of a high-latitude coral reef community at Sodwana Bay. Coral Reefs 36(2):369–382. https://doi.org/10.1007/s00338-016-1531-z

Portugal AB, Carvalho FL, Carneiro PBM, Rossi S, Soares MO (2016) Increased anthropogenic pressure decreases species richness in tropical intertidal reefs. Mar Environ Res 120:44–54. https://doi.org/10.1016/j.marenvres.2016.07.005

Potts DC, Jacobs JR (2000) Evolution of reef-building scleractinian corals in turbid environments: a paleo-ecological hypothesis. In: Proceedings 9th international coral reef symposium (Bali), pp 249–254

Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci 92:520–531. https://doi.org/10.1007/s00531-003-0328-9

Rocha LA, Pinheiro HT, Sheperd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P (2018) Mesophotic coral ecosystems are threatened and ecological distinct from shallow water reefs. Science 361(6399):281–284. https://doi.org/10.1126/science.aaq1614

Rodriguez L, Martínez B, Tuya F (2019) Atlantic corals under climate change: modelling distribution shifts to predict richness, phylogenetic structure and trait-diversity changes. Biodivers Conserv 28(14):3873–3890. https://doi.org/10.1007/s10531-019-01855-z

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends Ecol Evol 27 (7):404–413. https://doi.org/10.1016/j.tree.2012.04.007

Roitman S, López-Londoño T, Pollock J, Ritchie KB, Galindo-Martínez CT,Gómez-Campo K, González-Guerrero LA, Pizarro V, López-Victoria M, Iglesias-Prieto R, Medina M (2020) Surviving marginalized reefs: assessing the implications of the microbiome on coral physiology and survivorship. Coral Reefs 39:795–807. https://doi.org/10.1007/s00338-020-01951-5

Rossi S, Bramanti L, Gori A, Orejas C (2017) Animal forests of the world: an overview. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer, Cham. https://doi.org/10.1007/978-3-319-21012-4_1

Rossi S, Schubert N, Brown D, Soares MO, Grosso V, Rangel-Huerta E, Maldonado E (2018) Linking host morphology and symbiont performance in octocorals. Sci Rep 8:12823. https://doi.org/10.1038/s41598-018-31262-3

Rossi S, Isla E, Bosch-Belmar M, Galli G, Gori A, Gristina M, Ingrosso G, Milisenda G, Piraino S, Rizzo L, Schubert N, Soares M, Solidoro C, Thurstan RH, Viladrich N, Willis TJ, Ziveri P (2019) Changes of energy fluxes in marine animal forests of the Anthropocene: factors shaping the future seascape. ICES J Mar Sci 1:1–12. https://doi.org/10.1093/icesjms/fsz147

Rossi S, Schubert N, Brown D, Gonzales-Posada A, Soares MO (2020) Trophic ecology of Caribbean octocorals: autotrophic and heterotrophic seasonal trends. Coral Reefs 39:433–449. https://doi.org/10.1007/s00338-020-01906-w

Schleyer MH, Floros C, Laing SCS, MacDonald AHH, Montoya-Maya PH, Morris T, Porter SN, Seré MG (2018) What can South African reefs tells us about the future of high-latitude coral systems? Mar Pollut Bull 136:491–507. https://doi.org/10.1016/j.marpolbul.2018.09.014

Schoepf V, Stat M, Falter JL, McColluch MT (2015) Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci Rep 5:17639. https://doi.org/10.1038/srep17639

Schoepf V, Carrion SA, Pfeifer SM, Naugle M, Dugal L, Bruyn J, McCulloch MT (2019) Stress-resistant corals may not acclimatize to ocean warming but maintain heat tolerance under cooler temperatures. Nat Commun 10:4031. https://doi.org/10.1038/s41467-019-12065-0

Servetto N, Rossi S, Fuentes V, Alurralde G, Lagger C, Sahade R (2017) Seasonal trophic ecology of the dominant Antarctic coral *Malacobelemnon daytoni* (Octocorallia, Pennatulacea, Kophobelemnidae). Mar Environ Res 130:264–274. https://doi.org/10.1016/j.marenvres.2017.08.003

Shlesinger T, Grinblat M, Rapuano H, Amit T, Loya Y (2018) Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. Ecology 99(2):421–437. https://doi.org/10.1002/ecy.2098

Silva M, Etnoyer PJ, MacDonald IR (2016) Coral injuries observed at mesophotic reefs after the Deepwater Horizon oil discharge. Deep-Sea Res II Top Stud Oceanogr 129:96–107. https://doi.org/10.1016/j.dsr.2.2015.05.013

Skirving WJ, Heron SF, Marsh BL, Liu G, De La Cour JL, Geiger EF, Eakin CM (2019) The relentless march of mass coral bleaching: a global perspective of changing heat stress. Coral Reefs 38(4):547–557. https://doi.org/10.1007/s00338-019-01799-4

Smale DA, Wernberg T, Oliver ECJ, Thomsen MS, Harvey BP, Straub SC, Burrows M, Alexander LV, Benthuysen J, Donat M, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell H, Gupta AS, Payne BL, Moore PJ (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9(4):306–312. https://doi.org/10.1038/s41558-019-0412-1

Smith EG, Hume BCC, Delaney P, Wiedenmann J, Burt JA (2017) Genetic structure of coral-*Symbiodinium* symbioses on the world's harmest reefs. PLoS One 12(6):e0180169. https://doi.org/10.1371/journal.pone.0180169

Smithers S, Larcombe P (2003) Late Holocene initiation and growth of a nearshore turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef. Austr Coral Reefs 22:499–505. https://doi.org/10.1007/s00338-003-0344-z

Soares MO (2020) Marginal reef paradox: a possible refuge from environmental changes? Ocean Coastal Manage 185:105063. https://doi.org/10.1016/j.ocecoaman.2019.105063

Soares MO, Rossi S, Martins FAS, Carneiro PBM (2017) The forgotten reefs: benthic assemblage coverage on a sandstone reef (tropical South-western Atlantic). J Mar Biol Assoc UK (Online) 97:1585–1592. https://doi.org/10.1017/S0025315416000965

Soares MO, Tavares T, Carneiro PBM (2019a) Mesophotic ecosystems: distribution, human impacts, and conservation in the South Atlantic. Divers Distrib 25(2):255–268. https://doi.org/10.1111/ddi.12846

Soares MO, Teixeira CEP, Ferreira SMC, Gurgel ALAR, Paiva BP, Menezes MOB, Davis M, Tavares TCL (2019b) Thermal stress and tropical reefs: mass coral bleaching in a stable temperature environment? Mar Biodivers 49:2921–2929. https://doi.org/10.1007/s12526-019-00994-4

Soares MO, Araújo JT, Ferreira SMC, Santos BA, Boavida JR, Costantini F, Rossi S (2020a) Why do mesophotic coral ecosystems have to be protected? Sci Total Environ 138456. https://doi.org/10.1016/j.scitotenv.2020.138456

Soares MO, Teixeira CEP, Bezerra LEA, Rossi S, Tavares T, Cavalcante RM (2020b) Brazil oil spill response: time for coordination. Science 367(6474):155. https://doi.org/10.1126/science.aaz9993

Spalding M, Burke L, Wood SA, Ashpole J, Hutchinson J, Ermgassen PZ (2017) Mapping the global value and distribution of coral reef tourism. Mar Policy 82:104–113. https://doi.org/10.1016/j.marpol.2017.05.014

Steneck RS, Bellwood DR, Hay ME (2017) Herbivory in the marine realm. Curr Biol 27 (11):484–489. https://doi.org/10.1016/j.cub.2017.04.021

Stimson J (2018) Recovery of coral cover in records spanning 44 yr for reefs in Kane'ohe Bay, Oa'hu, Hawai'i. Coral Reefs 37:55–69. https://doi.org/10.1007/s00338-017-1633-2

Studivan MS, Milstein G, Voss JD (2019) *Montastraea cavernosa* corallite structure demonstrates distinct morphotypes across shallow and mesophotic depth zones in the Gulf of Mexico. PLoS One 14(3):e0203732. https://doi.org/10.1371/journal.pone.0203732

Suggett DJ, Kikuchi RKP, Oliveira MDM, Spanó S, Carvalho R, Smith DJ (2012) Photobiology of corals from Brazil's nearshore marginal reefs of Abrolhos. Mar Biol 159:1461–1473. https://doi.org/10.1007/s00227-012-1925-6

Sully S, Woesik RV (2020) Turbid reefs moderate coral bleaching under climate-related temperature stress. Glob Chang Biol 26(3):1367–1373. https://doi.org/10.1111/gcb.14948

Sully S, Burkepile DE, Donovan MK, Hodgson G, Woesik RV (2019) A global analysis of coral bleaching over the past two decades. Nat Commun 10:1264. https://doi.org/10.1038/s41467-019-09238-2

Suzuki G, Keshavmurthy S, Hayashibara T, Wallace CC, Shirayama Y, Chen CA, Fukami H (2016) Genetic evidence of peripheral isolation and low diversity in marginal populations of the *Acropora hyacinthus* complex. Coral Reefs 35(4):1419–1432. https://doi.org/10.1007/s00338-016-1484-2

Teixeira CD, Leitão RLL, Ribeiro FV, Moraes FC, Neves LM, Bastos AC, Pereira-Filho GH, Kampel M, Salomon PS, Sá JA, Falsarella LN, Amario M, Abieri ML, Peireira RC, Amado-Filho GM, Moura RL (2019) Sustained mass coral bleaching (2016-2017) in Brazilian turbid-zone reefs: taxonomic, cross-shelf and habitat-related trends. Coral Reefs 1:1–13. https://doi.org/10.1007/s00338-019-01789-6

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol Rev 92(2):698–715. https://doi.org/10.1111/brv.12252

Tuckett CA, Wernberg T (2018) High latitude corals tolerate severe cold spell. Front Mar Sci 5:1–5. https://doi.org/10.3389/fmars.2018.00014

Tuckett CA, de Bettignies T, Fromont J, Wernberg T (2017) Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves. Coral Reefs 36(3):947–956. https://doi.org/10.1007/s00338-017-1586-5

Venegas RM, Oliver T, Liu G, Heron SF, Clark SJ, Pomeroy N, Young C, Eakin CM, Brainard RE (2019) The rarity of depth refugia from coral bleaching heat stress in the Western and Central Pacific Islands. Sci Rep 9:19710. https://doi.org/10.1038/s41598-019-56232-1

Wang L, Shantz AA, Payet JP, Sharpton TJ, Foster A, Burkepile DE, Thurber RV (2018) Corals and their microbiomes are differently affected by exposure to elevated nutrients and a natural thermal anomaly. Front Mar Sci 5:1–14. https://doi.org/10.3389/fmars.2018.00101

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251. https://doi.org/10.2307/1218190

Woesik RV, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and losers a decade after coral bleaching. Mar Ecol Prog Ser 434:67–76. https://doi.org/10.3354/meps09203

Animal Forests in Submarine Caves

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Abstract In dark zones of submarine caves, photosynthesis-related production and water movement can be negligible or absent. This situation induces sessile animals like Porifera and Bryozoa to reduce their presence, shifting from massive to tiny encrusting morphologies. Notwithstanding this general rule, true engineer organisms can develop forming three-dimensional structures in particular situations. Near the entrance of Mediterranean submarine caves, where light and hydrodynamism are not limited, bio-concretions are similar to those found in the coralligenous. Coralline algae with their convolute calcareous thalli are the primary engineers, while Porifera, Cnidaria, and erect Bryozoa compete for more sheltered and dark positions. Epi- and endolithic Bivalvia are present as well, together with the boring Porifera Clionaidae, representing the demolition community which establishes a dynamic equilibrium with the building one. Due to light decrease, until complete darkness, bioconstructions of innermost cave sectors lack algae and consist of a simplified association if compared with that at the entrance. They are dominated by a few selected taxa of skeletonized invertebrates, essentially Polychaeta Serpulidae, Porifera, and Bryozoa, to which carbonate-producing bacterial communities add. These peculiar frames known as biostalactites are conical to cylindrical in shape and typically restricted to semi-dark and dark cave portions, reaching considerable sizes and protruding from the ceiling and/or walls. The gravity force shapes in a more tenacious arrangement the structure. The presence of boring organisms is strongly

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reduced. The complete set of growth/structural development has to be investigated yet. Due to the recent discovery and description of these biostalactites and their apparent rarity, data are scant, especially those related with the associated vagile faunas and the biodiversity.

Keywords Dark habitat · Biostalactites · Skeletonized metazoans · *Protula* · Bacterial communities · Carbonatogenesis

1 Introduction

Sessile animals are defined bio-engineers when their associations produce 3D frames named marine animal forests (Rossi et al. 2017), offering new space for attachment to sessile organisms and shelter and/or rest to vagile ones. Associated organisms are adapted to live in such a spatial frame, sometimes during all their life cycle or during limited life stages (Stella et al. 2011).

Contrarily to terrestrial habitats, where bio-engineers are autotrophs (plants) performing photosynthesis, in marine environment the presence of plants diminishes with depth and/or darkness, replaced by suspension feeding animals (Fig. 1). Largely lacking in coralline algae (the main bio-engineers of habitats outside caves), bio-concretions in marine caves exclusively consist of animal organisms that no more rely on light, but need to get food (Zabala et al. 1989).

Marine sessile animals gather their food from water currents (existing or created by themselves) intercepting suspended food particles (particulate to dissolved organic matter and microorganisms) and/or relying upon the mobile behavior of potential preys (Gili and Coma 1998). Sessile marine animals capture what touch their (extended) appendages or convey water flow by passing it throughout a sieve that retains food particles.

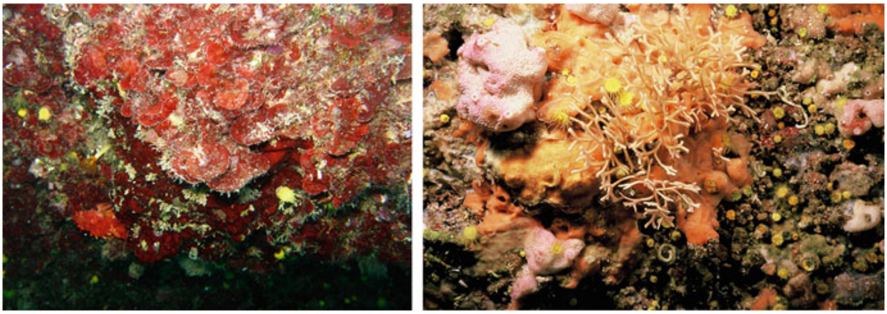

Fig. 1 Bio-concretions at different locations inside submarine caves. Left, red algae dominate at the entrance (Plemmirio MPA, courtesy of M. Catra; Univ. of Catania); right, animal-dominated association (Porifera, Bryozoa, Cnidaria, Serpulidae) thrive at about 20 m from the entrance (Ciolo cave, Otranto Channel; Univ. of Salento)

In dark caves not only light is completely absent, but also water motion is actually negligible, thus forcing sessile animals to rely on their own capability to move the water around them and/or to capture moving preys. In fact, low water circulation excludes passive filter feeders from the most confined, dark parts of submarine caves (Riedl 1966; Harmelin 1986; Bianchi and Morri 1994; Bianchi et al. 2003; Morri and Bianchi 2003). Probably due to the absence of water movement, sessile benthos of dark caves is typically dominated by active filter feeders species including Porifera, Polychaeta Serpulidae, Scleractinia, and Bryozoa (Gili et al. 1986; Bibiloni et al. 1989; Denitto and Licciano 2006), which move the surrounding water by ciliary activity of dedicated filtering apparatuses to catch suspended food. According to the confinement degree that increases from the entrance to the recesses of submerged caves, dissolved oxygen and trophic sources decrease dramatically inward (Pérès and Picard 1964; Riedl 1966; Fichez 1990). Consequently, sessile fauna progressively tends to be rarefied (Fig. 2) in dark sectors of the caves, and large portions of the walls can lack encrusting organisms (Bussotti et al. 2006). In such confined conditions, elevate or complex bio-concretions are not present. Encrusting organisms on walls and ceilings belong to small-sized species and show laminar and/or not elevated growths that generate low-profiled biogenic concretions.

Relevant discrepancies between such a model and observed distribution patterns of species assemblages are common and have often been reported (e.g., Harmelin 1969; Balduzzi et al. 1989; Corriero et al. 2000; Martì et al. 2004), possibly depending on the cave morphology, dimensions, extension, depth, sediment deposition, and/or presence of hydrothermal springs and freshwater inputs. Decrease in bio-encrusts seems not produced by a lack of larval recruitment in cave confined recesses but probably to unsuitable conditions for the survival of the benthic stages. Indeed, the occurrence of propagule settlement even in innermost parts of submerged caves (at about 100 m from the entrance) has been demonstrated by Palau et al. (1991) and Denitto et al. (2007). Nevertheless, settled organisms evidently were not able to develop sessile viable populations. This sometimes happens also in relation with the occurrence of fresh waters (with relatively low values of density and

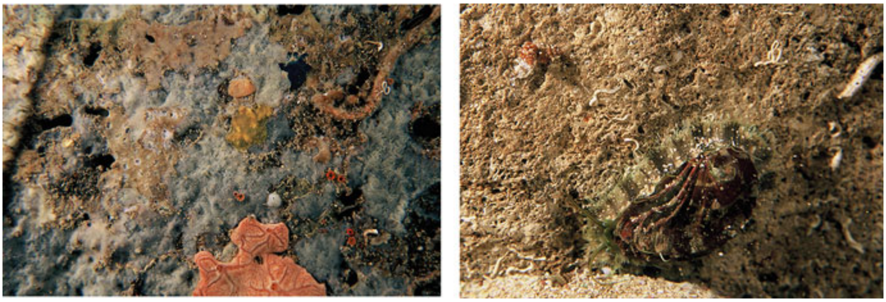

Fig. 2 Assemblage of encrusting organisms (Ciolo cave, Otranto Channel; Univ. of Salento). Left, Porifera, Bryozoa, and Serpulidae, at 60–80 m from the entrance; right Serpulidae and Bryozoa, at 80–100 m from the entrance. The structure simplification and the impoverishment of the assemblage, with few taxa and specimens, are evident

Fig. 3 Complex frames made by Polychaeta Serpulidae (several species) creating new available substrate, as well as numerous micro-spaces and cavities. Left: Lea cave (Gulf of Taranto, Ionian Sea; Univ. of Salento); right: Granchi cave, Plemmirio MPA (south Ionian Sea; Univ. of Catania)

pH) just below the ceiling and in the innermost part of the caves, where the development of a benthic coverage is impeded and barren substrata are evident (the so called *quartum veertel* of Riedl 1966). Just before these unsuitable conditions for sessile benthos, the transition area between poor benthic assemblages and barren substrata could be represented by the development of poorly diversified assemblages, consisting of the only taxa able to perform physiological adaptations. This is the case for Serpulidae, which are typical of the most confined parts of submarine caves, where in absence of high diversified communities, they realize complex frames of bio-concretions (Fig. 3).

The innermost parts of the caves appear as hostile to most marine invertebrates, but apparently not to Serpulidae and Bryozoa, as well as to bacterial communities.

Serpulidae and some Bryozoa often exploit early reproduction and are able to withstand starvation (Harmelin 1986, 2000; Okamura et al. 2001). Bryozoa in these areas often have spotlike colonies with “perennial zooids” continuously regenerating (e.g., Rosso et al. 2020). Bacterial communities inducing the formation of biomicrites are commonly associated with these invertebrate assemblages. The microbial carbonate derived by these bacteria is intermingled with invertebrate skeletons forming coating crusts and other microbialite structures in semi-dark and dark areas of caves (Guido et al. 2012, 2013, 2017a, b, 2019a, b; Sanfilippo et al. 2015). Here, local inflow of underground waters through fissures can produce salinity dilution and enrichment in organic matter. Among these variate conditions, the alteration of the ionic content (e.g., sulfates at place of chlorine) seems to favor a bacterial production of carbonates and the building of bio-concretions (Guido et al. 2012, 2013; Gischler et al. 2017a, b). Within this frame could be considered sizeable true bioconstructions of metazoans and microbial crusts, resembling stalactites in shape (biostalactites) recently described from Mediterranean sites (Onorato et al. 2003; Guido et al. 2013, 2017a; Sanfilippo et al. 2015).

2 Biostructures in Submarine Caves and Variability of Their Composition

Biostructures in any position within submarine caves are the result of engineer organisms, but their sizes and composition change greatly with distance from the entrance and/or depth of the cave and the nature of connections with the open sea (see paragraphs below and Onorato et al. 2003; Sanfilippo et al. 2015).

Normally, in submarine caves the most suitable substrate for building 3D structures is not the floor (often covered with mud) but the ceiling and/or lateral walls (that are rocky and less interested by sediment deposition). These positions imply biostructures must be more resistant to fractures than concretions rising from the bottom, where the same heaviness of the structure favors the stability.

Though investigations are still lacking, this upside-down growth habit probably requires chemical/structural solutions to minimize fractures and enhance robustness of biostructures. In coralligenous 3D structures (actively constructed by the superimposition of skeletons of subsequent generations of mostly encrusting organisms), cores and basal parts essentially are dead parts further steady by gravity force. In cave hanging structures, on the contrary, basal, ancient, and dead parts are not compacted by growth because they have to support new concretions that develop downward and are more solicited to be fractured. This situation requires a relative more robustness of the building and/or a possibly different arrangement of the species assemblages. Strengthening of these cave structures is favored by a relevant activity of carbonatogenetic bacteria that induce early cementation (microbialites) through autochthonous micrite precipitation in intra- and inter-skeletal cavities, with the result of consolidating the bioconstructions (Guido et al. 2013, 2016, 2017a; Gischler et al. 2017a, b).

Basing on light intensity and hydrodynamic energy, as well as on local factors such as richness/depletion of organic matter and salinity gradients, different types of biogenic structures can be recognized within caves.

2.1 Type 1: Coralligenous Type

Coralligenous-type bioconstructions usually develop at, or near, the entrances of submarine caves, when suitable conditions of shadowed light and decreasing hydrodynamic energy occur, even at very shallow depth. Species composition is roughly comparable to that of coralligenous concretions occurring on rocky bottoms outside caves (Onorato et al. 2003).

Calcareous algae are relevant components in these biostructures, usually accompanied by stony corals (Cnidaria, Scleractinia) and a few large-sized erect Bryozoa species, opposed to boring Bivalvia and Porifera promoting and enhancing erosive processes. Moreover, depending on different edaphic and environmental conditions, it is possible to recognize coralline algae-dominated from animal-dominated bioconstructions (Ingrosso et al. 2018).

Following the inward light decrease, bioconstructions of inner cave sectors substantially differ from those of cave entrances showing a progressive diminution of algal presence, up to their complete disappearance. In these conditions, a more sciaphilic coralligenous may develop, where the animal component largely dominates, locally with large erect engineer species among which colonies of the Bryozoa *Myriapora truncata*, *Smittina cervicornis*, *Adeonella calveti*, *Reteporella elegans*, and *Hornera frondiculata* (Harmelin 2000; Balduzzi and Rosso 2003).

The occurrence of a subordinate component of coralline algae could be at least partly responsible for the obliquity of the growing structures that, even if hanging from the ceiling, orient their growth toward a preferential direction, with an evident deviation of the structure main axis from the gravity force vector. However, oblique growth of bioconstructions could also result from inclination of suspension feeders to intercept incoming water flow enriched in food particles, as suggested by Rosso et al. (2018a). Sessile Bivalvia are well represented in such hanging bio-concretions, both with Ostraeidae of the genus *Neopycnodonte* (an engineer species of mesophotic habitats) (Angeletti and Taviani 2020; Cardone et al. 2020) and borers (Mytilidae of the genera *Lithophaga* and *Pholas*) (Fig. 4). Smaller borings are also produced by Porifera of the family Clionaidae.

Each biostructure is the result of a dynamic equilibrium between the two main components (builders and borers) which have different relevance during the building process (Ingrosso et al. 2018). It is expected that the growth rate is faster in early stages, but slows down in large and/or ancient buildings not simply for the age but for the increasing importance of competitive bio-erosive processes.

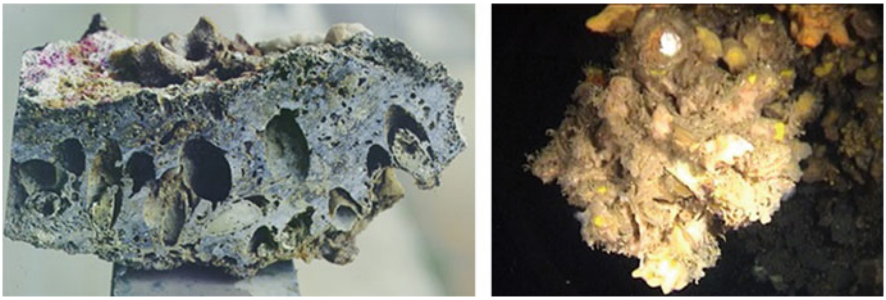

Fig. 4 Left, longitudinal section of a bioconstruction collected at the cave entrance (*lu Lampiùne* cave, Cape of Otranto, Italy). Borings produced by the bivalve *Lithophaga* are well evident. Right, a 3D concretion of the bivalve *Pycnodonte* (submerged cave of Otranto Channel, Italy)

2.2 Type 2: Other Bioconstructions

Some encrusting Bryozoa (e.g., *Rhynchozoon* spp., *Schizoporella* spp. and *Schizomavella* spp., *Onychocella marioni*) can also produce nodular structures, usually few centimeter in size that often remain isolated. Further species, such as *Celleporina caminata* can develop densely packed small nodular colonies or low crest-like concretions elongated in the current flow direction covering wide surfaces in the transitional zone between semi-dark and dark cave communities (Harmelin 1985; Rosso et al. 2013a, 2019).

2.3 Type 3: Biostalactites

Peculiar cave bio-concretions, only recently described, deserve a special place in the list of marine animal forests. First reported in the Mediterranean Sea as an unusual feature from a submarine cave of the Adriatic Italian coast (Onorato et al. 2003), fields of biostalactites (BSs) have been subsequently found in further caves in the Ionian Sea (Sanfilippo et al. 2015), the Levantine Sea (Guido et al. 2017a; Jimenez et al. 2019), and the Aegean Sea (Guido et al. 2019a, b; Gerovasileiou, personal communication).

Somewhat comparable bioconstructions were reported from present-day reef environments in Belize (the so-called pseudo-stalactites of Macintyre et al. 1982; Macintyre 1984; Gischler et al. 2017a, b), and fossil counterparts are known from Jurassic to Cretaceous shallow-water caves and reef cryptic environments in Europe (Olivier et al. 2003; Reolid and Molina 2010).

Belizean pseudo-stalactites are club-headed near cave entrances and elongated conical in the innermost cave portions. None of those structures exceed 50 cm in length, and Serpulidae tubes (genera *Vermiliopsis*, *Metavermilia*, and *Josephella*) are cemented together by a magnesium calcite matrix. Macintyre et al. (1982) also reported several invertebrate species (11 Porifera, 9 Bryozoa, 7 Bivalvia, and 5 epizoic algae) associated with, but not especially involved in, the construction of the pseudo-stalactites. The Belizean pseudo-stalactites are composed of still-living Serpulidae, at least on their surface. Calcareous tubes of the internal portion of each pseudo-stalactite were empty, abandoned structures, with a ^{14}C age of 820 years.

In Mediterranean submarine caves, biostalactites (BSs) typically develop in semi-dark and dark sectors of blind caves, hanging from ceilings and/or extending obliquely to nearly horizontally from lateral walls. Their oblique orientation observed in caves from Apulia and more recently from Cyprus and Lebanon caves could be the result of growth in a predominantly incoming water circulation (Belmonte et al. 2009; Quarta et al. 2010; Guido et al. 2017a) (Fig. 5).

Like true stalactites, BSs are usually conical or cylindrical in shape, some decimeters up to 2 m long. In some caves also dome-, mushroom-, and flabellate-

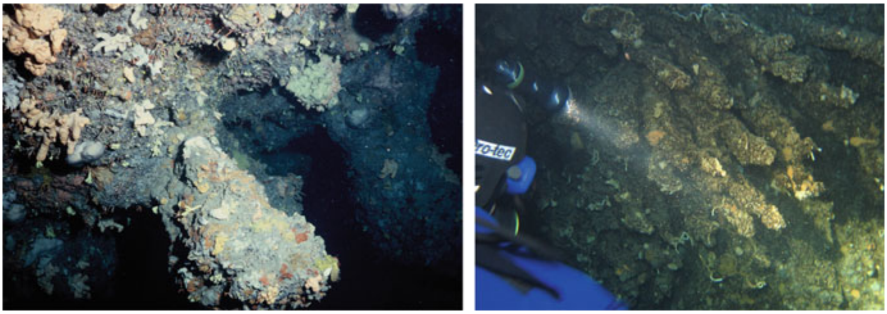

Fig. 5 Biostalactites growing obliquely from walls of Italian caves. Left: stout, isolated bioconstructions, about 60–70 cm long (caves of Marine Protected Area Porto Cesareo, Gulf of Taranto; Univ. of Salento); right: slender, about 100 cm long, tapering forms, packed together (cave *lu Lampiùne*, Cape of Otranto; Apogon Speleo Diving Association, Nardò, Italy)

shaped BSs have been recorded, which are centimeter- to decimeter-sized (Guido et al. 2013, 2017a; Sanfilippo et al. 2015).

BSs of different morphologies and sizes often co-exist close to each other and their distribution seems not closely related either to distance from the cave entrance or position on the ceilings or walls. Generally, BSs appear to be sparse, but they can be densely packed in some caves, as observed for southern Adriatic and eastern Mediterranean caves.

These bioconstructions usually exhibit a relatively smooth surface colonized by a low number of living epibionts belonging to few taxa (Serpulidae and Foraminifera), and an opposite rough surface, colonized by a more diversified and abundant community, including Serpulidae, Bryozoa, and Porifera. This differentiation, possibly resulting from selective larval settlement and species preference, has been explained with the onset of micro-environmental conditions probably linked to hydrodynamic energy and regime on the opposite sides of the BSs (Sanfilippo et al. 2015). In oblique and/or sub-horizontal BSs, these two sides are also differently interested by sediment deposition (siltation) (Guido et al. 2017a).

The BSs consist of invertebrate skeletons intermingled with carbonates whose precipitation is induced by microbial activity (see Guido et al. 2013). Serpulidae tubes are the main skeletal constituent of the core and contribute to the general framework. Foraminifera, Porifera, and Bryozoa are locally common. Mollusca, Brachiopoda, Hydrozoa, Scleractinia, Cirripedia Balanomorpha, and Polychaeta Terebellidae are subordinate or even rare and occur in only a few BSs (Sanfilippo et al. 2015). Subsequent colonizer generations occur within the same BSs, superimposed to each other during time and detectable thanks to their covering relationships and to their white or gray/blackish color in relation to the thickness of Fe/Mn coatings of the skeletons.

Most BSs, particularly those showing either conical or cylindrical elongate morphologies, possess an inner core, more or less easily distinguishable from the surrounding outer portion, owing to different composition and fabric (Sanfilippo

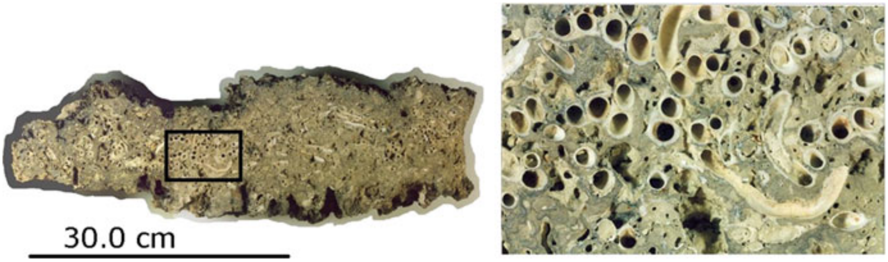

Fig. 6 Longitudinal section of a BS from the cave *lu Lampiùne* (cape of Otranto, Italy). Left: whole BS section; tip on the left, basis on the right. Right: magnification (black square area in the photograph on the left) of sectioned tubes of *Protula.* Note the absence of borers (see Fig. 4 for a comparison)

et al. 2015). Cores consist of irregularly coiled to plait-shaped aggregations of Serpulidae tubes (1.5–4 mm diameter) belonging to the genus *Protula* (Fig. 6). In elongated BSs, *Protula* tubes are roughly parallel to the main axes of BSs. Apertures of tubes with living specimens are usually exposed only at BSs tips. In contrast, lateral BSs surfaces are often covered with a metazoan-microbial crust consisting of superimposed tubes of smaller Serpulidae species. This crust, up to 1–2 cm thick, may completely envelop certain conical BSs, when *Protula* specimens of the core cease to actively grow (Sanfilippo et al. 2015).

It has been found that metazoans constituting BSs are not particularly diversified. *Protula* acts as an engineer organism (or primary builder *sensu* Fagerstrom 1964) with a gregarious behavior which produces relevant structures protruding from the substratum, thus providing space for further colonizers.

Few other skeletonized species actively contribute to the bioconstructions. In the Plemmirio caves, they are mostly represented by the medium-sized Serpulidae *Semivermilia crenata*, *S. pomatostegoides*, and the micro serpulid *Josephella marenzelleri*, which produces relatively thick carbonate crusts with the superimposition of a relevant number of specimens (Fig. 7). Bryozoa play as binders or dwellers (*sensu* Fagerstrom 1964) with rather inconspicuous runners such as *Aetea*

Fig. 7 Serpulidae associated with BSs from the Ionian coast of Sicily (Mazzere cave). Left: the gregarious *Spiraserpula massiliensis*, typical of dark cave sectors (tube diameter, 800 micrometers). Center: *Semivermilia crenata* and the foraminifer *Cornuspiramia adherens*. Right: *S. pomatostegoides*

truncata and *Annectocyma major* and with cryptic spots, including *Glabrilaria pedunculata* and *Setosella* spp. (Rosso et al. 2013a, 2020; Sanfilippo et al. 2015). The foraminiferan *Cornuspiramia adherens* locally forms extensive nets. Larger encrusting organisms are rare.

It can be remarked that not all species thriving on the BSs live on walls and ceiling of the same cave, as exemplified by Bryozoa (see Sanfilippo et al. 2015 in comparison with Rosso et al. 2013b). However, all these species are typical representative of submarine cave habitats (Rosso et al. 2013a, and references therein).

Overall, communities recognized from the internal and external parts of the BSs have similar species composition and substantially the same ecological meaning. The internal framework has numerous millimeter-sized voids that often open outward. Cavities are mainly formed by tube lumina of large Serpulidae and by spaces between convolute microbialite laminae. All BSs analyzed so far showed that both autochthonous (microbialite) and allochthonous (detrital) micrite occur within the metazoan framework (Guido et al. 2013). The former one is produced in situ by the mediation of microbial activities. It shows clotted peloidal and, subordinately, aphanitic (structureless) textures and suggests the presence of heterotrophic microbial communities (i.e., sulfate-reducing bacteria) thriving on decaying metazoan organic matter (Guido et al. 2013, 2017a), similar to those described for microbialite-metazoan facies of the Great Barrier Reef (Reitner 1993). Such micrite fills spaces inside and between skeletons, strengthening the bioconstructions, and especially occurs in the BSs inner and basal parts.

Guido et al. (2013) demonstrated that sulfate-reducing bacteria are responsible for the formation of the BSs autochthonous matrix, and their occurrence could contribute explanation for the presence of large structures in the innermost parts of submarine caves that are expected to be barren, according to Riedl (1966). On the one hand, springs of sulfuric water are common in the election area of BSs (the Otranto Channel) and could promote the formation and growth of the exceptionally long BSs of this area. On the other hand, the bacterial matrix of Otranto BSs shows typical growing rings of light and dark color, thus testifying a periodicity in growth and stasis, which could correspond to emission cycles of sulfuric water inside the caves.

Fe/Mn crusts have been reported coating external surfaces and also visible in the internal fabric as irregular thin dark-brown layers alternating with frame builders and microbialites. The occurrence of these crusts and of *Frutexites*-like structures has been interpreted as the result of the local activity of oxidizing bacteria (Guido et al. 2016, 2017b) (Fig. 8).

Protula specimens in the core of the structures could represent pioneer populations forming aggregates during an early phase of the cave colonization, soon after its flooding, due to the relatively high food supply from both seawater inflow at shallow depth location and intruding underground fresh waters (Onorato et al. 2003; Sanfilippo et al. 2015). Associated carbonate-producing microbial communities probably also benefit of the salinity gradient produced at these sites (Sanfilippo et al. 2015). The outer layer that completely seals the *Protula* cores in the

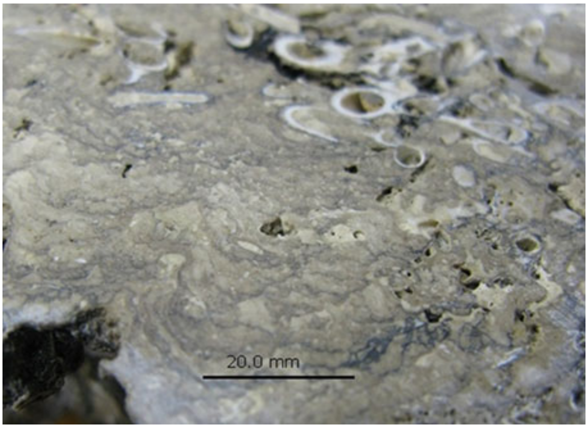

Fig. 8 Close-up of a BS section from the *lu Lampiùne* cave (Cape of Otranto, south Adriatic Sea) with large Serpulidae tubes in the core (up right) and wavy microbialites alternating with Fe/Mn crusts in the outer covering (bottom left) (Univ. of Salento)

Plemmirio caves (Sanfilippo et al. 2015), possibly formed during increasing confined conditions, occurred during the Holocene sea level rises.

^{14}C dating of *Protula* tubes allowed to establish an age of about 6000 years for south Adriatic (Otranto) BSs located at 8 m below the today sea level (Belmonte et al. 2009). This dating is fully compatible with presumed submersion time during last post-glacial sea level rising. Furthermore, the matrix coating which envelopes *Protula* tube plaits is younger than tubes at the same distance from the BS basis, at each point (Belmonte et al. 2016; Quarta et al. 2019). This suggests that BSs were completely produced during marine submersion and no trace of subaerial concretion has been found so far in the BSs from Otranto caves.

On the basis of descriptions of Onorato et al. (2003) and Onorato et al. (2020), it has been hypothesized that BS formation starts with the gregarious *Protula* forming tubule plaits and continues with aggregation of further *Protula* specimens, and a subsequent bacterial coating completely envelopes the structure after *Protula* death (Fig. 9).

The bacterial matrix shows an evident periodicity of accretion; and growth of *Protula* tube plait is not constant during time as demonstrated by ^{14}C dating recording phases of growth and stasis (Belmonte et al. 2009). Although ^{14}C dating suggests periodicity for both bacterial micrite precipitation and worm accretion, it is not evident a synchronism between them. Bacterial micrite is produced inside the micro-cavities of the skeletal framework and there is no relation with the stasis of worm growth. The *Protula* species responsible for the core formation of these BSs is still not identified, and does not correspond to *Protula* commonly reported from outside cave environments of the Mediterranean Sea (Causio et al. 2015). This gives unicity to such bioconstructions but also raises questions about the species and its adaptation to a millennial scale of isolated existence inside caves.

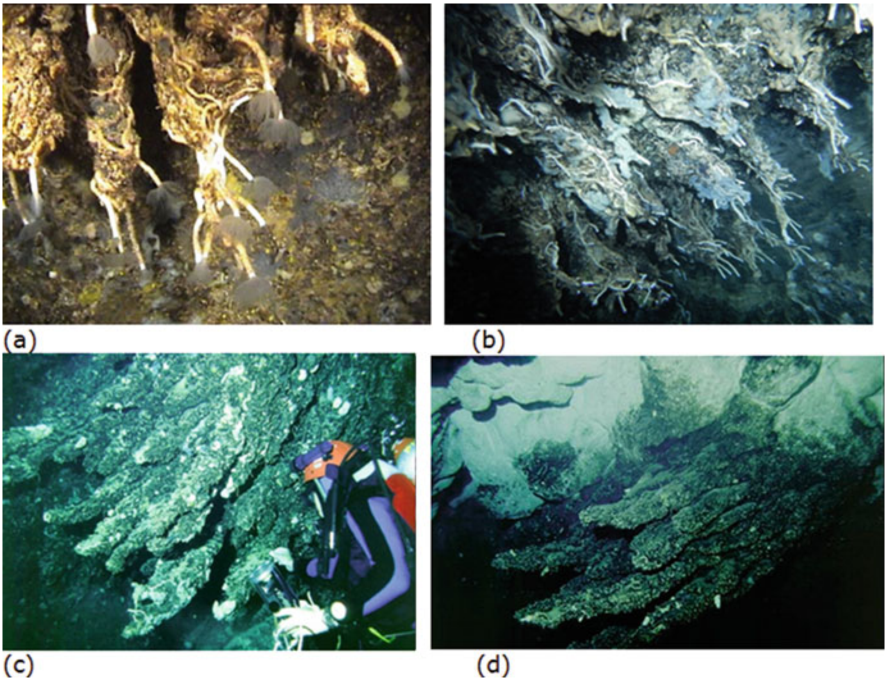

Fig. 9 "Young" biostalactites hanging from the ceiling (**a**) of the *Tau-Manhattan* cave, at Cape of Otranto, and (**b**) of the *Enzo Manieri-Elia* cave, at Santa Caterina. Living and gregarious *Protula* are still visible (with the gill fan extended outside the tubes) and characterizing the whole structure ((a) University of Salento, (b) Apogon Speleo Diving Association, Nardò, Italy). (**c**, **d**) BSs showing Serpulidae tubes completely enveloped by the bacterial coating and encrusted by additional organisms in in two different sites of the *lu Lampiùne* cave at Cape of Otranto. (Apogon Speleo Diving association, Nardò, Italy)

3 The Animal Forests of Submarine Caves

Whatever the origin, composition, and story of cave BSs, they undoubtedly realize a 3D space complexity that should host and shelter sessile as well as vagile organisms. According to available space (and to bioconstruction sizes), community of mobile organisms can span from medium-sized fish to microscopic meiobenthos. Although cave fishes are commonly detectable among such biostructures, the existence of a microscopic world of living organisms is only supposed.

Recently, Russo et al. (2015) studied the vagile meiobenthos from rocky walls of a submarine cave. They gave a first information about vagile microscopic life existing on cave rocky walls and found a relevant species richness in a community dominated by Harpacticoida (Crustacea, Copepoda). Although spaces between biostalactites and their surfaces were not especially examined, this study suggests the possible occurrence of an interesting fauna moving between BSs.

The peculiarity of the marine cave biodiversity is testified by the finding of a high number of faunal novelties, as for the Salento Peninsula (central Mediterranean Sea) where 60 species have been reported as new for Italian fauna and 27 new for science (see Onorato and Belmonte 2017; for a review on faunal reports). In addition, the particular position of BSs (whose growth appears favored by underground freshwater seeps, possibly rich of Sulfur) adds characterization and unicity to these animal forests, in comparison with other marine bioconstructions, thus enhancing the possibility to be habitat for unknown species. BSs distribution and functionality are, however, still largely unknown.

4 Perspectives

Studies on submarine animal forests (bioconstructions) are necessary for MPAs mapping and/or delimitation because they represent a relevant feature of submarine caves, and these latter are often comprised inside protected areas. With reference to southern Italy, already erected MPAs, such as the Ustica and the Plemmirio MPAs, host several submarine caves, and the Otranto-Leuca coast has been recently considered in the instituting process of a new MPA specifically dedicated to marine caves.

The Marine Strategy Framework Directive 2008/56/EC asks for the evaluation of Good Environmental Status (GES) of natural areas considered for protection. Studies on submarine caves are involved in at least 5 of the 11 GES indicators: (1) biodiversity; (2) NIS (Nonindigenous Species); (3) populations of commercially important species; (6) sea floor integrity; and (10) marine litter. This information will allow local environment managers to respect EU directive. Apart from practical management approach, exploration and description of marine animal forests in submarine caves will add important data to the knowledge of the marine habitats and biodiversity.

Another interesting point is related with studies on evolution. Because of their recent formation following sea level rise during the Holocene and their proposed role as refuge habitats, submarine caves could represent evolution laboratories. Species which find protection or refuge in submarine caves can isolate and evolve adaptations to such a particular environment (e.g., Silén and Harmelin 1976; Rosso et al. 2020, and references therein, for Bryozoa), and species new for local and/or regional fauna, and/or for science, could potentially enrich the assessment of cave biodiversity, thus increasing their bio-ecological importance.

Finally, we expect also faunal novelties from arrival of Nonindigenous Species that can easily enter caves and affirm themselves (Rosso et al. 2018b). An articulated study on carbon sink in dark habitat communities will be a relevant output. The evaluation of C sequestration in submarine caves has never been considered and requires the collaboration between marine biologists, geologists, chemists, and physicians. A large amount of data on ^{14}C presence in marine carbonate biostructures will be available for comparisons with the already dating of the

Holocene (last 11,700 years) of southern Italy. This already available data from the same geographic area will ensure the reliability to ^{14}C measures conducted on samples coming from marine habitats and, on the other hand, the building of a Holocene calendar of marine C ages which is uncommon.

An economic impact is also possible from studies on submarine caves, in general. Knowledge of submarine caves can be employed to promote dissemination, and images and virtual visits will enhance attractiveness of local submarine environments and MPAs. Collections of images, videos, and virtual visits, also mediated by Spelean scuba divers, can allow touristic fruition of these dark habitats (and their organisms), promoting virtual access of this superb, fascinating but still uncommonly and/or hardly accessible world to the large public.

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References

Angeletti L, Taviani M (2020) Offshore *Neopycnodonte* oyster reefs in the Mediterranean Sea. Diversity 12:92. https://doi.org/10.3390/d12030092

Balduzzi A, Rosso A (2003) Briozoi. In: Cicogna F, Bianchi CN, Ferrari G, Forti P (eds) Grotte marine. Cinquant'anni di ricerca in Italia. Ministero dell'Ambiente e della Tutela del Territorio, pp 195–202

Balduzzi A, Bianchi CN, Boero F, Cattaneo-Vietti R, Pansini M, Sarà M (1989) The suspension-feeder communities of a Mediterranean sea cave. Sci Mar 53:387–395

Belmonte G, Ingrosso G, Poto M, Quarta G, D'Elia M, Onorato R, Calcagnile L (2009) Biogenic stalactites in submarine caves at the Cape of Otranto (S-E Italy): dating and hypothesis on their formation. Mar Ecol Evolut Perspect 30:376–382

Belmonte G, Calcagnile L, Quarta G, D'Elia M, Russo R (2016) Biostalactites from Cape of Otranto (south east Italy). ^{14}C dating of extra-tubular calcareous matrix. 51st EMBS, Rhodes 26–30 September 2016, Abstract book: 55

Bianchi CN, Morri C (1994) Studio bionomico comparativo di alcune grotte marine sommerse: definizione di una scala di confinamento. Ist Ital Speleologia, Memorie 6, s. II:107–123

Bianchi CN, Morri C, Russo GF (2003) Deplezione trofica. In: Cicogna F, Bianchi CN, Ferrari G, Forti P (eds) Grotte marine, Cinquant'anni di ricerche in Italia. Ministero dell'Ambiente e della Tutela del Territorio, Roma, pp 297–305

Bibiloni MA, Uriz MJ, Gili JM (1989) Sponge communities in three submarine caves of the Balearic Islands (Western Mediterranean): adaptations and faunistic composition. Mar Ecol 10(4):317–334

Bussotti S, Terlizzi A, Fraschetti S, Belmonte G, Boero F (2006) Spatial and temporal variability of sessile benthos in shallow Mediterranean marine caves. Mar Ecol Prog Ser 325:109–119

Cardone F, Corriero G, Longo C, Mercurio M, Tarantini OS, Gravina MF, Lisco S, Moretti M, De Giosa F, Adriana G, Nonnis Marzano C, Pierri C (2020) Massive bioconstructions built by *Neopycnodonte cochlear* (Mollusca, Bivalvia) in a mesophotic environment in the central Mediterranean Sea. Sci Rep 10:6337. https://doi.org/10.1038/s41598-020-63241-y

Causio S, Giangrande E, Belmonte G (2015) Identification of Serpulidae (Polychaeta) responsible of stalactite cores in Italian submarine caves. 50th EMBS, Helgoland, 21–25 September 2015, Abstract book: 44

Corriero G, Scalera LL, Ruggiero D, Pansini M (2000) The sponge community of a semi-submerged Mediterranean cave. PSZN I Mar Ecol 21:85–96

Denitto F, Licciano M (2006) Recruitment of Serpuloidea (Annelida: Polychaeta) in a marine cave of the Ionian Sea (Italy, Central Mediterranean). J Mar Biol Assoc UK 86:1373–1380

Denitto F, Terlizzi A, Belmonte G (2007) Settlement and primary succession in a shallow submarine cave: spatial and temporal benthic assemblage distinctness. Mar Ecol 28(Suppl. 1):35–46

Fagerstrom JA (1964) Fossil communities in paleoecology: their recognition and significance. Bull Geol Soc Am 75:1197–1216

Fichez R (1990) Absence of redox potential discontinuity in dark submarine cave sediments as evidence of oligotrophic conditions. Est Coastal Shelf Sci 31:875–481

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13(8):316–321

Gili JM, Riera T, Zabala M (1986) Physical and biological gradients in a submarine cave on the Western Mediterranean coast (North-East Spain). Mar Biol 90:291–297

Gischler E, Heindel K, Birgel D, Brunner B, Reitner J, Peckmann J (2017a) Cryptic biostalactites in a submerged karst cave of the Belize barrier reef revisited: pendant bioconstructions cemented by microbial micrite. Palaeogeogr Palaeoclimatol Palaeoecol 278:34–51

Gischler E, Birgel D, Brunner B, Eisenhauer A, Meyer G, Buhre S, Peckmann J (2017b) A giant underwater stalactite from the Blue Hole, Belize, revisited: a complex history of massive carbonate accretion under changing meteoric and marine conditions. J Sediment Res 87:1260–1284

Guido A, Mastandrea A, Rosso A, Sanfilippo R, Russo F (2012) Micrite precipitation induced by sulphate reducing bacteria in serpulid bioconstructions from submarine caves (Syracuse, Sicily). Rend Online Soc Geol Ital 21:933–934

Guido A, Heindel K, Birgel D, Rosso A, Mastandrea A, Sanfilippo R, Russo F, Peckmann J (2013) Pendant bioconstructions cemented by microbial carbonate in submerged marine caves (Holocene, SE Sicily). Palaeogeogr Palaeoclimatol Palaeoecol 388:166–180

Guido A, Mastandrea A, Rosso A, Sanfilippo R, Tosti F, Riding R, Russo F (2014) Commensal symbiosis between agglutinated polychaetes and sulfate reducing bacteria. Geobiology 12:265–275

Guido A, Rosso A, Sanfilippo R, Russo F, Mastandrea A (2016) *Frutexites* from microbial/metazoan bioconstructions of recent and Pleistocene marine caves (Sicily, Italy). Palaeogeogr Palaeoclimatol Palaeoecol 453:127–138

Guido A, Jimenez C, Achilleos K, Rosso A, Sanfilippo R, Hadjioannou L, Petrou A, Russo F, Mastandrea A (2017a) Cryptic serpulid-microbialite bioconstructions in the Kakoskali submarine cave (Cyprus, Eastern Mediterranean). Facies 63:21

Guido A, Rosso A, Sanfilippo R, Russo F, Mastandrea A (2017b) Microbial biomineralisation in biotic crusts from a Pleistocene marine cave (NW Sicily, Italy). Geomicrobiol J 34 (10):864–872. https://doi.org/10.1080/01490451.2017.1284283

Guido A, Gerovasileiou V, Russo F, Rosso A, Sanfilippo R, Voultsiadou E, Mastandrea A (2019a) Composition and biostratinomy of sponge-rich biogenic crusts in submarine caves (Aegean Sea, Eastern Mediterranean). Palaeogeogr Palaeoclimatol Palaeoecol 534:109338. https://doi.org/10.1016/j.palaeo.2019.109338

Guido A, Gerovasileiou V, Russo F, Rosso A, Sanfilippo R, Voultsiadou E, Mastandrea A (2019b) Dataset of biogenic crusts from submarine caves of the Aegean Sea: an example of sponges *vs* microbialite competition in cryptic environments. Data Brief 27:104745. https://doi.org/10.1016/j.dib.2019.104745

Harmelin J-G (1969) Bryozoaires des grottes sous marines obscures de la région Marseillaise. Faunistique et écologie. Téthys 11:214–229

Harmelin J-G (1985) Organisation spatiale des communautés sessiles des grottes sous-marines de Mèditerranée. Rapports de la Commisssion Internationale pour l'Exploration Scientifique de la Mer Mèditerranee 5:149–153

Harmelin J-G (1986) Patterns in the distribution of bryozoans in the Mediterranean marine caves. Stygologia 2:10–25

Harmelin J-G (2000) Ecology of cave and cavity dwelling bryozoans. In: Herrera CA, Jackson JBC (eds) Proceedings of the 11th international bryozoology association conference. Smithsonian Tropical Research Institute, Panama, pp 38–55

Ingrosso G, Abbiati M, Badalamenti F, Bavestrello G, Belmonte G, Cannas R, Benedetti-Cecchi L, Bertolino M, Bevilacqua S, Bianchi CN, Bo M, Boscari E, Cardone F, Cattaneo-Vietti R, Cau A, Cerrano C, Chemello R, Chimienti G, Congiu L, Corriero G, Costantini F, De Leo F, Donnarumma L, Falace A, Fraschetti S, Giangrande A, Gravina MF, Guarnieri G, Mastrototaro F, Milazzo M, Morri C, Musco L, Pezzolesi L, Piraino S, Prada F, Ponti M, Rindi F, Russo GF, Sandulli R, Villamor A, Zane L, Boero F (2018) Mediterranean bioconstructions along the Italian Coast. Adv Mar Biol 79:61–136

Jimenez C, Achilleos K, Petrou A, Hadjioannou L, Guido A, Rosso A, Gerovasoleiou V, Albano PG, Di Franco D, Andreou V, Abu AR (2019) A dream within a dream: Kakoskali Cave, a unique marine ecosystem in Cyprus (Levantine Sea). In: Öztürk B (ed) Marine caves of the Eastern Mediterranean Sea. Biodiversity, threats and conservation. Turkish Marine Research Foundation (TUDAV), Istanbul, pp 91–110. ISBN: 978-975-8825-45-5

Macintyre IG (1984) Extensive submarine lithification in a cave in the Belize barrier reef platform. J Sediment Petrol 54:11–25

Macintyre IG, Rutzler K, Norris JN, Fauchald K (1982) A submarine cave near Columbus Cay, Belize: a bizarre cryptic habitat. Smithson Contrib Mar Sci 12:127–141

Martì R, Uriz MJ, Ballesteros E, Turon X (2004) Benthic assemblages in two Mediterranean caves: species diversity and coverage as a function of abiotic parameters and geographic distance. J Mar Biol Assoc UK 84:557–572

Morri C, Bianchi CN (2003) Zonazione biologica. In: Cicogna F, Bianchi CN, Ferrari G, Forti P (eds) Grotte Marine, Cinquant'anni di ricerche in Italia. Ministero dell'Ambiente e della Tutela del Territorio, Roma, pp 257–265

Okamura B, Harmelin J-G, Jackson JBC (2001) Refuges revisited: enemies versus flow and feeding as determinants of sessile animal distribution and form. In: Jackson JBC, Lidgard S, McKinney FK (eds) Evolutionary patterns: growth, form, and tempo in the fossil record. University of Chicago Press, Chicago, pp 61–93

Olivier N, Hantzpergue P, Gaillarda C, Pittet B, Leinfelder RR, Schmid DU, Werner W (2003) Microbialite morphology, structure and growth: a model of the Upper Jurassic reefs of the Chay Peninsula (Western France). Palaeogeogr Palaeoclimatol Palaeoecol 193:383–404

Onorato M, Belmonte G (2017) Submarine caves of the Salento peninsula. Faunal aspects. Thalassia Salentina 39:47–72

Onorato R, Forti P, Belmonte G, Costantini A, Poto M (2003) La grotta sottomarina *lu Lampiùne*: novità esplorative e prime indagini ecologiche. Thalassia Salentina 26:55–64

Onorato M, Onorato R, Posi ME, Poto M (2020) A new underwater karst phenomenon along the west coast of the Salento Peninsula (Italy): the "Enzo Manieri-Elia" cave. Thalassia Salentina 42:47–58

Palau M, Tornet C, Riera T, Zabala M (1991) Planktonic gradients along a Mediterranean Sea cave. Oecol Aquat 10:299–316

Pérès JM, Picard J (1964) Nouveau manuel de bionomie benthique de la Mer Mediterranee. Recl Trav Stat Mar Endoume 31:1–137

Quarta G, D'Elia M, Calcagnile L, Belmonte G, Ingrosso G (2010) Reconstructing the formation mechanism of submarine biogenic stalactites: the contribution of AMS. Nucl Instrum Methods Phys Res B 268:1244–1247

Quarta G, D'Elia M, Belmonte G, Braione E, Scrimieri L, Calcagnile L (2019) ^{14}C dating on marine bio-constructions from a submarine cave in the Adriatic Sea. Nucl Instrum Methods Phys Res, Sect B 455:234–237

Reitner J (1993) Modern cryptic microbialite/metazoan facies from Lizard Island (great barrier reef, Australia): formation and concepts. Facies 29:3–40

Reolid M, Molina JM (2010) Serpulid-Frutexites assemblage from shadow-cryptic environments in Jurassic marine caves, Betic Cordillera, southern Spain. Palaios 25:468–474

Riedl R (1966) Biologie der Meereshohlen. Paul Parey, Hamburg

Rossi S, Bramanti L, Gori A, Orejas C (2017) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer Nature, Cham, 3 vol, 1350 pp

Rosso A, Sanfilippo R, Taddei RE, Di Martino E (2013a) Faunas and ecological groups of Serpuloidea, Bryozoa and Brachiopoda from submarine caves in Sicily (Mediterranean Sea). Boll Soc Paleontol Ital 52(3):167–176

Rosso A, Di Martino E, Sanfilippo R, Di Martino V (2013b) Bryozoan communities and thanatocoenoses from submarine caves in the Plemmirio marine protected area (SE Sicily). In: Ernst A, Schäfer P, Scholz J (eds) Bryozoan studies 2010. Proceedings of the 15th IBA conference, 2010 Kiel. Lecture notes in earth system sciences, vol 143. Springer, Berlin, pp 251–269

Rosso A, Sanfilippo R, Bonfiglio L, Richards D, Nita D (2018a) Exceptional Pleistocene vermetid crusts preserved in a cave located 130 m a.s.l. near Taormina (NE Sicily). Boll Soc Paleontol Ital 57(2):133–144

Rosso A, Di Martino E, Pica D, Galanti L, Cerrano C, Novosel M (2018b) Non-indigenous bryozoan species from natural and artificial substrata of Mediterranean submarine caves. Mar Biodivers 48(3):1345–1355. https://doi.org/10.1007/s12526-016-0602-2

Rosso A, Gerovasileiou V, Sanfilippo R, Guido A (2019) Bryozoans assemblages from two submarine caves in the Aegean Sea (Eastern Mediterranean). Mar Biodivers 49 (2):707–726

Rosso A, Di Martino E, Gerovasileiou V (2020) Revision of the genus *Setosella* (Bryozoa: Cheilostomata) with description of new species from deep-waters and submarine caves in the Mediterranean. Zootaxa 4728(4):401–442

Russo R, Valente S, Colangelo G, Belmonte G (2015) Meiofauna distribution on hard substrata in a submarine cave. J Mar Biol Assoc UK 95:1555–1564

Sanfilippo R, Rosso A, Guido A, Mastandrea A, Russo F, Ryding R, Taddei-Ruggiero E (2015) Metazooan/microbial biostalactites from modern submarine caves in the Mediterranean Sea. Mar Ecol 36:1277–1293

Sanfilippo R, Rosso A, Guido A, Gerovasileiou V (2017) Serpulid communities from two marine caves in the Aegean Sea, Eastern Mediterranean. J Mar Biol Assoc UK 97:1059–1068

Silén L, Harmelin J-G (1976) *Haplopoma sciaphilum* sp. n., a cave-living bryozoan from the Skagerrak and the Mediterranean. Zool Scr 5:61–66

Stella JS, Pratchett MS, Hutchings PA, Jones JP (2011) Coral associated invertebrates: diversity, ecological importance and vulnerability to disturbance. Oceanogr Mar Biol Annu Rev 49:43–104

Zabala M, Riera T, Gili JM, Barange M, Lobo A, Peñuelas J (1989) Water flow, trophic depletion, and benthic macrofauna impoverishment in a submarine cave from the Western Mediterranean. Mar Ecol 10(3):271–287

The Tubeworm Forests of Hydrothermal Vents and Cold Seeps

V. Tunnicliffe and E. E. Cordes

Abstract The deep sea is typified by habitats that are dependent upon organic matter delivery from the sunlit surface. However, a few unusual ecosystems are localized around the only source of autochthonous primary productivity in the deep sea: chemosynthesis. The chemical substrates that drive chemosynthesis can come from the rapid venting of hydrothermal fluids at the spreading centres between continents and in back-arc basins or can be transported along with pore fluids rich in methane or higher hydrocarbons that are mobilized by sediment compaction at cold seeps. Tubeworms at hydrothermal vents and cold seeps in the deep sea are highly modified to exploit the chemoautotrophic capabilities of symbiotic bacteria. These polychaetes of the family Siboglinidae from vents and seeps share a common ancestor. The vent tubeworms include eight genera that have diverged around the Pacific; they rely mostly on their anterior branchiae to take up dissolved gases. Seep tubeworms are restricted to three genera, but have a cosmopolitan distribution along the continental margins and methane-rich settings around the world. They are notable in their capacity to acquire hydrogen sulphide through posterior extensions of their tubes in addition to the branchiae.

The siboglinid worms are intimately tied to the flux of reduced compounds and commonly exceed a metre in length. The chitinous tubes can form dense clusters that extend over hundreds of square metres at both vents and seeps. In stable settings, the colonies may persist many decades or more. The physical presence of dense tube clusters alters fluid flows, often creating a large enclosed volume for chemosynthetic processes. As the tubeworms rely entirely on their symbionts for nutrition, they do not compete with the forest inhabitants for organic matter. When tubes grow densely, they can create complex bushes as new worms recruit. The tube surfaces can be covered with other sedentary invertebrates that also build structures for

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further colonization. Surface area for access to emerging fluids is greatly extended in this canopy.

Well over 50 other species are documented from *Ridgeia piscesae* bushes on Juan de Fuca Ridge and from *Lamellibrachia luymesi* aggregations in the Gulf of Mexico. Tube surfaces serve to foster growth of microbial assemblages that include autotrophic and heterotrophic microbes. Thus, grazers are attracted to the tubes, while suspension feeders have access to the fluids rising through the assemblage. Community composition and trophic structure shows marked shifts as colonies are situated further from the influence of reduced fluids. Similar changes are manifested over time as the conduits for fluid transport become occluded and more background fauna gain access to the elevated productivity. Tubeworms from both vents and seeps continue to provide shelter and useable surfaces for deep-sea animals where toxic fluid influences are low, even after the worm has died. These extraordinary polychaetes foster extensive communities in special environments of the deep sea.

Keywords Vestimentiferans · Community complexity · Habitat variability · Foundation species · Hydrothermal vents · Cold seeps

1 Introduction

1.1 *The Deep-Sea Setting*

The deep ocean below 200 m receives too little light to support photosynthesis; thus the planet's largest ecosystems must await the delivery of energy through primary organic matter from the overlying waters. Seafloor organisms are fuelled by photosynthetic production and have developed a vast array of adaptations to retrieve nutrients from sediments and overlying water. Surface productivity, proximity to land, and oceanographic features (e.g. upwelling) are key factors in diversification of deep-sea lineages (Woolley et al. 2016). However, the discovery of dense animal assemblages around hydrothermal vents in 1977, and at cold seeps soon after, opened the realization that energy from reduction-oxidation reactions can also fuel enough organic carbon formation through chemosynthesis to support complex ecosystems (Lonsdale 1977; Corliss et al. 1979). Subsequently, the discoveries of autotrophic microbial diversity and many carbon fixation pathways at these sites have led to greater understanding of metabolic evolution, the origin of the first cells, and the potential for extraterrestrial life (Hugler and Sievert 2011).

The tectonic setting largely governs the nature of both the substratum and fluid emerging through the seafloor. Mid-ocean ridges (MOR), formed by magma injections and tectonic plate separation, foster high-temperature rock-buffered hydrothermal fluids that form from downwelled seawater and exit through vents in the basalt; these fluids tend to have consistent chemical properties (Seyfried and Mottl 1995). Ocean plate subduction under a younger ocean plate forms the volcanic arcs and back-arc basins typical of the western Pacific. Back-arc basins also have segmented spreading axes with MOR-type venting although basalts may be more altered with more variable fluids. Here, and at slower spreading MORs, long duration venting can deposit large structures of massive sulphides—rocks precipitated from hot fluids that concentrate metals complexed to sulphide. The volcanic arcs, however, are independent volcanoes that form as magma is injected from the downthrust ocean plate; melt from old, altered basalt can include the sediment overburden and volatiles. Hydrothermal fluids may be rich in SO_2 and CO_2 resulting in low pH, excess sulphur and high variability along-arc (Stern et al. 2003).

Many plate margins, especially those of continents, accumulate sediments and organic matter that is converted to hydrocarbons by deep thermogenic and biogenic processes that may form hydrocarbon deposits and methane hydrates. Fluids that emerge as cold seeps are driven upward by growing pressure from several processes, including compaction of sediments. Levin (2005) describes the great variety of seep types and manifestations that reflect the multitude of sedimentary environments and chemical conditions in which they form. Seeps along passive margins are best known from sedimentary basins that have accumulated organic matter and are often associated with salt tectonics as in the Gulf of Mexico (Brooks et al. 1987). They can also be associated with large pockmarks that are probably linked to gas hydrate disassociation events, such as on the Atlantic margins of Africa and Norway (Olu-Le Roy et al. 2007; Vogt et al. 1997).

Seeps along active margins often form in accretionary prisms (i.e. Barbados) that build as sediment is scraped off the subducting plate and compacted (Olu et al. 1996). Active margin seeps can also include areas of subducting seamounts, such as off the Pacific coast of Costa Rica and the Aleutian Islands, where the seamounts deform the overlying plate and result in compaction that drives fluid flux to the surface. In some cases, the fluid flux is so rapid that it can carry with it a measurable and observable thermal anomaly of a few degree Celsius, resulting in what has been termed a “hydrothermal seep” (Levin et al. 2015). This setting contrasts with that of sedimented hydrothermal vents, such as in the Guaymas Basin, that have the extreme thermal signature of vents (Von Damm et al. 1985) but also possess characteristics of seeps including the presence of hydrocarbons (Simoneit and Lonsdale 1982) and the types of microbial communities (Dhillon et al. 2003). Levin (2005) emphasizes the likelihood that many seeps, and even types of seepage, remain unknown. The large number of discoveries in recent years—570 gas plumes along the east coast of the United States between 50 and 1700 m depth and over 800 methane bubble streams along the west coast of the United States between 100 and 1600 m depth—indicates that exploration will reveal more (Baumberger et al. 2018).

At vents, subsurface fluid interaction with host rocks can leach many reduced elements and compounds into the fluids, and inorganic carbon is injected from magma sources. In contrast, the ultimate source of CO_2 and CH_4 at seeps is photosynthetic in origin. It is this source of reduced compounds, the high volume flux of venting, and the heat content that largely distinguish vent from seep fluids. In both systems, hydrogen sulphide is formed as seawater sulphate circulates subseafloor and is stripped of oxygen by minerals and microbes.

Globally, the animals that inhabit hard substratum hot vents tend to be endemic to the habitat with about 10% also known from seeps (Chapman et al. 2019). However, study of sedimented vents and seeps in close proximity reveals a higher degree of shared fauna where the chemosynthetic habitats are more of a continuum than discrete and isolated ecosystems. For example, around Japan where more than 50 vent and seep sites are known, Watanabe et al. (2010) report a 20% similarity in species in the two chemosynthesis-based ecosystems. The unusual setting of the sedimented vents of Okinawa Trough that is forming on a continental margin creates the opportunity for habitats that suit both vent and seep animals. Similarly, continental turbidite sediments have filled a venting basin (Middle Valley) at the northern end of Juan de Fuca Ridge where vent animals on emergent massive sulphides live only metres from seep species in adjacent sediments (Juniper et al. 1992).

1.1.1 Chemosynthesis

Some microbes use the process of chemosynthesis to transform CO_2 into organic molecules. Energy in the form of ATP and NADPH to enable the process is acquired from reduction-oxidation (redox) reactions involving inorganic compounds. Many such reactions are exploited by a wide range of microbes (mostly in the Proteobacteria and Archaea) with a variety of electron donors such as reduced forms of dissolved sulphur, metals, and hydrogen. Oxygen is the electron acceptor that yields the most energy, but other oxidized molecules (e.g. NO_3^- and CO_2) are also used. The seafloor interface between reduced emerging fluids and oxygenated seawater is particularly productive for both vent and seep microbes. The metabolic pathways used to fix inorganic carbon are diverse and include not only the basic Calvin-Benson-Bassham cycle known in plants but also some very simple reaction chains that may reflect adaptations by early life (Hugler and Sievert 2011). While chemolithotrophy is common in many marine systems (oxygen minimum zones, decaying carcasses, subseafloor), the rates at which reduced compounds encounter electron acceptors at vents and seeps are able to sustain higher rates of microbial production and the symbiotic associations with invertebrates that support the large biomass in these ecosystems.

1.2 Forests in Environments of Chemosynthesis

The largest biomass at hydrothermal vents and seeps lies in the invertebrates that house microbes as symbionts within specialized structures. These species include mussels, clams, and the iconic “tubeworms” that are polychaetes in the family Siboglinidae. Dense growths of these worms form “forest analogues” at many vents and seeps where associated organisms create complex communities. The visual similarity of tubeworms to terrestrial forests is highlighted by their initial identification as sunken plant material until they were observed bleeding on the ship's deck during the discovery cruise in the Gulf of Mexico. These aggregations align with the definition presented by Rossi et al. (2017) that have "as a common trait, their three-dimensional architecture tiering from a few centimeters to tens of meters" (p. vii). Our contribution explores the nature of the tubeworms that dominate many vents and seeps and their role in sustaining associated communities. We do not provide detailed background on the habitats and ecology of vents and seeps; reviews can be found elsewhere (Tunnicliffe 1991; Van Dover 2000; Tunnicliffe et al. 2003b; Levin 2005).

2 Diversity and Distribution of Tubeworms

2.1 What Are Vestimentiferans?

There is likely not another animal that has travelled as far across the Linnaean systematic hierarchy as the vestimentiferan and pogonophoran tubeworms. This history, which includes status as two distinct phyla, is well documented and reflects the confusion generated from highly modified morphologies. Pleijel et al. (2009) combine the two groups, plus allied worms (total about 200 species), into the family Siboglinidae in phylum Annelida, class Polychaeta. However, the higher placement in the order Sabellida remains under some debate (Weigert et al. 2014). Within the family, Karaseva et al. (2016) suggest the use of four subfamilies to recognize the distinction of pogonophorans, the bone-worm *Osedax*, moniliferans, and vestimentiferans. They present a detailed examination of the distinguishing morphological features of the ten described genera of the proposed subfamily Vestimentifera, including updated comparative diagnoses and range information (note that some distribution records in this review are not consistent with the cited literature). Currently, there are over 20 species of vestimentiferans described with several "molecular species" that will require further assessment.

It is probable that an ancestral siboglinid occupied organic-rich sediments and diversified into progressively more reduced habitats (Schulze and Halanych 2003). The vestimentiferans appear to be the most derived of the siboglinids with monoliferans as the sister clade (Li et al. 2017). As hydrothermal venting is a very old geological process (potentially where life originated on Earth (Weiss et al. 2016)), the habitat itself is ancient, and thus it is likely that many organisms colonized this rich source of primary production early; numerous fossils are described from vent sulphide deposits, including those of Palaeozoic age (Little et al. 1999; Georgieva et al. 2019). However, identifying fossilized vestimentiferan tubes is not easy, and the best potential examples date from the middle Mesozoic, a timing that is in better agreement with the few molecular clock estimates available for the origination of vent tubeworms (Hilário et al. 2011a). Vestimentiferans likely first appeared in cold seep sediments before a later move to the more stressful vent conditions on hard substrata. The siboglinid "subfamilies" all have an obligate association with endosymbiotic bacteria. Each of the four groups, however, hosts a different clade of the Gammaproteobacteria (McMullin et al. 2003; Hilário et al. 2011a). Within vent vestimentiferans, host-bacterium specificity does not appear to be strong although seep symbionts emerge as a distinct lineage (Nelson and Fisher 2000). Full genome comparisons of symbionts from four vent species confirm the presence of a single phylotype but also document bacterial population structure by location and host (Perez and Juniper 2016).

2.2 Distribution of Hydrothermal Vent Tubeworms

To date, siboglinid tubeworms at hydrothermal vents occur, almost exclusively, in the Pacific Ocean. They are commonly encountered along the Juan de Fuca Ridge and the East Pacific Rise in the eastern Pacific (mid ocean spreading ridges) where four species occur in high numbers (Fig. 1)—these taxa are distinct enough morphologically to warrant separate genera; to date, molecular work has supported the distinctions. It is less certain to find vestimentiferans at vents in the volcanic arcs and back-arc spreading centres of the western Pacific where the vent settings can be highly variable. Southward (1991) describes two vestimentiferan species from the Lau back-arc vents (south of Tonga) noting their distinction from east Pacific genera. These species (*Lamellibrachia columna* and *Alaysia spiralis*) do not figure largely in

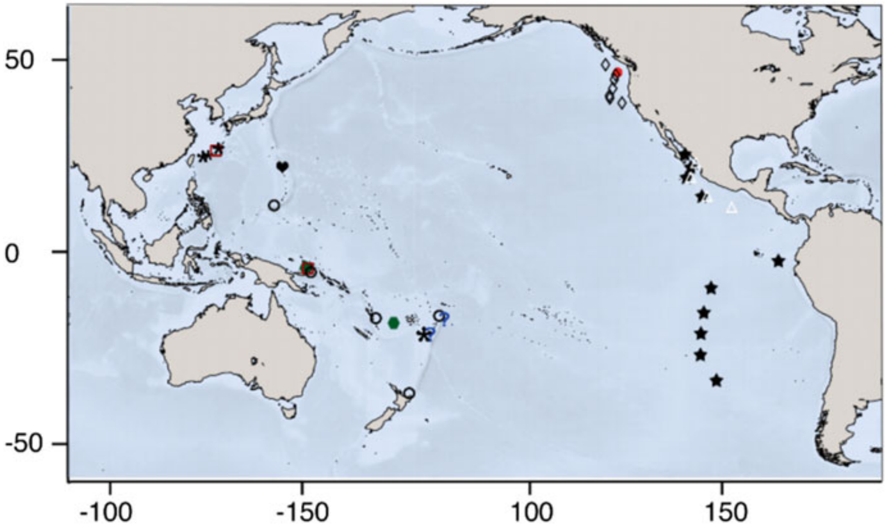

Fig. 1 Vestimentiferan distribution at hydrothermal vents: green hexagons, *Arcovestia ivanovi*; black flowers, *Alaysia* spp.; empty circle, *Lamellibrachia juni*; black heart, *Lamellibrachia satsumi*; hollow diamonds, *Ridgeia piscesae*; white triangles, *Oasisia alvinae*; black stars, *Riftia* and *Tevnia* combined. Several vent sites also have seep-related species observed in the periphery or vicinity: red hollow squares, *Paraescarpia echinospica*; blue question marks, *L. columna*; red circle, *L. barhami*. Base map provided by M. McCowin

subsequent descriptions of vents in this region, and the imagery from the collection sites shows very sparse worms. Possibly they are peripheral species that do not penetrate vigorous venting conditions. A third, and unusual, siboglinid also occurs in this region: *Siphonobrachia lauensis* is a monoliferan. As with others of its subfamily, it occupies sedimented habitat (Southward 1991). The vestimentiferans at vents on the Kermadec volcanic arc between New Zealand and Tonga constitute two more species: *L. juni* and *Oasisia fujikurai* (Miura and Kojima 2006). However, we know little of the habit or associates of either species in this area. *L. juni* is a widespread species, occurring on the Kermadec and Tonga Arcs, the Futuna Ridge near Vanuatu (VT, pers. obs.), in the Manus back-arc spreading centre, and on the southern Mariana back-arc spreading centre (Kojima et al. 2006). One more vent species in the southwest Pacific is *Arcovestia ivanova*, currently known from the Manus Basin and the Fiji Basin where they form short, tangled clusters of sinuous tubes on basalt (Southward and Galkin 1997).

The shallowest vent record is *L. satsuma* at Daikoku Seamount (Mariana Volcanic Arc) at 350 m depth (VT, pers. obs.). This species, however, also is abundant at cold seeps near Japan where it was first described from a collection in Kagoshima Bay less than 100 m (Miura 1997). The deepest Pacific record is probably those of *Oasisia alvinae* and *Riftia pachyptila* in the Gulf of California at 3685 m (Goffredi et al. 2017). Overall, there are more publications on molecular relationships of recovered vestimentiferans than there are taxonomic descriptions, with the consequence that many “molecular types” exist with no formal analysis. Thus, there is potential for greater diversity of vestimentiferans in Pacific vents; for example, there is likely more than one species of *Oasisia* on the East Pacific Rise (Goffredi et al. 2017).

Exploration of Indian Ocean vents has not reported, to date, any siboglinid tubeworms. Similarly, in the Atlantic Ocean, penetration of the hydrothermal vent habitat by vestimentiferans is almost non-existent, perhaps due to timing of diversification of the vent genera and closure of connecting seaways (Gebruk et al. 1997). Nonetheless, two species, well-known at cold seeps in the Gulf of Mexico (genera are *Lamellibrachia* and *Escarpia* with species designations taxonomically unclear), have ventured into weakly venting areas of the Mid-Cayman Spreading Center in the Caribbean Sea (Plouviez et al. 2015). In addition, *Lamellibrachia* has been observed on submarine volcanoes in the deep Mediterranean Sea (Southward et al. 2011). Although densities are very sparse, this occurrence highlights the opportunistic nature of sediment-/rubble-adapted seep species to encroach on hydrothermal vents. A final notable occurrence is the small tubeworm *Sclerolinum contortum*. As with the mention above of *Siphonobrachia* at Pacific vents, this worm is in the monoliferan subfamily, not the vestimentiferans. This species, present in Gulf of Mexico seeps, is also recorded at both Arctic and Antarctic vent sites where the thin tubes reaching 10 cm in length can form dense mats. Georgieva et al. (2015) refer to the species as a “chemosynthetic weed” that has accessed sites as far apart as 16,000 km. While data support the conspecific designation, it is clear the populations are genetically distinct with no gene exchange.

2.3 Distribution of Methane/Cold Seep Tubeworms

Tubeworms of various taxa are widespread at cold seeps throughout the world's oceans. *Lamellibrachia barhami* was the first species of the genus described (Webb 1969) and is widespread along the west coast of North and South America from Canada to Chile (Kobayashi and Araya 2018). It is present at the seep sites of Pacific Costa Rica, where it co-occurs with a recently described species, *L. donwalshi*, that is most closely related to Atlantic and Mediterranean species (McCowin and Rouse 2018). In the Gulf of Mexico, there are at least three species of *Lamellibrachia*, two species of *Escarpia*, and one species in the genus *Seepiophila* (Cordes et al. 2009; Cowart et al. 2014). The distribution of *Lamellibrachia luymesi* (300–1000 m depth) is largely restricted to the northern Gulf of Mexico, although it was originally described from Guyana (van der Land and Norrevang 1975). It (or another Gulf of Mexico *Lamellibrachia* species) may be conspecific with *Lamellibrachia* collected at the El Pilar site off Barbados at 1300 m depth (Olu et al. 1997; Cordes et al. 2008) and at the Cayman vents mentioned above. *E. laminata* (1000–3300 m depth) occurs beyond the Gulf of Mexico in the Caribbean and Barbados and is generally indistinguishable from *E. spicata* that is found in the Pacific along the west coast of the Americas. In the Gulf of Mexico, *Seepiophila jonesi*, closely related to species of *Escarpia*, inhabits shallower seep sites and co-occurs with *L. luymesi* and an undescribed species of *Escarpia* (Cordes et al. 2009).

Across the Atlantic, *Escarpia southwardae* occupies seeps of the African margin, and *Lamellibrachia anaximander* inhabits mud volcano and seep habitats of the Mediterranean (Olu-Le Roy et al. 2004; Hilário et al. 2011b; Taviani et al. 2013). There are no other reports of vestimentiferans from the Atlantic, although a small escarpid has recently been discovered at shallow (300 m) seeps along the southeast coast of the United States (EEC pers. obs.). As with vents, there are no reports of seep vestimentiferans in the Indian Ocean, although increased exploration may find both. However, the seeps of the Makran Accretionary Prism off Pakistan and the Bay of Bengal, India, have been reasonably well surveyed, with no siboglinid reports (Von Rad et al. 2000).

2.4 Intersecting Ecosystems

Some species are known from both vents and seeps such as *Escarpia spicata* in the Gulf of California (Vrijenhoek 2010). *Escarpia* and *Lamellibrachia* appear to occur at seeps and vents in the western Pacific although details are lacking in some cases. Around Japan, in particular, the intersection of oceanic and continental plates has created venting and seeping conditions (over 50 locations) in close juxtaposition (Watanabe et al. 2010). Kojima et al. (2002) propose two escarpid species: a shallow ("E1") species at northwest seeps and a deeper ("E2") species with broad distribution from Papua New Guinea to Japan where it occurs mostly in seeps but also at

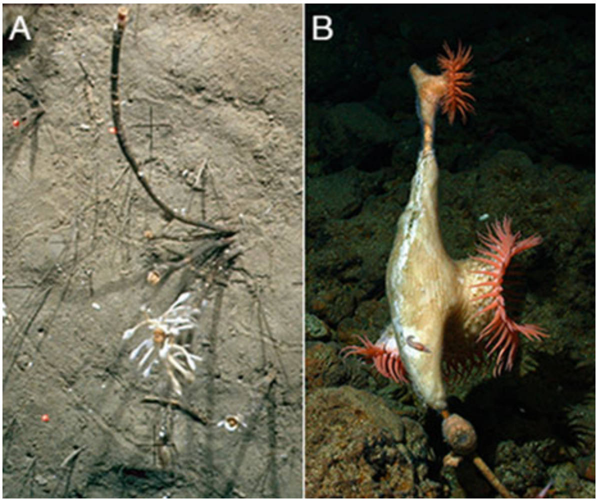

Fig. 2 Seep species observed near vents. Tubes are used as substratum for barnacles and anemones. Both images 25–30 cm across. (**a**) *Paraescarpia echinospicata* at type location (Edison Seamount, PNG) on a ridge with high methane anomaly. Image credit GEOMAR. (**b**) *Lamellibrachia* cf. *columna* on Niua Volcano (north Tonga Arc) between two large ventfields. Image credit Schmidt Ocean Institute and CSSF

hydrothermal vents. This latter species is now accepted as *Paraescarpia echinospica*, originally described from on Edison Seamount, PNG (Fig. 2a) where the authors note the methane anomaly, carbonate deposition, and sediments that indicate seep-like conditions; they are uncertain about vent affiliation (Southward et al. 2002). It has been observed also at seep sites in the South China Sea (Liang et al. 2017) and in the Nankai Trough.

Lamellibrachia columna may be another vestimentiferan that takes advantage of dissolved sulphide available in the periphery of vents. While the species description denotes a vent vestimentiferan (Southward 1991), field notes for the type locations note the habitat as “cold seeps” near the vents (Desbruyères et al. 1994). In the northern Tonga Arc, tubes and obturacula (from images, Fig. 2b) matching this species indeed cluster at the far edges of vents (VT, pers. obs.). More recently, McCowin et al. (2019) record this species in cold seeps on the eastern margin of New Zealand (800 m). These authors propose that *L. columna* and *L. sagami*, originally described from cold seeps in Japan (Kobayashi et al. 2015), along with “L.2”, are conspecific (interpreted by COI gene); thus, this seep species spans a very large west Pacific range, much as *L. juni* does at vents. In contrast, one species that does integrate very well into both vents and seeps is *L. satsuma* in the northwest Pacific. Here, it is the shallowest known vestimentiferan, collected from both seeps and whale falls between 80 and 100 m depth in Kagoshima Bay (Miura et al. 2002). It also flourishes at the hydrothermal vents on Nikko Seamount, Mariana Arc, where it forms dense thickets on bare substratum. The presence of these species at vents and seeps in the Pacific illustrates the soft boundaries of these reducing habitats and the opportunities for some vestimentiferans to access broader distribution ranges.

3 Nature of the "Trees in the Forest"

3.1 Siboglinid Biology

Several features of the vestimentiferan body plan are unique to this group of worms to accommodate the symbiosis with bacteria. Detailed descriptions are available in both taxonomic descriptions and reviews by Southward (2000), Southward et al. (2005), and Karaseva et al. (2016). In adult worms, four major body regions are evident: the obturacular region with the branchial plume that extends from the tube, the muscular collar or vestimental region, the long trunk region, and the basal segmented opisthosome. The obturaculum can be long (*Riftia*) or short (*Lamellibrachia*) relative to the body; several species have chitinous caps that plug the tube when the worm withdraws. The branchiae, usually red in life due to the haemoglobin in this heavily vascularized structure, are uptake sites for oxygen and metabolites that support both animal and bacteria (Scott et al. 1999). Muscles in the vestimentum that wedge the body in place also contract to expel gametes during spawning. Retraction occurs using longitudinal trunk muscles and setae on the opisthosoma to anchor the body. The trunk houses the gonads and the trophosome with extensive vascularization. Rimskaya-Korsakova et al. (2017) describe the more extensive blood system and modifications in *Riftia* that support the larger size and metabolic needs of this animal compared to smaller species. While early juveniles do have both mouth and gut (Southward 1988), the adult has neither as nutrition is derived from symbionts housed within host cells in the trophosome (Cavanaugh et al. 1981; Felbeck 1981). This organ can occupy the entire trunk, but it may also appear reduced and shrivelled in less optimal habitat (Tunnicliffe et al. 2014).

In these dioecious species, sperm bundles are released from the males and are captured by females where fertilization is internal in at least six species (Southward and Coates 1989; MacDonald et al. 2002; Hilário et al. 2005; Miyake et al. 2006). In *Ridgeia piscesae*, the males "fly" the sperm bundle on a long strand in flowing vent water where it can entangle in the branchiae of a female (Tunnicliffe et al. 2014); *Oasisia* cf. *alvinae* uses the same technique (VT, pers. obs.). Meiosis does not appear to occur until release of the fertilized egg in *R. pachyptila* and *L. luymesi* (and possibly all other species) so that embryogenesis occurs in the water (Hilário et al. 2005). In species where development to the larval form is known (*R. pachyptila and L. satsuma*), estimated lifespans of the nonfeeding trochophore larvae vary between 30 and 45 days (Marsh et al. 2001; Miyake et al. 2006). Laboratory observations of seep species *L. luymesi* and *S. jonesi* revealed that their larvae can persist for at least 21 days, at which point they still did not have a mouth or gut, suggesting a longer larval duration (Young et al. 1996). A settling larva (metatrochophore) is both mobile and able to feed but, as symbionts are acquired during metamorphosis, the gut closes, and the recruit becomes sessile (Southward 1988). The initial symbiotic bacteria are free-living in biofilms (Harmer et al. 2008) and can enter the host through the epidermis (Nussbaumer et al. 2006).

Comprehensive reviews of vestimentiferan biology detail the functional physiological adaptations of the host that enable access to the autotrophic food resources generated by the bacterial symbiont through chemosynthesis (Childress and Fisher 1992; Bright and Lallier 2010). Studies have focussed on only a few species, but they do involve both vent and seep adaptations. Key features are the mechanisms by which the animals transport the compounds to their symbionts and maintain internal ion balance as protons accumulate. The symbionts—Gammaproteobacteria—require sulphide (H_2S, HS^-) and inorganic carbon as carbon dioxide, as well as oxygen. The branchiae extract dissolved oxygen and hydrogen sulphide where emerging vent fluids mix with bottom water. A key difference between seep and vent species is that the latter obtain sulphides mostly across their plume, while the seep species examined can also obtain sulphide across a posterior extension of the body and tube, referred to as the "root" (Julian et al. 1999; Freytag et al. 2001). As sulphide is both toxic and highly reactive with oxygen, it cannot move as a free ion in the body; thus, *Riftia* and *Lamellibrachia* (and presumably the other species) have two or three types of haemoglobin in both blood and coelomic fluid to bind to these dissolved compounds and deliver to the symbionts (Arp and Childress 1983; Suzuki et al. 1989; Zal et al. 1998).

CO_2 is converted to HCO_3^- by carbonic anhydrase that maintains a P_{CO2} gradient to foster high inorganic concentrations in the blood (Goffredi et al. 1997). To counteract the proton build-up and potential pH drop, *Riftia* deploys ATPases to sustain an acid-base balance (Goffredi et al. 1999), while *Lamellibrachia luymesi* (at seeps) may augment ATPases with other proton channel mechanisms (Dattagupta et al. 2006). In some seep species, the sulphate that is produced as a by-product of sulphide oxidation is released into the sediments surrounding the worms to augment anaerobic methane oxidation and increase the supply of sulphide back to the worm (Cordes et al. 2005a; Dattagupta et al. 2006).

Vestimentiferan symbionts are Gammaproteobacteria of a few closely related phylotypes that tend to differ among location, substratum, and fluid source (Feldman et al. 1997; Di Meo et al. 2000; Duperron et al. 2009). The strongest differentiation lies between vents versus seeps where the distinct phylotypes in the symbionts do not reflect host evolutionary patterns (Vrijenhoek 2010). Across northeast Pacific vents, symbionts show low fidelity to any one host (Perez and Juniper 2016). It is likely that more than one population of symbiont within a phylotype inhabits a single host (Perez and Juniper 2018), perhaps thereby conferring wider metabolic flexibility on the association as fluid conditions change. To date, only sulphide is recognized as the substrate for oxidation. The endosymbiont is able to use two distinct metabolic pathways: the Calvin-Benson-Bassham cycle and the tricarboxylic acid cycle (Markert et al. 2007); metagenomic interpretations reveal that both pathways are widespread in vent and seep tubeworms (Thiel et al. 2012; Reveillaud et al. 2018). These two pathways provide a broad metabolic range for the worm-bacteria association that facilitate switches to optimize use of metabolites and ATP in variable chemical environments. Organic carbon is translocated to the host both directly and through symbiont digestion (Bright et al. 2000).

3.1.1 The Tubes

Some species can create a tube in excess of 2 m in length (*Riftia*, *Ridgeia*, several *Lamellibrachia* species). The vestimentiferan tube is closed at the base where it attaches to hard substrata or is buried in sediment; in many species, especially at seeps, the tube can grow in both directions. The tube is a tapered cone with the exception of *Riftia* which constructs a straight-sided cylinder. The tube material is a crystalline β-chitin secreted by glands on the vestimentum, body wall, and opisthosoma. Chitin microfibrils are embedded in a protein matrix in a twisted chain array forming swaths of strands that are then layered like plywood (Gaill et al. 1992); Shillito et al. (1995) note that protein content is higher in seep tubeworms. Tube thickness and rigidity vary among species to the point where cutting the tubes of seep species can be quite difficult. Tube material dehydrates slowly with outer layers hardening over the lifetime (Shillito et al. 1997); thus, older worms have thicker, harder tubes. Forward growth in many species appears to be incremental with stages that form flanges or funnels circling the tube, although these increments do not correspond to consistent time intervals. Tubes of *Riftia* are soft and without clear banding suggesting continuous growth. In contrast, *Ridgeia* has such a remarkable variety of tube forms that this trait contributed to the initial identification of multiple species (Southward et al. 1995). Tubes may resemble soft, smaller versions of *Riftia* or hard, flanged elongated tubes, or small tubes with extensive "roots" tangling within a bush. Such growth plasticity reflects the ability of this species to exploit a broad range of habitats from high to low sulphide flux (Urcuyo et al. 2007; Tunnicliffe et al. 2014).

Very high growth rates of vent tubeworms are estimated from sequential imagery and sampling: 85 cm year^{-1} and 160 cm year^{-1} *Riftia* (Lutz et al. 1994; Thiébaut et al. 2002) and 95 cm year^{-1} for *Ridgeia* where flux rates of sulphide were high (Tunnicliffe et al. 1997). However, the latter species may also grow very slowly in low fluid flows (0.3 cm year^{-1} from dye-stained tubes) yielding age estimates at 70 years (Urcuyo et al. 2007). Such older worms are often encrusted with mineral deposits, especially in fluids where excess metal ions accumulate (usually when free sulphide is reduced). Iron precipitation as oxides is mediated by microbial activity (Tunnicliffe and Fontaine 1987; Peng et al. 2009), resulting in masses of rusty-looking tubes; zinc and manganese accumulations are manifested as black tubes often in waning flows. These and other mineral coatings can slow the degradation process after the worm's death leaving a functional surface for other animals to inhabit. *Riftia* tubes with no mineral coating are degraded by microbial chitin lysis over the course of 2.5 years, while *Escarpia* and *Lamellibrachia* appear more resistant (Ravaux et al. 2003).

3.2 Extreme Age in Seep Tubeworms

In the species of seep tubeworms for which data exist, growth is slow, and longevity is very high. Growth data have been obtained primarily by staining the worms with a chitin stain and returning later (usually >1 year) to collect and measure the tubes (Bergquist et al. 2000). Growth is fastest in newly recruited worms (Fig. 3a), with the highest growth rate of approximately 10 cm per year measured in *L. luymesi* (Cordes et al. 2003). After this early phase, growth slows exponentially, with many larger worms exhibiting no growth between successive years of measurement (Bergquist et al. 2000; Cordes et al. 2007). In one study of *Escarpia laminata* over many years, a group tubeworms marked in 1992 was recovered in 2007; growth rates varied between 0.67 and 2.67 mm year^{-1} at the anterior ends of the tubes (Fig. 3c, d). Rates of growth at the posterior are unknown, although *L. luymesi* can lengthen posteriorly in the laboratory (EEC pers. obs.). Growth does not vary predictably within an aggregation, and worms whose anterior ends are next to each other do not necessarily possess similar growth rates (Cordes et al. 2007). However, growth does vary among nearby sites, suggesting that the primary determinant of growth is sulphide availability and acquisition of other resources (Cordes et al. 2007).

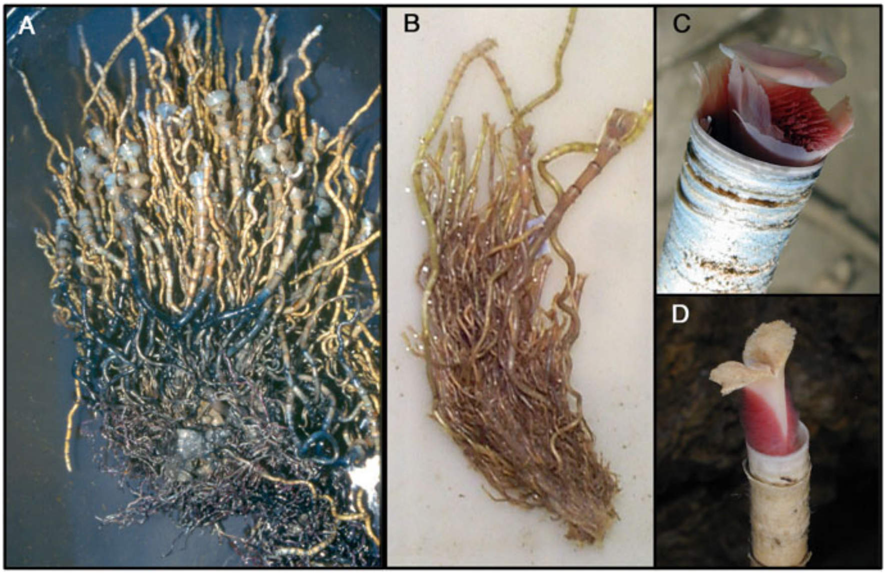

Fig. 3 Seep tubeworms. (**a**) Juvenile *Lamellibrachia luymesi*. (**b**) A mixture of *Lamellibrachia luymesi* (thin tubes) and *Seepiophila jonesi* (flared tubes) in a small aggregation, with the posterior extensions of the tubes and bodies (the root) visible at the bottom of the photograph. (**c**) The anterior end of a species of *Lamellibrachia* from the Gulf of Mexico showing the sheath lamellae that give this genus its name. Image credit: AquaPix, Ian MacDonald, Expedition to the Deep Slope. (**d**) The anterior end of *Escarpia laminata* from the Gulf of Mexico. Image credit AquaPix, Ian MacDonald, Expedition to the Deep Slope

Eventually, the worms reach an asymptotic size; growth is rarely observed and likely only occurs under ideal conditions. Thus, it is difficult to reach any definitive conclusions about their ultimate longevity, but modelled growth rates can provide some insight. Based on individual-based models, the maximum age of seep tubeworms varies between 200 and 800 years: *L. luymesi*, 200–250 years (Bergquist et al. 2000; Cordes et al. 2003); *Seepiophila jonesi*, 250–300 years (Cordes et al. 2007); and *Escarpia laminata*, 300–800 years (Durkin et al. 2017). Such extreme ages make these worms among the most long-lived non-colonial animals known. The contrasting life history strategies of seep and vent tubeworms is an interesting case of an extremely plastic condition of a highly selected trait within this single family of polychaetes.

4 The Tubeworm Forest Habitat

The forest analogy is appropriate in many ways to the habitat created by vestimentiferan tubeworms. Generally, the extent, vertical structure, density, and complexity are a function of the species that forms the forest and of the nature of the fluid supplying both the tubeworms and autotrophs associated with them. Nearly all three-dimensionality at hydrothermal vents is created from a hard substratum base (basalt, sulphide deposit, or altered rock), whereas the tubeworms at cold seeps also grow down into the sediments. Other key differences between the ecosystems, such as rate and nature of venting/seeping fluid, lead us to address these habitats separately in this section. We discuss the vent setting first as there is more work available over a longer time.

4.1 Formation of the Vent Tubeworm Habitat

The growth trajectory of a tubeworm is dictated by its access to the optimal interface between reduced sulphide in vent water and oxygen in deep-sea water. For most species, positioning the tube top—thus the branchiae—is a lifetime of adjustment that will affect the shape of the individual worm tube and of the local aggregation. Key factors that alter through time include the worm size, flow rate, or “quality” of the fluid due to subsurface changes and access to fluid due to bush formation and competition with neighbours. Physiological adjustments to dynamic chemical conditions include alteration in expression of the haemoglobin gene (Carney et al. 2007) and levels of carbonic anhydrase activity (Scott et al. 2012). However, modification of the growth form is another approach. *Riftia* will grow prone to maintain its branchiae close to fluid egress in meagre flows (Fig. 4a) but also in tall vertical stands in robust flows and even draped “head down” on chimneys.

Ridgeia, however, adopts another approach using a highly plastic morphology that results in a wide array of forms (Fig. 4e, f) occupying different venting

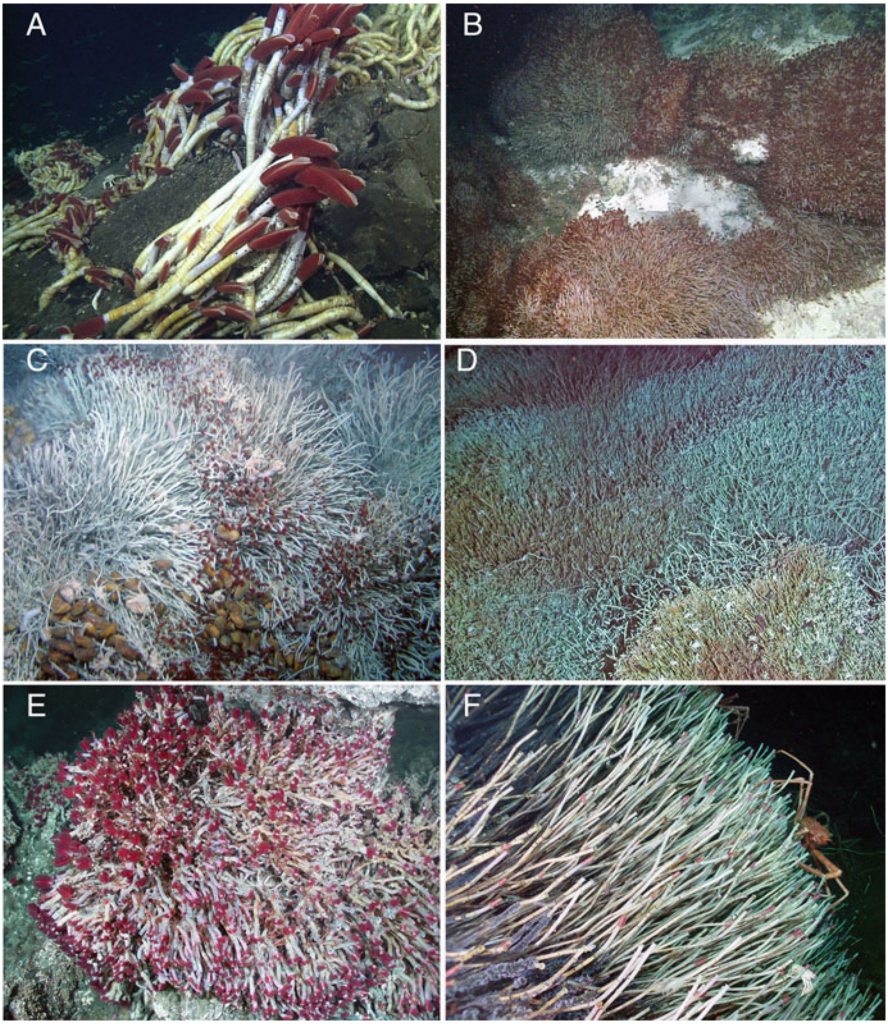

Fig. 4 Hydrothermal vent vestimentiferans in the Pacific Ocean. (**a**) *Riftia pachyptila*, Alarcon Rise, Gulf of California, in prone and recumbent positions. Image credit: MBARI. (**b**) *Oasisia* cf. *alvinae*, Pescadero Basin, Gulf of California, on carbonate chimney. Image credit: MBARI. (**c**) *Lamellibrachia juni*, Futuna Ridge, Vanuatu, with mussels and crabs. Image credit GEOMAR. (**d**) *Lamellibrachia satsuma*, Nikko Seamount, Mariana Arc. Image credit: NOAA. (**e**) *Ridgeia piscesae*, Endeavour Segment, Juan de Fuca Ridge, in short form on chimney. Image credit: CSSF/UVic. (**f**) *Ridgeia piscesae*, also Endeavour site, in long thin form with blue folliculinid mat and large spider crab. Image credit: CSSF/UVic

conditions (Govenar 2010; Tunnicliffe et al. 2014). Where many tubeworms have relative simple tubes, *Ridgeia* can intergrow, both forward and backward, to the extent that it is impossible to untangle the mass without breaking most tubes. In a tall, slender morph, this species grows vertically as “sticks” apparently accessing sulphide that is wafting laterally in bottom currents (Urcuyo et al. 2007). Little information is available on the growth conditions of *Oasisia alvinae* that mostly manifests as a small, sparse animal on East Pacific Rise (EPR) vents likely excluded by *Riftia* (Hunt et al. 2004). However, the discovery of the Pescadero ventfield in Gulf of California revealed large expanses of this (or a closely related) species on carbonate chimneys (Fig. 4b) where *Riftia* was nearly absent (Goffredi et al. 2017); it displayed a growth form and size similar to *Ridgeia*. *Lamellibrachia juni* at western Pacific vents has a similar aspect (Fig. 4c) and, in Nikko Seamount caldera, Mariana Volcanic Arc, *L. satsuma* forms dense fields where sulphide supply is pervasive (Embley et al. 2007) (Fig. 4d). At the other extreme, the small stringy siboglinid *Sclerolinum contortum* forms "grassy" turfs under about 20 cm high with up to 800 individuals m^{-2} (Sahling et al. 2005). It also has a highly variable tube that reflects the extensive range of habitats it occupies throughout its habitat (Georgieva et al. 2015).

4.2 "Forest" Architecture

The habitat created by tubeworms at hydrothermal vents can vary in form from tangled mats to sparse upright sticks to contorted bushes to dense towers reaching 3 m in height. As the tube never bifurcates, each one is a simple cylinder. However, settlement of juveniles can create "branches" and, thus, complexity. Recognizing that the internal architecture can affect the associated community, Tsurumi and Tunnicliffe (2003) proposed an index of complexity from one to five that reflects the many growth forms of *Ridgeia* on Juan de Fuca Ridge. In assessing the smallest of these bush forms (under 20 cm height), Lelièvre et al. (2018) estimate that 0.1 m^2 of bottom substratum can support over 4 m^2 of tubeworm surface area—a multiplying factor of 40. Urcuyo et al. (2003) describe one large "aggregation" of *Ridgeia* with maximum tube lengths of 55 cm and a top area of 1.1 m^2. At the bottom, however, was a "root-ball" of intergrown bases occupying a basalt depression 21 cm in diameter. These authors demonstrate that the thin walls of the basal mass are permeable to sulphide, thereby augmenting access to this compound in weak vent flow conditions. The entire bush comprised 4300 individuals and included several smaller clumps of recent recruits. In this case, a basal area under 0.04 m^2 supported an upper tube surface area of 6 m^2—a multiplying factor of 400. Given the variable growth rate measured within this aggregation, it is unlikely that tube size is a strong measure of recruitment timing, but conditions that support settlement of more tubeworms will create a more complex architecture.

Riftia forms an important habitat for vent animals that colonize its tubes on the East Pacific Rise (Fig. 5a). Tubeworm aggregations around fluid outlets in the basalt were estimated at over 2000 individuals from imagery (Shank et al. 1998). The

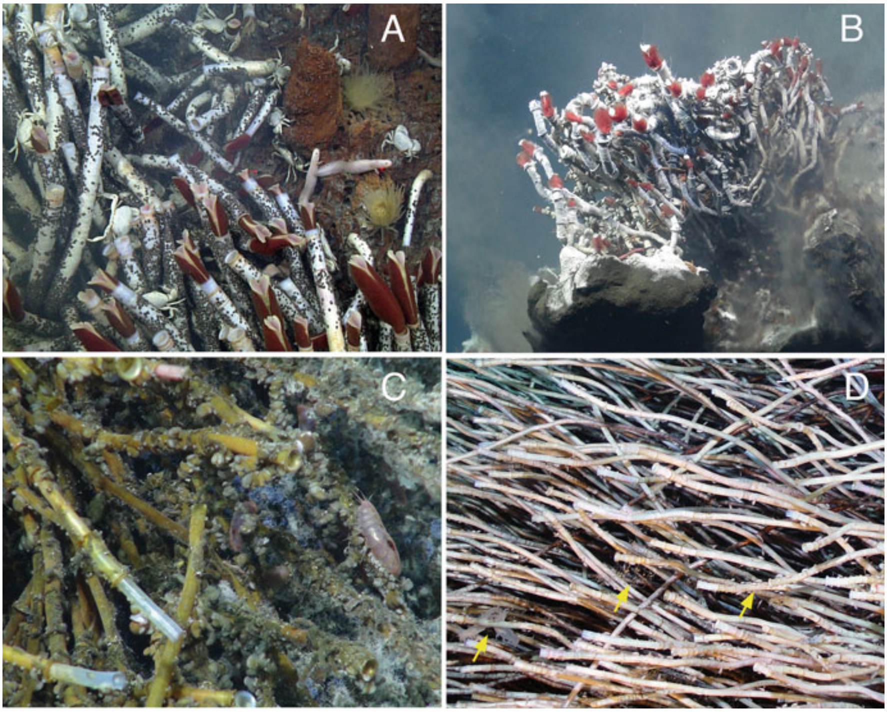

Fig. 5 Inhabitants of hydrothermal vent forests. (**a**) *Riftia* clump with black limpets, vent crabs, and zoarcid fish. Image about 70 cm across. Credit: MBARI. (**b**) *Ridgeia piscesae* in very warm, flowing fluid with white limpets and alvinellid polychaetes; white bacterial mat coats the surfaces. Image about 60 cm across. Image credit: ONC/CSSF. (**c**) Detail inside a *Ridgeia* bush with cooler flows: white bacterial filaments and blue protists; three species of gastropods, a tubicolous ampharetid polychaete, and predatory polynoid polychaete are visible. CSSF/UVictoria. (**d**) Senescent bush of *Ridgeia* with mostly empty tubes; arrows point to holothurian, hydroids, and amphipods on the tubes. Dark colouration on the tubes is likely a manganese coating. CSSF/UVictoria

"packing" of these worms can be much tighter than *Ridgeia* or *Oasisia* in good flow conditions. As juveniles recruit to the tubes, the surface area increases; Thiébaut et al. (2002) determine that 40–55% of the tubes sampled at one site were attached to others although many were small, recent recruits. Overall, this species forms masses that are less "bushes" than they are sprawling mounds or tight stands. In a study of eight collections at two ventfields, the ratio of tubeworm surface area to substratum area was highly variable; the mean value was around 70 to 1 (Govenar et al. 2005). All these estimates emphasize the importance of the tubeworms to create extensive surfaces for other animals that give greater access to food and space in the restricted volume of relatively undiluted vent fluid.

4.3 Features of the Vent Tubeworm Canopy Habitat

Unlike other marine forests in which lateral currents are modified by the dense stands (Guizien and Ghisalberti 2017), the most relevant flow at vents is from base to top as emerging fluids transport reduced compounds that fuel the tubeworm symbionts and other autotrophs. These fluids also bring suspended microbes that have grown in subsurface conduits where reduced compounds (such as H_2) support autotrophs, particularly thermophilic Archaea. Primary producers can form visible microbial mats on the tubes (Fig. 5b). López-García et al. (2002) speculate that chemoautotrophs in tube biofilms may belong to the ε-proteobacteria, a group with diverse members that can use the substrates in vent fluids for primary production. When examining the detritus within *Ridgeia* tubeworm bushes, Forget and Juniper (2013) find several candidate microbial groups that contribute to carbon fixation, including the facultative anaerobic mesophilic sulphur-oxidizing bacterium *Sulfurovum* and several ε-proteobacteria that are chemolithoautotrophs using hydrogen as the electron donor. Thus, the understory is also contributing to carbon production with the energy source delivered through the basal rock. However, one cannot assume that all such bacteria are metazoan food sources; it is not uncommon to see expanses of microbial mats with no associated macrofauna.

Habitat provision is a major community function of vent tubeworms in this ecosystem. Through an interesting experiment, Govenar and Fisher (2007) discovered that artificial tubes attracted nearly as many resident species, albeit in lower densities, as did *Riftia* tubes when placed in good to moderate fluid supply; thus, they conclude, the key features provided by this foundation species are substratum and shelter. While this outcome is likely applicable across most tubeworm species, a live tubeworm forest provides other services to create a favourable habitat. The worm itself is a food source, as discussed in the next section. In addition, the living "foundation" modifies the chemical habitat. Within a *Riftia* clump, sulphide is removed at a rate over four orders of magnitude greater than through passive oxidation by seawater (Johnson et al. 1988b). As sulphide is a metabolic poison for most metazoans, the worm provides a detoxifying function to its inhabitants.

The density of tubeworm growth will define the interaction with emergent fluid flow paths and with the ambient near-bottom currents. In general, the latter currents are not high, with ranges up to 10 cm s^{-1} and fluctuations with tidal signatures (Hautala et al. 2012), although such currents are highly setting dependent. These background flows import oxygen into the ventfield and export hydrothermal production and larvae. Thus, loose stands of vestimentiferans will experience a greater "internal renewal" compared to dense growths in which emerging reduced fluids dominate. Juvenile worms augment the density as they recruit to adult tubes (Fig. 6a). One may expect denizens to differ in this context, but the physicochemical environment within tubeworm bushes is not well characterized for most species. However, it is very likely that basal fluid delivery will result in vertical gradients. For example, temperature in *Ridgeia* masses can range from >40 °C at the base to 5 °C at the branchiae (VT pers. obs).

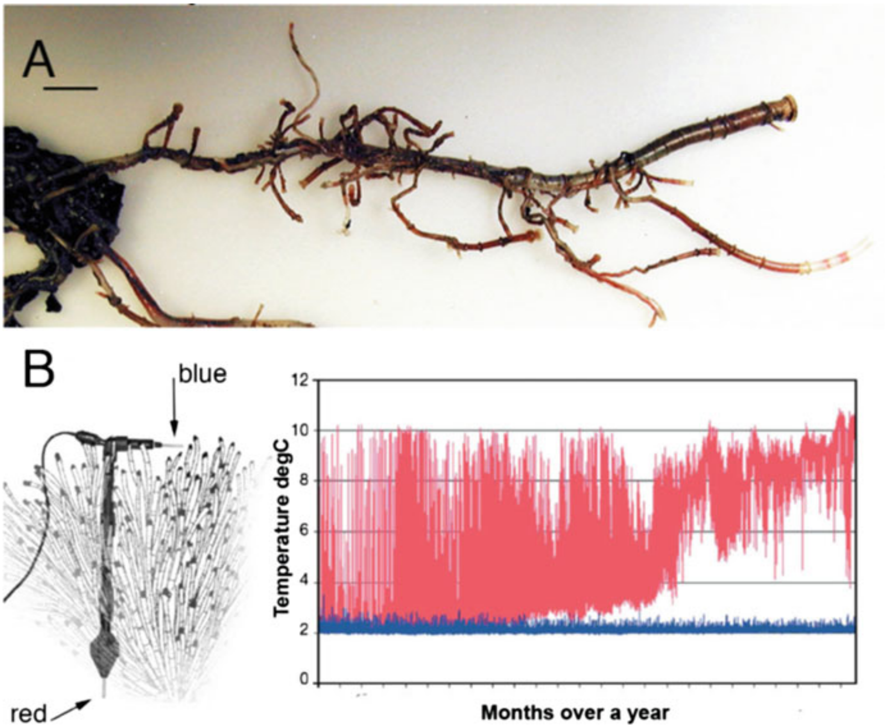

Fig. 6 *Ridgeia piscesae*, Juan de Fuca Ridge. (**a**) Tube with recent recruits showing flanges of interrupted growth; scale 2 cm. (**b**) Temperature record from base and top of a bush to illustrate short- and long-term temperature fluctuations (adapted from Urcuyo et al. 2007)

Short-term variability in temperature within bushes reflects the irregularity of fluid delivery and the turbulent mixing with cold seawater. Within one *Riftia* stand, measurements ranged from 2 to 15 °C over 3 days (Johnson et al. 1988a). Le Bris et al. (2006) report even greater variability from 10 to 50 °C at the base of a *Riftia* clump over the course of 5 min while pH ranged down to 4.4, and sulphide was also variable. Temperature measurements at base and branchiae of *Ridgeia* show similar variability sustained over many months (Fig. 6b) (Urcuyo et al. 2007). Temperature fluctuation represents changes in vent output and seawater mixing creating a highly variable setting for inhabitants. As tides change surface pressure, it is possible to detect both several components of the tide and surface storms at depth, in the temperature signals and animal behaviour (Tunnicliffe et al. 1990; Lelièvre et al. 2017). As also illustrated in Fig. 6b, longer-term variations in vent flows are manifested as small shifts in fluid supply occur subsurface. More marked changes result from magmatic and tectonic events that shut down or expand the conduits. For example, subsurface diking events can open new hydrothermal sites (Embley et al. 2000), and Johnson et al. (2000) record systemic fluid flow responses to an earthquake.

4.4 The Seep Tubeworm Forest

Seep tubeworms also seek a balance between sulphide and oxygen availability in their environment, but achieve it in ways that differ from most vent vestimentiferans. Rather than acquiring sulphide and oxygen at different times across the same surface (the plume), they spatially separate the acquisition of oxygen and sulphide (Fig. 7a). The anterior end of the worm remains in well-oxygenated seawater, while the posterior end of the worm, the root, extends into the anoxic layers of the sediment to acquire sulphide (Julian et al. 1999; Freytag et al. 2001).

Tubeworm larvae settle on hard substrata, typically authigenic carbonates at seep sites (Bergquist et al. 2002). Initially, they may acquire both sulphide and oxygen across the plume surface, as both are available in the boundary layer near the surface of the carbonate (Freytag et al. 2001; Cordes et al. 2005b). As the worm extends anteriorly, the plume would leave this favourable position, and the metabolism of the intact worm/bacterial symbiosis may become limited by sulphide access (Freytag et al. 2001). The anterior tube extension creates habitable space for colonization by associated fauna. Initially, this space is within the boundary layer that is relatively high in sulphide concentration, but as the distance from the sediment surface increases, the proportion of available space in ambient seawater increases (Cordes et al. 2005b).

Next, the posterior portion of the body and tube (Fig. 3b) would begin to grow into the sediment. The opisthosome would extend into deeper layers where sulphide is readily available, particularly at a nascent seep site. The rapid release of hydrogen ions, one of the major end products of sulphide oxidation, through the root also prevents authigenic carbonate precipitation on the root surface (Cordes et al. 2005b; Dattagupta et al. 2006). In some cases, it may even allow the root to dissolve and penetrate through carbonates (Cordes et al. 2005b). Sulphate, the other major metabolic product of sulphide oxidation, can also be released through the root (Julian et al. 1999; Cordes et al. 2003; Dattagupta et al. 2006). An exchange for bicarbonate ions may occur, thereby helping to supply an additional substrate for carbon fixation (Dattagupta et al. 2006). As the root continues to grow, the anterior end can increase in size and distance from the sediment surface without being limited by the distribution of sulphide. This spatial separation of the acquisition of sulphide and oxygen allows for continued growth at both ends of the worm while ensuring the availability of their metabolic requirements. There is relatively low habitat complexity in the tubeworm tubes, especially compared to the deep-sea coral habitats that often lie at the outer edges of the seeps (Cordes et al. 2008). Gregarious settlement of juveniles on adult tubes is rarely observed and is largely confined to the interior space of empty tubes that remain after the worms have died (Bergquist et al. 2002).

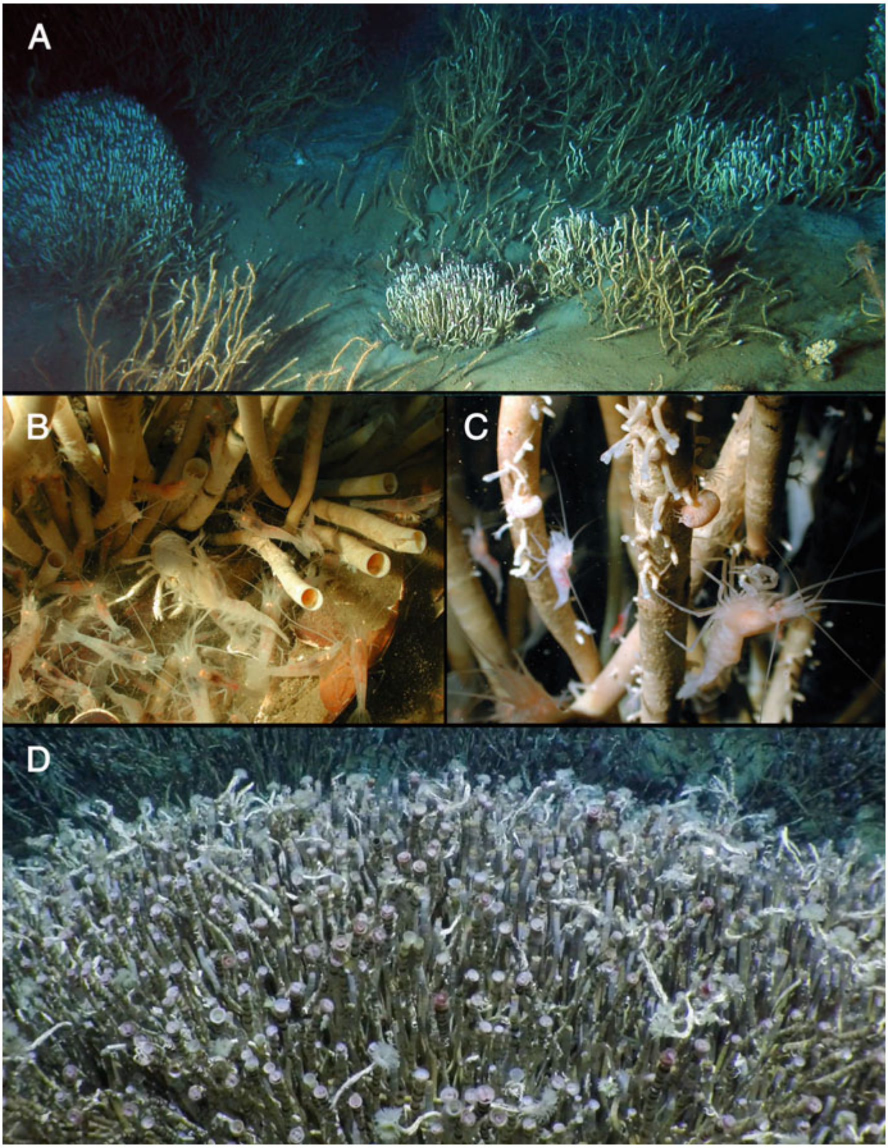

Fig. 7 Tubeworm forests at cold seeps. (**a**) Tubeworm aggregations from the upper slope of the Gulf of Mexico. White tubes in the foreground represent young aggregations, the larger group on the left of the image represent mid-succession stages, and the longer, darker tubes in the background represent later stages of succession. Mostly *Lamellibrachia luymesi* with some *Seepiophilia jonesi*. (**b**) *Escarpia laminata* from the Gulf of Mexico with *Alvinocaris stactophila* shrimp and *Munidopsis* sp. Image credit: AquaPix, Ian MacDonald, Expedition to the Deep Slope. (**c**) *Escarpia laminata* from the Gulf of Mexico with *Alvinocaris stactophila* shrimp, a small amphipod, and zoanthid anemones colonizing the tubes of later-stage aggregations. Image credit: AquaPix, Ian MacDonald, Expedition to the Deep Slope. (**d**) Dense tubeworm aggregation from the Pacific margin of Costa Rica made up of *Lamellibrachia barhami*, *Escarpia spicata*, and other undescribed species of vestimentiferans. Image credit: E. Cordes, with MISO GoPro courtesy of D. Fornari, WHOI

5 The Forest Denizens

Vent and seep tubeworms play a very important role in fostering the biomass and diversity of the communities in these chemosynthetic environments. These foundation species create complex physical habitat and modify adverse physico-chemical conditions to favour a multitude of colonists (Govenar 2010).

5.1 A Specialized Fauna

The animals that can tolerate the physiological stressors of the hydrothermal vent habitat are relatively few. From the first discoveries in the late 1970s, nearly all species collected close to venting fluids have been new to science. While many taxa remain undescribed, there are 675 named species (Chapman et al. 2019) of which 80% are currently not known elsewhere and another ~8% that are known only from vents and cold seeps. Novelty is also high at genus and family levels where many more taxa are shared with cold seeps. Animals such as the siboglinids illustrate the extent to which physiological, morphological, and genomic modifications have supported the penetration of these habitats. Other species, particularly in more marginal areas, show close affiliations with non-vent/seep species.

5.2 Character of the Inhabitants

In addition to the siboglinid tubeworms, a few other organisms may occur that also host symbionts. The protozoa are poorly known at vents, but the colonial ciliate *Folliculinipsis* hosts bacteria (Kouris et al. 2007); on Juan de Fuca Ridge, it can form extensive mats among *Ridgeia* tubes (Figs. 4f and 5c). This group also inhabits tubeworm tubes and other substrata at seeps of the Gulf of Mexico and along the eastern Pacific margin, where they contribute to overall methane oxidation rates (Pasulka et al. 2017). In addition, mussels of the subfamily Benthomodiolinae, all of which have large gills with intracellular symbionts, can be abundant among East Pacific Rise/Galapagos *Riftia* and within *Lamellibrachia* stands of western Pacific vents (Fig. 4c). These mussels are also foundation species at hydrothermal vents, but tend to occupy less vigorous hydrothermal flux on the EPR where a rich fauna nestles among the shells (Van Dover 2002). At cold seeps, mussels tend to occupy the most vigorous flow, including sites where bubble streams are visible and methane and sulphide concentrations are high (Olu et al. 1996; Bergquist et al. 2005).

In Juan de Fuca Ridge (JdF) tubeworm forests, a similar mussel is very rare, but, instead, the small limpet *Lepetodrilus fucensis* displays a unique relationship with bacteria that manifest as episymbionts attached to the gill surface. This animal exposes the bacteria to sulphide-rich water that fosters their growth, and then the bacterial filaments are pulled into a mucous strand that is ingested through the mouth (Bates 2007a). Where fluid flow is intense, the limpet forms large stacks, often smothering the tubeworms in numbers up to 100,000 s m^{-2}. However, the limpet is also capable of changing the gill morphology to a form that does not host symbionts when it adopts a grazing habit in peripheral areas of the vent (Bates 2007b).

Large animals are not common among tubeworms at vents with the exception of the zoarcid eelpout fish, *Thermarces cerberus*, that can reach 40 cm long. The majority of species are in the "macrofaunal" size range from 0.1 to 5 cm. Meiofauna, although abundant, are limited in diversity (Gollner et al. 2015); however, an important component of this size fraction is the multitude of juvenile animals that can inhabit the colony. Completely sessile epifauna on the tubes are rare, and they tend to occur in peripheral and senescent stands of tubes where an overlap with deep-sea species such as hydroids occurs (Fig. 5d). The tubes of polychaetes (which can vacate and rebuild) create additional structure: tubicolous alvinellid and maldanid species are often very abundant. Most species are sedentary, especially the grazers such as limpets and pycnogonids and deposit feeders such as many polychaetes. Highly mobile animals include large predatory polychaetes and decapods (crabs, shrimp, and amphipods), as well as zoarcid fish (Fig. 5a). While we can measure spatial gradients in heat, pH, oxygen, and dissolved compounds, there are no quantified data on distribution of animals within the tubeworm canopy that can be very difficult to penetrate with cameras. It is highly likely that "tiering" relates largely to the tolerance of each species to temperature and chemical stressors, the magnitude of which would differ in each aggregation. For example, gastropod species that occur on tubeworms show preferences for different thermal regimes (Bates et al. 2005; Mills et al. 2007).

At cold seeps, the tubeworm forest is typified by alvinocarid shrimp, provannid gastropods, limpets, and a wide variety of polychaetes (Fig. 7b, c). These species dominate the low-diversity, but high-biomass, communities when the tubeworms are relatively young and the tubes are nearly white (Bergquist et al. 2003; Cordes et al. 2005b). These lower trophic groups graze the free-living microbes on tubeworm tubes and surrounding hard substrata in a relatively simple food web consisting of weak trophic links, similar to vents (Cordes et al. 2010a; Portail et al. 2016). In contrast to vent communities, seep tubeworm aggregations are often colonized by background species as they age. The longevity of the seep tubeworms and their reliance on sulphide from the sediments results in a large, complex habitat in the deep benthos that can serve as shelter and host an abundance of prey for mobile predators (Carney 1994). At the Costa Rica cold seeps, large lithodid crabs will come into the seep habitat to feed on free-living bacteria (Niemann et al. 2013). At the Gulf of Mexico seeps, "vagrant" species that exhibit lighter carbon isotopic signatures include hagfish, spider crabs, and the giant isopod (MacAvoy et al. 2003).

5.3 Assemblage Structure

Several studies have examined the composition of the assemblages within the habitat formed by *Ridgeia piscesae* on Juan de Fuca Ridge (Table 1). Overall, comparison highlights two key features: (1) the adaptable nature of the tubeworm that allows it to occupy nearly all habitable settings of hydrothermalism means there is a wide range of associates depending on which habitat is sampled; and (2) the plastic morphology generates several degrees of "forest complexity" that are reflected in the composition and abundance of inhabitants. In a baseline study of a single 9-m-high edifice in the Endeavour Main Field, Sarrazin et al. (1997) use imagery to document six animal assemblages, of which four include the tubeworm; they note that venting vigour (including temperature and dissolved sulphide concentration) is correlated with the assemblage type. In subsequent work on the same structure, Sarrazin and Juniper (1999) report the biomass of the associated animals can nearly equal that of the tubeworms. Overall, biomass rivals other marine ecosystems and, compared to substratum area, numbers are often in the 100,000 s/m^2 (Table 1).

Along 140 km of ridgecrest on the southern Juan de Fuca Ridge, composition of the fauna within *Ridgeia* bushes does not reflect the location (Tsurumi and Tunnicliffe 2003). Instead, it is the number of species that a bush can house that drives similarities: thus, complexity of the branching and suitability of the habitat are important. Where the tubeworms are knotted with many secondary recruits, species numbers are much higher. This study finds a total of 50 species with four species that occur in 36 of the 51 samples: the gastropods *Lepetodrilus fucensis* and *Depressigyra globulus* and the polychaetes *Amphisamytha carldarei* and *Paralvinella pandorae*. Nearly all the studies listed in Table 1 at Endeavour site also record the first three species as the most abundant; an interesting difference is the fourth species, an alvinellid polychaete that appears more common in samples from early stages of vents developing after eruption disturbance. Another feature is that many assemblages from chimney structures group together and are significantly lower density. Overall, density averages greater than one animal per cm^2 of tube surface. Such crowding is possible because the limpets stack and the two tubicolous polychaetes named above will overgrow conspecifics. Compared to the more northerly Endeavour Segment, these southern JdF sites have few and small chimneys. However, even on Endeavour, it is the tubeworms living on basalt that also have higher species numbers. In a single sample of 4300 tubeworms (see description of Urcuyo's study in Sect. 4), Bergquist et al. (2007) recover more species than do 12 samples from nearby chimneys (Lelièvre et al. 2017; VT unpubl data). The growth complexity appears greater on basalt, but the metal-rich fluids (e.g. iron and manganese) venting through chimneys may also deter some species as suggested by Sarrazin et al. (1997).

The last study in Table 1 is on the East Pacific Rise (EPR) off Mexico where *Riftia* is the foundation species. There are many parallels with the outcomes from JdF. First, there was high similarity among assemblages within and among sites where samples were from diffuse flows through basalt (Govenar et al. 2005).

Table 1 Summary of studies that examine diversity within tubeworm bushes in the northeast Pacific where JdF = Juan de Fuca Ridge and EPR = East Pacific Rise

Site	# Vents	Substratum	# samples	# taxa[a]	# specimens	Density/m^2 substratum[b]	Outcome	Authors
Endeavour JdF	1	Chimney	6 small	na	na	250,000	Biomass compares to other rich systems	Sarrazin and Juniper (1999)
Endeavour JdF	1	Chimney	3 large to medium	10	69,450	164,000	Agree with above; diversity very low	Govenar et al. (2002)
Cleft, Axial, CoAxial JdF	41	Basalt and chimney	51 small to medium	36 macro, 14 meio	321,134 28,052	na	Density rivals other ecosystems; site and substratum variability; bush complexity effects	Tsurumi and Tunnicliffe (2003)
Endeavour JdF	1	Basalt	1 large	35 macro 10 meio	150,673 4130	4,423,000	Biomass and abundance mostly in a few species; diversity moderate	Bergquist et al. (2007)
Endeavour JdF	1	Chimney	6 medium	34 species	148,005	21,880	Gradients in bush allows partitioning of resources	Lelièvre et al. (2018)
Endeavour JdF	5	Basalt and chimney	7 medium	30 macro 13 meio	164,061 140,278	na	Higher diversity in moderate stress; meiofauna low diversity	Murdock et al. (in prep)
9° North EPR	2	Basalt	8 small to medium	46 macro; 33 meio	119,000 38,046	~716,000	High similarity due to common species; meiofauna with low similarity	Govenar and Fisher (2005, 2007)

All, but the EPR study, focus on the foundation species *Ridgeia piscesae*. A “chimney” is formed of polymetallic sulphides deposited by superheated water, and many still lack smokers near the top. “macro” means fauna >1 mm; “meio” is 0.06–1 mm

[a] Total macrofaunal species for the study; Branchinotogluminae reduced to one species in Juan de Fuca as now accepted; for JdF, meiofauna have not separated harpacticoid copepod or nematode species

[b] Highest density sample shown

Second, despite a near complete difference in the regional species pool, the same vent-endemic genera or families dominate the inhabitants of *Riftia* clumps, including species of *Lepetodrilus*, *Paralvinella*, and *Amphisamytha* as noted above. Important differences are that the overall diversity is higher (as it is for the entire EPR compared to JdF) and that biomass is higher in groups such as predatory crabs, grazing shrimp, and mussels. However, because *Riftia* is a relatively massive worm, the entire epifaunal assemblage represents a maximum of only about 2% of the biomass. Govenar et al. (2005) find that the numbers of species have a positive correlation with tube surface area. The numbers of meiofauna in these same samples were about one-third of the macrofauna and were represented mostly by nematodes and copepods (Gollner et al. 2007). The macrofauna-to-meiofauna ratio in the two JdF studies that looked at *Ridgeia* assemblages also hosted in basalt (Table 1) is even lower. However, one study (Murdock et al. in prep) examines bushes where meiofaunal abundances approach those of macrofauna. Here, a few species of copepods dominate the numbers. These copepods are in a family that has diversified extensively and nearly exclusively at hydrothermal vents: there are currently over 50 species described (Gollner et al. 2010). Three species on JdF are abundant in tubeworm bushes, especially on chimneys (Tsurumi et al. 2003) where densities can reach over five individuals cm^{-1}.

These studies within the vestimentiferan “canopy” discuss factors that affect the magnitude of diversity and abundance: bush architecture, physico-chemical factors, biological interactions, and succession stage. Available space to access microbial productivity from a restricted outlet is at a premium. Thus, surfaces that provide vertical structure over the vent—even artificial ones—are colonized (Govenar and Fisher 2007). As greater complexity develops with new recruits and interwoven tubes, more species accumulate. Within bushes on basalt, higher temperatures and greater productivity occur near the base, but more reduced compounds that induce metabolic stress are also located here. Temporal and spatial variability mean that animals must tolerate steep gradients. Vent animals move to preferred conditions that leave a buffer zone with the temperatures that will kill; in fact, vent animals are much more risk averse than similar species in other marine environments (Bates et al. 2010). However, in the general mid-range of conditions, temperature (and other chemical conditions) appears not to affect community structure (Tsurumi and Tunnicliffe 2003; Govenar et al. 2005). There are, however, limit effects in which macrofauna diversity is lower at both high and low temperatures, while meiofauna show a notable decline as temperature increases (Fig. 8). Size may constrain the adaptations in many groups of meiofauna that have less flexibility in mobility and physiology to deal with the variable, upper extremes of vent fluids (Gollner et al. 2015).

This pattern of high productivity, but high stress, is also present at seep tubeworm communities. While, typically, temperature remains ambient and sulphide concentrations are lower than vents, high methane concentrations are present. However, an interesting exception exists at the “hydrothermal seeps” of the Costa Rica margin (Fig. 7d) (Levin et al. 2012). Here, there are temperature anomalies reaching a few degrees C at point sources of rapidly seeping fluids. The community is dominated by grazing species, some of which also occur at the nearby Galapagos and East Pacific Rise vents (Levin et al. 2012). This discovery, along with the findings of similar community structure at seeps and vents, leads to the developing perception of these chemosynthetic systems as occupying a continuum of fluid flow types, rather than being completely distinct systems (Levin et al. 2012, 2016; Portail et al. 2016).

5.4 Species Interactions

Functional relationships of species within the vestimentiferan communities include space competition and trophic interactions. While imagery and counts indicate that tube surfaces can approach or exceed 100% cover, studies have not addressed space competition explicitly. The marked decrease in body size of an alvinellid polychaete in the second year a vent was sampled on Juan de Fuca Ridge coincided with the appearance of another species of the same genus (*Paralvinella*); competition with the second species or even overcrowding by conspecifics was likely (Tunnicliffe et al. 1997). Levesque et al. (2003) confirm this observation at another site and, adding a third alvinellid polychaete, demonstrate resource partitioning in terms of food resources among these species. Detritus within the bush supports microbes that contribute to the diet of bacterivores where fluid flux is high (Limén et al. 2007), but the particulate organic matter itself forms an increasingly important part of the diet of the inhabitants along habitat gradients of lower venting influence (Levesque et al. 2006). Interpretations of food web structure are based on stable isotope studies and mixing models of the amounts and signatures of source carbon that can be difficult to assess.

Three studies of *Ridgeia* community trophic relations (Levesque et al. 2006; Bergquist et al. 2007; Lelièvre et al. 2018) combine to portray the following general picture. Three sources of primary producers are distinguished: symbiotic bacteria within invertebrate hosts, the autotrophic bacteria free-living within the bush, and subsurface microbes (archaea and bacteria) suspended in rising fluids. The depleted carbon isotopic signature of the alvinellid worm *Paralvinella palmiformis* suggests a food source that relates mostly to the microbes suspended in the emergent fluid; this species is a modified suspension feeder that streams its buccal tentacles in high flows. For the most part, however, the food web is based in bacterivores feeding within the detritus and grazing on tubes. Curiously, three species of sea spiders in the genus *Sericosura* have adapted to feeding on bacterial filaments, whereas their non-vent relatives specialize on cnidarians (Brescia and Tunnicliffe 1998). The detritivores are prey to a variety of predators from larger zoarcid fish and whelks down to small polychaetes. The role of parasitism is poorly known at vents, but infection rates by protozoans and by parasitic copepods in limpets can be high and possibly play an important role in population control (Terlizzi et al. 2004; Tunnicliffe et al. 2008). A notable separate energy pathway centres around the highly abundant limpet *Lepetodrilus fucensis* that farms bacteria on its gills in high flow conditions. Overall, the high variability in isotopic values reflects small spatial gradient in productivity and food sources that vary in relation to the hydrothermal discharge.

An interesting trophic dynamic exists in hydrothermal systems on volcanoes at shallow depths where substantial sea surface production may enter the food web as illustrated in the Mariana Arc where photosynthetic carbon was present in hydrothermal invertebrates at 350 m depth (Stevens et al. 2015). On another seamount in the Arc (Nikko), extensive fields of *Lamellibrachia satsuma* dominate the caldera at 500 m. Yorisue et al. (2012) report a mix of primary carbon input on Nikko Seamount, including photosynthesis, especially in vent crustaceans and fish—all of which have a shallow larval stage feeding in the plankton.

The only predator that can extract an entire tubeworm is the spider crab (*Macroregonia macrochira*) that congregate on the periphery of vents (Fig. 4f), but rarely venture high onto chimney structures (Tunnicliffe and Jensen 1987). Otherwise, major damage is inflicted by two species of polynoid scaleworms (*Branchinotogluma tunnicliffeae* and *Lepidonotopodium piscesae*) as they attack the expanded tubeworm plume with jaws on a rapidly everted proboscis (Tunnicliffe et al. 1990). Among *Riftia* stands on the East Pacific Rise, most trophic interactions are based in anecdotal observations (Govenar 2012). Here, *Riftia* predators are few, but bythograeid crabs and zoarcids take their toll. The vestimentiferan tubes, however, can make up a major portion of the diet of some grazing limpets (Gaudron et al. 2015). At seeps, there is little evidence for direct grazing on tubeworms, although there is a small polychaete that inhabits the interior of the ends of the tubes of *Escarpia laminata* and appears to be a blood-sucking parasite (Becker et al. 2013).

6 Temporal Change in the Forest

The great range of adaptations in life cycles exhibited by vestimentiferans from vigorous vents through to slow seeps means that rates of colonization and subsequent stages of community development and change are also variable. There are few studies of complete cycles of these communities and then only in rapidly evolving vent communities. Here, we combine observations from various settings to sketch an overall concept of initiation, maturation, and extinction of tubeworm forests.

6.1 Recruitment of Vestimentiferans

Tubeworm larvae arrive as trochophores with a functional digestive system; before converting to a sessile stage, this stage must acquire the symbiont from the environment. Metamorphosis proceeds through the subsequent metatrochophore stage as the trophosome forms, and tube formation initiates as described by Bright and Lallier (2010). Larvae appear to need a solid surface for initial attachment, but the recruit may continue growth into sediments at seeps. Studies of *Riftia* arrival on deployed substrata describe high rates of settlement, possible facilitation among tubeworm species, and the role of predators in determining successful recruitment (Mullineaux et al. 1998; Micheli et al. 2002; Hunt et al. 2004). It is unclear whether *Riftia* recruitment is continuous as population size structure analyses have interpreted both discrete cohorts (Thiébaut et al. 2002) and constant settlement (Govenar et al. 2005). Gregarious settlement behaviour accounts for the dense packing of *Ridgeia* in aggregated locations (Urcuyo et al. 2003).

6.2 Arrival of the Denizens

We tend to observe only one end of the spectrum with most data accruing from "mature" tubeworm forests. Nonetheless, opportunities to observe community response to de novo creation of a new vent habitat arise after a magmatic eruption paves the seafloor and supplies a new heat source for venting. Formation of hydrothermal vent habitat occurs when magma injection and/or tectonic faulting creates new conduits for hot water to the seafloor. While most vent settings rarely experience "eruptions", some sites on fast-spreading ridges and on magmatic hotspots are very recent as lava rolls onto the seafloor, sometimes obliterating extant vent communities.

Three studies on Juan de Fuca Ridge on Axial Volcano and on East Pacific Rise near 9°N paint a similar overall picture (Tunnicliffe et al. 1997; Shank et al. 1998; Marcus et al. 2009): vigorous initial venting with high sulphide-to-heat ratios that diminish in subsequent years; tubeworm recruitment at many sites in the first year, with subsequent arrival by first colonizers such as alvinellid polychaetes and limpets; and arrival of other species in second and third "waves". In all cases, trajectories of succession were likely influenced by post-eruption changes in the fluid chemistry. On Axial Volcano, *Ridgeia piscesae* did not arrive at some new vents until the third year, and each vent on the new lava had a different specific trajectory in species accumulation (Marcus et al. 2009). While Metaxas (2004) records high numbers of larvae arriving at the seafloor adjacent to these new vents, successful recruitment for many of the species did not occur until after tubeworms were established. One species of alvinellid polychaete established on newly grown tubeworms with a second species arriving in later years. While species interactions, such as facilitation, competition, and predation, likely play roles in succession, two factors will have immediate consequences that may result in more stochastic patterns emerging: larval availability and habitat suitability.

After establishment of communities at a vent, the degree to which local patches change composition depends much upon the stability of the vent conduits and chemical composition of the fluids. For example, maps of the symbiont hosts inhabiting five chimney structures in the Lau back-arc basin revealed only small shifts in animal position over the course of a decade (Du Preez and Fisher 2018). In contrast, Sarrazin et al. (1997) record decimetre shifts in assemblages on a large chimney on Juan de Fuca Ridge over the course of 5 years as fluid flow rates and substratum character changed. They define several groupings of species associated with tubeworms that settle in preferred locations as venting rates change. Thus, the pattern is less "succession" than a shifting spatio-temporal mosaic. On shorter timescales, ocean tides influence the behaviour and movement patterns of animals in *Ridgeia* bushes; pressure changes affect volume flows out of a vent orifice, while lateral currents alter the flux of particulates and fluid access. Time-lapse imagery records the behaviour rhythms in tubeworms, snails, scaleworms, and pycnogonids reflecting diurnal through monthly responses to several tidal components (Tunnicliffe et al. 1990; Martell et al. 2002; Cuvelier et al. 2014). Even winter storms on the ocean surface cause deep pressure currents that are registered by scaleworms and pycnogonids as they position themselves higher or lower in the bush (Lelièvre et al. 2017).

The best studied seep tubeworm forest is from the Gulf of Mexico. Here, the initial stages of community succession are similar within a site, but can vary widely at different seep locations (Cordes et al. 2006). Differences may be due to the relative abundance of different tubeworm species at each site, small differences in habitat characteristics, or simply due to the random effect of larval dispersal and colonization of the initial tubeworm stage. Over time, these variable initial stages tend to converge on a community that represents the background fauna of the region. In the mature seep tubeworm forest, the majority of canopy space experiences ambient, deep-sea environmental conditions in terms of sulphide, methane, and dissolved oxygen concentrations. As deep-sea species take advantage of the habitat provided, a more homogenous community emerges in the later stages of succession. There is a trade-off in which seep endemic species decline in abundance and are replaced by species with similar niches from the background community that are presumably capable of replacing the endemic species in the absence of seep conditions (Cordes et al. 2005b).

6.3 Export of Productivity

Both hydrothermal vents and cold seeps are flow-through ecosystems in which the productivity is eventually exported to the surrounding deep sea (Carney 1994; Tunnicliffe et al. 2003a; Levin et al. 2016). The plume rising from a vent tubeworm colony includes organic particulates and microbes that may be advected laterally in bottom tidal currents or become entrained in a rising plume where zooplankton and nekton are attracted in dense aggregations (Burd and Thomson 1995; Skebo et al. 2006). The animals in these bushes also contribute gametes and larvae to the plume as a major part of their energy is devoted to reproduction (Tyler and Young 1999). These propagules can rise thousands of metres to into surface waters where development occurs. Predators also disperse production as large crabs, fish, and cephalopods are frequent visitors at the margins of vents and invade the interior of seeps; in areas of high chemosynthetic production, the density of these animals tends to increase. When the energy source for these chemosynthetic communities fades, the dependents die, and deep-sea scavengers are able to invade.

6.4 Senescence and Termination

Mortality is a fact of life. While predation by bush inhabitants, such as scaleworms, can reduce fitness in tubeworms (Tunnicliffe et al. 2014), death of the foundation species is more likely to result from incursion from deep-sea fish and large crabs (Tunnicliffe and Jensen 1987; Tunnicliffe et al. 1990). Replacement of these prey ensues by new recruits. However, the entire vestimentiferan forest at a hot vent will eventually die, and inhabitants disperse or perish. In conditions that sponsor rapid growth, senescence may play a strong role in rapid turnover in the population. Bodnar (2009) suggests that some marine invertebrates with high metabolic rates accumulate free oxidative radicals that accelerate cell death—investigation of short-versus long-lived vestimentiferans may confirm this scenario. The most evident cause of forest decline is cessation of the supply of reduced compounds. Klose et al. (2015) record not only the brief lifespans of *Riftia* and *Tevnia* as heat recedes in a newly formed vent but also the massive release of microbial symbionts into the adjacent environment.

As venting vigour decreases, assemblage composition shifts because the dilute hydrothermal fluid no longer supports intense autotrophic production. Robustness of the foundation species declines, fewer vent species occur, and mobile predators from the deep sea make more frequent incursions. The spatial zonation of vent animals represents this temporal sequence (Grassle 1987; Sarrazin et al. 1999; Gollner et al. 2015) where peripheral senescent assemblages clearly differentiate from those under vent influence (Marcus and Tunnicliffe 2002). Near-vent dying worms still host some vent species, but at markedly lower densities, and deep-sea species such as isopods, tanaids, ophiuroids, harpacticoids, and hydroids occupy the tubes (Tsurumi and Tunnicliffe 2003) (Fig. 5d). Here, the diversity remains high as non-vent species populate the tubes. Empty tubes also form habitat for species seeking shelter inside, such as phyllodocid polychaetes inside *Alaysia* tubes (Kobayashi and Kojima 2017).

Similarly, as the seep community wanes, background deep-sea species take advantage of the remaining habitat, especially the authigenic hard substratum carbonates that can occur in a typically sediment-dominated seascape. Such carbonates may have formed within the last 1000 years (Aharon et al. 1997) or can be tens to hundreds of thousands of years old and exhumed by currents and slope instability (Roberts and Aharon 1994). These substrata increase habitat heterogeneity in the region and result in elevated diversity at the seascape scale (Cordes et al. 2010b). Frequently, they are colonized by deep-sea corals that also augment habitat heterogeneity and regional diversity (Cordes et al. 2008).

7 Tubeworm Forests and Humans

Since their discovery in the late 1970s, exploration of hydrothermal vents and cold seeps has driven far-reaching studies of many deep ocean areas that have greatly expanded our understanding of these, and other, ecosystems. We have come to realize that vent and seep ecosystems do not function in isolation, but have a wide "sphere of influence" in the deep sea (Levin et al. 2016) such as transfer of production and habitat provision. Humans have remained fascinated with the bizarre life described, to the point that movies, books, and games have incorporated facets into popular culture (Van Dover et al. 2018). While biologists have mapped the biodiversity and conservation approaches for these ecosystems, some geologists have examined the extent of associated deposits that may prove of value to the commercial sector: polymetallic sulphides at vents and gas hydrates at seeps (Thompson et al. 2018).

7.1 Fundamental Knowledge of Life Processes

The discovery of hydrothermal vents and methane seeps fuelled a significant and substantial increase in our understanding of many biotic processes, including the early origin and diversification of life. The tubeworms themselves became a focus of many studies to detail the morphological and physiological transformation of an annelid bauplan into a factory for microbial growth and translocation of organic products to the host (e.g. Childress and Fisher 1992; Bright and Lallier 2010). Soon after recognition of the integrated symbiosis in tubeworms, other discoveries revealed a wide range of invertebrate-bacteria relationships in both deep and shallow ocean habitats where dissolved sulphide is available (Dubilier et al. 2008). The intimate relationship between invertebrates and bacteria remains a fertile area of research. Currently, new genomic techniques have spawned many novel studies of tubeworm symbionts such as the metabolic flexibility that associations with a variety of bacterial lineages can yield (Li et al. 2018). An intriguing aspect of vestimentiferan tubeworms is the wide range of growth strategies that exist within a single family of polychaetes: from massive, short-lived *Riftia* to small, twisting *Alaysia* to long, thin *Lamellibrachia* (Karaseva et al. 2016) that can live over 200 years (Bergquist et al. 2000) and *Escarpia* species that may live in excess of 300 years (Durkin et al. 2017). There can be marked variability in growth form, reproductive output, and age within species that have the capacity for phenotypic plasticity to adapt to a broad range of venting conditions (Robidart et al. 2011; Tunnicliffe et al. 2014).

7.2 Genetic Resources and Potential

Expectation usually far exceeds realization in discussions around lucrative genetic products from living organisms. Hot vents present an attractive focus for genetic resources because of adaptations to extreme conditions, although returns remain limited. Hyperthermophilic Archaea are common targets as they are able to stabilize enzyme activity at high temperatures during DNA replication; such discoveries transformed PCR accuracy (Pettit 2011). The blood of *Riftia* has oxygen-binding properties that may have therapeutic properties such as organ preservation in transport (Simoni 2014). The cosmetics industry has also investigated vent animal products (see "Abyssine Cream" from Kiehl, among others). The longevity of seep tubeworms is also a tantalizing prospect in terms of cell maintenance mechanisms. As discussions around a possible international agreement regarding Biodiversity Beyond National Jurisdiction continue at the United Nations, governance of such resource extraction may become more regulated (Harden-Davies 2017).

7.3 Anthropogenic Impacts

To date, apart from sampling by scientists, evidence of human-induced change at hydrothermal vents is lacking. In their study of functional traits of vent species, Chapman et al. (2018) test the relative contributions of rare and common species to community functional diversity to find a much stronger role of common species to functional uniqueness than is generally described in other ecosystems. They attribute the outcome to the lack of human attrition of the common species at vents, unlike shallow marine and terrestrial ecosystems. However, the possibility of habitat destruction from deep-sea mining is growing. This new industry is nearing readiness to initiate exploitation for manganese nodules (abyssal plains), massive sulphides (hot vents), and cobalt crusts (seamounts) as the International Seabed Authority (a UN organization) completes the Mining Code for high seas activities (Lodge and Verlaan 2018). In addition, several countries in the western Pacific have granted licences for exploration of hot vent sulphide deposits in state waters. Because we have a good estimate of the locations of deposits at or near active vents (Hannington et al. 2011), most contracts focus on these areas; however, it is likely that more lucrative prospects lie in larger, perhaps buried, inactive deposits (Petersen et al. 2018). There is currently low overlap between vents that support dense vestimentiferan forests and those of interest for mining; most of the larger ore deposits lie in the Mid-Atlantic Ridge and the Indian Ocean ridges. However, in some west Pacific locations, sulphide deposits of economic interest may intersect with tubeworm habitat.

Seep communities have experienced direct human impacts such as trawling activities as noted in New Zealand waters (Bowden et al. 2013). As deepwater fishing interests and seep distribution overlap on continental margins around the globe, habitat destruction is likely. Similarly, impacts from oil and gas drilling are possible, as this activity, by its nature, will often coincide with the presence of seep communities in tubeworm forests, as described off Trinidad and Tobago (Amon et al. 2017). In the Gulf of Mexico, there are regulations in place to avoid direct impacts on "high-density biological communities" in deep water, including seeps, which is not the case in many other areas of active oil and gas resource exploration and exploitation, particularly in developing nations (Cordes et al. 2016). During surveys following the Deepwater Horizon explosion and oil spill in 2010, no direct impacts were observed on seep communities, although less apparent, sublethal impacts may have gone undetected by the visual survey techniques used (EEC pers. obs). It is also possible that future gas hydrate extraction will have a significant impact on seep communities, particularly the long-lived species that form the tubeworm forest habitat.

Conservation questions concerning vents and seeps are now under examination at national and international levels. As fishing practices have highlighted potential effects on sensitive benthic habitats, several regulatory instruments are now in place after UN General Assembly resolutions urged states to protect special ecosystems such as hydrothermal vents. For example, the FAO (Food and Agriculture Organization) includes vents under its definition of vulnerable marine ecosystems (VME) and restricts fishing activities. Similarly, many states have placed hydrothermal vents into protected or conservation areas (Canada, Mexico, the United States, New Zealand, Portugal). With such precedents, the International Seabed Authority is urged to put active vents beyond mining influence using its regulatory power (Van Dover et al. 2018). Designing conservation strategies for hydrothermal vent ecosystems—especially around current contract areas—is challenging (Dunn et al. 2018). Seeps have garnered less attention, but the longevity of many of the inhabitants and high biomass of these habitats certainly fits the VME definitions of many regulatory bodies (Amon et al. 2017). Recognizing these characteristics, cold seeps are included in the list of protected habitats by the Pacific Fisheries Management Council on the west coast of the United States; similar measures are under consideration in Canada.

8 Summary

Discoveries of both vents and seeps continue as exploration is propelled by interests in the biological and geological novelties in these unusual chemosynthetic ecosystems. The giant tubeworms are the basis of many research programs because of the marked and extensive adaptations in their morphology and physiology to assimilate and service symbionts. These animals form dense masses of tubes up to 2 m long, thereby creating the framework of this marine "forest". At hydrothermal vents, we currently know vestimentiferan tubeworms from the Pacific Ocean only, whereas small monoliferans colonize some Atlantic vents. However, vestimentiferans are abundant at methane cold seeps throughout the Pacific, Atlantic, and into the

Mediterranean. All tubeworms grow upward, but those at seeps also extend down into sediments to access dissolved sulphide. In old worms (decades to centuries), hardened tubes provide long-term colonization surfaces. At vents, dense tangles can form as juveniles recruit to the adult tubes creating a complex three-dimensional habitat.

The forest inhabitants form a specialized fauna—mostly endemic at vents—adapted to the challenges presented by variable fluid flows carrying compounds that compromise metabolic and physiological functions. Inhabitants form a restricted food web based on the chemoautotrophic microbes in fluids and in mats among the tubes; a few species can prey on the tubeworms. Three to four dozen macrofaunal species inhabit tubeworm forests with a few taxa that dominate abundance in the eastern Pacific vents, while several studies find that meiofauna tend to be copepod-dominated and limited in diversity. The highly productive habitat and dense assemblages imply that many species interactions occur, but studies on the roles of competition, parasitism, and predation in structuring the assemblage are mostly lacking. Many species depend on the early colonization of new sites by the habitat-forming tubeworms. At vents, high variability of fluids supplying reduced compounds over time and space leads to a mosaic of assemblages that can change composition, sometimes over a few months. At seeps, toxic compounds are less limiting in the upper canopy, thus a mature community incorporates many background species. As much of the information on community structure and function derives from one vent and one seep system, more work is needed to examine those from other locations, especially the western Pacific.

The role that these tubeworms play in promoting diversity is very important. As summarized by Govenar (2010), this foundation species forms three-dimensional habitats with access to primary productivity, it creates potential niches through spatial variability, and it ameliorates stressors in the emergent fluids. Thus, understanding how human activities can modify or destroy these habitats is an important factor in deep-sea conservation (Turner et al. 2019). The presence of potential mineral resources on the seabed is attracting attention. Beyond national jurisdictions, the International Seabed Authority is encouraging the exploration for minerals, such as those in the metal-rich sulphide deposits at hydrothermal vents; regulations governing exploitation are due for finalization in 2022. Gas hydrates form mostly on continental shelves, thus fall under nation authorities. Precedent for protections may derive from definitions around Vulnerable Marine Ecosystems. Increased awareness of the ecosystem services provided by these habitats can augment protections through future management actions.

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References

Aharon P, Schwarcz HP, Roberts HH (1997) Radiometric dating of submarine hydrocarbon seeps in the Gulf of Mexico. Geol Soc Am Bull 109:568–579

Amon DJ, Gobin J, Van Dover CL, Levin LA, Marsh L, Raineault NA (2017) Characterization of methane-seep communities in a deep-sea area designated for oil and natural gas exploitation off Trinidad and Tobago. Front Mar Sci 4:342

Arp AJ, Childress JJ (1983) Sulfide binding by the blood of the hydrothermal vent tube worm *Riftia pachyptila*. Science 219:295–297

Bates AE (2007a) Feeding strategy, morphological specialization, and the presence of bacterial episymbionts in lepetodrilid gastropods from hydrothermal vents. Mar Ecol Prog Ser 347:87–99

Bates AE (2007b) Persistence, morphology, and nutritional state of a gastropod hosted bacterial symbiosis in different levels of hydrothermal vent flux. Mar Biol 152:557–568

Bates AE, Tunnicliffe V, Lee RW (2005) Role of thermal conditions in habitat selection by hydrothermal vent gastropods. Mar Ecol Prog Ser 305:1–15

Bates AE, Lee RW, Tunnicliffe V, Lamare MD (2010) Deep-sea hydrothermal vent animals seek cool fluids in a highly variable thermal environment. Nat Commun 1:1–6

Baumberger T, Embley RW, Merle SG, Lilley MD, Raineault NA, Lupton JE (2018) Mantle-derived helium and multiple methane sources in gas bubbles of cold seeps along the Cascadia continental margin. Geochem Geophys Geosyst 19:4476–4486

Becker EL, Cordes EE, Macko SA, Lee RW, Fisher CR (2013) Using stable isotope compositions of animal tissues to infer trophic interactions in Gulf of Mexico lower slope seep communities. PLoS One 8:e74459

Bergquist DC, Williams FM, Fisher CR (2000) Longevity record for deep-sea invertebrate. Nature 403:499–500

Bergquist DC, Urcuyo IA, Fisher CR (2002) Establishment and persistence of seep vestimentiferan aggregations on the upper Louisiana slope of the Gulf of Mexico. Mar Ecol Prog Ser 241:89–98

Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R et al (2003) Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico cold seeps. J Exp Mar Biol Ecol 289:197–222

Bergquist DC, Fleckenstein C, Knisel J, Begley B, MacDonald IR, Fisher CR (2005) Variations in seep mussel bed communities along physical and chemical environmental gradients. Mar Ecol Prog Ser 293:99–108

Bergquist DC, Eckner JT, Urcuyo IA, Cordes EE, Hourdez S, Macko SA et al (2007) Using stable isotopes and quantitative community characteristics to determine a local hydrothermal vent food web. Mar Ecol Prog Ser 330:49–65

Bodnar AG (2009) Marine invertebrates as models for aging research. Exp Gerontol 44:477–484

Bowden DA, Rowden AA, Thurber AR, Baco AR, Levin LA, Smith CR (2013) Cold seep epifaunal communities on the hikurangi margin, New Zealand: composition, succession, and vulnerability to human activities. PLoS One 8:e76869

Brescia LA, Tunnicliffe V (1998) Population biology of two pycnogonid species (Ammotheidae) at hydrothermal vents in the northeast Pacific. Cah Biol 39:233–236

Bright M, Lallier FH (2010) The biology of vestimentiferan tubeworms. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) Oceanography and marine biology: an annual review, vol 48. CRC Press, New York, pp 213–265

Bright M, Keckeis H, Fisher CR (2000) An autoradiographic examination of carbon fixation, transfer and utilization in the *Riftia pachyptila* symbiosis. Mar Biol 136:621–632

Brooks JM, Kennicutt MC, Fisher CR, Macko SA, Cole K et al (1987) Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. Science 238:1138–42

Burd BJ, Thomson RE (1995) Distribution of zooplankton associated with the Endeavour ridge hydrothermal plume. J Plankton Res 17:965–997

Carney RS (1994) Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. Geo-Mar Lett 14:149–159

Carney SL, Flores JF, Orobona KM, Butterfield DA, Fisher CR, Schaeffer SW (2007) Environmental differences in hemoglobin gene expression in the hydrothermal vent tubeworm, *Ridgeia piscesae*. Comp Biochem Physiol B Biochem Mol Biol 146(3):326–337

Cavanaugh CM, Gardiner SL, Jones ML, Jannasch HW, Waterbury JB (1981) Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. Science 213:340–342

Chapman AS, Tunnicliffe V, Bates AE (2018) Both rare and common species make unique contributions to functional diversity in an ecosystem unaffected by human activities. Divers Distrib 24:568–578

Chapman AS, Beaulieu SE, Colaço A, Gebruk AV, Hilario A, Kihara TC et al (2019) sFDvent: a global trait database for deep-sea hydrothermal-vent fauna. Glob Ecol Biogeogr 28:1538–1551

Childress JJ, Fisher CR (1992) The biology of hydrothermal vent animals: physiology, biochemistry and autotrophic symbioses. In: Barnes M (ed) Oceanography and marine biology. An annual review, vol 30. Aberdeen University Press, Aberdeen, pp 337–441

Cordes EE, Bergquist DC, Shea K, Fisher CR (2003) Hydrogen sulphide demand of long-lived vestimentiferan tube worm aggregations modifies the chemical environment at deep-sea hydrocarbon seeps. Ecol Lett 6:212–219

Cordes EE, Arthur MA, Shea K, Arvidson RS, Fisher CR (2005a) Modeling the mutualistic interactions between tubeworms and microbial consortia. PLoS Biol 3:e77

Cordes EE, Hourdez S, Predmore BL, Redding ML, Fisher CR (2005b) Succession of hydrocarbon seep communities associated with the long-lived foundation species *Lamellibrachia luymesi*. Mar Ecol Prog Ser 305:17–29

Cordes EE, Bergquist DC, Predmore BL, Dienes P, Jones C et al (2006) Alternate unstable states: convergent paths of succession in hydrocarbon-seep tubeworm-associated communities. J Exp Mar Biol Ecol 339:159–76

Cordes EE, Carney SL, Hourdez S, Carney RS, Brooks JM, Fisher CR (2007) Cold seeps of the deep Gulf of Mexico: community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. Deep-Sea Res Pt I 54:637–653

Cordes EE, McGinley MP, Podowski EL, Becker EL, Lessard-Pilon S, Viada ST et al (2008) Coral communities of the deep Gulf of Mexico. Deep-Sea Res Pt I 55:777–787

Cordes EE, Bergquist DC, Fisher CR (2009) Macro-ecology of Gulf of Mexico cold seeps. Annu Rev Mar Sci 1:143–168

Cordes EE, Becker EL, Fisherb CR (2010a) Temporal shift in nutrient input to cold-seep food webs revealed by stable-isotope signatures of associated communities. Limnol Oceanogr 55:2537–2548

Cordes EE, Cunha MR, Galeron J, Mora C, Olu-Le Roy K, Sibuet M et al (2010b) The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. Mar Ecol 31:51–65

Cordes EE, Jones DOB, Schlacher TA, Amon DJ, Bernardino AF, Brooke S et al (2016) Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. Front Environ Sci 4:58

Corliss JB, Dymond J, Gordon LI, Edmond JM, von Herzen RP, Ballard RD et al (1979) Submarine thermal springs on the Galapagos rift. Science 203:1073–1083

Cowart D, Halanych K, Schaeffer S, Fisher C (2014) Depth-dependent gene flow in Gulf of Mexico cold seep *Lamellibrachia* tubeworms (Annelida, Siboglinidae). Hydrobiologia 736:139–154

Cuvelier D, Legendre P, Laes A, Sarradin P-M, Sarrazin J (2014) Rhythms and community dynamics of a hydrothermal tubeworm Assemblage at Main Endeavour Field – a multidisciplinary deep-sea observatory approach. PLoS One 9:5

Dattagupta S, Miles LL, Barnabei MS, Fisher CR (2006) The hydrocarbon seep tubeworm *Lamellibrachia luymesi* primarily eliminates sulfate and hydrogen ions across its roots to conserve energy and ensure sulfide supply. J Exp Biol 209:3795–3805

Desbruyères D, Alayse-Danet A-M, Ohta S, Cruises tspoBS (1994) Deep-sea hydrothermal communities in Southwestern Pacific back-arc basins (the North-Fiji and Lau Basins): composition, microdistribution and food web. Mar Geol 116:227–242

Di Meo CA, Wilbur AE, Holben WE, Feldman RA, Vrijenhoek RC, Cary SC (2000) Genetic variation among endosymbionts of widely distributed vestimentiferan tubeworms. Appl Environ Microbiol 66:651–658

Du Preez C, Fisher CR (2018) Long-term stability of back-arc basin hydrothermal vents. Front Mar Sci 5:54

Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. Nat Rev Microbiol 6:725

Dunn DC, Van Dover CL, Etter RJ, Smith CR, Levin LA, Morato T et al (2018) A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining. Sci Adv 4:7

Duperron S, De Beer D, Zbinden M, Boetius A, Schipani V, Kahil N et al (2009) Molecular characterization of bacteria associated with the trophosome and the tube of *Lamellibrachia* sp., a siboglinid annelid from cold seeps in the eastern Mediterranean. FEMS Microbiol Ecol 69 (3):395–409

Durkin A, Fisher CR, Cordes EE (2017) Extreme longevity in a deep-sea vestimentiferan tubeworm and its implications for the evolution of life history strategies. Sci Nat 104:63

Embley R, Chadwick W, Perfit M, Smith M, Delaney J (2000) Recent eruptions on the CoAxial segment of the Juan de Fuca ridge: implications for mid-ocean ridge accretion processes. J Geophys Res Solid Earth 105:16501–16525

Embley RW, Baker ET, Butterfield DA, Chadwick WW Jr, Lupton JE, Resing JA et al (2007) Exploring the submarine ring of fire: Mariana Arc – Western Pacific. Oceanography 20:68–79

Felbeck H (1981) CO2 fixation in the hydrothermal vent tube worm *Riftia pachyptila* (Jones). Physiol Zool 58:272–281

Feldman RA, Black MB, Cary CS, Lutz RA, Vrijenhoek RC (1997) Molecular phylogenetics of bacterial endosymbionts and their vestimentiferan hosts. Mol Mar Biol Biotechnol 6:268–277

Forget NL, Juniper KS (2013) Free-living bacterial communities associated with tubeworm (*Ridgeia piscesae*) aggregations in contrasting diffuse flow hydrothermal vent habitats at the Main Endeavour Field, Juan de Fuca Ridge. Microbiologyopen 2:259–275

Freytag JK, Girguis PR, Bergquist DC, Andras JP, Childress JJ, Fisher CR (2001) A paradox resolved: sulfide acquisition by roots of seep tubeworms sustains net chemoautotrophy. Proc Natl Acad Sci USA 98(23):13408–13413

Gaill F, Persson J, Sugiyama J, Vuong R, Chanzy H (1992) The chitin system in the tubes of deep sea hydrothermal vent worms. J Struct Biol 109:116–118

Gaudron SM, Marqué L, Thiébaut E, Riera P, Duperron S, Zbinden M (2015) How are microbial and detrital sources partitioned among and within gastropods species at East Pacific rise hydrothermal vents? Mar Ecol 36:18–34

Gebruk AV, Galkin SV, Vereshchaka AL, Moskalev LI, Southward AJ (1997) Ecology and biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge. Adv Mar Biol 32:93–144

Georgieva MN, Wiklund H, Bell JB, Eilertsen MH, Mills RA, Little CTS et al (2015) A chemosynthetic weed: the tubeworm *Sclerolinum contortum* is a bipolar, cosmopolitan species. BMC Evol Biol 15(1):280

Georgieva MN, Little CTS, Watson JS, Sephton MA, Ball AD, Glover AG (2019) Identification of fossil worm tubes from Phanerozoic hydrothermal vents and cold seeps. J Syst Palaeontol 17:287–329

Goffredi S, Childress J, Desaulniers N, Lee R, Lallier F, Hammond D (1997) Inorganic carbon acquisition by the hydrothermal vent tubeworm *Riftia pachyptila* depends upon high external PCO2 and upon proton-equivalent ion transport by the worm. J Exp Biol 200:883–8196

Goffredi SK, Girguis PR, Childress JJ, Desaulniers NT (1999) Physiological functioning of carbonic anhydrase in the hydrothermal vent tubeworm *Riftia pachyptila*. Biol Bull 196:257–264

Goffredi SK, Johnson S, Tunnicliffe V, Caress D, Clague D, Escobar E et al (2017) Hydrothermal vent fields discovered in the southern Gulf of California clarify role of habitat in augmenting regional diversity. Proc R Soc B: Biol Sci 284:1859

Gollner S, Zekely J, Govenar B, Le Bris N, Nemeschkal HL, Fisher CR et al (2007) Tubeworm-associated permanent meiobenthic communities from two chemically different hydrothermal vent sites on the East Pacific Rise. Mar Ecol Prog Ser 337:39–49

Gollner S, Ivanenko VN, Arbizu PM, Bright M (2010) Advances in taxonomy, ecology, and biogeography of Dirivultidae (Copepoda) associated with chemosynthetic environments in the deep sea. PLoS One 5:e9801

Gollner S, Govenar B, Fisher CR, Bright M (2015) Size matters at deep-sea hydrothermal vents: different diversity and habitat fidelity patterns of meio- and macrofauna. Mar Ecol Prog Ser 520:57–66

Govenar B (2010) Shaping vent and seep communities: habitat provision and modification by foundation species. In: Kiel S (ed) The vent and seep biota: aspects from microbes to ecosystems. Springer, Dordrecht, pp 403–432

Govenar B (2012) Energy transfer through food webs at hydrothermal vents; linking the lithosphere to the biosphere. Oceanography 25:246–255

Govenar B, Fisher CR (2007) Experimental evidence of habitat provision by aggregations of *Riftia pachyptila* at hydrothermal vents on the East Pacific Rise. Mar Ecol 28:3–14

Govenar BW, Bergquist DC, Urcuyo IA, Eckner JT, Fisher CR (2002) Three Ridgeia piscesae assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar. Cah Biol Mar 43(3/4):247–252

Govenar B, Le Bris N, Gollner S, Glanville J, Aperghis AB, Hourdez S et al (2005) Epifaunal community structure associated with *Riftia pachyptila* aggregations in chemically different hydrothermal vent habitats. Mar Ecol Prog Ser 305:67–77

Grassle JF (1987) The ecology of deep-sea hydrothermal vent communities. In: Blaxter JHS, Southward AJ (eds) Advances in marine biology, vol 23. Academic, San Diego, pp 301–362

Guizien K, Ghisalberti M (2017) Living in the canopy of the animal forest: physical and biogeochemical aspects. In: Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, New York, pp 507–528

Hannington M, Jamieson J, Monecke T, Petersen S, Beaulieu S (2011) The abundance of seafloor massive sulfide deposits. Geology 39:1155–1158

Harden-Davies H (2017) Deep-sea genetic resources: new frontiers for science and stewardship in areas beyond national jurisdiction. Deep-Sea Res Pt II 137:504–513

Harmer TL, Rotjan RD, Nussbaumer AD, Bright M, Ng AW, DeChaine EG et al (2008) Free-living tube worm endosymbionts found at deep-sea vents. Appl Environ Microbiol 74:3895–3898

Hautala S, Johnson HP, Pruis M, Garcia-Berdeal I, Bjorklund T (2012) Low-temperature hydrothermal plumes in the near-bottom boundary layer at Endeavour segment, Juan de Fuca Ridge. Oceanography 25:192–195

Hilário A, Young CM, Tyler PA (2005) Sperm storage, internal fertilization, and embryonic dispersal in vent and seep tubeworms (Polychaeta: Siboglinidae: vestimentifera). Biol Bull 208(1):20–28

Hilário A, Capa M, Dahlgren TG, Halanych KM, Little CT, Thornhill DJ et al (2011a) New perspectives on the ecology and evolution of siboglinid tubeworms. PLoS One 6:e16309

Hilário A, Comas M, Azevedo L, Pinheiro L, Ivanov M, Cunha M (2011b) First record of a vestimentifera (Polychaeta: Siboglinidae) from chemosynthetic habitats in the western Mediterranean Sea—biogeographical implications and future exploration. Deep-Sea Res Pt I 58:200–207

Hugler M, Sievert SM (2011) Beyond the Calvin cycle: autotrophic carbon fixation in the ocean. Annu Rev Mar Sci 3:261–289

Hunt HL, Metaxas A, Jennings RM, Halanych KM, Mullineaux LS (2004) Testing biological control of colonization by vestimentiferan tubeworms at deep-sea hydrothermal vents (East Pacific Rise, 9° 50′ N). Deep-Sea Res Pt I 51:225–234

Johnson KS, Childress JJ, Beehler CL (1988a) Short-term temperature variability in the Rose Garden hydrothermal vent field: an unstable deep-sea environment. Deep-Sea Res Pt A 35:1711–1721

Johnson KS, Childress JJ, Hessler RR, Sakamoto-Arnold CM, Beehler CL (1988b) Chemical and biological interactions in the Rose Garden hydrothermal vent field, Galapagos spreading center. Deep-Sea Res Pt A 35:1723–1744

Johnson HP, Hutnak M, Dzlak RP, Fox CG, Urcuyo I, Cowen JP et al (2000) Earthquake-induced changes in a hydrothermal system on the Juan de Fuca mid-ocean ridge. Nature 407:174–177

Julian D, Gaill F, Wood E, Arp AJ, Fisher CR (1999) Roots as a site of hydrogen sulfide uptake in the hydrocarbon seep vestimentiferan *Lamellibrachia* sp. J Exp Biol 202:2245–2257

Juniper SK, Tunnicliffe V, Southward EC (1992) Hydrothermal vents in turbidite sediments on a Northeast Pacific spreading centre: organisms and substratum at an ocean drilling site. Can J Zool 70:1792–1809

Karaseva N, Rimskaya-Korsakova N, Galkin S, Malakhov V (2016) Taxonomy, geographical and bathymetric distribution of vestimentiferan tubeworms (Annelida, Siboglinidae). Biol Bull 43:937–969

Klose J, Polz MF, Wagner M, Schimak MP, Gollner S, Bright M (2015) Endosymbionts escape dead hydrothermal vent tubeworms to enrich the free-living population. Proc Natl Acad Sci USA 112:11300–11305

Kobayashi G, Araya JF (2018) Southernmost records of Escarpia spicata and *Lamellibrachia barhami* (Annelida: Siboglinidae) confirmed with DNA obtained from dried tubes collected from undiscovered reducing environments in northern Chile. PLoS One 13(10):e0204959

Kobayashi G, Kojima S (2017) First record of *Protomystides hatsushimaensis* (Annelida: Phyllodocidae) inhabiting vacant tubes of vestimentiferan tubeworms. Mar Biodivers Rec 10:25

Kobayashi G, Miura T, Kojima S (2015) *Lamellibrachia sagami* sp. nov., a new vestimentiferan tubeworm (Annelida: Siboglinidae) from Sagami Bay and several sites in the northwestern Pacific Ocean. Zootaxa 4018:97–108

Kojima S, Ohta S, Yamamoto T, Miura T, Fujiwara Y, Fujikura K et al (2002) Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific. Mar Biol 141:57–64

Kojima S, Watanabe H, Tsuchida S, Fujikura K, Rowden AA, Takai K et al (2006) Phylogenetic relationships of a tube worm (*Lamellibrachia juni*) from three hydrothermal vent fields in the South Pacific. J Mar Biol Assoc UK 86(06):1357–1361

Kouris A, Kim Juniper S, Frebourg G, Gaill F (2007) Protozoan–bacterial symbiosis in a deep-sea hydrothermal vent folliculinid ciliate (*Folliculinopsis* sp.) from the Juan de Fuca ridge. Mar Ecol 28:63–71

Le Bris N, Govenar B, Le Gall C, Fisher CR (2006) Variability of physico-chemical conditions in 9°50′N EPR diffuse flow vent habitats. Mar Chem 98:167–182

Lelièvre Y, Legendre P, Matabos M, Mihály S, Lee RW, Sarradin P-M et al (2017) Astronomical and atmospheric impacts on deep-sea hydrothermal vent invertebrates. Proc Natl Acad Sci USA 284:20162123

Lelièvre Y, Sarrazin J, Marticorena J, Schaal G, Day T, Legendre P et al (2018) Biodiversity and trophic ecology of hydrothermal vent fauna associated with tubeworm assemblages on the Juan de Fuca Ridge. Biogeosciences 15:2629–2647

Levesque C, Juniper K, Marcus J (2003) Food resource partitioning and competition among alvinellid polychaetes of Juan de Fuca Ridge hydrothermal vents. Mar Ecol Prog Ser 246:173–182

Levesque C, Kim Juniper S, Limén H (2006) Spatial organization of food webs along habitat gradients at deep-sea hydrothermal vents on Axial Volcano, Northeast Pacific. Deep-Sea Res Pt I 53:726–739

Levin LA (2005) Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) Oceanography and marine biology: an annual review, vol 43. CRC Press, New York, pp 1–46

Levin LA, Orphan VJ, Rouse GW, Rathburn AE, Ussler W, Cook GS et al (2012) A hydrothermal seep on the Costa Rica margin: middle ground in a continuum of reducing ecosystems. Proc Natl Acad Sci USA 279:2580–2588

Levin LA, Baco AR, Bowden D, Colaço A, Cordes E, Cunha MR et al (2016) Hydrothermal vents and methane seeps:rethinking the sphere of influence. Front Mar Sci 3:72

Li Y, Kocot KM, Whelan NV, Santos SR, Waits DS, Thornhill DJ et al (2017) Phylogenomics of tubeworms (Siboglinidae, Annelida) and comparative performance of different reconstruction methods. Zool Scr 46:200–213

Li Y, Liles MR, Halanych KM (2018) Endosymbiont genomes yield clues of tubeworm success. ISME J 12:2785–2795

Limén H, Levesque C, Kim JS (2007) POM in macro-/meiofaunal food webs associated with three flow regimes at deep-sea hydrothermal vents on Axial Volcano, Juan de Fuca Ridge. Mar Biol 153:129–349

Little CT, Maslennikov VV, Morris NJ, Gubanov AP (1999) Two palaeozoic hydrothermal vent communities from the southern Ural mountains, Russia. Palaeontology 42:1043–1078

Lodge MW, Verlaan PA (2018) Deep-sea mining: international regulatory challenges and responses. Elements. 14:331–336

Lonsdale P (1977) Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. Deep-Sea Res 24:857–863

López-García P, Gaill F, Moreira D (2002) Wide bacterial diversity associated with tubes of the vent worm *Riftia pachyptila*. Environ Microbiol 4:204–215

Lutz RA, Shank TM, Fornari DJ, Haymon RM, Lilley MD, Von Damm KL et al (1994) Rapid growth at deep-sea vents. Nature 371:663–664

MacAvoy SE, Macko SA, Carney RS (2003) Links between chemosynthetic production and mobile predators on the Louisiana continental slope: stable carbon isotopes of specific fatty acids. Chem Geol 201:229–2237

MacDonald IR, Tunnicliffe V, Southward EC (2002) Sperm transfer in the vestimentiferan *Ridgeia piscesae* Jones: an event observed at Endeavour segment, Juan de Fuca Ridge. Cah Biol 43:395–399

Marcus J, Tunnicliffe V (2002) Living on the edges of diffuse vents on the Juan de Fuca Ridge. Cah Biol 43:263–266

Marcus J, Tunnicliffe V, Butterfield DA (2009) Post-eruption succession of macrofaunal communities at diffuse flow hydrothermal vents on Axial Volcano, Juan de Fuca Ridge, Northeast Pacific. Deep-Sea Res Part II 56:1586–1598

Markert S, Arndt C, Felbeck H, Becher D, Sievert SM, Hügler M et al (2007) Physiological proteomics of the uncultured endosymbiont of *Riftia pachyptila*. Science 315:247–250

Marsh AG, Mullineaux LS, Young CM, Manahan DT (2001) Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411:77

Martell KA, Tunnicliffe V, MacDonald IR (2002) Biological features of a buccinid whelk (Gastropoda, Neogastropoda) at the Endeavour ventfields of Juan de Fuca Ridge, Northeast Pacific. J Molluscan Stud 68:45–53

McCowin MF, Rouse GW (2018) A new *Lamellibrachia* species and confirmed range extension for *Lamellibrachia barhami* (Siboglinidae, Annelida) from Costa Rica methane seeps. Zootaxa 4504:1–22

McCowin MF, Rowden AA, Rouse GW (2019) A new record of *Lamellibrachia columna* (Siboglinidae, Annelida) from cold seeps off New Zealand, and an assessment of its presence in the western Pacific Ocean. Mar Biodivers Rec. 12:10

McMullin ER, Hourdez S, Schaeffer SW, Fisher CR (2003) Phylogeny and biogeorgraphy of deep-sea vestimentiferan tubeworms and their bacterial symbionts. Symbiosis 34:1–41

Metaxas A (2004) Spatial and temporal patterns in larval supply at hydrothermal vents in the Northeast Pacific Ocean. Limnol Oceanogr 49:1949–1956

Micheli F, Peterson CH, Mullineaux LS, Fisher CR, Mills SW, Sancho G et al (2002) Predation structures communities at deep-sea hydrothermal vents. Ecol Monogr 72:365–382

Mills SW, Mullineaux LS, Tyler PA (2007) Habitat associations in gastropod species at East Pacific Rise hydrothermal vents (9°50′N). Biol Bull 212:185–194

Miura T (1997) *Lamellibrachia satsuma*, a new species of vestimentiferan worms (Annelida; Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan. Proc Biol Soc Washington 110:447–456

Miura T, Kojima S (2006) Two new species of vestimentiferan tubeworm (Polychaeta: Siboglinidae a.k.a. Pogonophora) from the Brothers Caldera, Kermadec Arc, South Pacific Ocean. Species Divers 11:209–224

Miyake H, Tsukahara J, Hashimoto J, Uematsu K, Maruyama T (2006) Rearing and observation methods of vestimentiferan tubeworm and its early development at atmospheric pressure. Cah Biol 47:471

Mullineaux LS, Mills SW, Goldman E (1998) Recruitment variation during a pilot colonization study of hydrothermal vents (9°50′N, East Pacific Rise). Deep-Sea Res Pt II 45:441–464

Nelson K, Fisher CR (2000) Absence of cospeciation in deep-sea vestimentiferan tube worms and their bacterial endosymbionts. Symbiosis 28:1–15

Niemann H, Linke P, Knittel K, MacPherson E, Boetius A, Brückmann W et al (2013) Methane-carbon flow into the benthic food web at cold seeps–a case study from the Costa Rica subduction zone. PLoS One 8:e74894

Nussbaumer AD, Fisher CR, Bright M (2006) Horizontal endosymbiont transmission in hydrothermal vent tubeworms. Nature 441:345–348

Olu K, Sibuet M, Harmegnies F, Foucher J-P, Fiala-Medioni A (1996) Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. Prog Oceanogr 38:347–376

Olu K, Lance S, Sibuet M, Henry P, Fiala-Médioni A, Dinet A (1997) Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. Deep-Sea Res Pt I 44:811–841

Olu-Le Roy K, Sibuet M, Fiala-Médioni A, Gofas S, Salas C, Mariotti A et al (2004) Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. Deep-Sea Res Pt I 51:1915–1936

Olu-Le Roy K, Caprais JC, Fifis A, Fabri MC, Galeron J et al (2007) Cold-seep assemblages on a giant pockmark off West Africa: spatial patterns and environmental control. Mar Ecol 28:115–30

Pasulka AL, Goffredi SK, Tavormina PL, Dawson KS, Levin LA, Rouse GW et al (2017) Colonial tube-dwelling ciliates influence methane cycling and microbial diversity within methane seep ecosystems. Front Mar Sci 3:276

Peng X, Zhou H, Yao H, Li J, Wu Z (2009) Ultrastructural evidence for iron accumulation within the tube of vestimentiferan *Ridgeia piscesae*. Biometals 22:723–732

Perez M, Juniper SK (2016) Insights into symbiont population structure among three vestimentiferan tubeworm host species at eastern Pacific spreading centers. Appl Environ Microbiol 82 (17):5197–5205

Perez M, Juniper SK (2018) Is the trophosome of *Ridgeia piscesae* monoclonal? Symbiosis 74 (1):55–65

Petersen S, Lehrmann B, Murton BJ (2018) Modern seafloor hydrothermal systems: new perspectives on ancient ore-forming processes. Elements 14:307–312

Pettit RK (2011) Culturability and secondary metabolite diversity of extreme microbes: expanding contribution of deep sea and deep-sea vent microbes to natural product discovery. Mar Biotechnol 13:1–11

Pleijel F, Dahlgren TG, Rouse GW (2009) Progress in systematics: from Siboglinidae to Pogonophora and Vestimentifera and back to Siboglinidae. C R Biol 332:140–148

Plouviez S, Jacobson A, Wu M, Van Dover CL (2015) Characterization of vent fauna at the mid-Cayman Spreading Center. Deep-Sea Res Pt I 97:124–133

Portail M, Olu K, Dubois SF, Escobar-Briones E, Gelinas Y, Menot L et al (2016) Food-web complexity in Guaymas Basin hydrothermal vents and cold seeps. PLoS One 11(9):e0162263

Ravaux J, Zbinden M, Voss-Foucart M, Compère P, Goffinet G, Gaill F (2003) Comparative degradation rates of chitinous exoskeletons from deep-sea environments. Mar Biol 143:405–412

Reveillaud J, Anderson R, Reves-Sohn S, Cavanaugh C, Huber JA (2018) Metagenomic investigation of vestimentiferan tubeworm endosymbionts from mid-Cayman Rise reveals new insights into metabolism and diversity. Microbiome 6:19

Rimskaya-Korsakova NN, Galkin SV, Malakhov VV (2017) The anatomy of the blood vascular system of the giant vestimentiferan tubeworm *Riftia pachyptila* (Siboglinidae, Annelida). J Morphol 278:810–827

Roberts HH, Aharon P (1994) Hydrocarbon-derived carbonate buildups of the northern Gulf of Mexico continental slope: a review of submersible investigations. Geo-Mar Lett 14:135–148

Robidart JC, Roque A, Song PF, Girguis PR (2011) Linking hydrothermal geochemistry to organismal physiology: physiological versatility in *Riftia pachyptila* from sedimented and basalt-hosted vents. PLoS One 6:7

Rossi S, Bramanti L, Gori A, Orejas C (2017) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, New York

Sahling H, Wallmann K, Dählmann A, Schmaljohann R, Petersen S (2005) The physicochemical habitat of *Sclerolinum* sp. at Hook Ridge hydrothermal vent, Bransfield Strait, Antarctica. Limnol Oceanogr 50:598–606

Sarrazin J, Juniper SK (1999) Biological characteristics of a hydrothermal edifice mosaic community. Mar Ecol Prog Ser 185:1–19

Sarrazin J, Robigou V, Juniper SK, Delaney J (1997) Biological and geological dynamics over four years on a high-temperature sulfide structure at the Juan de Fuca Ridge hydrothermal observatory. Mar Ecol Prog Ser 153:5–24

Sarrazin J, Juniper SK, Massoth G, Legendre P (1999) Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, Northeast Pacific. Mar Ecol Prog Ser 190:89–112

Schulze A, Halanych KM (2003) Siboglinid evolution shaped by habitat preference and sulfide tolerance. Hydrobiologia 496:199–205

Scott KM, Bright M, Macko SA, Fisher CR (1999) Carbon dioxide use by chemoautotrophic endosymbionts of hydrothermal vent vestimentiferans: affinities for carbon dioxide, absence of carboxysomes, and d^{13}C values. Mar Biol 135:25–34

Scott KM, Boller AJ, Dobrinski KP, Le Bris N (2012) Response of hydrothermal vent vestimentiferan *Riftia pachyptila* to differences in habitat chemistry. Mar Biol 159:435–442

Seyfried WE, Mottl MJ (1995) Geological setting and chemistry of deep-sea hydrothermal vents. In: Karl DM (ed) The microbiology of deep-sea hydrothermal vents. CRC Press, New York, pp 1–34

Shank TM, Fornari DJ, Von Damm KL, Lilley MD, Haymon RM, Lutz RA (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50′N, East Pacific Rise). Deep-Sea Res Pt II 45:465–515

Shillito B, Lechaire J-P, Goffinet G, Gaill F (1995) Composition and morphogenesis of the tubes of vestimentiferan worms. Geol Soc Lond, Spec Publ 87:295–302

Shillito B, Lechaire JP, Childress J, Gaill F (1997) Diffraction contrast imaging of extracellular matrix components using zero-loss filtering. J Struct Biol 120:85–92

Simoni J (2014) New approaches in commercial development of artificial oxygen carriers. Artif Organs 38:621–624

Skebo K, Tunnicliffe V, Garcia Berdeal I, Johnson HP (2006) Spatial patterns of zooplankton and nekton in a hydrothermally active axial valley on Juan de Fuca Ridge. Deep-Sea Res Pt I 53:1044–1060

Southward EC (1988) Development of the gut and segmentation of newly settled stages of *Ridgeia* (Vestimentifera): implications for relationship between Vestimentifera and Pogonophora. J Mar Biol Assoc UK 68:465–487

Southward EC (1991) Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-Arc Basin (Southwest Pacific Ocean). J Nat Hist 25:859–881

Southward EC (2000) Class Pogonophora. In: Polychaetes and allies: the southern synthesis fauna of Australia, vol 4, pp 331–51

Southward EC, Coates KA (1989) Sperm masses and sperm transfer in a vestimentiferan, *Ridgeia piscesae* Jones, 1985 (Pogonophora: Obturata). Can J Zool 67:2776–2781

Southward EC, Galkin SV (1997) A new vestimentiferan (Pogonophora: Obturata) from hydrothermal vent fields in the Manus Back-arc Basin (Bismarck Sea, Papua New Guinea, Southwest Pacific Ocean). J Nat Hist 31:43–55

Southward EC, Tunnicliffe V, Black M (1995) Revision of the species of *Ridgeia* from northeast Pacific hydrothermal vents, with a redescription of *Ridgeia piscesae* Jones (Pogonophora: Obturata= Vestimentifera). Can J Zool 73:282–295

Southward EC, Schulze A, Tunnicliffe V (2002) Vestimentiferans (Pogonophora) in the Pacific and Indian Oceans: a new genus from Lihir Island (Papua New Guinea) and the Java Trench, with the first report of *Arcovestia ivanovi* from the North Fiji Basin. J Nat Hist 36:1179–1197

Southward EC, Schulze A, Gardiner SL (2005) Pogonophora (Annelida): form and function. Hydrobiologia 535:227–251

Southward EC, Andersen AC, Hourdez S (2011) *Lamellibrachia anaximandri* n. sp., a new vestimentiferan tubeworm (Annelida) from the Mediterranean, with notes on frenulate tubeworms from the same habitat. Zoosystema 33(3):245–279, 35

Stern RJ, Fouch MJ, Klemperer SL (2003) An overview of the Izu-Bonin-Mariana subduction factory. Geophys Monogr 138:175–222

Stevens CJ, Juniper SK, Limén H, Pond DW, Metaxas A, Gélinas Y (2015) Obligate hydrothermal vent fauna at East Diamante submarine volcano (Mariana Arc) exploit photosynthetic and chemosynthetic carbon sources. Mar Ecol Prog Ser 525:25–39

Suzuki T, Takagi T, Okuda K, Furukohri T, Ohta S (1989) The deep-sea tube worm hemoglobin—subunit structure and phylogenetic relationship with annelid hemoglobin. Zool Sci 6:p915–p926

Taviani M, Angeletti L, Ceregato A, Foglini F, Froglia C, Trincardi F (2013) The Gela Basin pockmark field in the strait of Sicily (Mediterranean Sea): chemosymbiotic faunal and carbonate signatures of postglacial to modern cold seepage. Biogeosci Discuss 10:1

Terlizzi CM, Ward ME, Van Dover CL (2004) Observations on parasitism in deep-sea hydrothermal vent and seep limpets. Dis Aquat Org 62:17–26

Thiébaut E, Huther X, Shillito B, Jollivet D, Gaill F (2002) Spatial and temporal variations of recruitment in the tube worm *Riftia pachyptila* on the East Pacific Rise (9°50^{1}N and 13°N). Mar Ecol Prog Ser 234:147–157

Thiel V, Hügler M, Blümel M, Baumann HI, Gärtner A, Schmaljohann R et al (2012) Widespread occurrence of two carbon fixation pathways in tubeworm endosymbionts: lessons from hydrothermal vent associated tubeworms from the Mediterranean Sea. Front Microbiol 3:423

Thompson KF, Miller KA, Currie D, Johnston P, Santillo DS (2018) Seabed mining and approaches to governance of the deep seabed. Front Mar Sci 5:480

Tsurumi M, Tunnicliffe V (2003) Tubeworm-associated communities at hydrothermal vents on the Juan de Fuca Ridge, northeast Pacific. Deep-Sea Res Pt I 50:611–629

Tsurumi M, De Graaf RC, Tunnicliffe V (2003) Distributional and biological aspects of copepods at hydrothermal vents on the Juan de Fuca Ridge, north-east Pacific Ocean. J Mar Biol Assoc UK 83:469–477

Tunnicliffe V (1991) The biology of hydrothermal vents: ecology and evolution. Oceanogr Mar Bio Ann Reu 29:319–407

Tunnicliffe V, Fontaine A (1987) Faunal composition and organic surface encrustations at hydrothermal vents on the southern Juan de Fuca Ridge. J Geophys Res Solid Earth 92 (B11):11303–11314

Tunnicliffe V, Jensen RG (1987) Distribution and behaviour of the spider crab *Macroregonia macrochira* Sakai (Brachyura) around the hydrothermal vents of the northeast Pacific. Can J Zool 65:2443–2449

Tunnicliffe V, Garrett JF, Johnson HP (1990) Physical and biological factors affecting the behaviour and mortality of hydrothermal vent tubeworms (vestimentiferans). Deep-Sea Res Pt A 37:103–125

Tunnicliffe V, Embley RW, Holden JF, Butterfield DA, Massoth GJ, Juniper SK (1997) Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge. Deep-Sea Res Pt I 44:1627–1644

Tunnicliffe V, Baross J, Gebruk A, Giere O, Koschinsky A, Reysenbach A et al (2003a) Group report: what are the interactions between biotic processes at vents and physical, chemical, and geological conditions. In: Halbach P, Tunnicliffe V, Hein J (eds) Energy and Mass Transfer in Marine Hydrothermal Systems. Dahlem Press, Berlin, pp 251–270

Tunnicliffe V, Juniper S, Sibuet M (2003b) Reducing environments of the deep-sea floor. In: Tyler P (ed) Ecosystems of the world: the Deep Sea. Elsevier, Amsterdam, pp 81–110

Tunnicliffe V, Rose J, Bates A, Kelly N (2008) Parasitization of a hydrothermal vent limpet (Lepetodrilidae, Vetigastropoda) by a highly modified copepod (Chitonophilidae, Cyclopoida). Parasitology 135:1281–1293

Tunnicliffe V, St. Germain C, Hilário A (2014) Phenotypic variation and fitness in a metapopulation of tubeworms (*Ridgeia piscesae* Jones) at hydrothermal vents. PLoS One 9:e110578

Turner PJ, Thaler AD, Freitag A, Collins PC (2019) Deep-sea hydrothermal vent ecosystem principles: identification of ecosystem processes, services and communication of value. Mar Policy 101:118–124

Tyler PA, Young CM (1999) Reproduction and dispersal at vents and cold seeps. J Mar Biol Assoc UK 79:193–208

Urcuyo IA, Massoth GJ, Julian D, Fisher CR (2003) Habitat, growth and physiological ecology of a basaltic community of *Ridgeia piscesae* from the Juan de Fuca Ridge. Deep-Sea Res Part I 50:763–780

Urcuyo I, Bergquist D, MacDonald I, VanHorn M, Fisher C (2007) Growth and longevity of the tubeworm *Ridgeia piscesae* in the variable diffuse flow habitats of the Juan de Fuca Ridge. Mar Ecol Prog Ser 344:143–157

van der Land J, Norrevang A (1975) Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera). K Dan Vidensk Selsk Biol Skr 21:1–102

Van Dover CL (2000) The ecology of Deep-Sea hydrothermal vents. Princeton University Press, Princeton, 424 p

Van Dover CL (2002) Community structure of mussel beds at deep-sea hydrothermal vents. Mar Ecol Prog Ser 230:137–158

Van Dover CL, Arnaud-Haond S, Gianni M, Helmreich S, Huber JA, Jaeckel A et al (2018) Scientific rationale and international obligations for protection of active hydrothermal vent ecosystems from deep-sea mining. Mar Policy 90:20–28

Vogt PR, Cherkashev G, Ginsburg G, Ivanov G, Milkov A, Crane K, Sundvor A, Pimenov N, Egorov A (1997) Haakon Mosby mud volcano provides unusual example of venting. EOS Trans AGU 78(48):549–557

Von Rad U, Berner U, Delisle G, Doose-Rolinski H, Fechner N, Linke P et al (2000) Gas and fluid venting at the Makran accretionary wedge off Pakistan. Geo-Mar Lett 20:10–19

Vrijenhoek RC (2010) Genetics and evolution of deep-sea chemosynthetic bacteria and their invertebrate hosts. In: Kiel S (ed) The vent and seep biota: aspects from microbes to ecosystems. Springer, Dordrecht, pp 15–49

Watanabe H, Fujikura K, Kojima S, Miyazaki J-I, Fujiwara Y (2010) Japan: vents and seeps in close proximity. The vent and seep biota. Springer, New York, pp 379–401

Webb M (1969) *Lamellibrachia barhami*, gen. nov., sp. nov. (Pogonophora), from the northeast Pacific. Bull Mar Sci 19:19–47

Weigert A, Helm C, Meyer M, Nickel B, Arendt D, Hausdorf B et al (2014) Illuminating the base of the annelid tree using transcriptomics. Mol Biol Evol 31(6):1391–1401

Weiss MC, Sousa FL, Mrnjavac N, Neukirchen S, Roettger M, Nelson-Sathi S et al (2016) The physiology and habitat of the last universal common ancestor. Nat Microbiol 1:16116

Woolley SN, Tittensor DP, Dunstan PK, Guillera-Arroita G, Lahoz-Monfort JJ, Wintle BA et al (2016) Deep-sea diversity patterns are shaped by energy availability. Nature 533:393

Yorisue T, Inoue K, Miyake H, Kojima S (2012) Trophic structure of hydrothermal vent communities at Myojin Knoll and Nikko Seamount in the northwestern Pacific: implications for photosynthesis-derived food supply. Plankton Benthos Res 7:35–40

Young CM, Vázquez E, Metaxas A, Tyler PA (1996) Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps. Nature 381:514

Zal F, Leize E, Lallier FH, Toulmond A, Van Dorsselaer A, Childress JJ (1998) S-Sulfohemoglobin and disulfide exchange: the mechanisms of sulfide binding by *Riftia pachyptila* hemoglobins. Proc Natl Acad Sci USA 95:8997–9002

Bryozoans: The 'Forgotten' Bioconstructors

C. Lombardi, P. D. Taylor, and S. Cocito

Abstract Bryozoan constructions have been present in all major climatic zones of marine ecosystems for the past 450 million years, since the Early Ordovician. Some fossil species possessed large bioconstructional colonies that would have provided habitats for other marine animals and plants, just as similar colonies do at the present day. Today, biogenic calcareous structures vary greatly in size, ranging from a few centimetres to many kilometres, and in complexity, forming composite structures that are distributed globally. Despite the role of bioconstructional bryozoan species in promoting marine biodiversity worldwide, they have been excluded from several protection strategies. Information emerging from the literature provides only a very incomplete picture of the role of bryozoans as bioconstructors at the global level. The ability of bryozoans to form long-lasting carbonate structures makes them important carbonate producers, with a significant role in the carbon cycle. Bryozoan reefs are facing the challenges of climate change, which will be detrimental for some species and their associated biota. Better knowledge of the contribution of bryozoans to the carbon stock and the ecosystem services they provide will be of great importance to ensure their protection and to understand their potential in adaptation strategies under future ocean scenarios.

Keywords Bryozoan bioconstructions · Biodiversity · Fossil and recent bioconstructors · Climate change · Ecosystem services · Conservation

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1 Introduction

Bryozoans are able to develop bioconstructions including biogenic reefs (Hiscock 2014). Structurally complex ecosystems associated with bioconstructions are characterized by a higher density and greater macroinvertebrate species richness than most soft-sediment habitats. As biodiversity promoters, they increase benthic diversity by providing hard substrates with a complex architecture on which other species can settle, hide and seek protection, resulting in assemblages that are highly diverse and taxonomically complex (Cocito 2004; Wood et al. 2012; Lombardi et al. 2013). As well as their roles as bioconstructional organisms, bryozoans provide the foundation for many other ecosystem processes and can be pivotal for conservation (Crain and Bertness 2006). To date, biogenic bryozoan reefs are not protected by the European Habitats Directive (Council Directive 92/43/EEC) but in order to achieve the Good Environmental Status for marine habitats (EU 2020)—one of the main goal of the Marine Strategy Framework Directive (MSDF)—the conservation of biological diversity at species, habitat and ecosystem levels, including bryozoans, is necessary. This will help individual countries, and the EU as a whole, to improve and implement ecosystem-based marine spatial management.

There is growing evidence of the potential of bryozoan biogenic reefs to provide important ecosystem services from the tropics to polar environments, and from shallow seas to the deep ocean (Cocito 2004; Wood et al. 2012; Barnes 2015, 2016; Santagata et al. 2018). In the deep ocean, bryozoans together with sponges, cold-water corals, hydroids etc. form structurally complex ecosystems. These ecosystems are diverse in terms of community composition and structure, the geomorphological features they create and their geographical and bathymetric distributions. They are often impacted by deep-sea fisheries (i.e. bottom trawling), leading the FAO to categorize some of these organisms as indicators of vulnerable marine ecosystems (VMEs), meaning areas that would take very long times to recover or even would fail to recover after disturbance. Despite the presence of bryozoans in these deep ecosystems (Rosso et al. 2010; Santagata et al. 2018; Lombardi pers. obs.), they are not yet included in the VMEs list of taxa.

The aim of the present chapter is to provide an insight into bioconstructional bryozoans, summarizing aspects of their biology, ecology and distribution, and to highlight their vulnerability—but also their potential for mitigation and adaptation strategies—and thus to encourage their conservation globally.

2 Bryozoa: A Brief Review

Once referred to as ‘ectoprocts’, bryozoans are exclusively colonial animals formed of tens to thousands of modular units called zooids. Each zooid, generally less than a millimetre in size, comprises a polypide and a cystid. The polypide consists of a lophophore—an inverted cone or bell-shaped ring of tentacles for capturing planktonic food—and a U-shaped gut. The cystid comprises an organic cuticle, mineralized skeleton (in some taxa) and peritoneum (layer of cells of mesodermal origin; Hayward and Ryland 1999; Taylor 2005; Lombardi et al. 2013). The lophophore of the polypide can be extended to enable feeding, or retracted into the safety of the cystid.

Zooids belonging to the same colony are genetically identical: all originate from the ancestrula (founder zooid), which is formed by the metamorphosis of a larva, adding new zooids via asexual budding. The zooids of bryozoan colonies are commonly polymorphic and include autozooids, which filter feed on phytoplankton, as well as in some species structurally supportive kenozooids, specialized reproductive gonozooids and defensive avicularia with jaw-like mandibles. Bryozoans reproduce sexually and have a free-swimming larval stage which, in most species, has a short duration. The great majority of bryozoan colonies are benthic and sessile, typically attached to rocks, shells, seaweeds, other animals or other firm substrates, although a few species are free-living (Taylor 2020; Ryland 1970).

Colony forms range from encrusting uni- and multilaminar, to branches of radially arranged zooids, or erect uni- and bilaminate colonies (Hageman et al. 1998). Encrusting bryozoans create nano-habitats and act functionally as 'binders', which unite and expand other erect biogenic constructions (Cocito 2004). Within all these structural forms, rigidity and shape (lobes, sheets, discs, cylinders, nodules, spheroids or ellipsoids, cones and domes) are important, as these features potentially increase the types and numbers of species that can utilize the bryozoan colony as a habitat. Colony size varies enormously (Barnes and De Grave 2002), depending on environmental conditions and species characteristics. Some species attain sizes of 50–500 mm in three dimensions (Batson and Probert 2000; Cocito et al. 2003; Lombardi et al. 2008) and exceptionally can grow much larger, 700–1000 mm across (Cocito et al. 1998, 2004; Barnes and De Grave 2002). Although there is little data on longevity and growth rates, colonies can live for decades; e.g. *Melicerita obliqua* colonies in Antarctica were found to be up to 50 years old (Brey and Gerdes 1998). Most species have slow growth rates (Ryland 1977; Winston 1983); nevertheless, a few studies have reported growth rates of 30–40 mm/year (e.g. *Cellaria sinuosa* from the English Channel (Bader and Schäfer 2005) and *Pentapora fascialis* from the Ligurian Sea (Cocito et al. 1998)) (Fig. 1).

The phylum Bryozoa is moderately diverse, estimated in 2013 to contain 5869 living species (Bock and Gordon 2013), and has a good fossil record dating back to the Early Ordovician (Taylor and Ernst 2004). Most extant bryozoan species are marine and belong to the order Cyclostomata in the class Stenolaemata or the dominant order Cheilostomata in the class Gymnolaemata. The focus of this chapter is on bryozoans with calcified exoskeletons—Stenolaemata and Cheilostomata—because they are able to act as bioconstructors, providing habitat over timescales of years to decades (Smith et al. 2001). In contrast, species belonging to two less diverse taxa (class Phylactolaemata; order Ctenostomata in the class Gymnolaemata) lack mineralized skeletons. Large carbonate bryozoans have been categorized as 'frame-builders' (Duncan 1957). Here, we use the term 'frame-building' for those species that regularly grow to ≥50 mm in three dimensions, a size considered relevant as complex habitat for associated macroinvertebrate or algal species

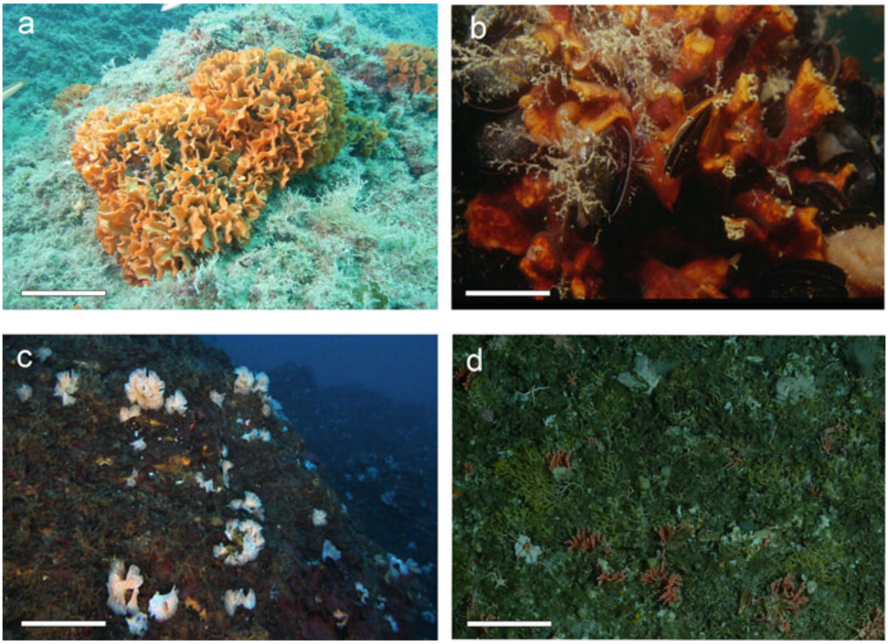

Fig. 1 Recent bioconstructional bryozoans from shallow and deep habitats. (**a**) Large colony of the frame-building bryozoan *Pentapora fascialis* in the Ligurian Sea (depth: 20 m); (**b**) Orange colonies of the encrusting bryozoan *Schizoporella errata* hosting mussels, hydroids and ascidians (depth: 50 cm); (**c**) *Reteporella* sp. colonies from the Panarea Island underwater volcano chimney of Basiluzzo (Italy) (depth: 70 m); (**d**) Deep bryozoan reefs from the Ross Sea (depth: 885 m). Scale bars: (**a**) 15 cm; (**b**) 5 cm; (**c**, **d**) 20 cm

(Wood et al. 2012). Frame-builders contribute significantly to the structural complexity of the substratum over an area greater than a few square metres, as single or multiple species.

3 Fossil Bryozoan Bioconstructions

Bioconstructional bryozoans range back almost to the earliest fossil record of the phylum in the Tremadocian stage of the Early Ordovician. Indeed, some of the oldest known metazoan reefs were constructed by bryozoans. These are found in the Fenhsiang Formation of the Yangtze Platform in central China and consist of numerous closely spaced, bifurcating columns formed by stacked domes of the esthonioporate genus *Nekhorosheviella*, each dome about 10–15 mm in diameter and 5–10 mm high (Cuffey et al. 2012; Adachi et al. 2012). Frame-building bryozoans have been described elsewhere in the fossil record but in general have become less common through geological time, largely supplanted by corals and sponges. Nevertheless, it is likely that many extinct bryozoans were important in providing habitats for other invertebrates. A good example is provided by a Miocene fossil assemblage from onshore northwest Nelson in New Zealand which contains some of the same bioconstructional bryozoan genera that today host numerous other animals in the nearby Tasman Bay (Gordon et al. 1994).

Fossil bioconstructional bryozoans exhibit a similar range of colony forms to bioconstructional bryozoans living at the present day. Most had ramose branching colonies, which in some cases were articulated during life, but others developed foliaceous colonies of convoluted, flattened fronds. They belong to a range of extinct orders (e.g. trepostomes and cystoporates) and extant orders (cheilostomes and cyclostomes). Dense accumulations of bryozoan colonies can be found in sedimentary rocks through most of the Phanerozoic. For example, Permian limestones in the Glass Mountains of Texas are replete with bryozoans (Fig. 2a), which in some cases

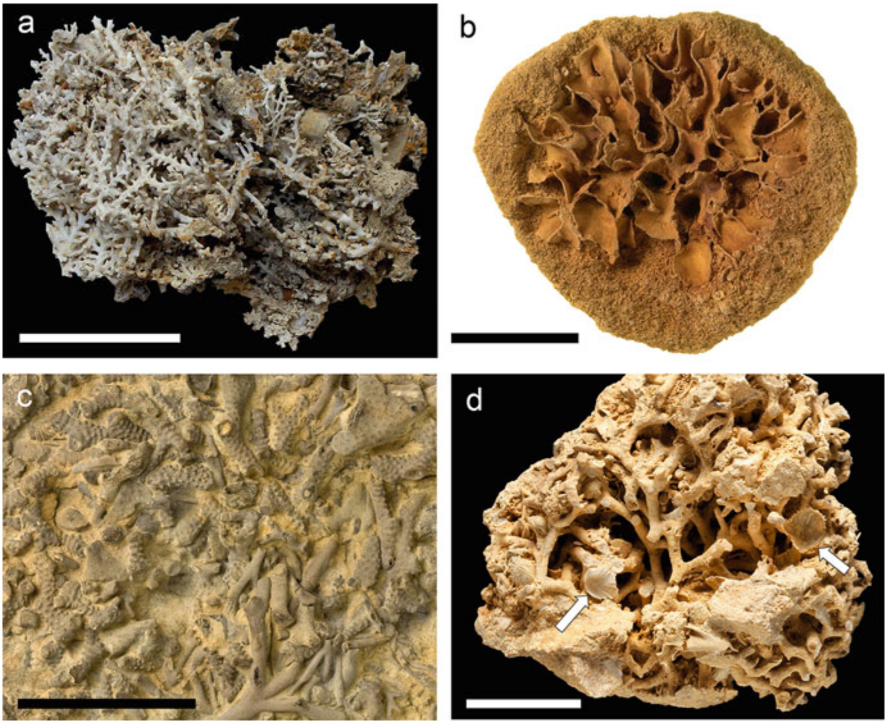

Fig. 2 Fossil bioconstructional bryozoans. (**a**) Silicified Permian acanthocladiids (order Fenestrata) forming small bioherms in the Glass Mountains, Texas, United States (Smithsonian Institution, Washington DC). (**b**) Large colony of the cheilostome bryozoan *Pentapora lacryma* from the Pliocene Coralline Crag Formation of Suffolk, England (Natural History Museum, London). (**c**) Bedding plane surface of an Ordovician limestone from the Cincinnati region of Ohio strewn with broken branches of bushy trepostome bryozoans (Natural History Museum, London). (**d**) Jurassic cyclostome bryozoan *Ceriocava corymbosa* from Calvados, France, with two small oysters (arrowed) cemented to the branches (Natural History Museum, London). Scale bars: (**a**, **b**, **c**) 5 cm; (**d**) 2 cm

may have formed small reefs or thickets (Zimmerman and Cuffey 1987). In much younger rocks, Hoffmeister et al. (1967) described a spectacular example of bryozoans in the Pleistocene Miami Limestone of southern Florida. The bryozoan facies of this limestone consist almost entirely of large multilayered colonies of the cheilostome *Schizoporella floridana*. At least 70% of the rock is estimated to be made of bryozoans. As the bryozoan facies of the Miami Limestone covers a total area of about 3000 km and can be often 2–3 m thick, the total volume of bryozoans may exceed 5 million cubic metres.

Large fossil bryozoan colonies are occasionally preserved intact (Fig. 2b, d), but more often they were broken up after death and survive in the fossil record as branch fragments covering bedding planes (Fig. 2c). Because the great majority of any associated animals and plants would have lacked fossilizable hard parts, it is difficult to evaluate the overall ecological importance of bioconstructional fossil bryozoans. The likelihood that bryozoans did host other organisms is, however, clear from the routine presence of skeletonized encrusters (e.g. oysters and serpulid polychaetes; Fig. 2d) on colony surfaces, as well as the trace fossils made by borers penetrating the skeletons of potential bioconstructional bryozoans.

A striking feature of the fossil history of bryozoans is that species with large and well-calcified colonies were distributed pan-globally during the Palaeozoic, whereas nearly all such bryozoans are found at higher latitudes in Mesozoic and Cenozoic deposits (Taylor and Allison 1998). Thus, the role of bryozoans as habitat formers is likely to have been much greater in the Palaeozoic tropics than it has been in equatorial seas during the last 250 million years.

4 Recent Bryozoan Bioconstructions

Nowadays, bryozoans are fairly ubiquitous across aquatic habitats from lakes to estuaries, shorelines to the deep sea and the tropics to polar oceans. They are found most commonly in continental shelf environments, attached to hard (e.g. rocks, shells) or firm (e.g. marine plants) substrata in places where water movement is relatively fast and consistent, thus guaranteeing an adequate supply of phytoplankton as a food resource (Taylor 2000; Wood et al. 2012). Conversely, high rates of sedimentation and/or disturbance as well as stagnant, low-oxygen conditions are unfavourable to bryozoans.

Globally, Antarctica holds the greatest expanses of habitat-forming bryozoans (Wood et al. 2012), with extensive communities covering >1000 km in the Weddell and Lazarev seas (Gutt and Starmans 1998) and densely structured communities in the Ross Sea (Parker and Bowden 2010). Bryozoan diversity in the Southern Ocean is estimated at more than 400 species, with the majority of species belonging to cheilostomes and cyclostomes (Barnes and Downey 2014; De Broyer and Danis 2011; Figuerola et al. 2014; Rosso 1992, 1994; Rosso and Sanfilippo 2000; Pabis et al. 2014) forming encrusting and erect colonial forms that are able to build significant biogenic reefs. Currently, at least 25% of all bryozoan species found in the Southern Ocean are deemed to be major bioconstructors, with taxa belonging to the genus- and species-rich families Flustridae and Cellaridae being particularly important in this role. Unusually, cyclostome bryozoans, which are otherwise rarely abundant (cf. the New Zealand continental shelf), have also been found to be bioconstructors in the Southern Ocean (Gutt and Starmans 1998). Over 95% of the bioconstructional Antarctic bryozoan species are distributed only on the Antarctic shelf (0–1000 m depth); however, important habitat-forming species (e.g. *Melicerita obliqua*) have been found at depths of up to 5000 m in the Weddell Sea. Although habitat-forming bryozoan communities have been documented worldwide (Wood et al. 2012), little is known about the species assemblages that create these unique habitats and their importance to Antarctic shelf communities as a whole. Santagata and coauthors (2018) reached the conclusion that flustrid bryozoans are more prevalent in the habitat-forming bryozoan communities in the Ross Sea and northern Palmer Archipelago/Scotia Sea. In contrast, sites in the eastern Weddell Sea investigated by these authors comprised mainly moderately to robustly mineralized, cellariiform, lepraliomorph and umbonulomorph cheilostome bryozoans. A research campaign of the Italian National Program for Antarctic Research conducted on Ross Sea banks in 2017 revealed a dominance of well-calcified bioconstructional bryozoans between 250 and 900 m deep on the Ross Sea banks (Pennel Banks and Rosse Sea Platform) (Lombardi pers. obs.). Bilaminar species (e.g. *Cellarinella watersi*, *Cellarinella rogickae*) and unilaminar species (e.g. *Lageneschara lyrulata*, *Thrypticocirrus contortuplicata*, *Pemmatoporella marginata* and *Bostrychopora dentata*) are dominant (Fig. 3). Species compositional differences observed among Antarctic sites and depths are likely influenced by the spatial and temporal variability inherent in seasonal ice scour, carbonate chemistry and primary productivity (Santagata et al. 2018).

In New Zealand, bryozoan bioconstructions are also abundant, providing habitats over hundreds of square kilometres of seafloor. The cheilostome *Celleporaria agglutinans* is widespread around New Zealand and Australia (Flynn et al. 2019) where it forms extensive beds up to 272 km^2 at depths of 10–35 m and is known as the ‘Tasman Bay Coral’. A thicket-forming cyclostome bryozoan, *Cinctipora elegans*, forms beds around 10 km long and 0.5 km wide. It provides an important habitat for juvenile blue cod on the Otago shelf and is the major frame-builder of biogenic reefs in Foveaux Strait between the South Island and Stewart Island, supporting invertebrates such as sponges, ascidians and the commercially important Bluff oyster, *Tiostrea chilensis* (Cranfield et al. 2014). Five other frame-building bryozoans occur in New Zealand in ecologically significant densities: the cyclostomes *Hornera robusta* and *Hornera foliacea* and the cheilostomes *Celleporina grandis*, *Hippomenella vellicata* and *Adeonellopsis* spp.

Other areas where habitat-forming bryozoans are abundant include the North Pacific around Japan, the northern Mediterranean, the southern edge of the North Sea and through into the English Channel, the waters northwest of the United Kingdom and the lagoons of South Australia and brackish inland waters of the Netherlands (Cocito 2004).

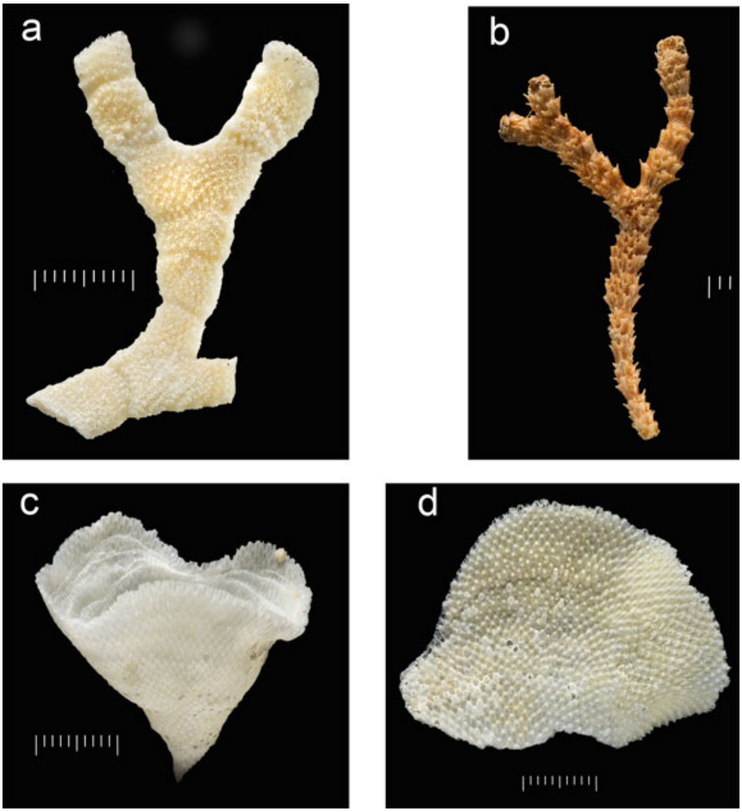

Fig. 3 Antarctic species from Ross Sea Platform (320 m). Bilaminar species (**a**) *Cellarinella rogickae*, (**b**) *Cellarinella* sp.; unilaminar species (**c**) *Thrypticocirrus contortuplicata*, (**d**) *Lageneschara lyrulata*. Scale bars (small unit): 1 mm

A recent update on the Mediterranean benthic fauna reported 556 species, 212 genera and 93 families (Rosso and Di Martino 2016). Some of these species contribute to bioconstructions, which vary in spatial extent, structure and taxonomic composition, being generally monospecific in high-energy, shallow-water environments but paucispecific in open, deep-water habitats. Bryozoan-dominated assemblages containing numerous species often occur in cryptic microhabitats (Harmelin 1985). In the Mediterranean, the main bioconstructional orders (Cyclostomata and Cheilostomata) are represented by 75 and 424 species, respectively, although many of these are encrusters or small erect species having no significant bioconstructional roles. The Mediterranean bryozoan fauna accounts for 9.6% of global bryozoan diversity, with cheilostomes fauna representing 8.6% of the global value and cyclostomes 13.8% (Rosso 2003; Rosso and Di Martino 2016). Interestingly, the richest bryozoan diversity belongs to Coralligenous (219 spp.) and the dark and semi-dark cave biocoenoses (220 spp.). Within all of these habitats, which are particularly suitable for bryozoans because of the availability of permanent hard substrates and reduced light levels, bioconstructional taxa are often dominant (i.e. the genera *Pentapora*, *Smittina*, *Reteporella*, *Adeonella* and *Myriapora*). Thus, bioconstructional bryozoan colonies provide habitat for other species that would not be able to cope with the depleted (caves) or overexploited substrates (Coralligenous), with intense competition for food and space (see Harmelin 1985, 1997, 2000; Rosso et al. 2013).

Bryozoan bioconstructions from the Mediterranean Sea comprise encrusting species forming dome-like colonies originating from multilaminar sheets and/or large erect branching colonies. Among the encrusters, there are perennial cheilostomes such as *Schizoporella* spp., *Schizomavella* spp., *Pentapora ottomulleriana*, *Schizobrachiella sanguinea*, *Rhynchozoon* spp., *Calpensia nobilis* and *Reptadeonella violacea*, characterized by fast and continuous growths. These species are able to colonize a wide range of substrates including living organisms, organogenic structures and different types of inert substrates, both natural and artificial (Cigliano et al. 2007; Cocito et al. 2012; Poluzzi and Coppa 1991). Regarding large bush-like well-skeletonized colonies, of special interest are *Pentapora* spp., *Reteporella* spp., *Smittina cervicornis*, *Myriapora truncata*, *Adeonella* spp. and *Schizoretepora serratimargo* because of their ability to act as frame-builders on semi-dark rocky environments as well as on unstable substrates (Cocito 2004; Cocito et al. 2004; Lombardi et al. 2008; McKinney and Jackson 1989; Novosel 2005).

Size and longevity are key characteristics which allow these species to erect three-dimensional structures that provide a substrate for huge variety of organisms to settle on such as bacteria, algae, sponges, hydrozoans, worms, molluscs and other bryozoans, but also inner cavities offering protection from predation, wave scour and high light irradiance.

Some of the richest associations recorded include 92 bryozoan species plus other invertebrates and fishes found living on *Celleporaria agglutinans* and *Hippomenella vellicata* beds in New Zealand (Bradstock and Gordon 1983).

Extensive patches of spheroidal colonies of a non-native bryozoan, *Schizoporella errata*, constitute 'bryoliths', 2–20 cm in diameter and 1 m across, forming reef-like structures on mudflats in San Francisco Bay, California (Zabin et al. 2010). These bryoliths facilitate colonization of the mudflats, hosting 50 species of algae and invertebrates that live on and within them. In the Mediterranean, 84 species were counted associated with mound-like *Pentapora fascialis* colonies in the Ligurian Sea (Ferdeghini and Cocito 1999), 58 epibiont species with *Cellaria salicornioides* branches in the Adriatic Sea (McKinney and Jaklin 2000) and 36 species on or inside buildups of the encrusting bryozoan *Schizoporella errata* growing on wharf piles in harbours (Ferdeghini and Cocito 1999). It is worth emphasizing that increase in the size of bryozoan bioconstructions induces modifications not only in the composition of the associated biota but also in the shape and growth rate of these structures (Cocito 2004) (Table 1).

Table 1 Occurrence of bryozoan constructions from different geographic areas: main bryozoan frame-builders, location, habitat formed and extent, associated biota and references

Bryozoan frame builders	Location	Habitat formed, extent	Associate biota diversity	References
Carbasea sp., *Nematoflustra* sp., *Isosecuriflustra* sp., *Kymella* sp., *Melicerita obliqua,* *Reteporella* sp., *Adelascopora* sp., *Bostrychopora* sp., *Cellarinella* sp., *Systenopora* sp.	Antarctica (Ross Sea, Scotia and Weddell seas)	0.6–103.3 m^2		Santagata et al. (2018)
Melicerita obliqua, Cellarinella sp., *Lageneschara lyrulata, Cellaria* spp., *Cellarinella* sp., *Austroflustra vulgaris*	Weddell and Lazarev Seas, Antarctica	>1000 km coastline sampled	Soonges, tunicates, bryozoans, ophiuroids, molluscs	Gutt and Starmans (1998)
Celleporaria agglutinans, Hippomenella vellicata	Tasman Bay, New Zealand	Beds up to 272 km^2	Bryozoans, serpulids, bivalves, foraminiferans, gastropods, ophiuroids, polychaetes, sponges, ascidians, holoturians, fishes	Bradstock and Gordon (1983)
Celleporaria agglutinans, Galeopsis porcellanicus, Galeopsis polyporus, Hornera robusta	Separation Point, South Island, New Zealand	Massive, heavy clumps attaining up to 50% cover and 50 cm height (patch reefs), area of 118 km^2		Bradstock and Gordon (1983); Grange et al. (2003)
Hippomenella vellicata	Torrent Bay, South Island, New Zealand	Coarse honeycombs up to 30 cm across and 15 cm tall, >300 km^2		Saxton (1980); Bradstock and Gordon (1983)
Cintipora elegans	South New Zealand	Linear reefs 10 km × 0.5 km		Bradstock and Gordon (1983)
Celleporaria agglutinans, Hornera spp., *Diaperoecia purpurascens, Heteropora neozelanica, Calvetia osheai,*	North Island, New Zealand	Thicket/patch reef ~100 km^2, thickets may be >100 km^2	Sponges, bryozoans, molluscs, cnidarians, arthropods, echinoderms, tunicates	Taylor and Gordon (2003)

(continued)

Table 1 (continued)

Bryozoan frame builders	Location	Habitat formed, extent	Associate biota diversity	References
Galeopsis porcellanicus, Spiritopora perplexa, Arachnopusia unicornis, Steginoporella perplexa				
Cinctipora elegans, Hornera foliacea, Hornera robusta, Celleporina grandis, Cellaria immersa, Cellaria tenuirostris, Celleporaria agglutinans, Adeonellopsis spp., *Hippomenella vellicata, Tetrocycloecia neozelanica, Diaperoecia purpurascens, Galeopsis polyporus, Hippellozoon novaezelandiae, Arachnopusia unicornis*	Otago shelf, South Island, New Zealand	Thicket/patch reef, structures 5–50 cm distributed across 500 km^2	Bryozoans, annelids, arthropods, molluscs, tunicates, poriferans, echinoderms, cnidarians, brachiopods, sipunculids, platyhelminthes, fish	Wood (2005); Probert et al. (1979)
Conopeum aciculata	South Australia		Bryozoans, serpulids	Bone and Wass (1990)
Celleporaria albirostris, Parasmittina munita, Rhyncozoon rostratum, Rhyncozoon tuberculatum,, Schizoporella cornuta, Smittipora americana, Steginoporella magnilabris, Stylopoma spongites	Bahamas	Biogenic reef, 0.3–3 m tall, up to 10 m across		Cuffey et al. (1977)

(continued)

Table 1 (continued)

Bryozoan frame builders	Location	Habitat formed, extent	Associate biota diversity	References
Schizoporella errata	Ubatuba, Brazil	Encrusters, cavity dwellers, fillers, many cm in dimension	Annelids, arthropoda, molluscs, echinoderms, sipunculans, echiuran, algae, poriferans, cnidarians, tunicates	Morgado and Tanaka (2001)
Schizoporella errata	Bermuda	Encrusters, cavity dwellers, fillers, many cm in dimension	Encrusters/cavity dwellers/fillers, many cm in dimension	Cuffey and Fonda (1976)
Myriapora orientalis, Phidolopora elongata	Bering Seas	Intensive spots 10 cm tall, up to 3 × 5 m across, individual colonies up to 12 cm tall, covering continuously 200 m^2	Bryozoans, molluscs, echinoderms, tunicates, poriferans, cnidarians, annelids, arthropoda, algae	Grischenko and Ivanjushina (2002)
Cellarinella spp., *Melicerita obliqua, Cellaria* spp.	Norvegia, NE Weddell Sea	Thickets >65% cover		Bader (2001a)
Pentapora foliacea	Bristol Channel, UK	1 colony m^2 over large areas		Natural England (2011)
Einhornia crustulenta	The Netherlands	Reef up to 1 m high, tens of m across, in waterways over 300 km^2	Bryozoans, serpulids, hydroids, gatropods, isopods, polychaetes, plants, algae	Bijma and Boekschoten (1985)
Cellaria salicornioides	Croatia	Meadow 80–90% cover, 5–10 cm thick, extends >100 × 100 m	58 species (algae, sponges, cnidarians, annelids, bryozoans, molluscs, ascidians)	McKinney and Jaklin (2000)
Cellaria sinuosa, Cellaria fistulosa	Roscoff, France	Dense patch thickets, >150 km^2	Bryozoans, molluscs, arthropoda, annelids, foraminifera, cnidarians, *Ciliophora*	Bader (2001b)
Adeonella calveti, Myriapora truncata, Pentapora fascialis, Reteporella grimaldii, Smittina cervicornis, Turbicellepora avicularis	Marseille, France	Outcrops on rock wall		Harmelin and Capo (2001)

(continued)

Table 1 (continued)

Bryozoan frame builders	Location	Habitat formed, extent	Associate biota diversity	References
Flustra foliacea, Securiflustra securifrons	Scotland	Dense band 1 m wide, turf of many square metres	Bryozoans, tunicates, poriferans, cnidarians, echinoderms	Connor et al. (2004)
Pentapora fascialis	La Spezia, Italy	Outcrops on rock wall	Molluscs, cnidarians, annelids, crustaceans, echinoderms, ascidians, bryozoans, fishes	Ferdeghini and Cocito (1999); Cocito (2004)
Schizoporella errata	Spain	Outcrops 15–25 cm across	Bryozoans, molluscs, cnidarians, annelids, crustaceans, echinoderms, ascidians, fishes	Maluquer (1985)
Schizoporella errata	La Spezia, Italy		Algae, sponges, hydroids, polychaetes, molluscs, bryozoans, crustaceans, ascidians, fishes	Ferdeghini and Cocito (1999)
Schizoporella errata	San Francisco Bay, California	20 cm × 1 m	Algae, other invertebrates	Zabin et al. (2010)

5 Mineralization Patterns Through Time

Cheilostomes and cyclostomes, as well as related extinct orders of stenolaemates (superorder Palaeostomata), have biomineralized skeletons of calcium carbonate. Bryozoans utilize two biominerals, calcite and aragonite. In all stenolaemates, the skeleton is made of calcite, but in cheilostomes it may be monomineralic calcite, monomineralic aragonite or a bimineralic combination of calcite and aragonite. As the earliest fossils of cheilostomes date from the Late Jurassic, no aragonitic bryozoans are known in the Palaeozoic. In fact, aragonitic bryozoans did not appear until the Late Cretaceous or possibly even later. Several clades of cheilostomes have independently evolved skeletons consisting wholly or partly of aragonite (Taylor et al. 2009). A trend through the Cenozoic towards aragonite biomineralization may have been driven by changing seawater chemistry, with an increase in Mg/Ca favouring secretion of aragonite over calcite, particularly in warmer waters.

In summary, all Ordovician–Early Cretaceous bryozoans appear to have had stable calcite skeletons. The high content of Mg in some of these (e.g. Ma et al. 2014) led to neomorphic changes, with the high-Mg calcite converting to low-Mg calcite containing microdolomite inclusions, but the skeleton as a whole remained intact during fossilization. Cheilostomes with aragonite in their skeletons probably first appeared in the Late Cretaceous. They initially comprised bimineralic taxa possessing skeletons of calcite overlain by aragonite, but some younger Cenozoic cheilostomes had skeletons consisting entirely of aragonite. The fossilization potential of such entirely aragonitic bryozoans is less than that of calcitic forms because of the greater solubility of aragonite during diagenesis. Therefore, bioconstructional cheilostome bryozoans with aragonitic skeletons, which are more common in the tropics (Taylor et al. 2016), may be lost entirely from the fossil record.

6 Bryozoan Bioconstructions Under Climate Change

Generally included among organisms forming ‘rocky reef ecosystems’ in official management documents (Bindoff et al. 2019; IPCC 2014), bryozoans as reef-forming organisms are very poorly known. Despite the 450 million-year evolutionary history of this phylum, an adequate understanding is lacking of the evolution and genesis of globally distributed bryoconstructions (Taylor et al. 2015).

In common with nearly all ecosystems, bryozoan bioconstructions are facing increasing pressure from multiple environmental drivers related to climate change. These drivers can produce additive and synergistic (i.e. amplifying) or antagonistic (i.e. dampening) effects, operating at individual, population and ecosystem scales (Boyd et al. 2018). Multiscale environmental signals act simultaneously at different biological levels producing physiological, ecological and evolutionary outcomes. Common ecological responses are modification in the temporal and spatial distribution of species, altered gene expression, physiology, reproduction or behaviour (Riebesell and Gattuso 2015). Some organisms may adapt, but others may not be able to tolerate the present and future rates of environmental change, and thus ecosystems can be altered in assemblage composition, productivity, diversity, trophic structure and nutrient cycling, ultimately affecting the ecosystem services they provide (Soliveres et al. 2016). Numerous research studies using in field and laboratory approaches have been conducted to evaluate the effects of global warming and ocean acidification, and their synergic effects, on different bioconstructional species (see Table 2).

Among Mediterranean and northeastern Atlantic bioconstructional bryozoans, the genus *Pentapora*, extensively studied in modern communities and represented in the fossil record (Fig. 2b), includes species whose colony growth, zooid size and skeletal mineralogy and geochemistry show correlations with seawater temperature (Cocito 2004; Cocito et al. 2004; Cocito and Sgorbini, 2013; Lombardi et al. 2008, 2010, 2013; Pagès-Escolà et al. 2018). Colonies of both *Pentapora foliacea* and *P. fascialis* show growth banding patterns, reflecting seasonal temperature-related variations in carbonate deposition (Patzold et al. 1987; Lombardi et al. 2006, 2008; Knowles et al. 2010). Colony growth, zooid size and skeletal mineralogy (i.e. the proportion of aragonite and Mg level in the calcite) can reflect seasonal as well as anomalous seawater temperature changes (Amui-Vedel et al. 2007; Knowles et al.

Table 2 Bioconstructional bryozoan responses to climate change drivers (factors): temperature and pH. All colonies from natural environments. Experimental approaches: in field and laboratory experiments, number of days of exposure to treatments, species' responses, and references

Species	Exp. approach	Factors	Days of exposure	Species responses	References
Pentapora fascialis 30% calcite 70% aragonite >8 wt% $MgCO_3$	Field	T		Reduced growth in cold water, larger zooids in cold water, higher wt% aragonite in warm waters	Lombardi et al. (2006, 2008, 2010, 2013)
	Field, lab	T	44	Reduced growth rate, decrease in oxygen consumption at high temperatures; species necrosis at 25–26 °C and death at 28–29 °C; skeletal damage, increase in Mg and aragonite content	Pagès-Escolà et al. (2018)
Myriapora truncata 100% calcite 8 wt%$MgCO_3$	CO_2 vents, transplant	T, pH	16, 36, 48, 87, 128	Reduced colony growth, decline in $MgCO_3$ content; increased organic cuticle thickness; upregulation of cuticular protein production	Rodolfo-Metalpa et al. (2010), Lombardi et al. (2010, 2011a)
	Field, lab	T	4	Reduced growth rate, decrease in oxygen consumption at high temperatures; necrosis at 28 °C and death at 30 °C; skeletal damage, increase in Mg content	Pagès-Escolà et al. (2018)
Schizoporella errata 40% calcite 60% aragonite 12wt% $MgCO_3$	CO_2 vents, transplant	T, pH	16, 36, 48, 87, 128	Reduced bud size; reallocation of colony resources to favour feeding zooids over defensive avicularia; skeletal corrosion	Lombardi et al. (2011b)
Calpensia nobilis 80% calcite 20% aragonite 7 wt% $MgCO_3$	CO_2 vents, transplant	T, pH	16, 36, 48, 87, 128	Reduced and retarded colony growth; plasticity of colony development at the growing edge; skeletal corrosion	Lombardi et al. (2015)

2010; Lombardi et al. 2008, 2010; Pagès-Escolà et al. 2018) (Table 2). These observations highlight the utility of *Pentapora* as an indicator of thermal conditions as well as its vulnerability to rising seawater temperatures (IPCC 2014).

Seawater warming in combination with ocean acidification is threatening important bioconstructional species, such as *Myriapora truncata*, a cheilostome bryozoan inhabiting semi-dark environments in the Mediterranean and north Atlantic waters where it promotes habitat complexity and biodiversity. Despite its higher tolerance to raised temperatures compared to *Pentapora fascialis* (Pagès-Escolà et al. 2018), when thermal anomalies occur with high pCO_2 levels, the effects on its physiology are detrimental (Lombardi et al. 2010, 2011a). The synergic effects will act on colony growth and skeleton formation, putting *M. truncata* at risk through exhausting biochemical energy in an attempt to cope with these environmental stressors (Lombardi et al. 2011a) (Table 2).

Warming and acidification are also affecting two encrusting frame-builders, *Schizoporella errata* and *Calpensia nobilis*. The genus *Schizoporella* is globally distributed, from polar to tropical environments, and *S. errata* has been described from the Mediterranean Sea and Atlantic Ocean and is also found as an alien species in the Pacific and Indian oceans, Australia and New Zealand (World Register of Marine Species http://www.marinespecies.org/aphia.php). Thermally tolerant, this shallow-water species grows in harbours and marinas where it develops massive bioconstructions, whose growth attitude is determined by the current conditions (Cocito et al. 2000). This biomineralic species is mainly aragonitic (60 wt%) and has a high content of Mg (12 wt%) in the calcite part of the skeleton. *Schizoporella errata* is extremely vulnerable to high pCO_2 conditions (Lombardi et al. 2011b) (Table 2); thus its bioconstructions may be corroded and unable to mineralize under future oceanic conditions (RCP 8.5, IPCC 2014). *Calpensia nobilis*, widespread in the Mediterranean from 10 to 30 m of depth, is also present in eastern Atlantic southwards along the northwest African coast and northwards to the Gulf of Saint-Malo and the Channel Islands (Zabala 1986; Poluzzi and Coppa 1991). Although temperature does not seem to affect the species, pH conditions could cause reallocation of energy resources within colonies, with preference given to maintenance of existing zooids relative to colony growth (Lombardi et al. 2015) (Table 2). In a future scenario, this species might be able to adapt but with a cost: bioconstructions of smaller size and a reduced number of niches available for hosting biodiversity.

7 The Role and Potential of 'Forgotten' Bioconstructions in Mitigation and Adaptation Strategies

Climate change increases the risk of impacts on ecosystem diversity, quality and services (Bindoff et al. 2019). Among coastal and deep ecosystems, the role of 'biogenic reefs', including those formed by bryozoans, is still under-investigated, and they have been excluded from valuable, heavily used and threated systems globally (cf. coral reefs) (Bindoff et al. 2019). Considered as 'secondary reefs', these important ecosystems are less known; thus the effects of climate change on ecosystem quality and services they provide are still unclear, as well as their potential in mitigation and adaptation strategies.

Ecosystem services or 'Nature's Contribution to People' (Díaz et al. 2018) are provided by the environment and its processes that render benefits and support the well-being of people (Tallis et al. 2010). Ecosystem services are divided into provisional services, regulating services, cultural services and supporting/habitat services, all interconnected to each other (Leadley et al. 2014). Bioconstructional bryozoans provide 'regulating services'—contributing to climate regulation (see Barnes 2015, 2016, discussed below), 'supporting/habitat services'—habitats or ecosystem functions that support or maintain biodiversity but also 'cultural services', product of both human experiencing nature and the availability of nature to provide experiences such as tourism, recreation and aesthetic experiences, similarly to other bioconstructions (Costanza et al. 2017). Despite the neglect of bryozoans even though they are a component of coastal ecosystems and deep benthic communities worldwide (Santagata et al. 2018; Rosso et al. 2010), their global loss or degradation will affect the three services they provide, causing a loss of biodiversity, ecosystem functions, impact of their recreation and cultural values, other than carbon capture and sequestration.

To reduce the scale of the physical changes to the ocean and their environmental impacts, transformative and near-total emission reductions are needed in all sectors of human activity and for all greenhouse gases (Myhre et al. 2013; UNEP 2017). According to the Paris Agreement (UN 2015), 'balance between anthropogenic emissions by sources and removals by sinks of greenhouse gases in the second half of this century' is needed; thus 'mitigation strategies' which bring to a reduction of greenhouse gas emissions and the active removal of greenhouse gases from the atmosphere are requested to all nations. There are two types of ocean-based mitigation approaches: (1) to decrease anthropogenically driven releases of greenhouse gases from the marine environment by maintaining the integrity of natural carbon stores in the coastal zone and (2) the potential to promote additional carbon uptake by marine ecosystems, both in the coastal zone and the open ocean, as a contribution to the additional gigaton-scale uptake (negative emissions) of CO_2 that is needed in most emission pathways that limit global warming to 1.5–2.0 °C (Anderson and Peters 2016).

The potential of biogenic reefs in mitigation strategies is related to their carbon sequestration rate, current carbon stocks (including the stability and permanence of those stocks), geographical area (i.e. their cover), anthropogenic drivers of system loss leading to carbon emissions or removals and emission rates from both degraded and intact states of the reefs. Despite the limited potential attribute by 'biogenic reefs' in IPCC reports (Bindoff et al. 2019), mainly due to the lack of information, recent works (Barnes 2015, 2016) have shown that, in Antarctica, they are very important sites of carbon immobilization (net annual carbon accumulation) by bioconstructional bryozoans, one of the few demonstrable negative feedbacks to climate change. Most polar benthos feeds on phytoplankton. The increased blooms coincident with sea ice losses due to global warming is causing an increase of growth in Antarctic benthos (Meredith et al. 2019), including calcifying bryozoan reefs. Barnes (2015, 2016) highlights strong increases in annual production of shelf seabed carbon in West Antarctic due to bryozoans: $>2 \times 105$ tonnes of carbon per year since the 1980s. Thus, an increased drawdown of ~2.9 × 106 tonnes of carbon resulted per year and then immobilized (=buried) for significant time periods. Carbon held in deep benthos skeletons, which is likely to be buried on death and remain out of the carbon cycle for significant time periods; it won't be available for negative feedbacks to the atmosphere (i.e. mitigation strategy). However, carbon gains from increased phytoplankton blooms because of ice shelf and sea ice losses could be reversed if predicted acidification happens (Barnes 2015). Modelled data (e.g. Orr et al. 2005) suggest insignificant change at typical Antarctic shelf depths before 2060, although it seems likely that in the longer term, acidification could negate many polar carbon immobilization increases. Biologically meaningful levels of acidification change have yet to be reported in West Antarctic seas, and initial change, like temperature and salinity, is occurring at the surface (Antarctic continental shelves are typically 500 m deep), which is important because otherwise raised acidity at the seabed could dissolve newly sequestered carbon (Meredith et al. 2019).

The role of ecosystems in adaptation strategies is well-recognized at the international level, under the United Nations Framework Convention on Climate Change (UNFCCC), the Convention on Biological Diversity (CBD) and the United Nations Convention to Combat Desertification (UNCCD). The IPCC Fifth Assessment Report highlighted that climate change impacts on human settlements and communities could be reduced through coastal protection activities (Wong et al. 2014) including 'Ecosystem Based Adaptation' (*EbA*) which consist on the use of biodiversity and ecosystem services as part of an overall adaptation strategy to help people to adapt to the adverse effects of climate change (Secretariat of the Convention on Biological Diversity 2010). *EbA* uses the range of opportunities for the sustainable management, conservation and restoration of ecosystems to provide services that enable people to adapt to the impacts of climate change (Narayan et al. 2016). It is a people-centric concept but acknowledges that human resilience depends critically on the integrity of ecosystems. Yet ecosystem health alone does not guarantee human resilience, so *EbA* is best implemented as an integrated element of a broader adaptation strategy. *EbA* approaches include, for example, coastal habitat restoration, agroforestry, integrated water resource management, livelihood diversification and sustainable forest management interventions that use nature to reduce vulnerability to climate change (IPCC 2014). This effectively gives natural-based adaptation solutions a cost-effective advantage over built infrastructure, besides providing other co-benefits, including biodiversity conservation, utility and recreational value.

In coastal environments, other than mangroves, seagrass meadows and salt marshes, most of the attention in *EbA* is given to coral reefs, whose traditional conservation measures, aimed at protecting reefs from human activities and allowing natural processes to mitigate human impacts, are being acknowledged as insufficient to address climate change. Instead, restoration measures are being called for restoring these ecosystems and make them more resistant (Rinkevich 2000; Bindoff et al. 2019; Barton et al. 2017). Coral reefs are not the only reefs with a potential as *EbA*. As previously shown, bryozoan reefs have a huge potential in *EbA*: (1) as a sink of carbon and playing a significant role in carbon sequestration (via carbon immobilization in the skeletons and in the sediment), (2) offering habitats that support rich biodiversity and biological productivity within and outside the ecosystems through the aggregation of their biogenic structures and (3) supporting local and international economies with their aesthetic value. However, there is a need to reveal this potential through scientific literature and policy documents. It is urgent to expand the knowledge on their distribution worldwide, in both coastal a deep oceans, and introduce them in conservation strategies, yet being excluded from several directives for marine ecosystem protection. Also, future strategies addressing ecosystem restoration in overexploited areas should consider them as a source, being extremely plastic, some of them potentially able to adapt to the fast-occurring changes, and a valuable source for marine biodiversity.

8 Conclusions

Bryozoan constructions have been present in marine ecosystems for the past 450 million years, since the Early Ordovician. The calcitic skeletons of most species have ensured a rich fossil record of bryozoans since the Ordovician. Bryozoans have inhabited all major climatic zones. Some fossil species possessed large bioconstructional colonies that would have provided habitats for other marine animals and plants, just as similar colonies do at the present day.

Despite the role of bioconstructional bryozoan species in promoting marine biodiversity worldwide (i.e. ‘supporting service’), this phylum has been always considered of secondary importance. As a result, biogenic bryozoan reefs have been excluded from several protection strategies (European Habitats Directive—Council Directive 92/43/EEC, IPCC reports, Vulnerable Marine Ecosystem—FAO). Other than the poor knowledge of the taxon, one possible explanation could be the variability of bryozoan colony forms (see Taylor and James 2013), with shapes that are not easy to quantify. Their ability to colonize different habitats, such as sandy and rocky substrates, dark and semi-dark caves and organic substrates, makes evaluation of their coverage and biomass technically demanding. This, together with difficulties in species-level identification, has led to bryozoans often being neglected in ecological studies. Information emerging from the literature provides only a very incomplete picture of the role of bryozoans as bioconstructors at the global level (Table 1)—the need to fill this knowledge gap should be a priority in future field studies.

Like other marine organisms forming biogenic reefs, bryozoans are facing the challenges of climate change, which will undoubtedly be detrimental for some species and their associated biotas. Better knowledge of bryozoan bioconstructions, their contribution to the carbon stock and the ecosystem services they can provide will be of great importance to ensure their protection and to understand their potential in *EbA* strategies under future ocean scenarios.

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References

Adachi N, Ezaki Y, Liu J (2012) The oldest bryozoan reefs: a unique early Ordovician skeletal framework construction. Lethaia 45:14–23

Amui-Vedel AM, Hayward PJ, Porter JS (2007) Zooid size and growth rate of the bryozoan *Cryptosula pallasiana* Moll in relation to temperature, in culture and in its natural environment. J Exp Mar Biol Ecol 353:1–12

Anderson K, Peters G (2016) The trouble with negative emissions. Science 354:182–183. https://doi.org/10.1126/science.aah4567

Bader B (2001a) Bryozoan communities in the Weddell Sea, Antarctica: a first overview. In: Wyse Jackson PN, Buttler CJ, Spencer Jones ME (eds) Bryozoan studies 2001; proceedings of the 12th International Bryozoology Association Conference, Balkema, pp 1–6

Bader B (2001b) Modern bryomol-sediments in a cool water, high energy setting: the inner shelf off northern Brittany. Facies 44:81–104

Bader B, Schäfer P (2005) Impact of environmental seasonality on stable isotope composition of skeletons of the temperate bryozoan *Cellaria sinuosa*. Palaeogeogr Palaeoclim Palaeoecol 226:58–71

Barnes DKA (2015) Antarctic Sea ice losses drive gains in benthic carbon drawdown. Curr Biol 25 (18):789–790. https://doi.org/10.1016/j.cub.2015.07.042

Barnes DKA (2016) Iceberg killing fields limit huge potential for benthic blue carbon in Antarctic shallows. Glob Change Biol 23:2649–2659. https://doi.org/10.1111/gcb.13523

Barnes DKA, De Grave S (2002) Temporospatial constraints in resources available to and used by hermit crabs: tests of models. Funct Ecol 16:714–726

Barnes DKA, Downey RV (2014) Bryozoa. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, Udekem d'Acoz C d' et al (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 195–199

Barton JA, Willis BL, Hutson KS (2017) Coral propagation: a review of techniques for ornamental trade and reef restoration. Rev Aquac 9:238–256. https://doi.org/10.1111/raq.12135

Batson PB, Proberts PK (2000) Bryozoan thickets off Otago Peninsula. New Zealand fisheries assessment report 2000/46, 31 p

Bijma J, Boekschoten GJ (1985) Recent bryozoan reefs and stromatolite development in brackish inland lakes, SW Netherlands. Senckenberg Marit 17:163–185

Bindoff NL, Cheung WWL, Kairo JG, Arístegui J, Guinder VA, Hallberg R, Hilmi N, Jiao N, Karim MS, Levin L, O'Donoghue S, Purca Cuicapusa SR, Rinkevich B, Suga T, Tagliabue A, Williamson P (2019) Changing ocean, marine ecosystems, and dependent communities. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds) IPCC special report on the ocean and cryosphere in a changing climate. https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/09_SROCC_Ch05_FINAL-1.pdf

Bock PE, Gordon DP (2013) Phylum Bryozoa Ehrenberg, 1831. Zootaxa 3703:67–74

Bone Y, Wass RE (1990) Sub-recent bryozoan-serpulid buildups in the Coorong Lagoon, South Australia. Austral J Earth Sci 37:207–214

Boyd PW, Collins S, Dupont S, Fabricius K, Gattuso JP, Havenhand J (2018) Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change – a review. Glob Chang Biol 24:2239–2261. https://doi.org/10.1111/gcb.14102

Bradstock M, Gordon DP (1983) Coral-like bryozoan growths in Tasman Bay, and their protection to conserve commercial fish stocks. N Z J Mar Freshw Res 17:159–116

Brey T, Gerdes D (1998) High Antarctic macrobenthic community production. J Exp Mar Biol Ecol 231:191–200. https://doi.org/10.1016/S0022-0981(98)00060-4

Cigliano M, Cocito S, Gambi MC (2007) Epibiosis of *Calpensia nobilis* (Esper) (Bryozoa: Cheilostomida) on *Posidonia oceanica* (L.) Delile rhizomes: effects on borer colonization and morpho-chronological features of the plant. Aquat Bot 86:30–36

Cocito S (2004) Bioconstruction and biodiversity: their mutual influence. Sci Mar 68:137–144

Cocito S, Sgorbini S (2013) Long-term trend in substratum occupation by a clonal, carbonate bryozoan in a temperate rocky reef in times of thermal anomalies. Mar Biol 161(1):17–27. https://doi.org/10.1007/s00227-013-2310-9

Cocito S, Sgorbini S, Bianchi CN (1998) Aspects of the biology of the bryozoan *Pentapora fascialis* in the north-western Mediterranean. Mar Biol 131:73–82

Cocito S, Ferdeghini F, Morri C, Bianchi CN (2000) Patterns of bioconstruction in the cheilostome bryozoan *Schizoporella errata*: the influence of hydrodynamics and associated biota. Mar Ecol Progr Ser 192:153–161

Cocito S, Sgorbini S, Peirano A, Valle M (2003) 3-D reconstruction of biological objects using underwater video technique and image processing. J Exp Mar Biol Ecol 297:57–70. https://doi.org/10.1016/S0022-0981(03)00369-1

Cocito S, Novosel M, Novosel A (2004) Carbonate bioformations around underwater freshwater springs in the north-eastern Adriatic Sea. Facies 50:13–17

Cocito S, Lombardi C, Ciuffardi F, Gambi MC (2012) Colonization of Bryozoa on seagrass *Posidonia oceanica* 'mimics': biodiversity and recruitment pattern over time. Mar Biodivers 42:189–201. https://doi.org/10.1007/s12526-011-0104-1

Connor DW, Allen JH, Golding N, Howell KL, Lieberknecht LM, Northen KO, Reker JB (2004) The marine habitat classification for Britain and Ireland version 04.05 JNCC, Peterborough, ISBN 1 861 07561 8 (internet version). jncc.defra.gov.uk/MarineHabitatClassification.

Costanza R et al (2017) Changes in the global value of ecosystem services. Glob Environ Chang 26:152–158. https://doi.org/10.1016/j.gloenvcha.2014.04.002

Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56(3):211–218

Cranfield J, Rowden A, Smith D, Gordon D, Michael K (2014) Macrofuanal assemblages of benthic habitat of different complexity and the proposition of a model of biogenic reef habitat regeneration in Foveaux Strait, New Zealand. J Sea Res 52:109–125

Cuffey RJ, Fonda SS (1976) "Giant" *Schizoporella* – sedimentologically important cheilostome bryozoans in Pleistocene and recent carbonate environments of Bermuda, the Bahamas, and Florida. Geol Soc Am 8:474–475

Cuffey RJ, Fonda SS, Kosich DF, Gebelein CD, Bliefnick DM, Soroka LG (1977) Modern tidal-channel bryozoan reefs at Joulters Cays (Bahamas). In: Proceedings: Third International Coral Reef Symposium. University of Miami, Florida, pp 339–345

Cuffey RJ, Chuantao X, Zhu Z, Spjeldnaes N, Zhao-Xun H (2012) The world's oldest-known bryozoan reefs: late Tremadocian, mid-Early Ordovician; Yichang, Central China. In: Ernst A, Schäfer P, Scholz J (eds) Bryozoan studies 2010. Lecture Notes in Earth System Sciences 143. Springer, Berlin, pp 13–27

De Broyer C, Danis B (2011) How many species in the southern Ocean? Towards a dynamic inventory of the Antarctic marine species. Deep-Sea Res Part II 58:5–17. https://doi.org/10.1016/j.dsr2.2010.10.007

Díaz S et al (2018) Assessing nature's contributions to people. Science 359:270

Duncan H (1957) Bryozoans. Geol Soc Am Mem 67:783–799

Ferdeghini F, Cocito S (1999) Biologically generated diversity in two bryozoan buildups. Biol Mar Medit 6:191–197

Figuerola B, Gordon DP, Polonio V, Cristobo J, Avila C (2014) Cheilostome bryozoan diversity from the Southwest Atlantic region: is Antarctica really isolated? J Sea Res 85:1–17

Flynn AJ, Donnelly D, Fejer AJ, Dutka TL (2019) Western port bryozoan reefs project: report 2 – reef type and extent. Report to La Trobe University, AGL and PP&WP CMA by Fathom Pacific Pty Ltd

Gordon DP, Stuart IG, Collen JD (1994) Bryozoan fauna of the Kaipuke Siltstone, northwest Nelson: a Miocene homologue of the modern Tasman Bay coralline bryozoan grounds. N Z J Geol Geophys 37:239–247

Grange KR, Tovey A, Hill AF (2003) The spatial extent and nature of the bryozoan communities at Separation Point, Tasman Bay. Marine biodiversity biosecurity report 4. Ministry of Fisheries, Wellington

Grischenko AB, Ivanjushina EA (2002) Hermatypic Bryozoa of the shelf zone of the Commander Islands. In: Conservation of biodiversity of Kamchatka and coastal waters. Materials of III scientific conference. Petropavlovsk-Kamchatsky, pp 32–35

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. Polar Biol 20:229–247

Hageman SJ, Bock PE, Bone Y, McGowran B (1998) Bryozoan growth habits: classification and analysis. J Paleontol 72:418–436

Harmelin J-G (1985) Bryozoan dominated assemblages in Mediterranean cryptic environments. In: Nielsen C, Larwood GP (eds) Bryozoa: Ordovician to Recent. Olsen and Olsen, Fredensborg

Harmelin J-G (1997) Diversity of bryozoans in a Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal processes and local factors. Mar Ecol Progr Ser 153:139–152

Harmelin J-G (2000) Ecology of cave and cavity dwelling bryozoans. In: Herrera CA, Jackson JBC (eds) Proceedings of the 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Panama, pp 38–55

Harmelin J-G, Capo S (2001) Effects of sewage on bryozoan diversity in Mediterranean rocky bottoms. In: Wyse Jackson PN, Buttler CJ, Spencer Jones ME (eds) Bryozoan Studies 2001, A.A. Balkema, pp 151–157

Hayward PJ, Ryland JS (1999) Cheilostomatous Bryozoa, part 2: Hippothooidea–Celleporoidea. In: Barnes RSK, Crothers JH (eds) Synopses of the British Fauna (new series). Field Studies Council, Shrewsbury

Hiscock K (2014) Marine biodiversity conservation, a practical approach. Earthscan from Routledge (Taylor and Francis Group), London and New York, 298 pp

Hoffmeister JE, Stockmann KW, Multer HG (1967) Miami Limestone of Florida and its recent Bahamian counterpart. Geol Soc Am Bull 78:175–190

IPCC (2014) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change

Knowles T, Leng MJ, Williams M, Taylor PD, Okamura B (2010) Interpreting seawater temperature range using oxygen isotopes and zooid size variation in *Pentapora foliacea* (Bryozoa). Mar Biol 157:1171–1180

Leadley P et al (2014) Interacting regional-scale regime shifts for biodiversity and ecosystem services. Bioscience 64:665–679. https://doi.org/10.1093/biosci/biu093

Lombardi C, Cocito S, Occhipinti Ambrogi A, Hiscock K (2006) The influence of seawater temperature on zooid size and growth rate in *Pentapora fascialis* (Bryozoa: Cheilostomata). Mar Biol 149:1103–1109. https://doi.org/10.1007/s00227-006-0295-3

Lombardi C, Cocito S, Occhipinti-Ambrogi A, Porter JS (2008) Distribution and morphological variation of colonies of the bryozoan *Pentapora fascialis* (Bryozoa: Cheilostomata) along the western coast of Italy. J Mar Biol Ass UK 88:711–717

Lombardi C, Rodolfo-Metalpa R, Cocito S, Gambi MC, Taylor PD (2010) Structural and geochemical alterations in the Mg calcite bryozoan *Myriapora truncata* under elevated seawater pCO_2 simulating ocean acidification. Mar Ecol 32(2):211–221. https://doi.org/10.1111/j.1439-0485.2010.00426.x

Lombardi C, Cocito S, Gambi MC, Cisterna B, Flach F, Taylor PD, Keltie K, Freer A, Cusack M (2011a) Effects of ocean acidification on growth, organic tissue and protein profile of the Mediterranean bryozoan *Myriapora truncata*. Aquat Biol 13:251–262. https://doi.org/10.3354/ab00376

Lombardi C, Gambi MC, Vasapollo C, Taylor PD, Cocito S (2011b) Skeletal alterations and polymorphism in a Mediterranean bryozoan at natural CO_2 vents. Zoomorphology 130:135–145

Lombardi C, Cocito S, Taylor PD (2013) Bryozoan bioconstructions in a changing Mediterranean Sea. In: Goffredo S, Dubinsky Z (eds) The Mediterranean Sea – its history and present challenges. Springer, New York, pp 373–384

Lombardi C, Cocito S, Gambi MC, Taylor PD (2015) Morphological plasticity in a calcifying modular organism: evidence from an *in situ* transplant experiment in a natural CO_2 vent system. R Soc Open Sci 2:140413. https://doi.org/10.1098/rsos

Ma J-Y, Taylor PD, Feng-Sheng X (2014) New observations on the skeletons of the earliest bryozoans from the Fenhsiang Formation (Tremadocian, lower Ordovician), Yichang, China. Palaeoworld 23:25–30

Maluquer P (1985) Algunas consideraciones sobre la fauna asociada a las colonias de Schizoporella errata (Waters, 1878) del puerto de Mahón (Menorca, Baleares). Publ Dept Zool Univ Barcelona 11:23–28

McKinney FK, Jackson JBC (1989) Bryozoan Evolution. Chicago University Press, Chicago

McKinney FK, Jaklin A (2000) Spatial niche partitioning in the *Cellaria* meadow epibiont association, northern Adriatic Sea. Cah Biol Mar 41:1–17

Meredith M, Sommerkorn M, Cassotta S, Derksen C, Ekaykin A, Hollowed A, Kofinas G, Mackintosh A, Melbourne-Thomas J, Muelbert MMC, Ottersen G, Pritchard H, Schuur EAG (2019) Polar regions. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Alegría A, Nicolai M, Okem A, Petzold J, Rama B, Weyer NM (eds) IPCC special report on the ocean and cryosphere in a changing climate. https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/07_SROCC_Ch03_FINAL.pdf

Morgado EH, Tanaka MO (2001) The macrofauna associated with the bryozoan *Schizoporella errata* (Walters) in southeastern Brazil. Sci Mar 65:173–181

Myhre G et al (2013) Anthropogenic and natural radiative forcing. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 659–740

Narayan S et al (2016) The effectiveness, costs and coastal protection benefits of natural and nature-based defences. PLoS One 11:e0154735. https://doi.org/10.1371/journal.pone.0154735

Novosel M (2005) Bryozoans of the Adriatic Sea. Denisia 16. Landesmuseen Neue Serie 28:231–246

Orr JC et al (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686. https://doi.org/10.1038/nature04095

Pabis K, Hara U, Presler P, Sicinski J (2014) Structure of bryozoan communities in an Antarctic glacial fjord (Admiralty Bay, South Shetlands). Polar Biol 37:737–751. https://doi.org/10.1007/s00300-014-1474-1

Pagès-Escolà M, Hereu B, Garrabou J, Montero-Serra I, Gori A, Gómez-Gras D, Figuerola B, Linares C (2018) Divergent responses to warming between two common co-occurrent Mediterranean bryozoans. Sci Rep 8:17455

Parker SJ, Bowden DA (2010) Identifying taxonomic groups vulnerable to bottom longline fishing gear in the Ross Sea region. CCAMLR Sci 17:105–127

Patzold J, Ristedt H, Wefer G (1987) Rate of growth and longevity of a large colony of *Pentapora foliacea* (Bryozoa) recorded in their oxygen isotopes profiles. Mar Biol 96:535–538

Poluzzi A, Coppa MG (1991) Zoarial strategies to win substratum space in *Calpensia nobilis* (Esper). Bull Soc Sci Nat Ouest Fr, Mém H.S. 1:337-360

Probert PK, Batham EJ, Wilson JB (1979) Epibenthic macrofauna off southeastern New Zealand and mid-shelf bryozoan dominance. N Z J Mar Freshw Res 13:379–392

Riebesell U, Gattuso J-P (2015) Lessons learned from ocean acidification research. Nat Clim Chang 5:12–14. https://doi.org/10.1038/nclimate2456

Rinkevich B (2000) Steps towards the evaluation of coral reef restoration by using small branch fragments. Mar Biol 136(5):807–812. https://doi.org/10.1007/s002270000293

Rodolfo-Metalpa R, Lombardi C, Cocito S, Hall-Spencer J, Gambi MC (2010) Effects of ocean acidification and high temperatures on the bryozoan *Myriapora truncata* at natural CO_2 vents. Mar Ecol 31:447–456

Rosso A (1992) Bryozoa from Terra Nova Bay (Ross Sea, Antarctica). In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografia in Antartide. Universidad de Concepcion, Chile, Centro Eula, pp 359–369

Rosso A (1994) Bryozoa of the first Italian Antarctic oceanographic expedition (Terra Nova Bay, Ross Sea). I. Flustridae Smitt, 1867. J Nat Hist 28:695–713. https://doi.org/10.1080/00222939400770321

Rosso A (2003) Bryozoan diversity in the Mediterranean Sea. Biogeographia 24:227–250

Rosso A, Di Martino E (2016) Bryozoan diversity in the Mediterranean Sea: an update. Medit Mar Sci 17:567–607

Rosso A, Sanfilippo R (2000) Shallow-water bryozoans and serpuloideans from the Ross Sea (Terra Nova Bay, Antarctica). In: Faranda FM, Guglielmo L, Ianora A (eds) Ross Sea ecology. Springer, New York, pp 515–525. https://doi.org/10.1007/978-3-642-59607-0_37

Rosso A, Vertino A, Di Geronimo I, Sanfilippo R, Sciuto F, Di Geronimo R, Violanti D, Corselli C, Taviani M, Mastrotaro F, Tursi A (2010) Hard and soft-bottom thanatofacies from Santa Maria di leuca deep-water coral province, Mediterranean. Deep Sea Res Part II: Trop Stud Oceanogr 57:360–379

Rosso A, Sanfilippo R, Taddei Ruggiero E, Di Martino E (2013) Faunas and ecological groups of Serpuloidea, Bryozoa and Brachiopoda from submarine caves in Sicily (Mediterranean Sea). Boll Soc Paleo Ital 52:167–176

Ryland JS (1970) Bryozoans. Hutchinson University Library, London

Ryland J (1977) Physiology and ecology of marine bryozoans. Adv Mar Biol 14:285–443. https://doi.org/10.1016/S0065-2881(08)60449-6

Santagata S, Ade V, Mahon AR, Wisocki PA, Halanych KM (2018) Compositional differences in the habitat-forming bryozoan communities of the Antarctic shelf. Front Ecol Evol 6:116. https://doi.org/10.3389/fevo.2018.00116

Saxton F (1980) Coral loss could deplete fish stocks. Catch 15–16

Secretariat of the Convention on Biological Diversity (2010). Year in Review 2009. Montreal, 42 pages. https://www.cbd.int/doc/reports/cbd-report-2009-en.pdf

Smith AM, Stewart B, Key MM Jr, Jamet CM (2001) Growth and carbonate production by *Adeonellopsis* (Bryozoa: Cheilostomata) in Doubtful Sound, New Zealand. Palaeogeogr Palaeoclim Palaeoecol 175:201–210

Soliveres et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459. https://doi.org/10.1038/nature19092

Tallis H et al (2010) The many faces of ecosystem-based management: making the process work today in real places. Mar Policy 34(2):340–348

Taylor PD (2000) Origin of the modern bryozoan fauna. In: Culver SJ, Rawson PF (eds) Biotic response to global change. The last 145 million years. Cambridge University Press, Cambridge

Taylor PD (2005) Bryozoans and palaeoenvironmental interpretation. J Palaeontol Soc India 50 (2):1-11

Taylor PD (2020) Bryozoan palaeobiology. Wiley Blackwell, Oxford, 320 pp

Taylor PD, Allison PA (1998) Bryozoan carbonates in space and time. Geology 26:459–462

Taylor PD, Ernst A (2004) Bryozoans. In: Webby BD, Paris F, Droser ML, Percival IG (eds) The Great Ordovician Biodiversification Event. Columbia University Press, New York, pp 147–156

Taylor PD, Gordon DP (2003) Endemic new cyclostome bryozoans from Spirits Bay, a New Zealand marine-biodiversity “hotspot”. N Z J Mar Freshw Res 37:653–669

Taylor PD, James NP (2013) Secular changes in colony-forms and bryozoan carbonate sediments through geological time. Sedimentology 60:1184–1212

Taylor PD, James NP, Bone Y, Kuklinski P, Kyser TK (2009) Evolving mineralogy of cheilostome bryozoans. Palaios 24:440–452

Taylor PD, Lombardi C, Cocito S (2015) Biomineralization in bryozoans: present, past and future. Biol Rev 90(4):1118–1150. https://doi.org/10.1111/brv.12148

Taylor PD, Tan S-HA, Kudryavstev AB, Schopf JW (2016) Carbonate mineralogy of a tropical bryozoan biota and its vulnerability to ocean acidification. Mar Biol Res 12:776. https://doi.org/10.1080/17451000.2016.1203951

The Natural Environment White Paper (2011) The natural choice: securing the value of nature. Department for Environment, Food and Rural Affairs. https://www.gov.uk/government/publications/natural-environment-white-paper-implementation-updates

UNEP (2017) The emissions gap report 2017. United Nations Environment Programme (UNEP), Nairobi

United Nation Sustainable Development Summit (2015). https://sustainabledevelopment.un.org/post2015/summit

Winston JE (1983) Patterns of growth, reproduction and mortality in bryozoans from the Ross Sea, Antarctica. Bull Mar Sci 33:688–702

Wong PP et al (2014) Coastal systems and low-lying areas. Climate Change 2104:361–409

Wood ACL (2005) Communities associated with habitat-forming bryozoans from Otago shelf, Southern New Zealand. Master of Science thesis, University of Otago, New Zealand

Wood ACL, Probert PK, Rowden AA, Smith AM (2012) Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. Aquat Conserv: Mar Fresh Ecosyst 22:547–563

Zabala M (1986) Fauna dels Briozous dels Països Catalans. Institut d’Estudis Catalans, Arxius de la Secció de Ciéncies, Barcelona 84:1–836

Zabin CJ, Obernolte R, Mackie JA, Gentry J, Harris L, Geller J (2010) A non-native bryozoan creates novel substrate on the mudflats in San Francisco Bay. Mar Ecol Prog Ser 412:129–139. https://doi.org/10.3354/meps08664

Zimmerman LS, Cuffey RJ (1987) Species involved on Permian bryozoan bioherms, West Texas. In: Ross JRP (ed) Bryozoa: present and past. Western Washington University, Bellingham, pp 309–316

Polychaetes as Habitat Former: Structure and Function

A. Giangrande, M. C. Gambi, and M. F. Gravina

Abstract Polychaetes are widespread across marine ecosystem reaching high density in various seabed habitats, where they play a relevant role in the functioning of benthic communities. Many polychaetes are sessile and tube-dwelling forms, often gregarious, which are able to create primary biogenic structures or to modify the abiotic characteristics of the pre-existing substrate. They act as real builders of forest-like structures that offer new substrates for other benthic species, affect habitat conditions and regulate ecosystem functioning. Thus, polychaetes are ascribed to the engineers of animal forests. In this chapter, the main evidences of polychaetes as habitat formers on both rocky and sedimentary bottoms are reported; the time-scale variations of the biogenic structures are considered and the sensitivity and threats of polychaete forests are exhibited for contributing in decision-making regarding protection measures and management of coastal ecosystems.

Keywords Bioconstructions · Polychaete reefs · Burrowing polychaete assemblages · Engineering species · Persistence · Recovery · Emerging threats

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1 Introduction

Marine seafloor is strongly impacted in its architectural features by many benthic organisms, mainly sessile and sedentary. The benthic communities dominated by sessile suspension feeders invertebrates form living three-dimensional structures, which provide architectural complexity and shelter for several species and in their structure are similar to the terrestrial forests; for these reasons such communities are denominated "animal forests" (Rossi 2013). In such communities, marine animals play the role of ecosystem engineers, owing to their ability to physically create, to modify and to maintain habitats upon which other species depend and through which the benthic community is formed and regulated (Jones et al. 1997; Rossi et al. 2017). In fact, such organisms act as structuring species providing new substrate for the colonization by other species or modifying the physical-chemical features of the surrounding environment and modulating the distribution and abundance of the resources for other species (Gribben et al. 2019). The roles of these animals on the rest of the community are various: they may provide food, offer nursery and spawning habitats and refuge from predation and reduce physical and chemical stresses; they also condition local hydrodynamics and biogeochemical cycles and act as carbon sink areas (Turner et al. 1999). Playing a role similar to plants in the terrestrial environment, many sessile invertebrates communicate by means of chemical language, producing a myriad of active substances (infochemicals) used as defence against epibionts, pathogens and competitors and so highlighting the force and the validity of the inter-species relationships (Gerhart et al. 1988).

The main organisms which form animal forests are cnidarian, sponges and molluscs (Bo et al. 2015; Cau et al. 2017; Longo et al. 2017; Donnarumma et al. 2018; Corriero et al. 2019), but also polychaetes exhibit their key role in edifying three-dimensional biogenic structures resembling forests, which create new substrate, drive community structure and provide biodiversity hotspot areas (Bruschetti 2019). Particularly this is recognized for reef building polychaetes, but also in soft bottoms some burrowing species are able to crease biogenic structures in a three-dimensional space, which affect habitat conditions and resources and thus regulate community structure and ecosystem functioning. For these reasons both of such groups of polychaetes are here ascribed to the engineers of animal forests.

In this chapter the main literature-based studies on polychaetes as ecosystem engineers are synthetized, and new results of current authors' researches are reported, with the objectives to summarize the main biogenic structures edified by polychaetes, to highlight their ecological role as habitat formers, to consider the timescale variations of the biogenic structures and to exhibit the sensitivity and threats of polychaete forests, in the light to the sustainable management and protection of marine coastal ecosystems.

2 Polychaetes Forming Biogenic Structures

2.1 Reef Building Polychaetes

Some sessile polychaetes act as real bioconstructors, producing solid calcareous or sand tubes where they live, and their tubes are cemented to each other and are crowded in three-dimensional aggregations; so these worms form monospecific reefs which create new secondary substrata and behave as trees in terrestrial forests. Polychaetes which are capable to build reefs are ascribed to the families Sabellariidae and Serpulidae.

Sabellariidae

The sedentary polychaetes belonging to the family Sabellariidae are sessile, tube-dwelling species which build tubes from sand and shell fragments cemented together with mucous. Such worms build reefs on sand flats where elements of hard substratum are exposed and used for the settlement of pioneering larvae. The reef is formed by gregariousness of larvae and is not the product of asexual reproduction. Sabellarid forming reefs include the worms of the genera *Sabellaria* and *Phragmatopoma*, commonly known as sandcastle worms and honeycomb worms, which are distributed in temperate and tropical regions. The largest biocontructions of *Phragmatopoma* occur along the South America and California coasts with the species *P. californica* and *P. lapidosa* (Main and Nelson 1988; Nunes et al. 2016), while along northern European and Mediterranean coastlines two species of the genus *Sabellaria* are reported: *S. alveolata* and *S. spinulosa* (Gruet 1986; Jackson and Hiscock 2008; Gravina et al. 2018; Bonifazi et al. 2019). In the Mediterranean Sea, *S. alveolata* bioconstructions cover an area of hundreds of square metre along Central Tyrrhenian coast (Ventura et al. 2018), while along the northern-eastern Atlantic coast they cover areas of approximately 100 ha, which are considered the largest reefs in Europe (Dubois et al. 2006). *Sabellaria* bioconstructions occur along the midlittoral-upper infralittoral zone, from the lower shore into the sublittoral, arising from the sandy seafloor or forming banks adhering to hard bottom. Such structures often reach the sea surface and emerge during the low tide. Along the Italian coast, *S. alveolata* reefs (Fig. 1) occur along southern Sicily (Schimmenti et al. 2016), Latium (La Porta and Nicoletti 2009; Bonifazi et al. 2019), Campania (Gambi et al. 1996), Liguria (Delbono et al. 2003) and Abruzzo (Gadaleta et al. 2015), while the only known actual reef constructed by *S. spinulosa* has been reported for the first time in the Mediterranean Sea along Apulian coast (Gravina et al. 2018).

Serpulidae

Polychaetes of the family Serpulidae include numerous species of sessile worms producing calcareous tubes where they withdraw plugging the opening by means of their characteristic operculum. They cemented their tubes to each other in both encrusting aggregations and vertical clumps and so forming belt- and reef-like structures on hard substrata. These latter may cover tens of square metres with a

Fig. 1 Mesolittoral *Sabellaria alveolata* reef from Tyrrhenian coast (Latium). Photo Bonifazi A

layer more than 1 m thick (ten Hove and van der Hurk 1993; Bianchi et al. 1995). Serpulids are important bioconstructors in tropical environments, where most of the species lives associated to coral reef, shallow barriers and mesophotic formations, but up to date the biology of such worms is scantily known and few information is available about the coral-boring polychaete *Spirobranchus giganteus* (Vine and Bailey-Brock 1984; Nishi 1996).

Thanks to their sessile habit, serpulids behave both as primary and secondary habitat formers; in particular, some species of the genera *Pomatoceros*, *Spirobranchus*, *Galeolaria* and *Pomatoleios* edify biogenic structures in the intertidal tropical zone. Recently the species *Pomatoceros kraussii*, native to Indo-Pacific, entered through the Suez Canal into Eastern Mediterranean (Belal and Ghobashy 2012) where large clumps were built and are acting as pest species. In tropical waters serpulids also live associated to coral reef, such as the coral-boring species *Spirobranchus giganteus* (ten Hove and Kupriyanova 2009). In temperate regions, other species ascribed to the genera *Serpula*, *Hydroides* and *Vermiliopsis* edify tube aggregations in sheltered enclosed coastal areas. Among them, *H. elegan*s is considered a fouling pest species, while *H. dianthus* build scattered small-medium reefs in the temperate lagoon areas (Bianchi and Morri 2001). The worldwide species *Serpula vermicularis* generally occur as solitary or with small clumps encrusting hard substrata such as bivalve shells and stones and only in very few sites this species forms large clumps. Such rare biogenic structures are made of calcareous tubes attached to stones on muddy sediment, reaching up to 2 m high in very sheltered waters, and are reported only from few sites in the UK: Loch Creran along the west coast of Scotland, where *S. vermicularis* occur with the most developed reefs (Moore et al. 1998), and Ardbear Lough and Killary Harbour along the west coast of Ireland (Bosence 1979; Minchin 1987). In Antarctic region similar sublittoral reefs are produced by *Serpula narconensis* in Ellis Fjord and South Georgia (Kirkwood and Burton 1988; Ramos and San Martin 1999) and along New Zealand coast by *Galeolaria hystrix* (Smith et al. 2005); the serpulid reef located at Ellis Fjord (Davis Sea), with its 8.3 km in length, is the largest known tubeworm reef in the world and the amount of *Serpula* tubes collected at the South Georgia island shelf was estimated at nearly 1.5 tonnes of wet weight.

Among serpulid worms, one of the most popular primary habitat former is *Ficopomatus enigmaticus*. This species, native from Indian Ocean, was firstly recorded along Atlantic coast of Europe in 1921 and in the Mediterranean Sea since the 1950s (Tenerelli 1966). Such species builds large bioconstructions in the brackish-water habitats of the warm-temperate regions, thanks to the gregarious settlement of the larvae and the calcareous tubes of the adults which are cemented to each other in massive aggregations. Such biogenic structures form both fringing reefs along the shoreline and dense patch hummocks growing from the bottom up to the surface.

All the before mentioned polychaete bioconstructions are the product of multiple settlement, since the larvae settle themselves on or near conspecific individuals to form monospecific aggregations; on the contrary asexual reproduction events are carried out in the case of the species of the genus *Filograna* spp., whose individuals engineer very delicate but consistent biogenic concretions in coralligenous Mediterranean habitats.

More often serpulids have the role of secondary builders, commonly cementing their calcareous tubes to all firm surfaces underwater and in epibiosis on skeletons of other organisms, i.e. mollusc shells, stony corals, bryozoan colonies and coralline red algae, so, thanks to their dominance, such sessile worms may participate to the architecture of biogenic primary structures built by other bioconstructors. For example in the Mediterranean Sea, serpulids are important components of the relevant habitats of biogenic origin, such as the sciaphilic coralligenous, the mesophotic coral reefs and the bathyal white coral banks (Ballesteros 2006; Mastrototaro et al. 2010; Corriero et al. 2019; Cardone et al. 2020) (Fig. 2). A large number of serpulids species, such as *Serpula concharum*, *Josephella merenzelleri*, *Semivermilia crenata*, *S. pomatostegoides*, *Pileolaria pseudomilitaris* and *Vinearia koehleri*, live associated to the sciaphilic and coralligenous habitats. Other typically deep-water species encrust the white corals skeletons, such as *Janita fimbriata*, *Vermiliopsis monodiscus*, *Filogranula gracilis*, *F. calyculata*, *Metavermilia multicristata*, *Protula tubularia* and *Plagosteus tridentatus*.

Moreover, serpulids are typical components of the bulk of submarine cave community, being the cave walls extensively covered by their encrusting tubes. These worms form tangled assemblages of their tubes several centimetres high, which are attached on the rocky cave walls and locally create small biogenic hummocks. Notwithstanding real exclusive species of cave biotope are missing, serpulids are typical components of the benthic communities of submerged cavities. Owing to the progressive decline of light penetration and of water movement

Fig. 2 Particular of a mesophotic reef from the Adriatic coast of Apulia showing the conglomerate of serpulid tubes. Photo Corriero G

intensity along the outside-inside cave gradient that reaches the total darkness conditions in the inner part, a parallel sharp impoverishment of benthic organisms occurs, and only few sessile suspension feeders taxa cover the bare rocky walls of dark caves. They are mostly sponges, hydroids, bryozoans and serpulids, and these latter organisms cover the substratum with dense populations. In the Mediterranean Sea, numerous serpulids species colonize either semi-dark and dark submarine caves, e.g. *Serpula cavernicola*, *Filogranula annulata*, *Hydroides pseudouncinata*, *Janita fimbriata*, *Josephella merenzelleri*, *Vinearia endoumensis*, *Semivermilia cribrata*, *Serpula massiliensis*, *Spirobranchus polytrema* and *Vermiliopsis striaticeps* (Bianchi and Sanfilippo 2003; Rosso et al. 2013). Peculiar bioconstructions in Mediterranean submerged caves are built by the serpulids of the genus *Protula*, with subordinate *Semivermilia* and *Josephella*, particularly in the Plemmirio Marine Protected Area along south-eastern Sicily coast and at Cape of Otranto off Apulian coast, where such serpulids erect rigid structures, synsedimentarily lithified by clotted-peloidal microbial carbonate, which are termed biostalactites (Belmonte et al. 2008).

2.2 *Soft Bottom Polychaetes Engineers*

Polychaetes modulate three-dimensional space in soft bottoms by biostructures and architectures of sediment, so notably, that such worms can be assimilated to engineer species which edify forests. In fact, these worms burrow into the sediment where they form dense aggregations of tube- and tunnel-living species, which alter soft bottom environmental conditions and enhance both the associated infauna and the aboveground epifauna. Such polychaetes are mainly represented by species belonging to various families living permanently within their tubes, such as Terebellidae, Oweniidae, Sabellidae, Serpulidae and Chaetopteridae, and also living in non-permanent tubes, such as Onuphidae and Spionidae.

Terebellidae

The tube-dwelling polychaete *Lanice conchilega* is well-known habitat former in soft bottom environments: large aggregations of this species occur mainly in subtidal areas of the English Channel where they extend for approximately 1–12 m^2 alternate with tube-free areas (Rabaut et al. 2007).

Oweniidae

Owenia fusiformis is a thin worm up to 10 cm long living in a tough but flexible tube buried in the sand; its tubes are composed of sand grains or shell fragments glued together in an overlapping, imbricate fashion, and they are slightly longer than the worm so their tops protrude to up to 2 cm from the surface. This species is recorded both in the Mediterranean Sea and in the English Channel, with high density of individuals in fine to coarse sedimentary habitats where it behaves as an efficient sediment stabilizer and habitat former (Gambi 1989; Pinedo et al. 2000; Somaschini 1993).

Chaetopteridae

Similar capability in modulating the original soft bottom features is shown by some species of Chaetopteridae, e.g. *Mesochaetopterus sagittarius*. Worms of such species live in sandy bottoms inhabiting their sandy tubes, reaching very high densities particularly in the Gulf of Naples in the Mediterranean Sea (Guglielmo et al. 2006).

Onuphidae

The tubeworms of the genus *Diopatra* includes species living in intertidal and shallow bottoms of tropical and temperate regions; particularly *Diopatra neapolitana* and *D. cuprea* occur, respectively, in the Mediterranean, Eastern Atlantic and Western Atlantic coasts. These worms consolidate the muddy-sandy sediments, where they build vertical tubes embedded up to a depth of 50–60 cm with their hook-shaped cap emerging 2–5 cm above the sediment surface (Berke and Woodin 2008; Santos and Aviz 2018). Their parchment tube walls are reinforced with fragments of shell, algae and other debris, conferring the appellative of plumate or decorator to these worms.

Sabellidae

Some sabellid species are large habitat former polychaetes producing parchment tubes generally perpendicular to bottom surface, which may form dense canopies of feeding fans sometimes completely covering the substratum (Fig. 3). One of the most common Mediterranean species is *Sabella spallanzanii*, which typically colonizes natural and artificial substrates (Giangrande et al. 2000), often associated to other sabellids, e.g. *Sabella pavonina* and *Bispira viola*. Other species,

Fig. 3 Canopy of sabellid tubes from a shallower fouling community in the Gulf of Taranto (Ionian Sea). Photo Mastrototaro F

i.e. *Perkinsiana littoralis* and *Myxicola sulcata*, reach high densities in Antarctic shelf coast (Gambi 1999; Gambi et al. 2000).

Serpulidae
Differently from the other serpulids, the endobenthic species *Ditrupa arietina* inhabits calcareous, curved, tusk-shaped tubes not adhering to solid surfaces but free in the sediment, resembling the shells of scaphopods. The tubes, up to 23 mm long and about 3 mm across, are buried in the sediment with the narrowest posterior end down and the anterior end protruding the sediment-water interface. These worms live in muddy-detritic sediments in the Mediterranean Sea, where they reach very high densities, modify and consolidate the sediment structure so strongly to be considered real ecosystem engineers of soft bottoms (Gambi 1986; Gambi and Ierace 1997; Labrune et al. 2007).

3 Polychaete Biogenic Structure Functionalities

The biogenic structures edified by polychaetes exhibit their crucial role in changing environmental conditions and in structuring benthic communities and reveal these worms to be real habitat formers, both in rocky and in soft seabeds. In fact, polychaetes act as bioengineers, being able to influence the physical-chemical and biological characteristics of the habitats, and so they play various and significant roles that condition the ecosystem functioning.

3.1 Habitat Formers Building Biogenic Reefs

Gregarious tube-dwelling worms act as primary bioconstructors, thanks to their capability to build real biogenic structures by the assemblage of their habitation tubes, which have different effects.

The reefs of *Sabellaria* are compact bioconstructions, developing on hard and soft substrates through multiple settlements of larvae that have a gregarious behaviour. The reef is formed by the compaction of the tubes of individuals positioned in close proximity to each other, so producing a honeycomb-like structure, which gives these polychaetes the name "honeycomb worms". The larvae preferentially settle on the existing reef of *Sabellaria* or on their dead remains, in shallow marine areas where adequate sedimentological and hydrodynamic conditions occur. Their tubes, in fact, are made up of grains of sand and bioclasts cemented with mucus whose construction requires a good supply of sand grains from the water column. Therefore, according to the different environmental situations, *Sabellaria* reefs can develop in multiform aspects, from thin crusts, to mound-like, hummocks, tubular or barrier aggregations. Such biogenic structures provide a diversity of microhabitats hosting hard and sandy bottom species, sheltering rare species, and so they promote coastal biodiversity. For example, the Mediterranean *S. spinulosa* and *S. alveolata* reef, although not sheltering a distinctive associated fauna, show to be a significant biodiversity hotspot (Gravina et al. 2018; Bonifazi et al. 2019). Because of their composition in sandy grains and their coastal location, the *Sabellaria* bioconstructions have the same compositional features of the beach, and therefore, such structures have noteworthy physical roles in retaining suspended sandy grains and in creating a barrier against storms. So they represent a temporary sedimentary repository that may provide sands to the beach during the high-energy storm and wave events, and, at the same time, they act as defence of the coast from erosion: in both cases being important in beach-sand stabilization (Lisco et al. 2017, 2020).

On the contrary, serpulids are the main biomineralizer annelids and play a significant role in the ocean carbonate sink, because they build calcareous tubes. As an example, for the *Ficopomatus* reefs in the Sacca del Canarin at Po River Delta (North Adriatic Sea), it was computed to have an annual production of 21.269 kg m^{-2} $year^{-1}$ dry weight that corresponds to about 30,000 tonnes of calcium carbonated stored up in 6 km^2 of surface area (Bianchi and Morri 1996). Indeed, the species *Ficopomatus enigmaticus* occurs in most of the Mediterranean lagoons, where it plays the role of real habitat former building the most extensive sheltered biogenic reefs and so enhancing biodiversity too. In fact, these worms cement their tubes to hard substratum, such as shells, cobbles and other hard fragments, resulting in spread-out patchy bioconstructions with different shapes: belts fringing the shoreline in a continuous layer up to 1–3 m thick or hemispherical mounds up to 2 m height and 4 m in diameter growing from the bottom. Such biostructures result from many generations of worms and may cover several square metres of substrate in very shallow waters (Bianchi and Morri 1996). The architecture of the structure is stabilized by other sessile invertebrates including barnacles and mussels, which contribute to the reef formation acting as secondary builders, as well as by encrusting bryozoans, e.g. *Conopeum seurati*, which act as the main binders. Both the belt-reef and the mound-reef, thanks to their thickness, often reach the water surface especially at low tide and provide refuge for many other benthic species (Nonnis Marzano et al. 2007). Additionally, such bioconstructions can be attractive for fish with a high conservation value, which get space and food in the reef, such as *Syngnathus abaster*, *Aphanius fasciatus* and *Knipowitschia panizzae*, this latter being an interesting Mediterranean endemism (Cardone et al. 2014). However, in the shallow coastal areas where such submerged structures are very extensive, they can exceedingly reduce the oxygen content in the water and cause dystrophic crises. On the other hand, the worm filtration activity, carried out by millions of individuals, removes particulate organic matter from the water, promoting water clarity and favouring the trophic state of the entire lagoon system.

Notwithstanding their very locally restricted distribution, the reefs of *Serpula vermicularis* notably alter the uniform sedimentary bottom, enhancing the habitat heterogeneity and acting as promoters and attractors of local biodiversity. As an example, in Scottish Loch the *Serpula vermicularis* reefs grow up vertically from the bottom and form solid substrata in otherwise muddy seabed, reaching over 1–2 m in height and up to 2 m wide (Dodd et al. 2009). The worms cement their tubes to small hard surfaces, such as cobbles, pebbles and shells, which are scattered throughout the sedimentary seabed, and so they form aggregations of winding tubes resulting in underwater islands, which take many years to develop. Such biogenic reefs provide food and living space for a large variety of animals and algae that otherwise could not live in the area. The rich associated biota includes many sessile invertebrates, e.g. sponges, ascidians, hydroids, bivalves, other serpulids, encrusting bryozoans and red algae, and also motile animals, e.g. crustaceans, sea urchins, brittle stars, starfishes and the whelk *Buccinum undatum* (Connor 1990; Poloczanska et al. 2004). Similarly, the Antarctic *Serpula narconensis* reefs harbour a very rich biota, embracing other filter feeder organisms as well as motile invertebrates, thus demonstrating their role as habitat refuge.

In cave environments, besides their role in shaping the primary rocky walls particularly in the inner part, the peculiar action of serpulids consist in affecting the hydrodynamics which is, together with the light and food supply decrease, the main factor constraining the colonization process of the cave's fauna. In fact, serpulids, as active filter feeders, with their branchial crown movements create those water currents that are necessary for the food supply available for themselves and for the other suspension feeders. In this way they considerably affect the ecosystem trophic web dynamics.

In Mediterranean deep-water habitats, such as mesophotic reefs and white corals, the main functional role of serpulids consists in their activity as secondary builders, because of their capability to binder the primary biogenic structures, with the results of making the surface more rough and wrinkled, increasing the habitat heterogeneity and thus promoting biodiversity.

3.2 Polychaete Aggregations in Soft Bottoms

Tubicolous polychaetes, including sabellids, chaetopterids, oweniids, terebellids and onuphids, which live with large number of individuals inserted in the sediment, are able to modulate the original soft bottom changing its features, such as compactness, size grain composition, organic matter and oxygen content, and so they are able to increase the spatial complexity of the soft sediments. The worms, with their tubes embedded in the substratum, act as sediment stabilizers, producing additional three-dimensional structures suitable for settlement and attachment of other organisms; indeed, the worms, thanks to turbulence caused around their tubes, act as traps for fine particles and larvae (Bell 1985; Luckenbach 1987; Thomsen et al. 2010). Moreover, soft bottom tube-dwelling polychaetes play the crucial role in enhancing local biodiversity, since they, increasing habitat complexity, provide protected living space for other invertebrates and, by buffering water movement, also provide food supply to numerous benthic species. For these reasons, the sedimentary areas inhabited by tube-building polychaetes harbour a benthic macrofauna more rich in species than the areas of bare sands. A significant example is shown by the species *Ditrupa arietina*, which acts as sediment stability promoter; since their tubes constitute a solid substrate for the attachment of various organisms, they also enhance larval settlement and give refuge from predators to associated fauna, including foraminiferans, other serpulids and bryozoans (Gambi 1986; Gambi and Ierace 1997; Somaschini 1993; Pinedo et al. 2000).

In fouling habitats, the tubes of sabellids provide shelter for predation and constitute a secondary solid habitat for algae and other sessile invertebrates (Callaway 2003); particularly in the Mediterranean Sea, the current researches conducted during the last years by one of us (GA) have exhibited the crucial role played by tubicolous sabellids as ecosystem engineers, due to their capability of creating the stratification of the associated benthic assemblage (Giangrande et al. 2014). Additionally, the filtration activity of *Sabella spallanzanii* modulates direction and velocity of water flow and significantly enhances the removal of dissolved and particulate organic matter and bacteria from the water column, as well as it influences oxygen water content (Licciano et al. 2005; Stabili et al. 2006). *S. spallanzanii* assemblages are also observed to enhance biodiversity of the fouling community, which progressively increases in relation to the higher density of such sabellid (Pierri et al. 2019). Therefore, our current studies highlight that this species, besides to act as habitat former, is a useful candidate for bioremediation of aquaculture wastes and for bacterial density control in marine waters.

4 Temporal Variations: Persistence, Degeneration and Recovery

Contrarily to most of the animal forest engineering species, polychaete habitat formers reproduce sexually and use different dispersal strategies, which are essential for both local populations and for connectivity among distant populations. So their reproductive and dispersal autogenic adaptations mainly affect persistence and recovery of the biogenic structures which polychaetes build, whereas degeneration is commonly affected to allogenic anthropogenic factors. Temporal variations of polychaete biogenic structures are different in intertidal, subtidal and deep habitats, where the worm bioconstructions show their persistence in time to be mainly influenced by sediment regime and hydrological factors.

Among the largest biogenic concretions, the reefs built by *Sabellaria* worms consist of gregarious aggregations of tubes made by sand grains and shell fragments cemented together. The incoherent characteristics of such constituent elements give an ephemeral, rather than stable, nature to the *Sabellaria* bioconstructions. They strictly depend on the precarious balance between local physical factors, i.e. hydrodynamic forces, seabed topography, sandy particles supply, water clarity and temperature, and biological factors, i.e. reproduction mode and recruitment mechanism of the pelagic larvae. On the other hand, *Sabellaria* larval behaviour, which consists in larvae preferential settling on living bioconstructions or either on their ruins, can ensure both reef persistence and promote its recovery. So, the age of the bioconstruction greatly exceeds the age of the living worms, since the reef may repeatedly follow a cyclical progression that is described in detail along northern-eastern Atlantic coasts. This cycle is characterized by the primary beginning phase with the settlement of new individuals which build small structures; the secondary growth phase occurs when the reef grows, becomes dense and mound or barrier shaped; the subsequent destruction phase is caused by the vigorous wave action, the strong tidal currents and the sand abrasion which erode the construction; the new growth phase is supported by the rapid tube growth rate, which reaches 4.4–6 mm/day; so the complete cycle lasts quite several months to also more than 10 years (Gruet 1986). *Sabellaria* reefs are therefore extremely dynamic systems: the reef may persist in an area although individual clumps may regularly form and disintegrate themselves. In the Mediterranean Sea, the *S. spinulosa* and the *S. alveolata* reefs showed cyclical fluctuations over a period of 1 year, both along Apulia and Latium Italian coasts (Gravina et al. 2018; Bonifazi et al. 2019). Persistence of *Sabellaria* reefs is also influenced by interactions with other organisms, particularly with *Mytilus*. A cyclical succession of *Sabellaria–Mytilus edulis* occurred along northern-eastern Atlantic coasts for around 30 years (Cunningham et al. 1984); similarly, a progression through the *Sabellaria spinulosa–Mytilus galloprovincialis* spread over a period of 15 years along the southern Adriatic coasts (Gadaleta et al. 2015).

Historical data from the North Sea have documented the persistence of *Sabellaria* reef over a period of approximately one century (Firth et al. 2015), whereas long-term information about *S. alveolata* reef has revealed a documented age of 60 years for Italian bioconstructions. Indeed, along Latium and Sicily coasts, the bioconstructions persist in their extension and in good status since the 1950s (Giordani Soika 1956; Taramelli-Rivorecchi 1961; Molinier and Picard 1953) to present (Gravina MF personal observations; Schimmenti et al. 2016).

Serpulid reefs built by *Ficopomatus* are extremely dynamic in both space and time, being characterized by very short cycles, according to the sudden environmental changes occurring in the brackish-water ecosystems. In fact, the reefs expose themselves to rapid growth phases (up to 30 mm per month); to periodic collapses due to the extreme tube aggregation's weight, which makes unstable the reef; and to subsequent reset of new reefs formed from consolidating remains. This cycle may last about 1 year (Bianchi and Morri 1996) and highlights that *Ficopomatus* is able to respond to sudden environmental changes and to recover from damage in a still short time. However various environmental factors affect the reef development, the main of them are as follows: hydrodynamics which has to be low, salinity range with optimum from 10 to 30.0‰, temperature ranging from 10 to 27 °C and the water trophic state and phytoplankton level, both these latter two factors strongly enhancing the settlement of *Ficopomatus* larvae.

The other serpulid species *Serpula vermicularis* shows its biogenic structures to be transient over decade timescale (Hughes 2011). On the contrary, polychaetes crust-like forms and reefs in deep habitat and particularly in submarine caves show persistence in time, without exhibit cyclical variations because of the low rate of worms' growth and of the quite stability of hydrological and environmental conditions. Serpulids grow more slowly in cave habitats than in the shallow ones, in caves they reach longer sizes of their tubes (Bianchi and Sanfilippo 2003), and, in addition, the old tubes of dead worms durably encrust the substrate, thus enhancing habitat topographic complexity and biodiversity levels for a long time (Rosso et al. 2013).

Persistence also characterizes the aggregations of the terebellid *Lanice conchilega* in soft bottoms. Sediment elevation and consolidation due to the very dense aggregation of these worms have been found to persist for several years, though the renewal of existing aggregations through juvenile settlement yearly occur (Rabaut et al. 2009).

A very long persistence has been observed for the fouling community dominated by the sabellid *Sabella spallanzanii* in the of Gulf of Taranto in the Ionian Sea, where aggregations formed by such sabellid, which have been studied for about 30 years, highlight to persist notwithstanding the introduction of alien sabellids in the fouling (Giangrande et al. 2014).

5 Perspectives in Conservation: Sensitivity and Threats

Polychaete biogenic structures are delicate dynamic systems suffering several threats, both by natural perturbations and by anthropogenic disturbances.

Sabellaria reefs are sensitive to various direct and indirect impacts from human activities. In Mediterranean Sea along Italian coasts, a consistent damage to *Sabellaria* reefs is the physical disturbance caused by human trampling, which is often performed to directly remove *Sabellaria* for employing the worms as baits for recreational fishery (Plicanti et al. 2016). Similarly, along North European coasts, physical damage seriously impacting the *Sabellaria* reefs is caused mainly by trawling for shrimps and dredging for oysters and mussels (Dubois et al. 2002, 2006). The health status and dynamics of the reef is also threatened by biological factors, such as the colonization by epibionts. First of all are the mussels *Mytilus galloprovincialis* which, with their intensive settlement on the surface of the biostructures, are responsible for weakness and deterioration of the *Sabellaria* reef, as it has been observed for the Adriatic bioconstruction at Torre del Cerrano (Gadaleta et al. 2015). Moreover, differences in the degradation and recovery time of the two *Sabellaria* species are connectable to differences in life cycle span, being *Sabellaria alveolata* a long-life species which live up to 9 years, while *S. spinulosa* is a fast-growing annual species.

Another main threat affecting the *Sabellaria* reefs is water eutrophication. Despite *Sabellaria* worms are tolerant to poor water quality, the increasing inputs of nutrients from coastal agriculture are responsible for indirect impact on the reef, causing massive green algae blooms, which in turn significantly reduce the rate of *Sabellaria* larval recruitment (Dubois et al. 2006). Evidence for such damage have been observed along the Sicily coasts (Badalamenti F., personal communication). *Sabellaria* reefs are also potentially vulnerable to changes in hydrological and sedimentary regime resulting from coastal engineering works and likely to recent climate changes. Mostly such human pressures are the cause of strong deterioration of the reefs and of reducing in their recover capacity (Firth et al. 2015).

Differently, *Ficopomatus* is able to respond to the environmental changes and to recover from damage in a short time. Notwithstanding, considerable environmental variations in water flow cause damages to the reef by causing its covering and smothering with sediment, as well as mechanical anthropogenic disturbances, produced by human tools such as fishing gears and anchors, also damage the reef; both these impacts are possible causes of the disappearance of *Ficopomatus* reefs in various suitable habitat. Moreover, other significant threats for serpulids reefs are the increase of water eutrophication and the dystrophic crises, which have been the causes of the decline of the *Serpula vermicularis* reefs (Hughes 2011).

Lastly, it is important to emphasize that, owing to the calcareous composition of serpulids tubes, increasing ocean warming and ocean acidification in particular, could be causes of net calcification decrease, of reduction in growth and reproduction rate and of decreasing in abundance and diversity of such worm biogenic structures.

6 Conclusions

In both hard and soft benthic ecosystems from shallow to deep habitats, polychaetes play an important role in creating habitats, maintaining bottom stability and modulating the functioning of benthic communities. Thanks to their large adaptive radiation, which makes these organisms successful colonizers of the seabed, in a large number of marine habitats, they reach high densities and show a high diversity in morphological/ethological habits and feeding strategies. Tube-dwelling polychaetes form aggregations which create peculiar three-dimensional structures on the substrate, principally when they build real reefs, but also in the cases of small groups of individuals. Moreover, other tubicolous polychaetes, due to their dominance in some sediments, may change the features of the bottoms: with their biogenic tubes embedded in the three-dimensional layer of sediment, they consolidate the substrate and produce secondary hard substrate with strong influence on the habitat heterogeneity and the associated fauna.

In conclusion, sessile and sedentary polychaetes can be ascribed to true ecosystem engineers, thanks to their capability in structuring space and forming complex architecture in many seafloor ecosystems, with the result to create stable oasis enhancing the local benthic diversity. So, polychaetes behave as real habitat formers and thus play a remarkable role among the organisms forming the animal forests.

Literature

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr Mar Biol Annu Rev 44:123–195

Belal AAM, Ghobashy AF (2012) Settlement behaviour and description of the Lessepsian immigrant of the serpulid polychaete *Pomatoleios kraussii* in the Suez Bay. Egypt J Aquat Res 38:23–30

Bell SS (1985) Habitat complexity of polychaete tube-caps: influence of architecture on dynamics of a meioepibenthic assemblage. J Mar Res 43:647–671

Belmonte G, Ingrosso G, Poto M, Quarta G, D'Elia M, Onorato O, Calcagnile L (2008) Biogenic stalactites in submarine caves at the Cape of Otranto (SE Italy): dating and hypothesis on their formation. Mar Ecol 30:376–373

Berke SK, Woodin SA (2008) Tube decoration may not be cryptic for *Diopatra cuprea* (Polychaeta: Onuphidae). Biol Bull 214:50–56

Bianchi CN, Morri C (1996) Ficopomatus 'reefs' in the Po River Delta (Northern Adriatic): their constructional dynamics, biology, and influences on the brackish-water biota. Mar Ecol 17:51–66

Bianchi CN, Morri C (2001) The battle is not to the strong: serpulid reefs in the Lagoon of Orbetello (Tuscany, Italy). Est Coast Shelf Sci 53:215–220

Bianchi CN, Sanfilippo R (2003) Policheti Serpuloidei. In: Cicogna F, Bianchi CN, Ferrari G, Forti P (eds) Grotte marine: cinquant'anni di ricerca in Italia. Ministero dell'Ambiente e della Tutela del Territorio, Rome, pp 175–185

Bianchi CN, Aliani S, Morri C (1995) Present-day serpulid reefs, with reference to an ongoing research project on *Ficopomatus enigmaticus*. Publ Serv Geol Luxemb 29:61–65

Bo M, Bavestrello G, Angiolillo M, Calcagnile L, Canese S, Cannas R, Cau A, D'Elia M, D'Oriano F, Follesa MC, Quarta G, Cau A (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10(3):1–21

Bonifazi A, Lezzi M, Ventura D, Lisco S, Cardone F, Gravina MF (2019) Macrofaunal biodiversity associated with different developmental phases of a threatened Mediterranean *Sabellaria alveolata* (Linnaeus, 1767) reef. Mar Environ Res 145:97–111

Bosence DWJ (1979) The factors leading to aggregation and reef formation in *Serpula vermicularis* L. In: Larwood G, Rosen BR (eds) Biology and systematics of colonial organisms. Systematics association, vol 11. Academic, London, pp 299–318

Bruschetti M (2019) Role of reef-building, ecosystem engineering polychaetes in shallow water ecosystems. Diversity 11(9):168

Callaway R (2003) Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* banks. J Exp Mar Biol Ecol 283:115–132

Cardone F, Corriero G, Fianchini A, Gravina MF, Nonnis MC (2014) Biodiversity of transitional waters: species composition and comparative analysis of hard bottom communities from the south−eastern Italian coast. J Mar Biol Assoc UK. 94:25–34

Cardone F, Corriero G, Longo C, Mercurio M, Tarantini SO, Gravina MF, Lisco S, Moretti M, De Giosa F, Giangrande A, Nonnis Marzano C, Pierri C (2020) Massive bioconstructions built by *Neopycnodonte cochlear* (Mollusca, Bivalvia) in a mesophotic environment in the Central Mediterranean Sea. Sci Rep 10:633

Cau A, Moccia D, Follesa MC, Alvito A, Canese S, Angiolillo M, Cuccu D, Bo M, Cannas R (2017) Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep Sea Res Part I: Oceanogr Res Papers 122:60–70

Connor D (1990) Survey of Lochs Linnhe, Eil, Creran and Aline. Nature Conservancy Council, Peterborough, CSD report no 1073 (Marine Nature Conservation Review Report MNCR/SR/12), pp 139–141

Corriero G, Pierri C, Mercurio M, Nonnis Marzano C, Tarantini SO, Gravina MF, Lisco S, Moretti M, De Giosa F, Valenzano E, Giangrande A, Mastrodonato M, Longo C, Cardone F (2019) A Mediterranean mesophotic coral reef built by non-symbiotic scleractinians. Sci Rep 9:3601

Cunningham PN, Hawkins SJ, Jones HD, Burrows MT (1984) The geographical distribution of *Sabellaria alveolata* (L.) in England, Wales and Scotland, with investigations into the community structure of, and the effects of trampling on *Sabellaria alveolata* colonies. The Department of Zoology, The University of Manchester, Manchester. Contract for the Nature Conservation Council HF3/11a/22

Delbono I, Bianchi CN, Morri C (2003) Le biocostruzioni di *Sabellaria alveolata* come indicatori ambientali: area costiera fra Chiavari e Sestri Levante. In: Ferretti O (ed) Studi per la creazione di strumenti di gestione costiera: Golfo del Tigullio. ENEA, Centro Ricerche Ambiente Marino, La Spezia, pp 130–140

Dodd J, Baxter L, Hughes DJ (2009) Mapping *Serpula vermicularis* (Polychaeta: Serpulidae) aggregations in Loch Teacuis, western Scotland, a new record. Mar Biol Res 5(2):200–205

Donnarumma L, Sandulli R, Appolloni L, Di Stefano F, Russo GF (2018) Morpho-structural and ecological features of a shallow vermetid bioconstruction in the Tyrrhenian Sea (Mediterranean Sea, Italy). J Sea Res 131:61–68

Dubois S, Retière C, Oliver F (2002) Biodiversity associate with *Sabellaria alveolata* (Polychaeta, Sabellariidae) reefs: effects of human disturbances. J Mar Biol Assoc UK 82:817–826

Dubois S, Commito JA, Olivier F, Retière C (2006) Effect of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. Estuar Coast Shelf Sci 635–646

Firth LB, Mieszkowska N, Grant LM, Bush LE, Davies AJ, Frost MT et al (2015) Historical comparisons reveal multiple drivers of decadal change of an ecosystem engineer at the range edge. Ecol Evol 5(15):3210–3222

Gadaleta F, Mercurio M, Cardone F, Corriero G (2015) Indagini biocenotiche sui popolamenti bentonici di substrato duro dei fondali marini dell’Area Marina Protetta Torre del Cerrano. Relazione Conclusiva. Univ degli Stud Bari 1–32

Gambi MC (1986) Ecological implication in the tube morphology and epibiota of a population of *Ditrupa arietina* (Polychaeta, Serpulidae). Rapp P-V Comm Int Expl Sci Mer Medit 30(2):19

Gambi MC (1989) Osservazioni su morfologia funzionale e comportamento trofico di *Owenia fusiformis* Delle Chiaje (Polychaeta, Oweniidae) in rapporto ai fattori ambientali. Oebalia 15:145–155

Gambi MC (1999) Preliminary observations on distribution, biology and feeding ecology of some suspension feeding polychaetes in the Eastern Weddell Sea. In: Arntz WE, Gutt J (eds) with contribution of the participants. The expedition ANTARKTIS XV/3 (EASIZ II) of R/V “Polarstern” in 1998. Berich polarforsch, vol 301, pp 83–94

Gambi MC, Ierace S (1997) Epibiosis on the tubes of the polychaete *Ditrupa arietina* Serpulidae in some populations of the soft bottoms off the southern Tyrrhenian Sea. Biol Mar Mediterr 4:380–383

Gambi MC, Giangrande A, Fraschetti S (1996) Policheti dei fondi mobili del Golfo di Policastro (Mar Tirreno Meridionale): distribuzione e ruolo di alcune specie. In: Virzo De Santo A, Alfani A, Carrada GC, Rutigliano A (eds) Atti S.It.E, vol 17, pp 349–353

Gambi MC, Giangrande A, Patti FP (2000) Comparative observations on reproductive biology of four species of *Perkinsiana* (Polychaeta, Sabellidae). Bull Mar Sci 67(1):299–309

Gerhart DJ, Rittschof D, Mayo SW (1988) Chemical ecology and the search for marine antifoulants. J Chem Ecol 14(10):1905–1917

Giangrande A, Licciano M, Pagliara P, Gambi M (2000) Gametogenesis and larval development in *Sabella spallanzanii* (Polychaeta, Sabellidae) from Mediterranean Sea. Mar Biol 136:847–861

Giangrande A, Licciano M, Lezzi M, Pierri C, Caruso L, Stabili S (2014) Allochthonous *Branchiomma* species (Anellida, Sabellidae) in the Mediterranean Sea. A case of study in the Mar Grande of Taranto. Biol Mar Mediterr 21(1):93–96

Giordani Soika A (1956) Scogliera pseudocorallina intercotidale di *Sabellaria alveolata* (L.) nelle coste del Lazio (Ann. Polych.). Boll Mus Civ Venezia 9:11–13

Gravina MF, Cardone F, Bonifazi A, Bertrandino MS, Chimienti G, Longo C, Nonnis Marzano C, Moretti M, Lisco S, Moretti V, Corriero G, Giangrande A (2018) *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: habitat mapping, dynamics and associated fauna for conservation management. Estuar Coast Shelf Sci 200:248–257

Gribben PE, Angelini C, Altieri AH, Bishop MJ, Thomsen MS, Bulleri F (2019) Facilitation cascades in marine ecosystems: a synthesis and future directions. Ocean Mar Biol Ann Rev 57:127–168

Gruet Y (1986) Spatio-temporal changes of sabellarian reef built by the sedentary polychaete *Sabellaria alveolata* (L). Mar Ecol 7:303–319

Guglielmo R, Flagella S, Gambi MC (2006) Dinamica della comunità a policheti dei fondi sabbiosi in alcune stazioni selezionate del Golfo di Napoli. In: Capobianco L, Del Gaizo S, Saggiomo V, Zucato E (eds) Gestione e tutela dell’ambiente marino-costiero in Campania. ARPAC, Napoli, pp 85–100

Hughes DJ (2011) Where’s the ‘reef’? A five-year study of serpulid tube bioerosion in a Scottish sea loch. Mar Ecol Prog Ser 430:273–280

Jackson A, Hiscock K (2008) *Sabellaria spinulosa* Ross worm. In: Tyler-Walters H, Hiscock K (eds) Marine life information network: biology and sensitivity key information reviews [on-line]. Marine Biological Association of the United Kingdom, Plymouth. Available from: https://www.marlin.ac.uk/species/detail/1133

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 8:1946–1957

Kirkwood JM, Burton HR (1988) Macrobenthic species assemblages in Ellis Fjord, Vestfold Hills, Antarctica. Mar Biol 97:445–457

La Porta B, Nicoletti L (2009) *Sabellaria alveolata* (Linnaeus) reefs in the Central Tyrrhenian Sea (Italy) and associated polychaete fauna. Zoosymposia 2:527–536

Labrune C, Gremare A, Amouroux JM, Sarda R, Gil J, Taboada S (2007) Assessment of soft bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuar Coast Shelf Sci 71:133–147

Licciano M, Stabili L, Giangrande A (2005) Clearance rate of two filter feeding polychaetes candidate for bioremediation in aquaculture. Water Res 39(18):4375–4384

Lisco S, Moretti M, Moretti V, Cardone F, Corriero G, Longo C (2017) Sedimentological features of *Sabellaria spinulosa* biocontructions. Mar Petroleum Geol 87:203e212

Lisco S, Acquafredda P, Gallicchio S, Sabato L, Bonifazi A, Cardone F, Corriero G, Gravina MF, Pierri C, Moretti M (2020) The sedimentary dynamics of *Sabellaria alveolata* bioconstructions (Ostia, Tyrrhenian Sea, Central Italy). J Palaeogeogr 9:1–18

Longo C, Cardone F, Pierri C, Mercurio M, Mucciolo S, Nonnis Marzano C, Corriero G (2017) Sponges associated with coralligenous formations along the Apulian coasts. Mar Biodivers 48:2151–2163

Luckenbach MW (1987) Effects of adult infauna on new recruits: implications for the role of biogenic refuges. J Exp Mar Biol Ecol 105:197–206

Main MB, Nelson WG (1988) Sedimentary characteristics of sabellariid worm reefs *Phragmatopoma lapidosa*. Oceanogr Mar Biol Annu Rev 44:123–195

Mastrototaro F, D'Onghia G, Corriero G, Matarrese A, Maiorano P, Panetta P et al (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. Deep-Sea Res 27(5):412–430

Minchin D (1987) *Serpula vermicularis* L. (Polychaeta: Serpulidae) reef communities from the west coast of Ireland. Irish Nat J 22:314–316

Molinier R, Picard J (1953) Notes biologiques à propos d'un voyage d'étude sur les côtes de Sicilie. Ann Inst Océanogr Monaco 28(4):163–188

Moore CG, Saunders GR, Harries DB (1998) The status and ecology of reefs of *Serpula vermicularis* L. (Polychaeta: Serpulidae) in Scotland. Aquat Conserv: Mar Freshw Ecos 8:645–656

Nishi E (1996) Serpulid polychaetes associated with living and dead corals at Okinawa Island, Southwest Japan. Publ Seto Mar Biol Lab 37(3/6):305–318

Nonnis Marzano C, Baldacconi R, Fianchini A, Gravina MF, Corriero G (2007) Settlement seasonality and temporal changes in hard substrate macrozoobenthic communities of Lesina Lagoon (Apulia, Southern Adriatic Sea). Chem Ecol 23:479–491

Nunes F, Wormhoudt AV, Faroni-Perez L, Fournier J (2016) Phylogeography of the reef-building polychaetes of the genus *Phragmatopoma* in the wester Atlantic region. J Biogeogr 44 (7):1612–1625

Pierri C, Colangelo P, Del Pasqua M, Longo C, Giangrande A (2019) Consequences of the experimental removal of *Sabella spallanzanii* (Gmelin, 1791) from fouling assemblage of a Mediterranean harbour. Mediterr Mar Sci 20(3):476–486

Pinedo S, Sarda R, Rey-Rassat C, Bhaud M (2000) Effect of sediment particle size on recruitment of *Owenia fusiformis* in the Bay of Blanes (NW Mediterranean Sea): an experimental approach to explain field distribution. Mar Ecol Progr Ser 203:205–213

Plicanti A, Domínguez R, Dubois S, Bertocci I (2016) Human impacts on biogenic habitats: effects of experimental trampling on *Sabellaria alveolata* (Linnaeus, 1767) reefs. J Exp Mar Biol Ecol 478:34–44

Poloczanska ES, Hughes DJ, Burrows MT (2004) Underwater television observations of *Serpula vermicularis* (L.) reefs and associated mobile fauna in Loch Creran, Scotland. Esuar Coast Shelf Sci 61:425–435

Rabaut M, Guilini K, Van Hoey G, Vincx M, Degraer S (2007) A bioengineered soft-bottom environment: the impact of *Lanice conchilega* on the benthic species-specific densities and community structure. Estuar Coastal Shelf Sci 75(4):525–536

Rabaut M, Vincx M, Degraer S (2009) Do *Lanice conchilega* (sandmason) aggregations classify as reefs? Quantifying habitat modifying effects. Helgol Mar Res 63:37–46

Ramos A, San Martin G (1999) On the finding of a mass occurrence of *Serpula narconensis* Baird, 1885 (Polychaeta, Serpulidae) in South Georgia (Antarctica). Polar Biol 22:379–383

Rossi S (2013) The destruction of the 'animal forests' in the oceans: towards an oversimplification of the benthic ecosystems. Ocean Coast Manag 84:77–85

Rossi S, Bramanti L, Gori A, Orejas C (2017) An overview of the animal forest in the world. In: Rossi S (ed) Marine animal forest. Springer International, New York

Rosso A, Sanfilippo R, Taddei Ruggiero E, Di Martino E (2013) Faunas and ecological groups of Serpuloidea, Bryozoa and Brachiopoda from submarine caves in Sicily (Mediterranean Sea). New Adv It Paleont 2:1–10

Santos TMT, Aviz D (2018) Macrobenthic fauna associated with Diopatra cuprea (Onuphidae: Polychaeta) tubes on a macrotidal sandy beach of the Brazilian Amazon Coast. J Mar Biol Ass UK 1–9. https://doi.org/10.1017/S0025315418000711

Schimmenti E, Musco L, Lo Brutto S, Mikac B, Nygren A, Badalamenti F (2016) Mediterranean record of *Eulalia ornata* (Annelida Phyllodocidae) corroborating its fidelity link with the *Sabellaria alveolata* reef habitat. Mediterr Mar Sci 17(2):359–370

Smith AM, McGourty CR, Kregting LA, Elliot M (2005) Subtidal *Galeolaria hystrix* (Polychaeta: Serpulidae) reefs in Paterson Inlet, Stewart Island, New Zealand. N Z J Mar Freshw Res 39 (6):1297–1304

Somaschini A (1993) A Mediterranean fine-sand polychaete community and the effect of the tube-dwelling *Owenia fusiformis* Delle Chiaje on community structure. Int Rev Ges Hydrobiol 78:219–233

Stabili L, Licciano M, Giangrande A, Fanelli G, Cavallo RA (2006) *Sabella spallanzanii* filter-feeding on bacterial community: ecological implications and applications. Mar Environ Res 61:74–92

Taramelli-Rivorecchi E (1961) Osservazioni sulle biocenosi del banco a *Sabellaria* di Lavinio. Rend Accad Naz dei XL Ser IV 12:147–157

ten Hove HA (1979) Different causes of mass occurrence in serpulids. In: Larwood G, Rosen BR (eds) Systematics Association. Biology and systematics of colonial organisms, vol 11. Academic, London, pp 281–298

ten Hove HA, Kupriyanova EK (2009) Taxonomy of Serpulidae (Annelida, Polychaeta): the state of affairs. Zootaxa 2036:1–126

ten Hove HA, van der Hurk P (1993) A review of recent and fossil serpulid "reefs"'; actuopaleontology and the "Upper Malm" serpulid limestones in NW Germany. Geol Mijnb 72:23–67

Tenerelli V (1966) Sulla presenza di *Mercierella enigmatica* Fauvel lungo la costa orientale di Sicilia (Polychaeta, Serpulidae). Boll Zool 24:735–748

Thomsen MS, Wernberg T, Altieri A, Tuya F, Gulbransen D, McGlathery K, Holmer M, Silliman BR (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol 50:158–175

Turner SJ, Thrush SF, Hewitt JE, Cummings VJ, Funnell G (1999) Fishing impacts and the degradation or loss of habitat structure. Fish Manag Ecol 6:401–420

Ventura D, Bonifazi A, Gravina MF, Belluscio A, Ardizzone GD (2018) Mapping and classification of ecological sensitive marine habitat using unmanned aerial vehicle (UAV) imagery and object-based image analysis (OBIA). Remote Sens 10(9):1331

Vine PJ, Bailey-Brock JH (1984) Taxonomy and ecology of coral reef tube worms (Serpulidae, Spirorbidae) in the Sudanese Red Sea. Zool J 80:135–156

Chemical War in Marine Animal Forests: Natural Products and Chemical Interactions

C. Avila

Abstract Forests are characterized by many different species living together, a high biodiversity, and many kinds of relationships among them, resulting from an advanced degree of mutual adaptations along evolution. Interactions occur both at interspecific and intraspecific levels, including many different types, such as competition (for food, light, space, etc.), predation, fouling, parasitism, symbiosis, etc. Many organisms evolved to defend or protect themselves against all sort of aggressive interactions. Reactions may include chemical, physical, and/or behavioral strategies. Chemical interactions are very common in terrestrial forests, regulating many of these relationships among species. Natural products are the molecules involved in these regulations and usually consist of secondary metabolites. In marine animal forests, many interactions are regulated just the same way as in terrestrial forests, with all sorts of relationships controlled by natural compounds, but studying these ecosystems is often challenging because many species are cryptic, small, and/or rare and belong to poorly known taxonomic groups. In this chapter, the different chemical strategies commonly found in marine animal forests are reviewed, as well as how relevant they are in the structuring and functioning of these ecosystems. This chapter also shows how high biodiversity is correlated to high chemical diversity in marine animal forests.

Keywords Chemical ecology · Chemical defense · Marine benthic invertebrates · Symbiotic microorganisms · Global change

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1 Introduction

Marine animal forests are composed of many zoological taxa forming three-dimensional architectures and growing from a few centimeters to tens of meters, thus providing shelter for many other species (Rossi et al. 2017a). They occur in all oceans, from the tropics to the poles and from shallow water to deep sea, over a wide geographical range of seascapes, including tropical shallow-water coral reefs, shallow communities in the Mediterranean and in Central America, mesophotic coral communities on the continental slope, bathyal cold-water coral gardens on seamounts at the Mid-Atlantic Ridge, and deep-sea cold-water ecosystems, as well as in northern and southern cold-temperate and polar regions (Rossi et al. 2017a). The structuring ecosystem engineers comprise the entire variety of hermatypic and soft corals, notably gorgonians, but also other cnidarians, sponges, bryozoans, polychaetes, bivalves, and other taxa which emerge from the seafloor (Rossi et al. 2017a, b). It is considered that the high diversity associated with these animal-dominated communities is the result of the high heterogeneity in the environmental conditions also induced by these structuring organisms (Rossi et al. 2017a, b).

As in terrestrial forests, there is a very active chemical war in marine animal forests, where chemical interactions and natural products play a crucial role. Chemical ecology is a multidisciplinary science that includes both chemical and biological research (Paul 1992). Secondary metabolites, or natural products, are the organic molecules produced by organisms that regulate their specific biology, coexistence, and coevolution, without direct participation in their primary metabolism (Torssel 1983; Pietra 2002). They have a restricted distribution, occurring only in some taxonomically related groups, or even individual species, and a wide heterogeneity (Torssel 1983; Pietra 2002). Their functions, mostly unknown, are being elucidated with increasing frequency over the recent decades. The complexity of their chemical structures and biosynthetic pathways has contributed to making it difficult to ascertain their roles. However, all organisms produce a vast and diverse assortment of natural products, many of which have been shown to have important adaptive significance in protection against predation and microbial infection, as attractants and allelopathic agents (influencing competition among species), among others. In particular, marine benthic invertebrates living in animal forests are exposed to strong predation, fouling, and potentially infectious waterborne microorganisms, and they must also compete for substrate upon which to settle. All these ecological functions largely affect organisms' survival.

In contrast to terrestrial studies that developed over centuries, not so much is known regarding the biological role of secondary metabolites in the marine environment. Actually, terrestrial chemical ecology, focusing on animal–plant relationships, has been and still is a model for marine chemical ecology studies (Paul 1992; Pietra 2002; Paul et al. 2007). The oceans cover 70% of the world's surface, with 95% of them deeper than 1000 m (Castro and Huber 2005) and thus opening up an incredible arsenal of natural compounds. The research on marine toxins started in the 1960s, together with the increasing development of marine animal taxonomy. In the

1970s–1980s, the search for new natural products and new chemical skeletons further advanced. Later, the priority moved towards activity-driven studies of the natural products because of the potentially huge biomedical interest of the new compounds found. By the end of the 1980s and beginning of the 1990s, the field expanded towards the wide marine chemical ecology field. Nowadays, there are >34,000 natural products reported in the MarinLit database, and the study of marine natural products and their bioactivity has developed further. Contrastingly, the chemical ecology of marine natural products is still growing quite at a snail's pace, as many chemical and ecological key aspects remain yet to be analyzed and well understood. This is particularly obvious in geographic areas where access to the field is difficult and/or expensive. Research in chemical ecology in marine animal forests is still an open field, with far more questions than answers. Nevertheless, marine natural products are known to play critical roles in the chemical defense of many marine organisms and may influence the community structure of entire ecosystems (Paul et al. 2007, 2011). The way in which marine consumers perceive chemical defenses can influence their health and survival and determine whether some natural products persist through a food chain. In addition to mediating a variety of trophic interactions, these compounds may be responsible for community-scale ecological impacts of chemically defended organisms, such as shifts in benthic and pelagic community composition (Paul et al. 2007). Examples may include harmful algal blooms; the invasion of the Mediterranean by the algae *Caulerpa taxifolia*; overgrowth of coral reefs by chemically rich macroalgae and cyanobacteria; invertebrate chemical defenses, including the role of microbial symbionts in compound production; and others (Paul et al. 2007). The study of the "chemical network" (chemical ecology interactions) structuring the communities provides information about the ecology and biology of the involved species and the function and the structure of the community (e.g., Avila 1995; Lebar et al. 2007; Avila et al. 2008; Figuerola et al. 2012).

Even if there are thousands of published chemical studies describing the compounds present in marine organisms (see Blunt et al. 2018 and previous reviews), still very few studies provide ecological information about the functional significance of these compounds (e.g., Paul 1992; Avila 1995, 2006; Hay 1996; McClintock and Baker 1997, 2001; Harborne 2001; Paul and Puglisi 2004; Lebar et al. 2007; Avila et al. 2008; McClintock et al. 2010; Núñez-Pons and Avila 2015; Puglisi et al. 2018). Marine organisms are under intense pressure for space, light, and food, and therefore, during evolution, a range of defensive mechanisms, including behavioral, physical, and chemical strategies, were favored by selection. While studying the ecological roles for marine natural products has become a broad research area encompassing studies of the chemical mediation of a variety of ecological interactions among organisms, including predator–prey interactions, spatial competition, avoiding fouling, symbioses, competition for space or food, mate recognition, reproductive cues, larval settlement, UV protection, and others, the most investigated activity so far is the ability to deter predators (Paul 1992; Pawlik 1993; Avila 1995; Hay 1996; Zimmer and Butman 2000; Stachowicz 2001; Hadfield and Paul 2001; Rittschof 2001; Amsler et al. 2001; McClintock and Baker 2001; Iken et al.

2002; Paul and Puglisi 2004; Bowden et al. 2006; Avila et al. 2008; Peters et al. 2010; Puglisi et al. 2014). Also, a major focus has been how chemical defenses of macroalgae and invertebrates do mediate predator–prey and competitive interactions (Paul and Puglisi 2004). In fact, as natural product chemists and marine ecologists started collaborating, the field developed rapidly to address questions of how organisms use their natural products. Further, chemical ecology has developed into including the biochemistry of marine plant–animal and animal–animal interactions and also including research into the chemical recognition of prey items and chemotaxis, i.e., directed movement oriented by chemical gradients, predator–prey and seaweed–herbivore interactions, defenses against fouling organisms, infection by microorganisms, competitive interactions, invasive species, and settlement cues (Paul and Puglisi 2004; Puglisi et al. 2014).

In temperate and tropical marine ecosystems, it has been recognized that natural products act as important mediators in intra- and interspecific biological interactions and in regulating the structure of the communities (e.g., Scheuer 1990; Paul 1992; Pawlik 1993; Hay 1996). However, other areas of the planet, such as the poles or the deep sea, remain mostly unexplored. It is well-known that in shallow, warm oligotrophic tropical waters, with strong light penetration, tropical coral reefs dominate, but also cold-water coral reefs, comparable to their tropical counterpart in terms of structural and functional complexity, are widely distributed in the world oceans, mostly at 200–1500 m depth (Rossi et al. 2017a, b). In temperate seas, gorgonians, sponges, and bryozoans may form dense forests, both in shallow coastal areas and in some deeper areas (Rossi et al. 2017a, b). At polar latitudes, for instance, in Antarctica, suspension feeders, such as sponges, gorgonians, and bryozoans, often dominate benthic communities (Fig. 1).

Antarctic ecosystems are unique because of their environmental characteristics, which result in communities that are structured mostly by biotic interactions, i.e., predation and competition, as well as by abiotic factors, i.e., seasonality and ice-scouring, where benthos inhabitants are mainly sessile suspension feeders (Dayton et al. 1974, 1994; Arntz et al. 1994; Orejas et al. 2000). Antarctic benthos comprises some of the most ancient and stable marine ecosystems worldwide. Alas, very little is known yet about the evolution of natural products in marine Antarctic

Fig. 1 Shallow Antarctic marine animal forests at Deception Island (South Shetland Islands), at about 15 m depth, dominated by suspension feeders. Left: sponge-covered rocky area. Right: *Doris* sea slugs preying upon a sponge

organisms and how ecological factors may prompt chemical mechanisms as a reaction for increasing survival (Avila et al. 2008). Over the last years, some studies showed that defensive compounds are present in many Antarctic species. For some groups, such as microorganisms, planktonic organisms, and deep-sea fauna, their chemical ecology remains mostly unexplored so far. Moreover, studies have usually been done in the laboratory, with only a few examples carried out in an ecologically relevant context.

Antarctic and sub-Antarctic benthic organisms are exposed to an intense predation pressure provoked by many vagile macroinvertebrates (Avila et al. 2008; Taboada et al. 2013; Moles et al. 2015). Therefore, defenses are anticipated to be frequent in organisms living in these ecosystems, either these being chemical mechanisms or other defensive strategies (physical, behavioral, etc.). The role that chemical defenses play mediating predator–prey interactions has attracted much interest in tropical and temperate areas as well as in the shallow sub-Arctic and Antarctic waters (Scheuer 1990; Paul 1992; Pawlik 1993; Hay 1996; McClintock and Baker 1997; Amsler et al. 2001; Lippert et al. 2004; Avila et al. 2008). Benthic invertebrates inhabiting deep waters in Antarctic and sub-Antarctic areas are also well defended against sympatric predators by using natural products, similar to shallow-water species (Taboada et al. 2013; Moles et al. 2015). Actually, more than half of the deepwater Antarctic and sub-Antarctic benthic invertebrates tested so far are chemically protected from the sympatric keystone predator, the sea star *Odontaster validus*, with sessile taxa displaying the highest repellence activities and ascidians, cnidarians, and sponges being the best chemically protected groups (Taboada et al. 2013; Moles et al. 2015). The Southern Ocean fauna is characterized by the poor presence of fish and decapods as either competitors or predators (Clarke et al. 2004; Gili et al. 2006). In fact, the absence of sharks and crabs, together with the low biodiversity and biomass of teleost fish, is a clear indication of low predation pressure on hard-bodied organisms, which has benefited, during evolution, groups like echinoderms (Aronson and Blake 2001). Therefore, in Antarctic communities, echinoderms are the dominant vagile megafaunal organisms in terms of abundance and diversity (Dayton et al. 1974; Clarke et al. 2004), with many species representing important generalist predators. There, asteroids replaced fish as major potential predators, and the pressure caused by these macrobenthic predators is as intense as that reported in temperate and even tropical areas (Dearborn 1977; McClintock 1994). This pressure, added to the environmental stability and isolation of Antarctic ecosystems from surrounding waters (ca 23–41 My; Lyle et al. 2007), has been a strong selective force for the evolution and acquisition of defensive natural products in many invertebrates (e.g., McClintock and Baker 1997; Amsler et al. 2000, 2001; Avila et al. 2008). Indeed, a quite large number of natural products and potential chemical defenses have been reported from Antarctic marine organisms in recent years (Lebar et al. 2007; Avila et al. 2008; Núñez-Pons and Avila 2015). In most cases the full understanding of either the molecular structure or the ecological relevance of most compounds is still missing (Avila et al. 2008; Moles et al. 2015; Núñez-Pons and Avila 2015). Overall, these studies provide further support for the hypothesis that Antarctic benthic marine invertebrates are rich in chemical defenses even if there is no fish predation (Amsler et al. 2000; Avila et al. 2008; Núñez-Pons et al. 2012b; Figuerola et al. 2013a; Moles et al. 2015; Núñez-Pons and Avila 2015). Benthic invertebrates from the Southern Ocean ecosystems seem to be efficiently protected from echinoderm predation through chemical defenses.

The deep sea, due to its high biodiversity, is another interesting marine environment. As already mentioned, over the past decades, >34,000 natural products have been reported from marine flora and fauna, and yet less than 2% of those derive from deepwater marine organisms (MarinLit database). Although it is difficult to access these depths, and this has previously hindered deep-sea research, nowadays with improved technologies and easier access to submersibles, deep-sea exploration is uncovering extensive deepwater coral reefs that are home to many species on continental shelves and seamounts worldwide (Roberts et al. 2006; Skropeta 2008). Environmental conditions and oceanographic parameters at play in the deep sea are very particular (Gage and Tyler 1991; Thistle 2003). Pressure increases by 1 atm for every 10 m below sea level, varying from 10 atm at the shelf–slope interface to >1000 atm in the deepest part of the trenches; temperatures taper off rapidly with increasing depth down to ca. 2 °C at bathyal depths of >2000 m; light penetration decreases exponentially with depth, such that below 250 m essentially no light penetrates (Skropeta 2008). In those conditions, in the dark cold depths of the ocean, vision becomes less critical, and the assumption is that chemoreception and mechanoreception play greater roles (Skropeta 2008).

Estimations indicate that the number of species inhabiting the world's oceans may be as high as ten million species (Grassle and Maciolek 1992), and the ocean fringe with its high concentration of competing species was thought to possess the highest species diversity. However, recent studies showed that the deep sea is one of the most biodiverse and species-rich habitats on the planet, rivalling that of coral reefs and rainforests (Grassle and Maciolek 1992; Gage 1996; Sibuet and Olu 1998; Snelgrove and Smith 2002; Venter et al. 2004; Brandt et al. 2007; Skropeta 2008). Deep-sea organisms survive under extreme conditions in the absence of light, under low levels of oxygen and intensely high pressures, and all these factors probably affect their primary metabolic pathways and consequently their secondary metabolites (Bull et al. 2000; Wright et al. 2003; Skropeta 2008). Thus, deep-sea fauna is expected to have a larger genetic diversity than their shallow-water counterparts and a higher probability of containing structurally unique metabolites (Skropeta 2008). Many species are found exclusively at the deep sea, with high levels of biodiversity extending to abyssal depths down to 5000 m (Gage and Tyler 1991; Thistle 2003). Skropeta (2008) compiled 390 novel natural products isolated from deep-sea fauna (down to 1000 m), with deepwater natural products from Antarctica to the tropical waters of the Caribbean. Over 50% of these metabolites were found in depths from 100 to 400 m, with 10% from depths of 500–600 m and only 8% from below 1000 m. Deep-sea metabolites have been reported from a diverse range of phyla including Porifera, Cnidaria, Echinodermata, and Chordata, along with a range of microorganisms such as archaea, bacteria, and fungi (Skropeta 2008).

From the tropics to the poles, from the deep sea to the shallows, we aim to summarize here the role of natural products and the chemical interactions in marine animal forests. However, this is not a comprehensive review of the topic, but an overview on the current state of the art, including some selected examples of relevant cases.

2 Interactions and Natural Products

2.1 Chemical Ecology

Interactions among organisms include a wide range of combinations, such as competition, commensalism, mutualism, parasitism, fouling, diseases, and others. Prey–predator interactions and their related defensive strategies are also a particular case of interaction that will be dealt with in a separate section below. In marine environments, megabenthic communities dominated by sessile suspension feeders (such as sponges, corals, and bivalves) generate three-dimensional habitats structurally complex that give shelter to other species (Fig. 2) and where many of these interactions exist (Rossi et al. 2017a, b). For regulating these interactions, seaweeds, sponges, corals, ascidians, and other sessile and vagile organisms use a diverse array of natural compounds, including terpenes, acetogenins, alkaloids, and polyphenols (Hay and Fenical 1996). Some of these compounds differ fundamentally from terrestrial natural products in that they are often halogenated and possess chemical structures that are unprecedented among terrestrial organisms (Faulkner 1994; Blunt et al. 2018).

Chemical ecology includes the study of all chemically mediated interactions, and as such, it comprises many different aspects, from chemical communication,

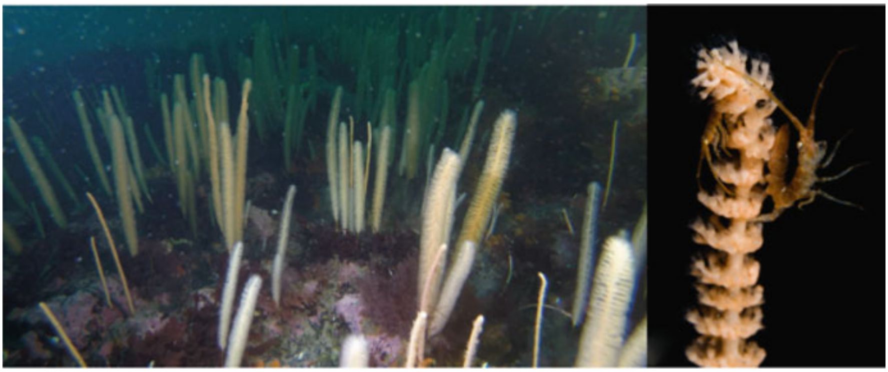


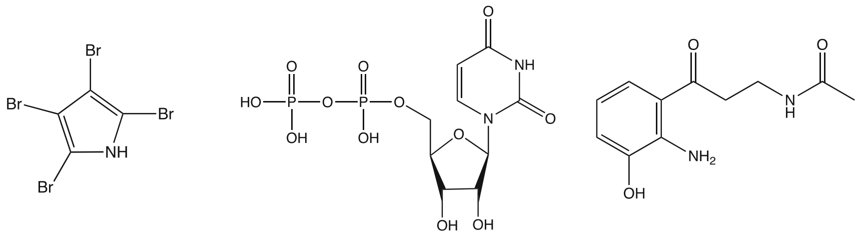
Fig. 2 Gorgonian gardens at 25 m depth in Livingston Island (South Shetland Island, Antarctica). Left: general view of the three-dimensional structure of the community. Right: isopods living on top of the gorgonians, probably being commensals

chemical sensing, and chemical defenses. Defenses may be developed against competitors, predators, foulers, and pathogens (see below). Other functions may include UV protection (Frederik et al. 1989; Karentz 2001; Karentz and Bosch 2001; Núñez-Pons et al. 2018a) or heavy metal chelation (e.g., phlorotannins from macroalgae that bind to metal ions potentially reducing the toxicity of heavy metal pollutants such as Cu and Pb; Toth and Pavia 2000; Amsler and Fairhead 2006). Chemical defenses against predators typically involve production of natural compounds that are toxic, distasteful, or both to potential consumers (Paul 1992; Roitberg and Isman 1992; Pawlik 1993; Eisner and Meinwald 1995; Avila 1995; Hay 1996; McClintock and Baker 1997; Faulkner 1998; Amsler et al. 1999). Interactions between sympatric organisms are typically defined as mutualistic if both interacting species derive benefit, such as protection from a predator or from the environment; dispersal of spores, gametes, larvae, seeds, or other propagules; transport away from unsuitable habitats; or provision of energy, nutrients, or other substances necessary for growth (Boucher et al. 1982; Ricklefs 1990; Bronstein 1994). Although a wide range of such interactions has been examined, interactions of plants and animals with the plants obtaining a reproductive benefit are particularly well documented (Bronstein 1994; Amsler et al. 1999). Similar processes may happen at the sea, although they are not yet well documented.

2.2 *Reproduction, Settlement, and Recruitment*

Chemical cues involved in reproduction, settlement, and recruitment have been recently reviewed by Harder et al. (2018). In macroalgae, motile brown male gametes from a wide variety of species locate female gametes using pheromones secreted by the female gametes (Amsler and Fairhead 2006). At least 12 specific pheromones are known to be released by zygotes or settled female gametes from over 60 species in 13 orders, with most species releasing more than one of the pheromones in addition to some of their biosynthetic precursors (Pohnert and Boland 2002; Amsler and Fairhead 2006). The effective distance at which male gametes could perceive the pheromones has been estimated as 0.5–1 mm, or even a few mm, although this is likely to decrease with increasing water motion (Amsler and Fairhead 2006).

The role of tannins in sponge recruitment has been studied in a mangrove sponge, *Tedania ignis*, in the field (Hunting et al. 2010). Since more sponge larvae settled on mangrove roots with high tannin concentrations with respect to control and roots with lower tannin amounts, the authors propose that there is a positive feedback in *T. ignis* larval recruitment. Also, to analyze the effect of sponges in the production of tannins in the mangrove roots, *T. ignis* was transplanted from populated to bare mangrove roots, demonstrating a significant increase in tannin and polyphenolic concentrations when sponges were attached, either naturally or artificially (Hunting et al. 2010). This is relevant for the sponge larvae to find a suitable habitat in the vast ocean. Another study tested larval settlement in two common Great Barrier Reef



1. Tetrabromopyrrole 1 2. Uridine diphosphate 3. Erebusinone

Fig. 3 Structures of some chemical cues used by marine invertebrates. *1*. Tetrabromopyrrole 1 induces settlement in several coral species. *2*. Uridine diphosphate is a sex pheromone in crabs. *3*. Erebusinone promotes reduced molting and increases mortality in an amphipod

sponges, *Coscinoderma matthewsi* and *Rhopaloeides odorabile*, using methanol extracts from the crustose coralline alga *Porolithon onkodes* (Whalan et al. 2012). In both cases, settlement was observed to be higher with crustose coralline algae, thus showing that sponge larvae are capable to select the best suitable habitats for their successful recruitment (Whalan et al. 2012). All these results suggest that sponges have the potential to recognize diverse signaling molecules for larval recruitment.

The crucial role of bacteria in the settlement of Caribbean corals has also been demonstrated. *Porites astreoides* larvae will settle in response to natural biofilms, and in particular to a strain of *Pseudoalteromonas* isolated from the surface of crustose coralline algae (Sneed et al. 2014). Crude organic extracts of *Pseudoalteromonas* sp. also induced settlement, and the compound tetrabromopyrrole 1 was identified as the active metabolite (1, Fig. 3). Tetrabromopyrrole 1 was also reported to induce settlement in two other Caribbean coral species, *Orbicella franksi* and *Acropora palmata*, which overall represent a diverse array of coral taxa and life history strategies, suggesting a potentially relevant role for this compound in a wide variety of Caribbean corals (Sneed et al. 2014).

Another study examined water-soluble chemical cues from live reefs compared to dead reefs to see how these cues influenced the larval settlement of crustaceans, cephalopods, and fishes in Japan (Lecchini et al. 2014). In a flume experiment, larvae of the fish *Chromis viridis*, a shrimp (Palaemonidae), and the mollusc *Sepia latimanus* spent more time in the water collected next to the live coral reef. The water from a dead coral reef never induced any of the larvae. Thus, water-soluble cues from live corals act as indicators for appropriate larval settlement, but the effects are less likely as the distance from the reef increases.

Chemical cues are often responsible for inducing settlement behaviors in many invertebrate larvae, including molluscs (Harder et al. 2018). The role of chemical cues in mate-seeking behavior has been demonstrated, for example, in sexually mature cuttlefish (*Sepia officinalis*), which are able to detect and are attracted to chemical compounds from the reproductive females (Boal et al. 2010). Cuttlefish usually form aggregations to lay their eggs, and thus, chemicals from the spawn have been suggested to act as pheromones to coordinate their reproductive behavior. Similarly, chemical cues used as metamorphosis signals are described in echinoderms (Swanson et al. 2012). In sea urchins larvae, the common chemical cue for identifying habitat and starting metamorphosis is reported to be histamine, released from algae and seagrasses (Swanson et al. 2012).

Also in crustaceans chemical cues are relevant in reproduction, in order to find a potential mate. In the green crab *Carcinus maenas*, uridine diphosphate (2, Fig. 3) has been identified as a sex pheromone, being released in female urine and found in female-conditioned seawater (Hardege et al. 2011). In shrimp, some studies have characterized the contact sex pheromones produced by *Lysmata boggessi*, where a complex mixture of chemicals probably regulates its mating behavior (Zhang et al. 2011). For further larval survival, it is also crucial to be able to detect potential predators. In fact, a study showed that, in laboratory assays, megalopae of the crab *Hemigrapsus sanguineus* were able to detect water-soluble cues from putative fish predators, showing that chemical cues may be used against predation (Rasch and O'Connor 2012).

Hippolyte inermis is a benthic shrimp characterized by a peculiar mechanism of sex reversal influenced by diatom foods (Zupo et al. 2007; Nappo et al. 2009). The appearance of primary females in spring is due to an apoptotic early disruption of the androgenic gland and of the male gonad, triggered by still unknown compounds present in benthic diatoms of the genus *Cocconeis* (Nappo et al. 2009). The action of diatoms delivered with the diet is very specific and time limited. It takes place from the second to the 12th day of postlarval development and is targeted only against the androgenic gland and the male gonad (Sagi 1988; Zupo and Messina 2007). Thus, it is a very fast and specific process leading to the complete disruption of the androgenic gland in the first days of postlarval growth and to the appearance of the female sex within a single molt cycle (Zupo et al. 2007). The influence of diatoms on the reproductive ecology and life cycle of planktonic crustaceans has been demonstrated previously: some planktonic diatoms produce aldehydes inducing apoptosis in the embryos and in the larvae of marine copepods, reducing their viability (Zupo et al. 2007). These phenomena are similar to what happens in the terrestrial environments with plants and insects. Both benthic and planktonic diatoms produce compounds having an apoptotic effect on tissues of target crustaceans, although the ecological significance of the two processes is different: deleterious for copepod populations and regulative for shrimps associated with *Posidonia oceanica* (Zupo et al. 2007). Also, the diatom compounds are different, since both planktonic diatoms and their aldehydes had negligible effects on the sex ratios of cultured shrimps. The apoptotic activities promoted by planktonic and benthic diatoms, both producing effects on the physiology of various crustaceans (reducing the size of recruitment in planktonic copepods and stabilizing the natural populations in benthic crustaceans), are analogous, because they are based on different chemical compounds (Zupo et al. 2007).

Even though it is rarely tested, chemical cues from predators might have an impact on the next generation of a species. Reproduction in the mud snails *Ilyanassa* *obsoleta* was assessed in the presence of chemical cues from the predatory green crab *Carcinus maenas* and in the presence of the non-predatory urchin *Strongylocentrotus droebachiensis* in the NE Atlantic (Schwab and Allen 2014). The study showed that predator cues in the natural environment affect egg capsule and larval morphology, but different morphologies were not always equally effective deterring predators. Erebusinone (3, Fig. 3) from the Antarctic demosponge *Isodictya erinacea* was found to mediate another peculiar allelopathic interaction, by promoting reduced molt events and increased mortality in the omnivore amphipod *Orchomene plebs*, when the amphipod was fed on eribusinone-enriched diets (Moon et al. 2000).

As said, few studies have investigated the potential activity of marine compounds against sperm and early life stages of common predators and competitors, although this is also a well-known process in terrestrial forests. The example of the Mediterranean *H. inermis* above is one of the few reported cases. In Antarctica, some experiments tested the activity of extracts from benthic invertebrates against sperm and early life stages of the common Antarctic echinoid *S. neumayeri* (McClintock et al. 1990, 1992; Heine et al. 1991; Slattery et al. 1995; Figuerola et al. 2012, 2013b). A high amount of sperm toxicity and cytotoxicity against *S. neumayeri* and copepods was found in most species of different benthic invertebrates tested by Figuerola et al. (2012, 2013b). *S. neumayeri* feeds mostly on diatoms (Pearse and Giese 1966), and it has been suggested that sea urchin grazing could be responsible for the mortality of settling larvae and juveniles of other benthic invertebrates (Bowden 2005; Bowden et al. 2006). Moreover, the settlement of pelagic larvae on or near their prey is frequent in marine predatory invertebrates (Pawlik 1992). Therefore, the presence of cytotoxic compounds in a good number of benthic invertebrates may play an important role in reducing the recruitment of this sea urchin and, consequently, the grazing pressure and the colonization of the surfaces (McClintock et al. 1990; Bowden et al. 2006; Figuerola et al. 2012, 2013b).

2.3 Habitat Specificity

In Antarctica, community-level non-consumptive effects occur when amphipods chemically sense fish predators and respond by seeking refuge in chemically defended macroalgae (McClintock et al. 2010). Also, the common sea star *Odontaster validus* and the limpet *Nacella concinna*, two ecologically relevant species inhabiting marine benthic communities along the Western Antarctic Peninsula, present chemosensory behaviors that are very important in determining conspecific and interspecific interactions impacting population and community ecology (McClintock et al. 2010).

It is now well-known that marine herbivores are active participants in seaweed–herbivore interactions and can greatly influence the structure of benthic algal communities (Cronin and Hay 1996a). Thus, seaweeds are not passive actors in these interactions, but actively alter their susceptibility to herbivores in ecological time.

Induced responses to herbivory help explain both spatial (i.e., within-thallus, within-site, and among-site) and temporal variation in the chemical defenses of algae (Cronin and Hay 1996a). Analogously, this may happen in marine animal forests, although the available information is scarce. In Antarctica, a relationship between macroalgae (*Phyllophora antarctica* and *Iridaea cordata*), the sea urchin *Sterechinus neumayeri*, and the sea anemone *Isotealia antarctica* was described (Amsler et al. 1999). Both macroalgal species are chemically defended against herbivory by *S. neumayeri*, and the urchins use macroalgae as cover, holding the vast majority of available drift. Their experiments showed that urchins make an active behavioral choice to cover with macroalgae when available. Macroalgal cover, in turn, acts as a defense against the major sea urchin predator, *I. antarctica*. The anemone tentacles attach to the algae and are subsequently released, being described as a physical defense (Amsler et al. 1999). Macroalgae benefit from this relationship because fertile drift plants are retained in the photic zone where they can continue to contribute to the gene pool, while the urchins also extend the effective horizontal and vertical distributions of the macroalgae, which may help sustain the range of these algal populations in periods of reduced light availability. Therefore, even if the macroalgae are chemically protected from urchin herbivory, this is a mutualistic relationship which benefits both the macroalgae and the urchin (Amsler et al. 1999). It seems reasonable to expect many mutualistic relationships like these in marine animal forests, although information is just starting to be compiled. For example, sponges are among the most abundant macroinvertebrates in Antarctic benthic communities, playing a key role in community structure and dynamics. They are used as food sources for many diverse predators (e.g., echinoderms, nemerteans, and gastropods; Cerrano et al. 2000; Schiaparelli et al. 2003; Avila et al. 2018), as well as substrates for epibionts and endobionts (e.g., isopods, amphipods, gastropods, bivalves, and polychaetes), which colonize external surfaces and also interstices of ostia and oscula (McClintock et al. 2005; Núñez-Pons et al. 2012b). Probably many mutualistic relationships remain to be discovered here.

A typical example of mutualistic relationship in the Mediterranean is that of pagurid crabs and anemones or sponges, for example, the crab *Dardanus arrosor* with the anemone *Calliactis parasitica* or with the sponge *Suberites domuncula*. While the crabs obtain chemical protection while travelling within the mollusc shell (chemical defenses and cnidocytes), both anemone and sponges obtain better access to food resources as well as improved water circulation and access to different habitats through the crab mobility. Another example includes the sponge coverage of some sessile bivalve molluscs, such as *Arca noae* with the sponge *Crambe crambe*, which is very rich in bioactive chemical compounds. In Antarctica, similar associations exist, for example, between the vagile mollusc *Harpovoluta charcoti* and the anemone *Isocyonis alba*, although in this case the mollusc is the transporting species. How these interactions are chemically regulated remains to be further elucidated. Interestingly, hermit crabs may also use chemical cues to evaluate possible resources, for example, empty shells (Tricaricoa et al. 2011). In this study, the authors compared the amount of time taken by the hermit crabs

Clibanarius erythropus and *Pagurus bernhardus* to touch an empty shell and for how long they investigated the shell, showing that these two crab species responded differently to the water-soluble cues related to these putative resources.

Many examples of species providing habitat for others include those of Antarctic ophiuroids with many different organisms (Martín Ledo 2010). This study reported the associations between *Ophioplinthus brevirima* and several foraminifera, *Ophioplinthus gelida* and some thecate colonial hydrozoa, *Ophioplinthus gelida* and some endoparasitic nematoda, *Ophionotus victoriae* and some endoparasitic nematoda, as well as many others. Among them, *Ophioplinthus gelida* seems to be the species with the highest symbiotic pressure. The most common interaction, however, is the well-known relationship with the covering sponge *Iophon* sp., with almost 100% of the *Ophioplinthus brevirima* specimens found covered by the sponge or presenting symptoms of having been covered by the sponge before. The main advantage of possessing the sponge has been suggested to be the chemical defenses of *Iophon*.

Large sponges usually act as refuges for many small vagile species that gather chemical protection. Sea slugs are good examples of organisms obtaining benefit from them (Avila et al. 2018). Hexactinellid sponges, for example, may host many sea slugs, but also diverse ophiuroids, polychaetes, and other organisms using the sponge as a support for gaining elevation in the three-dimensional forest and thus getting better access for food (Kunzmann 1996; Martín Ledo 2010). This has also been described for ophiuroids (*Astrotoma agassizii*, *Astrohamma tuberculatum*, *Ophioplinthus relegata*, *Ophioplinthus gelida*) crawling on top of different gorgonian species (*Thouarella*, *Fannyella*), or even hydroids (see Fig. 2). Some examples also report interactions between molluscs or bryozoans with ophiuroids (Martín Ledo 2010). The chemistry of all these interactions is still unknown.

The tropical pinnotherid crab *Tunicotheres moseri* has a variety of potential tunicate hosts, but the chemical cues implicated in host recognition are not fully understood yet. *T. moseri* living associated with the tunicates *Styela plicata*, *Molgula occidentalis*, and *Phallusia nigra* were analyzed for sensory cues used in host recognition and mating (Ambrosio and Brooks 2011). Their results suggest that *T. moseri* uses multiple waterborne cues together with tactile cues to select the appropriate host, even if the crabs responded to waterborne cues from the three tunicates with search behavior. Also, male crabs are capable to detect cues from non-gravid females. Moreover, it was suggested that *T. moseri* prefers *Styela plicata*, even if it is a generalist, preferring *S. plicata* even after conditioning with *Molgula occidentalis* and *Phallusia nigra* (Ambrosio and Brooks 2011).

Crustaceans display behavioral adaptations to increase their ability to find potential prey (Page et al. 2011a, b). For example, blue crabs can detect food cues and distinguish food cues from repellent cues, with chemosensory organs located in their antennules (Weissburg et al. 2012). Also, crustacean parasites have been described to use chemical cues to find their host species. The pea crabs that live on the two echinoids *Meoma ventricosa* and *Plagiobrissus grandis* also have been reported to use chemical cues to distinguish between host species (De Bruyn et al. 2011). The crab *Cissocactylus primitivus* is also able to detect chemical cues from the heart urchin *M. ventricosa*, its host, more than from seawater or the non-host echinoid *Clypeaster rosaceus*. Crabs collected from *M. ventricosa* were attracted to this species more than to *P. grandis*, but crabs collected from *P. grandis* did not show preferences between the two echinoids. The symbiotic shrimp, *Gnathophylloides mineri*, was also tested for attraction towards its host, the sea urchin *Tripneustes gratilla*, and significantly more shrimp moved towards *T. gratilla* than to water or to the non-host urchins *Heliocidaris tuberculata* and *Pseudoboletia indiana* (Williamson et al. 2012).

Nudibranch molluscs are well-known for their use of potent chemical defenses, but other interactions exist and have been reviewed recently (Avila et al. 2018). Sea slugs have an astonishing variety of trophic strategies, which often correlate to their chemical defenses. They may accumulate natural products directly from their diet on marine algae and other invertebrates, biotransform them, and/or de novo biosynthesize them. In fact, there may be several mechanisms coexisting in the same species for different compounds and roles (Avila et al. 2018).

Another remarkable example is the bioactive compounds described in the mucus nets of the vermetid mollusc *Dendropoma maxima* (Klöppel et al. 2013). This sessile suspension-feeding worm snail is a dominant, very abundant encrusting species of outer tropical reefs, and it is widespread throughout the Indo-Pacific. It secretes a mucus net to capture its planktonic prey, spreads over the corals, and often has remarkable deleterious effects on them, such as changes in growth, shape, and pigmentation, even resulting in tissue necrosis. Also, fish was observed to avoid the plankton-load nets. At least two active compounds exclusively present in the worm snails were found, with an antibiotic effect that may be useful to reduce the degradation of food items by bacteria while they are trapped within the net.

3 Chemical Defenses

3.1 Types of Chemical Defenses and Potential Uses

As in terrestrial organisms, defensive strategies in marine animals include a wide variety of mechanisms to ensure survival, which may include mechanical or physical structures, electrical pulses, behavioral trends, and/or chemical compounds. All these defensive systems interact in any given relationship, although usually they are studied separately. Marine organisms live under a constant and intense pressure for space and food, and therefore, during evolution they have developed the ability to communicate and defend themselves by means of species-specific chemical compounds (Paul 1992; Pawlik 1993; Hay 1996). Natural products play an important role in regulating predator–prey interactions and structuring benthic communities. Consequently, as described in terrestrial habitats (Firn and Jones 2009), the ability to generate new chemicals is viewed as crucial for the biological success of a marine species. Chemical defense is a particular interaction where natural compounds are used to mediate in the relationship and may include predator deterrence (Amsler et al. 2001; Koplovitz et al. 2009; Slattery 2010), competition for space or for food (Barnes and Rothery 1996; Bowden et al. 2006), and fouling avoidance (Peters et al. 2010; Avila et al. 2008; McClintock et al. 2010).

In the Antarctic benthos, the marked seasonality of food availability drives consumers to develop opportunistic behaviors, favoring the evolution of defensive chemistry in potential prey. The main predators of Antarctic benthic organisms are vagile invertebrates, including sea stars and dense amphipod populations (Núñez-Pons et al. 2012b). Also, habitat choice is a very important aspect of community structure, and one of the most important factors influencing this choice by prey species is predation risk, either by direct consumption or, secondarily, through "intimidation" (Amsler and Fairhead 2006). As an example, estimated amphipod densities may attain levels as high as 308,000 individuals/m^2 in Antarctic nearshore habitats (Huang et al. 2007; Amsler et al. 2008), much higher than in other latitudes (Nelson 1980). In this case, macroalgal-associated amphipods may play locally significant roles in nutrient and energy flow within Antarctic Peninsula shallow-water communities, by direct consumption of macroalgae or indirectly as grazers of endo- and epiphytic algae living associated with macroalgae (Huang et al. 2006; Amsler et al. 2009a). The marine benthos along the Western Antarctic Peninsula is particularly rich in both sponges and amphipods, and thus, the understanding of amphipod–sponge relationships is very relevant in determining factors that influence the ecology of these biologically diverse seafloor communities (Jazdzewski et al. 1991; McClintock et al. 2005; Huang et al. 2007; Lockhart and Jones 2008). Antarctic amphipods strongly influence population dynamics of benthic biota, feeding on a wide variety of taxa, including macroalgae, sponges, cnidarians, holothurians, bryozoans, and diatoms (Huang et al. 2006, 2007; Amsler et al. 2009b; McClintock et al. 2009), and are very relevant in terms of energy flux in shelf ecosystems, because they are a very important food source for demersal fishes (Richardson 1975). We now know that feeding deterrents are widespread in Antarctic communities, but the effect of generalist amphipods on the prevalence of defensive metabolites in their prey species has received scarce attention (Avila et al. 2008; McClintock et al. 2010). In Antarctic benthic communities, peracarid crustaceans, and especially amphipods, are by far the most species-rich group and probably the most diversified with respect to lifestyles, trophic types (including necrophagy, carnivory, herbivory, suspension feeding, detritivory, and omnivory), habitats, and size spectra (De Broyer and Jazdzewski 1996). They commonly associate temporarily with living substrata which are often also their potential (direct or incidental) prey (De Broyer et al. 2001). In tropical areas, these small crustaceans are effective inducers of chemical defense in their associated host and potential prey, because of the intense localized pressure they exert on these species (Cronin and Hay 1996a; Toth et al. 2007). In this sense, a broad study of chemical defenses among Antarctic benthic invertebrates and algae proposed a new method for testing feeding repellence that consists in including lipophilic extracts into caviar-textured alginate food pearls (Núñez-Pons et al. 2012b). The study tested 31 species of invertebrates, including sponges, cnidarians, ascidians, a bryozoan, an echinoderm, a hemichordate, and some algae, and most of the species resulted deterrent for the circumpolar omnivorous amphipod *Cherimedon femoratus* (Núñez-Pons et al. 2012b). The rate of feeding repellence was the highest in ascidians (91.7% of the extracts showing deterrent activity), followed by sponges (86.7%) and cnidarians (85.7%). For some species there was evidence for localization of defenses within certain body parts. For example, the extracts from the axial body region of the pennatulacean *Umbellula antarctica* were deterrent, while those from the polyparium were not, and the basal-external and visceral extracts of the tunicate *Synoicum adareanum* were repellent, but the apical extract was not. The high proportion of extracts that were unpalatable towards *C. femoratus*, with samples from a broad depth range of the Weddell Sea and South Shetland Archipelago, may reflect the importance of this amphipod as generalist consumer affecting the evolution of defenses and indicates that chemical defenses are broadly used among Antarctic benthic organisms to avoid predation by this opportunistic amphipod. Thus, chemical ecology plays a key role in the functioning of Antarctic marine animal forests.

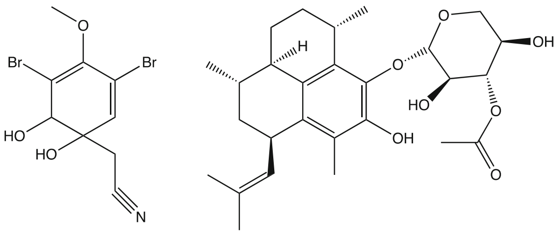
Exactly in the same way that many terrestrial insects avoid chemical defenses of their host plants and perform behaviors like vein cutting or leaf trenching to reduce exposure to their defenses (Dussourd and Denno 1991), marine herbivores could avoid the chemical defenses of their algal prey, or predators could act on their animal prey. Herbivore feeding activity creates intraspecific and interspecific variation in the distribution and abundance of plants, and plants actively alter their tissue quality affecting the distribution of herbivores and enemies of herbivores (Rowell-Rahier and Pasteels 1990, 1992; Schultz 1992). All these phenomena are probably occurring also in marine animal forests, even if we have not been able to prove it yet. In fact, some experiments showed that the gammarid *Ampithoe* avoids detection and consumption by omnivorous fishes by being relatively immobile and living on chemically defended plants that are avoided by fishes (Hay et al. 1987; Duffy and Hay 1991, 1994; Cronin and Hay 1996a). If these amphipods, or other herbivores, increase movement as algal resources change, they could become more susceptible to these visual predators, or alternatively, if grazing induces plant defenses that the amphipods can tolerate better than the fishes, then plants may be even better refuges when grazed (Cronin and Hay 1996a). The active responses of seaweeds to herbivores affect the dynamics of seaweed–herbivore interactions and may influence higher-order interactions, thus inducing cascade effects throughout the community (Cronin and Hay 1996a).

The concentration and body allocation of natural products among and within individuals may vary with life history, season, and ecological interactions (López-Legentil et al. 2005; Loh and Pawlik 2014; Avila et al. 2018). There is evidence of heterogeneity in intraspecific secondary metabolite chemistry over both local (a few km) and regional (thousands of km) spatial scales in Antarctic benthic macroinvertebrates, such as nudibranchs and sponges, but also in other taxa and other geographical regions (Avila 1995; Avila et al. 2008, 2018; McClintock et al. 2010). Many reasons may be behind this chemical variability: chemical selection may operate across a broad spectrum of spatial scales, there may be phenotypic plasticity in response to changes in grazing pressure, abiotic stress may affect, differences in the microbiome may be relevant, or genetic variability may exist. Some examples are mentioned below for the different taxa reported.

Natural products may have multiple defensive roles for the producer, and many marine organisms may produce a variety of these substances which affect different species of predators, competitors, foulers, and/or pathogens (Paul 1992; Figuerola et al. 2012). This was reported for the Antarctic soft corals *Alcyonium paessleri* and *Gersemia antarctica*, which possess compounds with feeding deterrence, antifouling, and toxicity properties (Slattery and McClintock 1995; Slattery et al. 1995, 1997), and several sea slugs (Avila 1995; Avila et al. 2018), among others. In Antarctic benthos, many species of Porifera, Cnidaria, and most Tunicata tested showed multiple activities too (Figuerola et al. 2012). In all cases, more field experiments are necessary for examining deterrent activities and other ecological roles of these compounds in situ.

Activated chemical defenses are produced constitutively but maintained in a biologically inactive form until wounding inflicted by an herbivore or a predator causes an enzymatic conversion of this precursor into a bioactive form (Amsler 2001; Amsler and Fairhead 2006). In terrestrial plants this has been known for nearly 50 years where Green and Ryan (1972) showed that potato and tomato plants wounded by beetles quickly accumulated high levels of a protease inhibitor effective against animal digestion in both damaged and undamaged portions of the plants (Amsler 2001). Now it is known that a small polypeptide is produced in response to leaf damage and it spreads through the plants via their vascular systems, controlling the expression of over 15 defense genes (Ryan and Pearce 1998). Enzymatic conversion of inactive storage compounds into biologically active defense metabolites has been demonstrated, for example, for cyanogenic glycosides from higher terrestrial plants (Luchner 1984; Amsler and Fairhead 2006). In marine ecosystems, activated defenses were first identified in green macroalgae (Paul and Van Alstyne 1992) and have since been identified in a number of other macroalgae and microalgae, as well as in animals (Van Alstyne 1988; Yates and Peckol 1993; Cronin and Hay 1996a; Pavia and Toth 2000; Toth and Pavia 2000; Cetrulo and Hay 2000; Amsler and Fairhead 2006). In terrestrial systems, inducible defenses can also be triggered by volatile compounds (Farmer and Ryan 1990, 1992) that spread through the air to induce defenses in neighbors and even to attract predators and parasites of the attacking herbivore (Paré and Tumlinson 1999; Kessler and Baldwin 2001). Significantly, even in the earliest studies of this phenomenon, it was recognized that the specific method of wounding had important effects on the induced response. In marine animal forests, sadly, we are still far of having this knowledge, although work in progress may yield soon some interesting results.

Because proving the induction of chemical defenses in marine macroorganisms is extremely difficult, it has rarely been demonstrated (Hay 1996). Rasher and Hay (2014) have reported the first experimental evidence of the induction of allelochemicals in a seaweed in the presence of its coral competitor *Porites cylindrica*, damaging corals. The sponge *Aplysina (Verongia) aerophoba* was probably the first example of an induced chemical defense mechanism in marine benthic invertebrates (Teeyapant et al. 1993). In this sponge, the potent cytotoxic metabolites aeroplysinin-1 (4, Fig. 4) and dienone, as well as their antimicrobial activity, seem to be very relevant for chemical defense (Teeyapant et al. 1993; Ebel et al.



4. Aeroplysinin-1

5. Pseudopterosin C

Fig. 4 Induced chemical defenses of marine benthic invertebrates. *4*. Aeroplysinin-1 from the sponge *Aplysina (Verongia) aerophoba*. *5*. Pseudopterosin C from the gorgonia *Pseudopterogorgia elisabethae*

1997; Steinberg et al. 2002). Isofistularin-3 and aerophobin 2 are brominated isoxazoline alkaloids that are rapidly converted to aeroplysinin-1 and a dienone when sponges are wounded. The products of the conversion have been shown to be more active against microorganisms and fish predators than the isoxazoline precursors (Weiss et al. 1996; Ebel et al. 1997).

The induction and activation of herbivore and antimicrobial chemical defenses in response to artificial predation have been studied for eight species of sponges in Guam (Rhode et al. 2015). The extracts from seven species were unpalatable to the fish *Canthigaster solandri* before incurring physical damage. Induced defenses were observed for the sponges *Stylissa massa* and *Melophlus sarasinorum*, while *M. sarasinorum* also showed activated defense in response to wounding. Induced antimicrobial defenses were observed in the sponges *Aplysinella* sp., *Cacospongia* sp., *M. sarasinorum*, and *S. massa*. Therefore, wounding selects for induced antimicrobial defenses to protect sponges from pathogens that could invade the sponge tissue via feeding scars (Rhode et al. 2015).

Thorton and Kerr (2002) reported that high levels of predation by the gastropod mollusc *Cyphoma gibbosum* induced pseudopterosin C (5, Fig. 4) production by the gorgonia *Pseudopterogorgia elisabethae*. Some experimental evidence suggests that *C. gibbosum* may use biotransformation enzymes to detoxify gorgonian metabolites (Vrolijk and Targett 1992), being this the first example where a specialist has been shown to induce the production of a gorgonian metabolite. Interestingly, induction did not occur after high levels of predation by the butterfly fish *Chaetodon capistratus* or artificial wounding of the sea fan. However, similar results to *C. gibbosum* predation were obtained using decreased levels of UV/Vis radiation (Thorton and Kerr 2002).

The snail *Nucella lamellosa* can change morphological traits after being exposed to chemical cues released from predators, as well as from predators feeding on conspecifics (Bourdeau 2010). It has been shown that snails that have been exposed to chemical cues from the crab predator *Cancer productus* decrease their body mass and increase their shell thickness with respect to the controls. Similarly, snails that were in contact with chemical cues from crabs feeding on conspecifics presented thickened apertural lips and teeth, while those exposed to chemical cues from crabs that had been feeding on fish or on the snail *Littorina sitkana* did not show changes in thickness. Thus, this work showed that snails may display different morphological defensive strategies based on what threat they confront, and not only if they detect distressed conspecifics (Bourdeau 2010). In a similar case, waterborne cues from crustacean predators caused inducible mechanical defenses in the prey, the oyster *Crassostrea virginica*, which altered shell thickness in response to chemical cues from the crabs *Callinectes sapidus* and *Panopeus herbstii*, therefore improving their ability to survive predation (Robinson et al. 2014).

The plutei larvae of the Pacific sand dollar *Dendraster excentricus* exhibit a peculiar response to the chemical cues of the mucus of predatory fish by cloning via anteroposterior fission (Vaughn and Strathmann 2008). A further detailed analysis tested the putative benefits that cloning may provide as a defensive mechanism for plutei larvae against three planktivorous fish, *Microstomus pacificus*, *Gasterosteus aculeatus*, and *Ammodytes hexapterus* (Vaughn 2010). Experiments exposing larvae to fish mucus resulted in smaller cloned plutei with respect to their sister unexposed plutei, while feeding experiments showed that uncloned sibling plutei were more eaten by fish when compared to the cloned smaller clones. Thus, asexual reproduction induced by fish chemical cues resulting in a fast size decrease is a viable defense against planktivory fishes, because the smaller size of the clones results in visual predators not detecting them (Vaughn 2010).

Limiting the production of costly chemical defenses to just when an organism is under attack would only benefit the producer if the defenses are made in time to significantly reduce consumption (Amsler 2001). Consequently, temporal and spatial patterns of consumption are expected to influence the patterns of defense induction (Amsler 2001). Hay (1996) suggested that inducible chemical defenses would be most effective if produced in response to small, relatively immobile mesograzers, such as small crustaceans and gastropods, which over short time intervals may cause only partial damage to the prey. Mesograzers often feed on individual prey for long enough periods for a chemical response to be produced, and many are only deterred by relatively high concentrations of defensive chemicals (Hay 1996; Paul et al. 2001; Amsler 2001). The relative impact of mesograzers compared to larger consumers varies spatially and has been long discussed, but mesograzers do have a significant impact in a variety of communities and throughout their life histories (Hay et al. 1987; Duffy and Hay 1991, 2000; Paul et al. 2001). Many mesograzers feed on individual prey for long times or are limited to feeding within small spatial ranges (Paul et al. 2001), while larger consumers can be relatively immobile and sometimes prey on an individual for long periods of time (Amsler 2001). For example, Antarctic sea stars can be very large and prey on individual sponges during many months (Dayton et al. 1974). Therefore, not all small consumers feed in ways that would be predicted to be influenced by induced defenses, while some larger consumers do.

Ecological relationships between macroalgae, sea urchins, and predators of sea urchins are often regarded as having major roles in the determination of benthic community structure (Lawrence 1975; Mann 1982; Dayton 1985; Elner and Vadas 1990; Lobban and Harrison 1994; Estes and Duggins 1995; Amsler et al. 1999). The sea urchins are there viewed as the major consumers of macroalgae, and when urchins are abundant, they may devastate macroalgal communities by overgrazing. Urchins, though, are prevented from becoming too abundant by predators such as sea otters or lobsters (or other biotic or abiotic factors; Elner and Vadas 1990; Lobban and Harrison 1994). In Antarctica, although the urchin *Sterechinus neumayeri* can be very abundant, is a major benthic consumer, and feeds upon some macroalgae (Pearse and Giese 1966; McClintock 1994; Brey et al. 1995; Angulo-Preckler et al. 2017a), it is prevented from overgrazing algae such as *Phyllophora antarctica* and *Iridaea cordata* by their chemical defenses while their macroalgal competitors are preferentially grazed (Estes and Duggins 1995; Amsler et al. 1998, 1999). The mutual benefits of this relationship have been mentioned before.

Another chemically mediated macroalga–herbivore–carnivore relationship has been described between the alga *Dictyota menstrualis*, the decorator crab *Libinia dubia*, and omnivorous fishes (Stachowicz and Hay 1999). Although there are some differences in their interactions, the decorator crabs obtain camouflage with the chemically defended *D. menstrualis* and use it as a low-priority food item, and the chemically defended macroalgal camouflage in turn reduces the susceptibility of the crabs to fish predation (Amsler et al. 1999). Similarly, the passive defense of the clam *Chama pellucida* by macroalgae (and other sessile epibionts) was described by Vance (1978). Predation by the sea star *Pisaster giganteus* on the clam is reduced by the presence of algal and other epibionts on the shells. The epibionts, which also grow on other substrata, derive benefit from the rough surface provided by the clams, as well as because clams live in habitats with generally less epibiont-grazing sea urchins (Vance 1978). The epibionts protect the clams by making it less likely that a sea star will recognize them as a food item (Vance 1978), and most probably for the algal chemical defenses. For example, Antarctic macroalgae are commonly unpalatable to sympatric consumers, and much of this unpalatability is the result of chemical defenses (Amsler et al. 2005).

Another interesting symbiotic relationship involving chemical defense in Antarctic organisms is that of the pelagic pteropod mollusc *Clione antarctica*, quite different from the macroalgae–urchin mutualism described above. The mollusc is chemically defended from predation by fish (McClintock and Janssen 1990; Bryan et al. 1995; Yoshida et al. 1995; McClintock and Baker 1998). There is a hyperiid amphipod, *Hyperiella dilatata*, that captures *C. antarctica* resulting in individual amphipods holding individual pteropods on their backs. The chemical defenses of the captured pteropods then also defend the amphipods from predation by fish (McClintock and Janssen 1990; McClintock and Baker 1998). However, the pteropod ceases feeding when captured, while the amphipod is not a potential pteropod predator. Although this is a pelagic example, similar cases are likely to exist in marine animal forests.

An additional response that could be used as a defense against pathogens, biofoulers, and/or consumers is the release of volatile halogenated organic compounds (VHOCs), such as bromoform, dibromomethane, dibromochloromethane, bromodichloromethane, and chloroiodomethane (Amsler and Fairhead 2006). As for terrestrial plants living in forests, in marine systems it has been proven that brown algae also release these potentially defensive compounds, although there is little evidence of an ecological role for them (see Amsler and Fairhead 2006). These compounds have received significant attention because they impact on atmospheric processes. An ecological role has been established for the antiepiphyte activity of VHOCs from a coralline red alga (Ohsawa et al. 2001). It has also been suggested that VHOCs are related to oxidative defense mechanisms in algae, while the enzymes responsible for VHOC production (e.g., bromoperoxidases) are involved in cross-linking phlorotannins in cell walls, which could certainly be related to responses to damage by grazers or pathogens (Colin et al. 2003, 2005; Amsler and Fairhead 2006). Some studies showed also that bromoform, the most abundant VHOC identified previously from Antarctic macroalgae, was a feeding deterrent against the common, herbivorous Antarctic amphipod *Gondogeneia antarctica* (Amsler and Fairhead 2006).

3.2 Chemical Defenses in the Different Taxa

Sessile marine invertebrate chemical defenses have been regularly reviewed, and a considerable amount of progress has been made in understanding the ecological roles of their chemical defenses (Paul 1992; Pawlik 1993; Paul and Puglisi 2004). Marine sponges (Porifera) have yielded the greatest number and diversity of natural products so far, being the Phylum where our knowledge of chemical defenses is the most extensive of all marine invertebrates (Harper et al. 2001, Paul and Puglisi 2004, Blunt et al. 2018, MarinLit database). Many of their compounds are used in defense against predators, competitors, and microorganisms (Pawlik 1993; Hay 1996; Engel et al. 2002). Some chemical ecology studies tried to analyze how natural products and other defenses may provide evolutionary advantages on the survival of sponges (Puglisi et al. 2014). It has been observed that sponges of the same genus and often the same species from different localities produce different compounds with distinct chemical structures, being effective also against diverse potential consumers. *Hymeniacidon heliophila* from Atlantic Brazil was tested in laboratory towards the hermit crab (*Calcinus tibicen*), the sea urchin (*Lytechinus variegatus*), and generalist fishes in the field (Ribeiro et al. 2010). Different extracts significantly reduced feeding by the hermit crab *C. tibicen*, while only one extract resulted deterrent to the sea urchin *L. variegatus*, and only two deterred fish feeding in the field (Ribeiro et al. 2010).

The distribution of chemical defenses in sponges is not ubiquitous, and it could regulate their geographical distributions. Ruzicka and Gleason (2009) investigated the relationship between sponge predators and the distribution of sponges on temperate reefs in the South Atlantic. In the scarp sponge community, encrusting and amorphous sponges were observed, while in the sponge community of the plateau, pedunculate, digitate, and arborescent growth forms were found. In the field, feeding assays using crude extracts and structural components from 19 sponges against natural assemblages of generalist fish showed that chemical extracts from scarp sponges were significantly more deterrent to fish than the structural components, while the structural components of >50% of the plateau sponges were significantly more deterrent to fish than the chemical extracts (Ruzicka and Gleason 2009). Transplant experiments resulted in significant volume changes, and predation scarring was observed in sponges transplanted from the plateau to the scarp (Ruzicka and Gleason 2009).

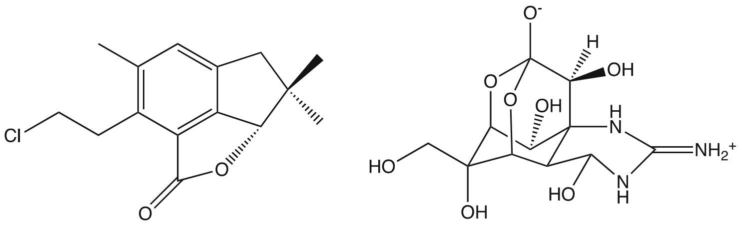
Hexactinellids (glass sponges) are an understudied class traditionally thought to lack defensive natural products and to suffer low predation because of their poor nutritional quality and particular habitats (Barthel 1995; Leys et al. 2007; Núñez-Pons et al. 2012c). Although hexactinellids represent tridimensional shelters for quite diverse fauna, as mentioned above, they are quite pristine in bacteria (Leys et al. 2007). Hexactinellids are typical inhabitants of deep waters, although in Antarctic marine animal forests they dominate the shallow upper shelf, providing shelter and food supply to many opportunistic mesograzers and macroinvertebrates (isopods, amphipods, polychaetes, molluscs, and others), which exert strong ecological pressures on them (Dayton et al. 1974; Dayton 1979; Barthel and Tendal 1994; Kunzmann 1996; McClintock et al. 2005). For example, spongicolous amphipods do occur in large abundances and diversity, with no obligate associations (Kunzmann 1996; De Broyer et al. 2007; Amsler et al. 2009b), and they may exert larger localized predation pressures than more wandering asteroids, thus favoring the production of chemical defenses (Toth et al. 2007). Feeding experiments conducted using lipophilic fractions of Antarctic hexactinellids and demosponges against the asteroid *Odontaster validus* and the amphipod *Cheirimedon femoratus* as sympatric, omnivorous consumers showed that hexactinellids yielded greater unpalatable activities towards the amphipod, with no apparent allocation of defenses (Núñez-Pons et al. 2012c). The lipidic compounds 5α(H)-cholestan-3-one and two glycoceramides were also isolated from these hexactinellids. Hexactinellid extracts displayed little activity against the sea star (McClintock 1987; Núñez-Pons et al. 2012c), but they displayed strong unpalatability towards the amphipod *C. femoratus* (Núñez-Pons et al. 2012c). Interestingly, sponges are rich and accessible resources of sterols for crustaceans, which are unable to de novo biosynthesize vital steroids, such as ecdysteroid hormones for molting (Goad 1981; Blumenberg et al. 2002). Also, amphipods seem to be more susceptible to lipidic defenses (Cruz-Rivera and Hay 2003; Aumack et al. 2010), along with being more discriminative for unpalatabilities when comparing both assays (Núñez-Pons and Avila 2014). All these facts may explain the stronger deterrent activities found towards *C. femoratus* with respect to *O. validus* using lipophilic sponge extracts (Núñez-Pons et al. 2012c).

Cnidarians are also rich sources of novel natural products. From 2000 to 2010, >2000 many new natural products were reported from cnidarians (Rocha et al. 2011; Puglisi et al. 2014). Some reviews described sea anemone toxins and the genes for toxin production (Frazao et al. 2012). There has been also a great interest in studying the production of toxins associated with nematocysts (Puglisi et al. 2014). Different toxins are found in the diverse types of nematocysts in the jellyfish *Aurelia aurita* (Wiebring et al. 2010), while in some sea anemones potent neurotoxins assumed to be in nematocysts were in fact located in ectodermal gland cells (Moran et al. 2012).

The prevalence of nematocyst or chemical defenses was studied in non-scleractinian zoantharians (sea anemones, zoanthids, and mushroom polyps) in order to ascertain whether there are trade-offs between different defensive strategies (Hines and Pawlik 2012). The evidence for a trade-off was found to be limited, because 65% of the species had only one type of defense, while the remaining 35% presented either both defensive systems or none.

Fire corals also possess toxins that may be useful in toxicological and pharmacological studies (Puglisi et al. 2014). The role of symbiotic algae (zooxanthellae) in producing these toxins was analyzed, trying to determine whether periods of coral bleaching do affect the presence of toxins in the hydrocorals (García-Arredondo et al. 2011). The bioactive chemicals from the aqueous extracts of *Millepora* are de novo biosynthesized by the coral independently from the presence of symbiotic algae. Thus, it seems probable that the corals keep their ability to synthesize the toxins for their defense even when suffering bleaching events.

Chemical ecology studies of alcyonarians (Octocorallia), especially the Alcyonacea (soft corals) and Gorgonacea (gorgonians, including sea whips and fans), have largely focused on predator defense (Puglisi et al. 2014). Numerous feeding studies with crude extracts and secondary metabolites from alcyonaceans and gorgonians have shown that with the exception of a few specialist predators, fishes and invertebrates do not readily consume them (Lasker 1985; Kelman et al. 1999). Soft corals are particularly interesting for their ability to chemically defend themselves against predation and fouling; since they lack physical or skeletal defenses and their nematocyst system is weak, they mainly rely on chemistry for protection from predators and microbes (Núñez-Pons et al. 2013). Moreover, their chemicals are usually exuded in the mucus surface layer, thus explaining the general lack of heavy fouling and predation in corals (Miyamoto et al. 1994; Slattery et al. 1997; Kelman et al. 1999; Wang et al. 2008). Among the substances exuded within the mucus of soft corals are sterols, wax esters, terpenoid toxins, and unidentified UV-absorbing compounds (Miyamoto et al. 1994; Slattery et al. 1997; Wang et al. 2008; Núñez-Pons et al. 2013). Chemical investigation of the lipophilic extract of the Antarctic soft coral *Alcyonium grandis* yielded nine unreported sesquiterpenoids, members of the illudalane class and in particular to the group of alcyopterosins (6, Fig. 5; Carbone et al. 2009). Repellency experiments against predation by the omnivorous Antarctic sea star *Odontaster validus* revealed a strong activity. Later, five Antarctic species of the genus *Alcyonium* were tested in feeding bioassays with the sea star *O. validus* and the amphipod *Cheirimedon femoratus* as potential sympatric predators (Núñez-Pons et al. 2013). Repellent activities were observed towards both consumers in all but one of the samples assessed. Furthermore, three of the extracts caused inhibition to a sympatric marine bacterium. The lipophilic extracts afforded characteristic illudalane sesquiterpenoids in two of the samples, as well as particular wax esters in all the analyzed colonies. Both kinds of metabolites displayed significant deterrent activities, thus demonstrating their role in defense. In general, Alcyonacea are rich in bioactive compounds that have a role in defense against predators but also in competition for space, antifouling, and reproduction enhancement (Wang et al. 2008; Núñez-Pons et al. 2013). Most of



6. Alcyopterosin P

7. Tetrodotoxin

Fig. 5 Chemical defenses from marine benthic invertebrates. *6*. Alcyopterosin P from the Antarctic soft coral *Alcyonium grandis*. *7*. Tetrodotoxin found in several nemertean species

these products are lipid-soluble, with terpenoids (di- and sesquiterpenes) and sterols predominating, but the specific molecules responsible for these bioactivities have rarely been identified (Wang et al. 2008; Fleury et al. 2008; Núñez-Pons et al. 2013). The ecological success of soft corals in Antarctic marine animal forests is probably related to the presence of feeding repellents and antifouling compounds, derived from both primary and secondary metabolism (Núñez-Pons et al. 2013).

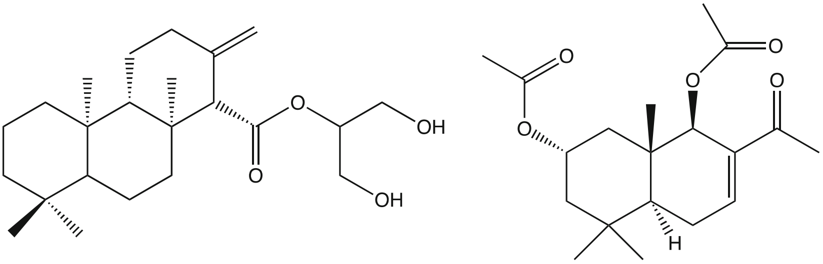
Very few studies deal with vagile invertebrate phyla such as Annelida or Nemertea. Feeding deterrent properties of 11 worm species collected from the southern Florida coast against predation by the wrasse *Thalassoma bifasciatum* showed that extracts of *Cirriformia tentaculata*, *Ptychodera bahamensis*, and *Eupolymnia crassicornis* were unpalatable and chemically defended (Kicklighter et al. 2003). Some Antarctic species have also shown repellent activity (Avila et al. 2008; Taboada et al. 2013; Moles et al. 2015). Most ribbon worms in marine environments are predators and scavengers, and they are characterized by an eversible proboscis used to hunt for prey and a thick mucus layer covering their skin (Göransson et al. 2019). Both proboscis and epidermal mucus mediate toxicity to predators and prey, but research into the chemical nature of the compounds that render toxicity has not been extensive. Göransson et al. (2019) provided a complete account of the current status of research into nemertean toxins. Certain nemertean species are known to contain remarkably potent toxins: pyridine alkaloids, tetrodotoxin (7, Fig. 5), and cytolytic or neurotoxic peptides. Pyridine alkaloids have mainly been found in hoplonemerteans, but the discovery efforts are scarce. Tetrodotoxin is probably not produced by nemerteans themselves, and the role of the compound in nemerteans is unclear (Göransson et al. 2019).

Although bryozoans have been studied for their natural products chemistry (Harper et al. 2001), much less is known about the role of bioactive metabolites in ecological interactions (Blackman and Walls 1995; Sharp et al. 2007; Blunt et al. 2018). Bryozoans are one of the most abundant and diverse members of the Antarctic marine animal forests and are preyed upon by diverse kinds of predators (Figuerola et al. 2014). They seem to be casual food items of the common Antarctic sea urchin *Sterechinus neumayeri* and the ubiquitous omnivorous amphipod

Cheirimedon femoratus. Chemical ecology of bryozoans has recently been reviewed (Lim-Fong and Kabir 2018). The cytotoxic activity of 13 Antarctic bryozoan species against embryos and sperm of the sea urchin *S. neumayeri* and the substrate preferences of the amphipod *C. femoratus* were assessed in order to determine the presence of chemical defenses (Figuerola et al. 2014). While no cytotoxicity was detected against embryos of *S. neumayeri*, almost all the species were cytotoxic to sperm at natural concentrations, and the amphipod *C. femoratus* was repelled by most species in the substrate preference assays. Amphipods are considered deleterious to bryozoans for their direct and indirect predation and the burden of commensality (Figuerola et al. 2014). Inter- and intraspecific variability in chemical defenses was also found, suggesting environmental-induced responses, symbiotic production, and/or genetic variability. These results clearly support the fact that chemically mediated bioactivity in Antarctic bryozoans is common, and most bryozoan species display cytotoxicity, reducing the reproductive success of the sea urchin, and/or repellent activity, as ecologically relevant defensive strategies. By inducing reduction in sea urchin sperm viability, natural products used by bryozoans may regulate adult grazing at a local scale, although further work is required to confirm this hypothesis. All these facts support that chemical mechanisms are highly relevant in the ecology of Antarctic marine animal forests (Avila et al. 2008; McClintock et al. 2010).

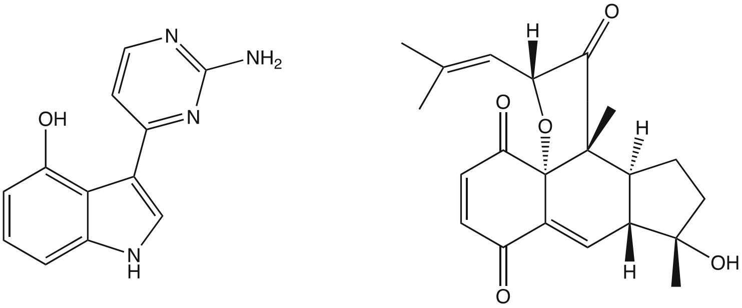
Molluscs are well studied for their chemical defenses, particularly heterobrachs because of the evolutionary reduction or loss of the shell, the classical mechanical defense of gastropods (Avila et al. 2018). As an example, *Doris (Austrodoris) kerguelenensis* is an Antarctic marine slug possessing a wide array of deterrent biosynthetic di- and monoterpene diacylglycerides (8, Fig. 6), with at least eight different skeletons (Gavagnin et al. 1999; Iken et al. 2002; Cutignano et al. 2011). The interindividual variability of these compounds indicated several chemotypes may exist in the same population and suggested the presence of terpene synthase variants involved in the biosynthesis of these defensive molecules. The remarkable variability of terpene skeletons in *D. kerguelenensis* is consistent with the massive genetic diversification reported for this mollusc (Wilson et al. 2009). In fact, morphological, ecological, and chemical traits of this Antarctic nudibranch appear to be variable and can also be explained by an unprecedented cryptic speciation (Wilson et al. 2009, 2013). Evolutionary radiation could have been responsible for the successive variation of the terpene synthase (TPS) genes within the single morphological "species," with a consequent neofunctionalization of the gene products (Cutignano et al. 2011; Avila 2016). *D. kerguelenensis* compounds provide protection against predation by the sympatric sea star, *Odontaster validus*. In a similar way, the dorid nudibranch *Bathydoris hodgsoni* possesses hodgsonal (9, Fig. 6), a sesquiterpene that also protects the slug from *O. validus* (Iken et al. 1998; Avila et al. 2000). In these two sea slugs, natural products are located in specific, external body parts, maximizing their effectiveness (see below).

Sea slugs play a crucial role within the benthos, occupying many different ecological niches and displaying a wide array of trophic relationships with organisms from many different phyla, such as Chlorophyta, Ochrophyta, Rhodophyta



8. Terpene glyceride

9. Hodgsonal



10. Meridianin A

11. Rossinone B

Fig. 6 Chemical defenses of selected marine benthic invertebrates. *8*. A terpene glyceride from the mantle of the Antarctic dorid nudibranch *Doris kerguelenensis*. *9*. Hodgsonal from the mantle of the Antarctic sea slug *Bathydoris hodgsoni*. *10*. Meridianin A from the Antarctic colonial ascidians *Aplidium meridianum* and *Aplidium falklandicum*. *11*. Rossinone B from Antarctic tunicates of the genera *Aplidium* and *Synoicum*

(green, red, and brown algae, respectively), Porifera, Cnidaria, Bryozoa, Chordata (tunicates), other Mollusca, and so on (Avila et al. 2018). Thus such interactions comprise macroalgal or plant herbivory, as well as carnivore prey–predator relationships, and occasional cannibalism. Sea slug defenses may include chemicals obtained directly from their prey, transformed dietary metabolites, or even de novo biosynthesized bioactive compounds. In fact, there may be several mechanisms coexisting in the same species for different compounds and roles. The abilities to steal functional structures or chemical products from other organisms through cleptoplasty and cleptochemistry, respectively, are considered to be a key innovation in the evolutionary success of sea slugs. In cleptoplasty, slugs retain certain functional structures from their prey, such as chloroplasts from algae to obtain energy and camouflage (Händeler et al. 2009) or nematocysts (cleptocnides) from cnidarians to be used as protection (Putz et al. 2010). Cleptochemistry, instead, is the incorporation of natural products from the diet (cleptochemicals), being called cleptochemodefenses when used for their own defensive means, and we have many examples in chromodoridid slugs and sponges, aeolid slugs with different cnidarians, and others (Avila 1992, 1993, 1995; Avila and Durfort 1996; Avila et al. 2018). The accumulation of bioactive products in characteristic glandular bodies seems to serve a dual role, as a strategy against predators and also simultaneously preventing autotoxicity in the slug (Wagele et al. 2006). Wägele (2004) argued that storing toxic dietary chemicals in MDFs could have fostered the radiation in chromodorids, by allowing them to benefit by feeding upon toxic sponges and expand their dietary resources. Biotransformation consists in modifications of dietary compounds, either by detoxification when the original products are highly toxic or by transformation to obtain more stable or more toxic metabolites (Avila 1995). Usually, all these processes entail energy costs (Avila et al. 2018).

Echinoderms are known for their production of saponins (Harper et al. 2001), but they have also been shown to be chemically defended against consumers (Bryan et al. 1997; McClintock et al. 2003). Holothuroids are known to produce a large number of diverse triterpene glycosides (saponins), and while they have been shown to selectively bind to cell wall proteins, their role in chemical defense for the host organism has not been well studied (e.g., Antonov et al. 2008, 2009, 2011; Silchenko et al. 2013). In the Mediterranean *Holothuria forskali*, the location of saponins and the ability of fish (*Coris julis* and *Symphodus ocellatus*) to detect the presence of these compounds suggested that these molecules act as an aposematic signal, warning predators away (Van Dyck et al. 2011).

Tunicates, and ascidians in particular, are rich in nitrogenous secondary metabolites that can deter feeding by predators (Lindquist et al. 1992; Davidson 1993; Pawlik 1993; Harper et al. 2001; Blunt et al. 2018). Actually, both natural products and inorganic acids have been proposed to protect adult ascidians from predation (Pawlik 1993). Some studies have showed that there is intra- and interspecific variation in chemical defenses. The known indole alkaloids meridianins A–G (10, Fig. 6) isolated from the Antarctic colonial ascidians *Aplidium meridianum* and *Aplidium falklandicum* chemically defend the tunicates from predation by the sea star *Odontaster validus* (Núñez-Pons et al. 2010). In fact, species belonging to the genus *Aplidium* are known as prolific producers of bioactive natural products exhibiting an extensive structural variability and including non-nitrogenous compounds, such as prenyl hydroquinones and prenyl quinones, and nitrogenous metabolites, like nucleosides, peptides, and a high variety of alkaloids (Zubía et al. 2005; Menna 2009; Núñez-Pons et al. 2010; Menna et al. 2011). While most ascidian metabolites are amino acid derived (Wang and Namikoshi 2007), the genus *Aplidium* is known for possessing also terpene derivatives (Zubía et al. 2005; Núñez-Pons et al. 2012a). The finding of rossinones B and related 2,3-epoxy-rossinone B, 3-epi-rossinone B, and 5,6-epoxy-rossinone B in *A. fuegiense* was consistent with that, since meroterpenes are typically found in sponges and seaweeds (Riguera 1997; Núñez-Pons et al. 2012a). In studies on colonial Antarctic ascidians from the Weddell Sea, chemical defenses of tunicates in the genera *Aplidium* and *Synoicum* were investigated against the starfish *O. validus*, the amphipod *Cheirimedon femoratus*, and a sympatric bacterium. New molecules, such as rossinone B (11, Fig. 6), 2,3-epoxy-rossinone B, 3-epi-rossinone B, and 5,6-epoxy-rossinone B, were also identified (Carbone et al. 2012; Núñez-Pons et al. 2012a). Almost all crude extracts tested were unpalatable to the amphipod *C. femoratus*, while the compounds deterred feeding against both predators, and some of them inhibited the growth of an unidentified sympatric marine bacterium, confirming therefore that meridianins may serve multiple roles in the chemical defense of tunicates (Núñez-Pons et al. 2012a). Interestingly, the presence of ecdysteroid-like compounds in the Antarctic ascidian *Synoicum adareanum* suggests a potential to defend their tissues from arthropod predators, such as crustacean amphipods, by employing a strategy similar to that found in terrestrial plants that elaborate ecdysteroids that short-wire molting in herbivorous insects (McClintock et al. 2010).

Antimicrobial and antifouling chemical defenses from lipophilic and hydrophilic extracts, as well as the seawater-soluble fractions of Antarctic ascidians, were assayed from four solitary and ten colonial species (Koplovitz et al. 2011). The bacterial screening panel consisted of 16 strains of g-proteobacteria, 1 strain of *Flavobacterium*, and 2 unidentified strains isolated from the surface of invertebrates from the same habitat. Mortality of the diatom *Syndroposis* sp. was used as a measure of antifouling activity. Only the extracts of *Distaplia colligans* exhibited significant antibacterial activity against all strains, while almost all extracts caused diatom mortality at natural concentration, leading the authors to propose that ascidians use chemical defenses to prevent diatom fouling (Koplovitz et al. 2011).

3.3 Antifouling and Antimicrobial Defenses

All surfaces in the benthic domain (external body surfaces of organisms as well as nonliving substrates, including rocks and rubble) are susceptible to colonization by bacteria and subsequent surface biofilm formation (Puglisi et al. 2014). Competition for space is a remarkable ecological force, comparable to predation, which produces a strong selective pressure on benthic invertebrates, and therefore, many of them possess antimicrobial compounds to reduce surface bacterial growth (Clare et al. 1992; Angulo-Preckler et al. 2015a). Settlement on the surfaces of living organisms (i.e., epibiosis) can be both advantageous and disadvantageous to the host. Advantages may include the production of antifouling substances by symbiotic epibiota or providing nutrients to the host (Clare et al. 1992; Walls et al. 1993; Mercado et al. 1998; Faulkner 2000; Harder et al. 2003; Piel 2004), while disadvantages may include growth inhibition, necrosis, or even death of the host (Wahl and Mark 1999). Antimicrobial inhibition is the first step in avoiding being overgrown by other organisms, which may have a negative impact in feeding, respiration, reproduction, and others. Thus, many algae, sponges, corals, ascidians, and other taxa produce antifouling substances which keep them free from undesirable encrusting organisms in nature (Hentschel et al. 2001; Dobretsov and Qian 2002; Harder et al. 2003). Regarding marine benthic chemical defenses, it has been proven to be very difficult to demonstrate that observed bioactivities against epiphytic bacteria or fouling organisms in vitro actually have in situ ecological relevance. Many authors performed bioassays on extracts or purified compounds from marine organisms at concentrations somehow equivalent to those present in the intact organism, and some authors outplanted gels containing such extracts into the sea to test their effectiveness in preventing fouling (Henrikson and Pawlik 1995; Da Gama et al. 2002; Amsler and Fairhead 2006; Sacristán-Soriano et al. 2017; Angulo-Preckler et al. 2015a, 2017b). Particularly difficult is to show that the compounds are present at the surface of the organism or in the boundary layer at bioactive concentrations (Steinberg and de Nys 2002; Steinberg et al. 2001; Amsler and Fairhead 2006). In situ inhibition of bacterial biofilm was used as an indicator of antifouling activity in a study testing hydrophilic extracts of 12 Antarctic invertebrates at natural concentrations (Angulo-Preckler et al. 2015a). Using two different approaches (genetics and confocal techniques), different levels of activity were found in the tested organisms, and differences within body parts were also detected. Most extracts had negative effects on fouling after 28 days submerged in Antarctic waters. Thus, although chemical defenses may be quite species-specific in their ecological roles, these results suggest that different chemical strategies exist to deal with space competition (Angulo-Preckler et al. 2015a).

Microbial biofilms can be disrupted in many ways, via interference with the signal exchange that leads to biofilm formation or through degradation of the extracellular polymers that make up the matrices of the biofilms (Dobretsov et al. 2013). Interference with bacterial quorum sensing (QS) is a potential approach for controlling biofouling (Dobretsov et al. 2009; Xiong and Liu 2010). Quorum sensing pathways, which allow density-dependent changes in bacterial phenotype, modulate biofilm formation as well as virulence and symbiosis (Callow and Callow 2006; Krug 2006). Although this type of information is usually missing in marine ecosystems, the mechanisms by which marine organisms inhibit the settlement of fouling have been investigated from molecular to ecological approaches along the years (Dobretsov et al. 2013). The extent of microbial colonization on soft-body marine organisms is probably influenced by the chemical effects of bioactive metabolites produced either by the host itself or by symbiotic microorganisms (Lee et al. 2001; Kelly et al. 2003). The ubiquity of fouling organisms in the marine environment and the negative consequences of fouling are likely strong evolutionary pressures for marine organisms to develop defenses to protect their surface from fouling (Wahl 1989; Steinberg et al. 1997). The planktonic pool of free bacteria, algal spores, and competent larvae imposes a strong selective pressure on benthic invertebrates (Krug 2006). One type of defense thus is the production of natural compounds preventing the initial steps in the bacterial fouling process, such as attachment, growth, and surface spreading (Steinberg et al. 1997). Although difficult, it is essential to test antifouling effects in situ in order to obtain ecologically significant results, thus indicating the potential effects against the bacteria that would be naturally found in the environment.

As an example, the fungus *Penicillium* sp. associated with the gorgonian coral *Dichotella gemmacea* was reported to significantly inhibit two bacterial strains and larval settlement of *Balanus amphitrite* (Bao et al. 2013). Further investigation yielded two new polyketides, 6,8,5′6′-tetrahydroxy-3′-methylflavone and paecilin C, and six known analogs with different biological activities. Secalonic acid D, the major metabolite in the extract, and two other compounds inhibited the growth of *Micrococcus luteus*, a larval settlement-inducing strain, and the marine pathogen *Pseudoalteromonas nigrifaciens*, while other metabolites significantly inhibited settlement of *Balanus amphitrite* (Bao et al. 2013).

3.4 Geographical Considerations

Antimicrobial chemical defenses are particularly common in the biodiversity-rich benthic communities of the tropics and temperate waters (Paul 1992; Pawlik 1993). As shown above, also in Antarctica antimicrobial defenses are abundant, but this has only been demonstrated recently. In fact, the geographical distribution of chemical defenses has been the subject of several discussions in the past. An earlier latitudinal hypothesis postulated that chemical defenses would decline with increasing latitude, based on lower biodiversity and fewer competitive interactions driving the development of chemical defenses at high latitudes (Bakus and Green 1974). This hypothesis has been solidly refuted for southern high latitudes, as all sort of chemical defenses have been proved to be both common and diverse in Antarctic benthic communities (Lebar et al. 2007; Avila et al. 2008, 2018; McClintock et al. 2010; Núñez-Pons and Avila 2015; von Salm et al. 2018). In fact, the incidence of chemical defenses in Antarctic sponges is as high as, or even slightly higher than, that found in tropical species (Pawlik et al. 1995; Peters et al. 2009; McClintock et al. 2010). In contrast, little is known about chemical defenses in Arctic ecosystems, but some data indicate that antimicrobial natural products are also present in marine invertebrates (Lippert et al. 2003; Angulo-Preckler et al. 2015b). The relatively short evolutionary history of the Arctic has been suggested to be the cause of its relatively low benthic biodiversity, due to a short time period for adaptation and speciation (Gray 2001). Low diversity could then reduce the competitive interactions that drive the development of bioactive natural products compared to the more biodiverse, lower latitudes. However, the latitudinal hypothesis has already been refuted at least for the Southern Hemisphere (see above), and now many studies are reporting that the Arctic is more diverse than previously thought (Piepenburg et al. 2011). All these suggest that Arctic marine benthic organisms are also likely to evolve chemically mediated defensive strategies and thus that we are just starting to understand the chemical relationships existing among Arctic invertebrates (Tadesse et al. 2008). A recent study investigated the presence of chemical defenses in sessile or slow-moving marine invertebrates from the Beaufort Sea, using organic extracts of 16 species (ten sponges, three soft corals, two bryozoans, and one holothurian) against 6 allopatric bacterial strains (Angulo-Preckler et al. 2015b). Most lipophilic fractions showed different degrees of activity against at least one bacterial strain at natural concentration, while none of the hydrophilic extracts did. This indicates that antimicrobial defenses are also a common trend among sessile or slow-moving marine benthic invertebrates from the Arctic.

Most research on marine invertebrate's chemical ecology focused on tropical and temperate environments, with a noteworthy increase observed in the last decade in studies in the Pacific Ocean, particularly in Japan, China, and South Korea (Costa Leal et al. 2012; Blunt et al. 2018). In order to make geographical comparisons in chemical ecology strategies, a good set of data is essential, but this is not existing yet for many marine animal forests around the planet. Sea slugs are one of the best known groups where we have enough data to start making comparisons (Avila et al. 2018). Some nudibranchs (such as *Bathydoris*, *Doris*, *Cuthona*, *Doto*, *Tritonia*), pleurobranchomorphs (*Bathyberthella*, *Tomthompsonia*), cephalaspideans (*Cylichna*, *Diaphana*, *Newnesia*, *Philine*, *Scaphander*, *Toledonia*), and pteropods (*Clione*, *Spongiobranchaea*) inhabit ecosystems from the tropics to the poles. Amazingly, their chemical defensive strategies are similar in the different geographic areas, even if the chemicals are used against very different kinds of predators (Avila et al. 2018). Effective protection from potential predators, thus, is achieved in very different ecosystems by using similar chemical defensive strategies. Similar sesquiterpenes from the Mediterranean and temperate *Dendrodoris* species and hodgsonal from the Antarctic *Bathydoris hodgsoni* or the wide distributed *Doris* species and the similar compounds from *Doris kerguelenensis* from Antarctica are just some examples of this (Avila 2006; Avila et al. 2018). Furthermore, most Antarctic species present biosynthetic defensive compounds, and this has been related to the fact that no herbivore sea slugs have been reported from the South pole, and thus no algal chemicals can be obtained, while sponge, bryozoan, and cnidarian feeders rely on biosynthesized defenses too. The evolutionary implications of this have been discussed elsewhere (Avila et al. 2018), but it seems clear that in these ecosystems it was more effective to rely on biosynthesis than on diet for defense and that all these data fit well with both RAM and EST models (see below). However, because data are still scarce, these hypotheses should be carefully considered.

4 Evolution and Chemical Theories

4.1 Chemical Defense Theories

In plant ecosystems, ecologists became quickly aware that plants are active participants in the dynamics of plant–animal interactions (Rhoades 1979, 1985; Karban and Meyers 1989; Cronin and Hay 1996a). Plants not only produce nectar, flowers, and fruits to attract pollinators and dispersers but also produce structures that mimic butterfly eggs or grazer scars to deter herbivores or to attract enemies of herbivores (Cronin and Hay 1996a). In marine animal forests, we are still far to reach this knowledge. In all cases, producing chemical defenses is believed to be energetically expensive because it uses resources that could be instead allocated to growth or reproduction (Herms and Mattson 1992). The induction of increased concentrations of chemical defenses allow costs of defenses to be delayed until enemies are detected, when the costs can be offset by the benefits of protection (Rhoades 1985; Karban and Meyers 1989; Cronin and Hay 1996a), and minimizes the costs by keeping defenses low until they are needed (Harvell 1990; Cronin and Hay 1996a).

It is well-known that organisms must balance the energetic costs of defense against those of growth and reproduction. However, why and how an organism invests in defense is obviously a key question in chemical ecology, and several theories and models have been proposed around this topic (Ianora et al. 2006). According to the Optimality Theory (OT), common defensive traits should be effective against a variety of enemies in order to save energy and should be mostly addressed towards generalists (Herms and Mattson 1992; Sotka et al. 2009). Furthermore, the Optimal Defense Theory (ODT) predicts that chemical defenses should be concentrated in those tissues that are most vulnerable (in terms of fitness), most valuable, and frequently targeted by predators in coordination with other defensive mechanisms (Rhoades and Gates 1976; Rhoades 1979). Therefore, defenses have to be concentrated in the most external zones, where they would be most effective against a number of predators. However, in prey that have bodies with holes (e.g., sponges), where small grazers may access internal parts, defenses could also be found there (Núñez-Pons et al. 2012b). Since this theory includes both evolutionary and ecological time scales, it may explain intraspecific, interspecific, and biogeographical variation in chemical defenses. However, ODT was proposed for the common and often marked differences observed in defensive compound allocations to various organs and tissues in terrestrial plants (Denno and McClure 1983; McKey 1974, 1979). In marine ecosystems, most tests of ODT predictions have used macroalgae, mostly brown algae, with most but not all the studies providing support for the theory (Amsler and Fairhead 2006). Similarly, for marine invertebrates, ODT has been supported in many but not all studied cases (Avila and Paul 1997; Avila et al. 2008; Taboada et al. 2013; Figuerola et al. 2014; Núñez-Pons and Avila 2014, 2015; Moles et al. 2015; Avila 2016). Some studies found no support for ODT in some Antarctic sponges (McClintock et al. 2010). However, the Antarctic sponge *Latrunculia apicalis* sequesters more defensive alkaloids in its external than internal layers, offering effective protection against sea star predators (Furrow et al. 2003). Also, the distribution of antifoulants in different body parts according to the ODT has been demonstrated for the tunicate *Synoicum adareanum* and for the sponges *Phorbas glaberrima* and *Cinachyra barbata* (Angulo-Preckler et al. 2015a). Surprisingly *C. barbata* showed antifouling activity in the internal instead of the external part, and this could be related to the body shape of the sponge with the surface, especially on the upper part, covered with dense spicule masses with crowns of longer spicules around the oscules and inhalant areas usually covered by sieve plates (Barthel and Gutt 1992). Although differential allocation has been observed, this may not be useful for metabolites with antimicrobial or antifouling activity, as microbes will encounter the inner cell layers of a sponge with similar likelihood as outer layers when a sponge pumps water during feeding (Angulo-Preckler et al. 2015a).

The allocation of resources and thus differences in growth strategy have been considered a possible explanation for the presence or absence of chemical defenses in sponges (Puglisi et al. 2014). To further explore this hypothesis, an indirect study of the reproductive output of known undefended and defended sponges was conducted using the undefended species *Iotrochota birotulata*, *Niphates erecta*, *Callyspongia armigera*, and *C. vaginalis* and the defended species *Aplysina cauliformis*, *A. fulva*, and *Amphimedon compressa* (Leong and Pawlik 2011). When the reproductive output index was compared among the sponge species, there was considerable interspecific variability, and no significant differences were found between undefended and chemically defended species (Leong and Pawlik 2011). The authors reported, however, how challenging it is to measure and compare trade-offs among sponge species with different modes of reproduction, and perhaps this could explain their negative results (Leong and Pawlik 2011). This is a field where more studies are urgently needed.

The induced defense model (IDM) follows from the ODT prediction that defense production should be directly correlated with the risk of an attack (Harvell 1990; Karban and Meyers 1989). When predation pressure is variable in space and/or time, one mechanism by which defense costs might be reduced is for the organism to produce them only when they are being attacked (Amsler and Fairhead 2006). Conversely, ODT and IDM would predict constitutive defense production when predation pressure is consistent and strong. However, temporal and spatial scales of predation are critical, because limiting the production of defenses to a given attack would only be beneficial if the defenses are produced fast and timely (Amsler and Fairhead 2006). Hay (1996) proposed that inducible chemical defenses in benthic marine organisms would be most effective if produced in response to mesograzers, because they cause only partial damage to their prey, at least over short time intervals, and because they often feed on individual prey for long enough periods for a chemical response to be produced. However, not all mesograzers feed on individual prey for long times or are limited to feeding within small spatial ranges (Paul et al. 2001; Amsler and Fairhead 2006). Furthermore, macropredators, such as Antarctic sea stars, sometimes prey on an individual organism for very long periods of time (Amsler 2001; Dayton et al. 1974), and therefore, not all small consumers feed as it would be predicted by the IDM to select for induced defenses, while some larger consumers feed over temporal and spatial scales that would be predicted (Amsler and Fairhead 2006). In fact, information is still very scarce, and more data are needed to test these theories in marine animal forests.

According to the growth–differentiation balance hypothesis (GDBH), there is a trade-off between resources allocated to differentiation processes (such as production of chemical defenses and cellular specialization) and growth, with differentiation occurring only after growth (Herms and Mattson 1992). One prediction of the GDBH is that newly produced cells, such as those at younger tissues, should contain lower levels of defenses than older, more differentiated cells (Amsler and Fairhead 2006). This contrasts with the ODT (see above), which predicts that younger individuals and younger reproductive parts of organisms should be better defended, because these are under a higher risk of predation because they usually are more nutritious (McKey 1974; Rhoades and Gates 1976; Rhoades 1979). This assumes that organisms should defend themselves maximizing fitness and thus protecting preferentially their tissues in function of their vulnerability or ecological value. The problem is that different models lead to completely different predictions. In part, this is due to the fact that in making these models completely different organisms were used, whether plants or animals, and thus many of the predictions of the ODT and GDBH relate to well-developed, complex organisms that may differentially invest in different organs or body parts. Chemical defense allocation is particularly common in sea slugs, with extensive literature reporting bioactive products stored in exposed, vulnerable areas, such as the mantle, foot, gills, and rhinophores; within mucus or ink secretions; in specialized glands, like mantle dermal formations (MDFs); and also occasionally in eggs, embryos, and larval stages (Avila 1995; Wagele et al. 2006; Avila et al. 2018).

The carbon–nutrient balance hypothesis (CNBH) tries to explain how resource availability affects the phenotypic expression of chemical defenses, suggesting that the allocation of resources to chemical defenses will change as environmental conditions, such as light or nutrient availability, change (Amsler et al. 2005; Amsler and Fairhead 2006). The CNBH predicts that because plants have a relative excess of fixed carbon, nitrogen-limited plants should produce compounds such as phenols and terpenes that do not contain nitrogen as defensive chemicals and that they should produce more of these compounds as nitrogen limitation increases relative to light availability (i.e., carbon fixation) (Bryant et al. 1983). Conversely, light-limited (i.e., carbon-limited) plants should use nitrogen-containing defenses, such as alkaloids and cyclic peptides, which are often effective at much lower concentrations than phenolics or terpenes. Again, these theories were initially formulated for plants in the terrestrial environment. The closely related resource allocation (or availability) model (RAM) makes similar predictions about defensive compound variation between species over evolutionary time scales (Coley et al. 1985). RAM predicts also that species that evolved in a nutrient-rich environment are inherently fast-growing species, with low investment in defenses, since they can easily replace lost tissues, while species that evolved in growth-limiting environments should produce relatively high levels of defensive compounds and tend to be slow growers, because replacing tissue lost to consumers should be more costly (Amsler et al. 2005; Amsler and Fairhead 2006). Only a few studies have tested CNBH and RAM in macroalgae (Amsler and Fairhead 2006). Cronin and Hay (1996b) and Van Alstyne et al. (1999) compared and contrasted these predictions, and while the results of Van Alstyne et al. (1999) did not support GDBH, the results of Cronin and Hay (1996b) did fit better with GDBH than with ODT. Almost nothing is known in marine animal forests regarding these theories yet.

All organisms that have to thrive under environmental stress (temperature or salinity fluctuations, high UV radiation, etc.) have probably more difficulties to acquire resources. The environmental stress theory (EST) predicts that under stress conditions the levels of chemical defenses would be lower, and thus, organisms would become more vulnerable to predation (Rhoades 1979). EST also suggests that environmental stresses, which may either reduce growth due to inadequate nutrient supply or cause damage due to adverse conditions, such as desiccation or UV radiation, will affect predator–prey interactions (Paul and Puglisi 2004; Núñez-

Pons et al. 2018a). Environmental stress often results in increased palatability to consumers, which may be due to either increases in nutritive value or decreases in defenses in the affected organisms (White 1984; Rhoades 1985; Cronin 2001). In general, it is accepted that stressed organisms would be able to devote fewer resources to defense and, therefore, be more palatable than unstressed individuals (Rhoades 1985). Recent experiments done by our research group showed changes in chemical composition of defenses in several marine benthic invertebrates when exposed to higher than usual temperatures (unpublished data). Further studies should focus on this research area.

In nature, all these phenomena do not occur in isolation but simultaneously, although very few studies have tested these theories combined (Amsler and Fairhead 2006). Some studies combined tests of IDM and CNBH (Hemmi et al. 2004; Jormalainen et al. 2003; Pavia and Brock 2000; Peckol and Yates 1997; Peckol et al. 1996; Weidner et al. 2004; Yates and Peckol 1993), while others combined IDM and UV radiation stress (Macaya et al. 2005; Pavia and Brock 2000; Pavia et al. 1997). Many more studies have to be done in order to clearly establish the validity of these theories in marine animal forests.

4.2 Coevolution

When a species is related to another by a trophic relationship, each one of them represents a selection factor that acts upon the other species, and therefore, their evolution remains mutually influenced (Margalef 1982). Along the previous sections, we have mentioned a few clear examples of coevolution. In terrestrial forests a plethora of examples exist, documenting the coevolution of plants–plants, insects–plants, and others. In marine animal forests, much research is still needed to understand these phenomena with the same degree of detail.

Comatulid crinoids possess polyketide sulfate pigments that inhibit fish feeding (Rideout et al. 1979). In contrast to comatulids, stalked crinoids seem to lack these defensive compounds, and this could explain why shallow-water adaptive radiation occurred in comatulid but not in stalked crinoids following the Mesozoic marine revolution (Meyer and Macurda 1977; McClintock et al. 1999). Observations indicate that two species of deepwater stalked crinoids, *Endoxocrinus parrae* and *Neocrinus decorus*, are not chemically defended from predation by a natural assemblage of reef fish, and this would support the predation hypothesis that restriction of stalked crinoids to deepwater habitats may have resulted from the Mesozoic radiation of durophagous fishes in shallow seas, resulting in a reduction of stalked crinoids from shallow water (McClintock et al. 1999).

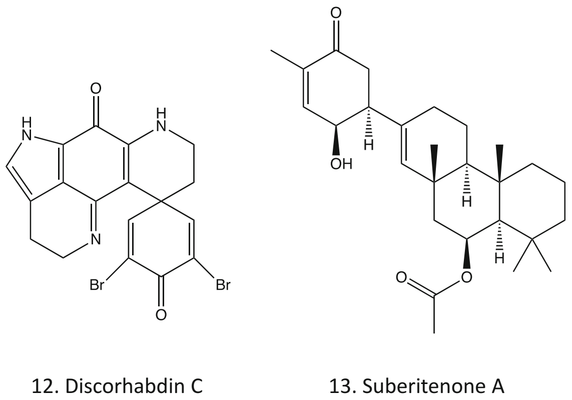
Predator–prey relationships are usually considered a coevolutionary arms race between predators and prey, in a reciprocal interaction in which better prepared predators increase the selection on better defended prey, which will in turn increase the selection on better armed predators in an interactive succession (Brodie 1999; Dietl and Kelley 2002; Da Cruz et al. 2012). The "escalation theory" proposes enemy-related selection as the most relevant factor of natural selection among individual organisms (Vermeij 1987, 1994). Thus, when hazardous to predators, prey might be considered enemies that influence predator evolution (Da Cruz et al. 2012). Opisthobranch molluscs that prey on chemically defended prey are an interesting study case for this (see below), because chemistry paved the way for them to enter in an arms race, developing means to detoxify and/or excrete harmful compounds, which led to the sequestration of those compounds and their self-defensive use, an escalation of defenses (Faulkner and Ghiselin 1983; Avila 1995; Cimino and Ghiselin 2001; Da Cruz et al. 2012; Avila et al. 2018). Sequestration of defensive chemical compounds from diet is well-known from terrestrial forests, for example, in insects (Opitz and Muller 2009), and it is very effective as it provides a defensive system for free. Thus, similar to insects (Opitz and Muller 2009), the acquisition of defensive chemicals in slugs coevolved with the selection of living host substrata, serving as habitat and as food source. The escalation of chemical defenses in slug molluscs, with chemically better protected predators than their prey, might also be related to their aposematism (Da Cruz et al. 2012).

Examples of marine benthic predator–prey relationships sharing the same natural products include *Bugula* bryozoans–polycerid slugs (see below), *Dysidea* sponges–*Hypselodoris* slugs, and cyanobacteria–*Stylocheilus* sea hares, among others (Avila et al. 2018). As said, sea slugs are clear examples of defensive escalation, because they often acquire better protection than their defended prey (Vermeij 1987, 1994; Avila et al. 2018). Other examples include some aeolidid species of *Phyllodesmium* feeding upon cnidarians (Bogdanov et al. 2014; Affeld et al. 2009; Slattery et al. 1998) and chromodoridid slugs feeding on sponges (Da Cruz et al. 2012; Carbone et al. 2013), among others. The accumulation of defensive molecules in specific glands has been described in the aposematic chromodorid slugs, which possess the typical mantle dermal formations (MDFs), but also in other groups that present different morphological structures. Dorid slugs are a clear example of defense allocation (Avila and Durfort 1996; Wagele et al. 2006), while many cladobranch dendronotids possess also other special cells, and many arminids present marginal sacs suggested to be involved in chemical defense too (Wagele et al. 2006; Putz et al. 2010).

4.3 Colors and the Role of Pigments

In nature, many chemical ecology strategies are accompanied by color displays, including crypsis, aposematism, mimetism, etc. (Avila et al. 2018). Some sea slugs, for example, possess an indistinguishable coloration (homochromy), shape (homomorphy), or texture, from the surrounding environment, using cryptic camouflage to hide from predators, combined (or not) with chemical strategies. Chemical defenses may be used in association with warning (aposematic) colorations, allowing species to survive in exposed habitats where predators learn to associate bright colorations to bad taste (Margalef 1977, 1982; Avila et al. 2018). Many pigments, in fact, possess bioactive properties themselves (e.g., alkaloids), while being part of photosynthetic systems, or may act as sunscreens protecting from UV light (Núñez-Pons and Avila 2015; Núñez-Pons et al. 2018a). As in other animals, several parallel strategies of using warning colorations appeared during evolution. Batesian mimicry is used by several taxa (sea slugs, sea cucumbers, and others) as a false warning appearance to discourage potential predators by imitating chemically defended species, without containing real toxic chemistry. Müllerian mimicry, instead, involves species that possess defensive metabolites and use similar coloration patterns, making the warning effect more effective against potential predators (Margalef 1977, 1982). Typical colors with warning effect in the sea often include dark blue–black background, combined with yellow, white, light blue, red, and orange lines or dots. These are common chromatic patterns of phyllidid and chromodoridid nudibranchs, and some sacoglossan slugs, which may be considered well-known examples of Müllerian or Batesian mimetic groups (see Avila et al. 2018). All these examples are equivalent to insect color–chemical strategies in terrestrial forests with similar ecological implications. However, very few examples exist so far in marine animal forests proving that color is really warning for potential predators (Tullrot and Sundberg 1991; Tullrot 1994; Cortesi and Cheney 2010). Further research is needed to fully demonstrate these phenomena in marine systems and to reach the deep knowledge existing in terrestrial forests.

Marine invertebrates are often brilliantly colored, inhabiting both shallow waters exposed to light, or dark, deeper areas (Núñez-Pons and Avila 2015). Colors may result from several different processes and serve diverse purposes. The most abundant pigments are nitrogenous compounds, but in fact they may belong to any major structural class of natural products. Pigments are usually employed by photosynthetic organisms in energy capture, in photoprotection, and as antioxidants, but they can also possess other roles, including protection against other organisms, where they may act directly as chemical defenses or indirectly by providing aposematic colorations. Discorhabdins (12, Fig. 7) from *Latrunculia apicalis*, the 4,5,8-trihydroxyquinoline-2-carboxylic acid from *Dendrilla membranosa*, an



12. Discorhabdin C

13. Suberitenone A

Fig. 7 Structures of selected pigments from Antarctic marine benthic sponges. *12*. Discorhabdin C from *Latrunculia apicalis*. *13*. Suberitenone A from *Suberites* sp.

uncharacterized purple compound from *Kirkpatrickia variolosa*, the tryptophan-related eribusinone (3, Fig. 3) from *Isodictya erinacea*, and suberitenones (13, Fig. 7) from *Suberites* sp. are all bioactive conspicuous pigments from Antarctic sponges (Núñez-Pons and Avila 2015). Moreover, the bioactive, bright yellow meridianins (10, Fig. 6) are found in several colonial *Aplidium* and *Synoicum* ascidians, as well as in some sponges. All these pigments, responsible for the intense colorations of the species, are not useful in Antarctica, where visually oriented predators such as fish or crabs are usually missing. Thus, it was hypothesized that pigmented chemical defenses in current Antarctic fauna may represent "relict pigments" that evolved under aposematic selection in ancient (ca. 22 Mya), warmer Antarctic seas when visual consumers, including fish and turtles, were important predators (Núñez-Pons and Avila 2015). Then, pigments could have been retained under selective pressure because they provided ecological advantages, even if the aposematic coloration was not useful anymore.

Typical generalist predators in tropical and temperate waters are fish and crabs, which are visually oriented towards their potential prey. In Antarctic ecosystems, instead, predation is mainly ruled by sea stars, which are chemically oriented towards food items. Most Antarctic chemically defended slugs, for example, seem to be cryptic. This fact may indicate that predators and food availability are the key factors in the evolution of defensive trends in sea slugs, rather than climate stability and high biodiversity levels only, as proposed by other authors (Avila et al. 2018). A simplistic assumption proposed that in polar zones the typical sea slugs would be cryptic and use biosynthetic defenses, while tropical sea slugs would be mostly aposematic and contain diet-derived defensive chemicals (Avila et al. 2018), although more data are needed to further prove this.

5 The Role of Microorganisms

Currently, organisms are no longer seen as single pluricellular beings, but as "holobionts," that is, metaorganisms formed by a macroscopic host harboring a wide array of functionally dynamic assemblages of bacteria, archaea, fungi, virus, and algal symbionts (Bosch and McFall-Ngai 2011). Although many studies described the compositions of the host-associated microbiota and the metagenome of the host and microbiome, little is known yet about the mechanisms by which host-associated microbiomes are structured and maintained (Puglisi et al. 2014). Several authors provided examples in which bacteria produce small molecules to allow or prevent selective, specific bacterial infection of eukaryotic tissues and/or surfaces (Goecke et al. 2010; Steinberg et al. 2011; Wahl et al. 2012; Krediet et al. 2013). Regardless of whether the bacteria are beneficial, commensal, or pathogenic, the molecules involved in the interactions between microorganism and eukaryotic hosts seem to be relatively conserved across a broad range of marine and terrestrial animals (Bosch and McFall-Ngai 2011).

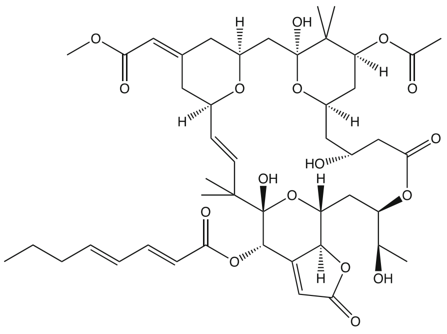
The microbial colonization of living surfaces may be affected by environmental and biological factors and may play an important role in the development and evolution of the holobiont (Lo Giudice et al. 2019). The holobiont and the hologenome act as a unique biological entity, playing a fundamental role in the adaptation and evolution of the holobiont itself (Rosenberg and Zilber-Rosenberg 2016, 2018). In fact, the holobiont maintains its unique characteristics (morphology, development, behavior, physiology, and resistance to diseases) due to the transmission through generations of the host genome and the associated microbiome. Changes in either genome can result in variations that can be selected for or against (Rosenberg and Zilber-Rosenberg 2018). Thus, many marine invertebrates host phylogenetically diverse microbial populations, also known as endosymbionts, which include symbiotic, pathogenic, or transient species (Taylor et al. 2007; Ueoka et al. 2015). Hentschel et al. (2002) demonstrated that sponges from different coasts contained microbes more closely related to each other than those from their surrounding waters. The nature of the relationship between microbes and macroorganisms has rarely been clarified, requiring complex metabolic and vertical hereditary transmission studies (Gordon and Leggat 2010). However, symbiotic relationships are often crucial, since they provide greater availability of nutrients for hosts, as well as protection against predation and fouling through defensive metabolites (Webster et al. 2004; Gordon and Leggat 2010). In Antarctica, bacterial symbiosis in sponge communities and soft corals, in particular, are among the scarcely studied examples (Webster et al. 2004; Webster and Bourne 2007). However, they are far from being fully described and still farther from establishing their relationship with guests. Sessile organisms such as sponges and corals represent complex ecosystems which harbor a rich bacterial community, not yet well-known. In the case of sponges, it has been reported that microbial populations may account for up to 40% of the total biomass (Wilkinson 1978). Bacterial symbionts are believed to play significant roles in the physiology of the sponge and have attracted the interest of researchers in the last years since they represent a source for the search of novel bioactive compounds. Proteobacteria and actinobacteria, for example, have been shown to produce secondary metabolites which supplement the host immune defenses (Hentschel et al. 2001). So far, more than 30 phyla have been found in close association with sponges worldwide (Fuerst 2014). Distinct microbial communities have been associated with different sponge species collected from a single location (Jackson et al. 2012), supporting the importance of these communities in the evolutionary history of the sponge. Breakdown of these associations due to perturbations in the ecosystems may result in the host's death. On the other hand, soft corals are usually covered by a protective layer of mucus which interacts with diverse forms of microbial life which include microbial representatives of Bacteria, Archaea, and Eukarya, making corals a model system for the study of symbiosis (Rosenberg et al. 2007). Mucus-associated bacteria also have an important ecological function as they can serve as food source for corals, providing beneficial metabolic capabilities such as carbon and nitrogen fixation, together with a more efficient uptake of limiting nutrients. They also serve as a physical barrier for coral pathogens occupying niches and spaces and produce antibiotic compounds to inhibit pathogens' growth or enhance the ability of corals to defend themselves against predator or competitors. This immunity strategy has been defined as the "coral probiotic hypothesis" (Reshef et al. 2006). Again, the breakdown of this relation can result in disease and mortality for the coral (Knowlton and Rohwer 2003).

In Antarctica, the peculiar and often strict interactions established between a benthic host and its symbionts have been only seldom investigated, resulting in fragmented and poor information (Lo Giudice et al. 2019). A recent review summarized the current knowledge on prokaryotic (bacteria and archaea) and eukaryotic (yeasts and diatoms) microbial symbionts of Antarctic benthic invertebrate hosts (Lo Giudice et al. 2019). Available data on Antarctic benthic hosts and prokaryotic symbionts are reduced to a small number of sponges, the soft coral *Alcyonium antarcticum*, the sea urchin *Sterechinus neumayeri*, and the oligochaete *Grania* sp. Among marine microorganisms from Antarctic sponges, bacteria, archaea, and benthic diatoms have been frequently observed in external surfaces (Hamilton et al. 1997; Amsler et al. 2000; Cerrano et al. 2000; Papaleo et al. 2012; Mangano et al. 2014; Rodríguez-Marconi et al. 2015). However, porifera from different oceans usually have a distinct microbial phylogenetic signature, different from that of marine plankton and sediments in the surroundings, usually species-specific (Hentschel et al. 2002). Another study showed that the host can be directly involved in the selection of symbiotic bacteria by producing bioactive metabolites (Soldatou and Baker 2017). Therefore, it is plausible to assume that the host maintains a stable associated microbial community to obtain benefits from such interaction (Lo Giudice et al. 2019). Also, a number of studies in polar regions have highlighted that sponge-associated microbial communities might be sponge-specific and different from that occurring in the external environment (Webster et al. 2004; Rodríguez-Marconi et al. 2015). Furthermore, some studies suggested that the interpopulation interactions occurring among bacterial populations inhabiting the same/different host species as well as the production of N-acyl homoserine lactones (involved in quorum sensing) may play an important role in the bacterial community associated with Antarctic sponges (Mangano et al. 2009, 2018). Similar to that observed for temperate and tropical climates, in Antarctic Porifera the associated communities display host specificity, and this suggests a positive interaction between the holobionts and their microbial symbionts (Lo Giudice et al. 2019).

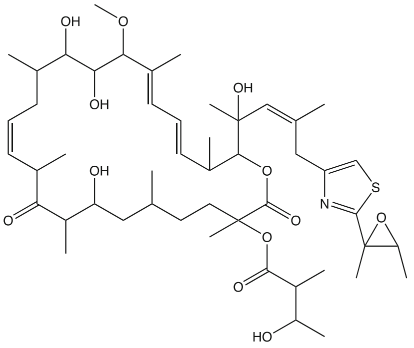
A recent study has dealt with the associated microbial communities of *Mycale* sponges, which are commonly and widely distributed across the oceans and represent a significant component in the benthos biomass, which in many species is mostly composed of bacteria (Cárdenas et al. 2018). The study provided a description of the microbiota of two *Mycale* species inhabiting the sub-Antarctic Magellan region and the Western Antarctic Peninsula, two geographically distant areas with contrasting environmental conditions. High-throughput sequencing of both sponges, *Mycale (Aegogropila) magellanica* and *Mycale (Oxymycale) acerata*, revealed a remarkable similarity in their microbiota, dominated by *Proteobacteria* and *Bacteroidetes*, with both species sharing more than 74% of the OTUs. These results showed a significant overlap among the microbiota of both species and suggested the existence of a low level of specificity of the most dominant symbiont groups (Cárdenas et al. 2018). The relationship between this microbiota and their chemical defenses remains to be further elucidated.

As said above, marine benthic invertebrates are known to be prolific sources of novel and diverse bioactive compounds (Blunt et al. 2018; Puglisi et al. 2014, 2018). Because some compounds are structurally similar to known microbial compounds, as research increases both in terrestrial and marine organisms, many natural products isolated from invertebrates are suggested to be in fact synthesized by symbiotic microorganisms (Kobayashi and Ishibashi 1993; Piel 2004; Paul et al. 2007). However, the potential bacterial origin for marine natural products has been demonstrated only seldom, because of the complexity of naturally occurring microbial assemblages in most marine invertebrates and the difficulties for culturing them outside their hosts (Piel 2006). Unlike one-host/one-symbiont associations, such as the well-described squid–bacteria symbiosis (*Euprymna scolopes*–*Vibrio fischeri*), sponges, ascidians, and bryozoans harbor abundant, very diverse bacterial and archaeal assemblages, making it very difficult to identify species-specific associations (Paul et al. 2007). As mentioned above, porifera, for example, seem to maintain long-term species-specific symbioses with diverse groups of bacteria through vertical transmission (Schmitt et al. 2007; Sharp et al. 2007; Taylor et al. 2007). Microbial ecology and genomics have provided support for biosynthetic origin studies, allowing the symbiotic sources of a few marine natural products to be identified, as well as molecular approaches to clone and express biosynthetic genes from symbionts have become a good way to overcome the problem of natural levels of supply (Hildebrand et al. 2004b; Piel 2006).

Examples of symbiotic sources of natural products include the bryozoan *Bugula neritina*, where there is conclusive evidence that a symbiotic bacterium produces the chemical defense compound for its host. *B. neritina* is a temperate intertidal bryozoan that usually fouls docks and boat hulls across the globe, forming chitinous, upright, branching colonies (Woollacott and Zimmer 1977). Bryostatins (14, Fig. 8), complex polyketides, were long suspected to be produced by symbiotic bacteria



14. Bryostatin 3



15. Patellazole B

Fig. 8 Natural products from symbiotic sources in marine benthic invertebrates. *14*. Bryostatin 3 from *Endobugula sertula* and the bryozoan *B. neritina*. *15*. Patellazole B from the symbiotic g-proteobacterium *Endolissoclinum faulkneri* and the ascidian *Lissoclinum patella*

(Anthoni et al. 1990). Bryostatins are well-known compounds because they also display anticancer activity (Pettit et al. 1982; Pettit 1991). The symbiotic bacterium has been identified, and a putative bryostatin biosynthetic gene cluster has been sequenced (Davidson et al. 2001; Hildebrand et al. 2004a; Sudek et al. 2007). The ecological implications of this specific symbiosis include the protection of the host, particularly the larval and early life stages. In general, it is known that bioactive natural products of invertebrates affect larval morphology and behavior rendering the larvae unpalatable to predators or preventing microbial fouling (Lindquist et al. 1992; Lindquist and Hay 1995; McClintock and Baker 1997; Iyengar and Harvell 2001). A single species of symbiotic g-proteobacterium was shown to reside in the pallial sinus of *B. neritina* larvae, and TEM studies demonstrated the presence of bacteria also at the funicular cords in adult *B. neritina* (Woollacott and Zimmer 1975; Haygood and Davidson 1997; Woollacott 1981). Interestingly, at least three cryptic species of *B. neritina* inhabit in the North Atlantic coasts, and each one of them presents different bryostatin profiles and possesses phylogenetically distinct but closely related symbionts (Davidson and Haygood 1999; McGovern and Hellberg 2003). Remarkably, the dorid nudibranch *Polycera atra*, which is cryptic on *B. neritina* colonies, feeds on colony tips and swimming larvae (both of which present high concentrations of bryostatins) and lays conspicuous white egg masses on *B. neritina* colonies (Davidson 1999; Davidson et al. 2001; Lopanik et al. 2004; Paul et al. 2007). These studies showed that bryostatins influenced the evolution of highly integrated relationships between the symbiont *Endobugula sertula*, the chemically defended bryozoan *B. neritina*, and its nudibranch predator *P. atra*, which uses that chemical defense for protecting its conspicuous egg masses.

Another example is the Pacific ascidian *Lissoclinum patella*, possessing the symbiotic cyanobacterium *Prochloron didemni*, which produces patellamides, cyclic peptides found in some specimens of the tunicate (Schmidt et al. 2005). Moreover, the genome of an uncultured symbiotic g-proteobacterium, *Endolissoclinum faulkneri*, includes a biosynthetic gene cluster that matches the predicted sequence for patellazoles (Kwan et al. 2012). Thus, it has been suggested that the bacterium specialized over evolution to produce patellazoles (15, Fig. 8), which have a defensive role in *L. patella*. The patellazole-producing symbionts are localized within bacteriocytes and are likely transmitted vertically, given their localization and their reduced genome (Kwan et al. 2012).

Tetrodotoxin (7, Fig. 5) is a naturally occurring toxin found in many bacteria species isolated from several marine organisms. Examples include *Vibrio alginolyticus* from the starfish *Astropecten polyacanthus*, *Vibrio* spp. from the puffer fish *Fugu vermicularis radiates*, *Aeromonas* sp. from the puffer fish *Takifugu obscurus*, *Vibrio* and *Pseudomonas* spp. from the gastropod *Niotha clathrata*, and others (Bane et al. 2014). Tetrodotoxin and its analogs are found, among others, in fish, nemerteans, prosobranchs, sea slugs, octopuses, copepods, crabs, and asteroids (Bane et al. 2014; Göransson et al. 2019). The proposed mechanism for tetrodotoxin accumulation in many marine organisms that do not contain the symbiotic bacteria is thought to be through the food web but also through other indirect mechanisms (Bane et al. 2014).

6 Chemical Ecology and Global Change

Global change is affecting all ecosystems at planetary scale, and marine animal forests are not an exception. Temperature shifts affect tropical, temperate, and polar animal forests, stressing species with narrow metabolic thresholds and causing changes in the composition of benthic communities (Schubert et al. 2017; Rossi et al. 2017a). Chemical interactions are being affected at different levels, although our understanding of these effects is still very low (Campbell et al. 2011). Knowing how environmental changes will impact chemically mediated interactions, however, is crucial for assessing and addressing the overall impact of climate change on marine ecosystems (Puglisi et al. 2014). Changing environmental conditions, especially increasing sea surface temperature and ocean acidification, have been shown to alter the composition and metabolism of beneficial bacterial communities associated with benthic hosts (Mouchka et al. 2010; Sharp and Ritchie 2012; Puglisi et al. 2014). Some studies have also analyzed the influence of environmental factors such as seasonal changes, depth, and light on the biosynthesis of natural compounds (Turon et al. 1996; Swearingen and Pawlik 1998; Duckworth and Battershill 2001; Peters et al. 2004; Ferretti et al. 2009). Furthermore, polar marine benthic species are exposed to major environmental challenges, including higher temperatures, ocean acidification, increasing UV radiation, and altered levels of sea ice and iceberg scouring (Peck 2018; Núñez-Pons et al. 2018a), although other potentially important stressors, such as salinity and hypoxia, have also been reported (Clark and Peck 2009a, b; Tremblay and Abele 2016). Ocean acidification and global climate change can also result in widespread disease outbreaks, sometimes causing phase shifts from coral reefs to algal dominated communities (Burge et al. 2014). The phase shifts have implications in chemically mediated interactions, notably the loss of chemical cues that disrupt the recruitment of juvenile fishes to those habitats (Lecchini et al. 2013).

Ocean acidification has been proven to interrupt chemical signaling on fish, thus hindering the ability of fish to detect predators, prey, and habitats and thus affecting their behavior and survival (Puglisi et al. 2014). There is also evidence that ocean acidification can alter microbial communities that may produce chemical cues for coral larval settlement (Mouchka et al. 2010; Sharp and Ritchie 2012). Ocean acidification also influences plant–animal interactions. An example is the effect of the diatom *Cocconeis scutellum parva* on the sex reversal of the shrimp *Hippolyte inermis*, already mentioned above. In seagrass meadows, including acidified environments, abundant epiphytic diatoms play key ecological roles. A still unknown apoptogenic compound produced by *Cocconeis* triggers the suicide of the androgenic gland of *H. inermis*, a protandric hermaphroditic shrimp distributed in *Posidonia oceanica* meadows both at normal pH and in acidified vents (Mutalipassi et al. 2019). Diatoms cultured at acidified conditions changed their metabolism and, in fact, produced in *H. inermis* a significantly lower proportion of females than diatoms grown at normal pH (Mutalipassi et al. 2019). The effects of reduced pH conditions on hermit crab shell selection behavior have been also proven (de la Haye et al. 2011). *Pagurus bernhardus* hermit crabs kept at a pH of 6.8 for 5 days showed increased time until they changed shells, lower rates of antennular flicking, and less time spent moving compared to crabs incubated at a control pH of 8.2. *P. bernhardus* response to food cues is also inhibited at lower pH (de la Haye et al. 2011). Crabs incubated at a lower pH took longer to find the food cue and also spent less time in contact with the cue. The crab behavior did not change when the cue was exposed to lower pH, indicating that the lower pH did not affect the chemical properties of the cues, but instead it decreased the ability of the crabs to detect and respond to the chemical cues (de la Haye et al. 2011). Moreover, the potential calcification problems in groups like bryozoans, molluscs, and echinoderms could dramatically affect their trade-offs between chemical and physical defenses and thus challenge their survival in the near future. Hopefully more research on the production, detection, and stability of natural products in a high CO_2 environment will take place in the near future, since potentially very complex mechanisms will determine the future of marine relationships in acidified oceans.

Anthropogenic environmental change is a global phenomenon, having a strong impact on biodiversity at planetary level (IPCC 2018). Polar regions are suffering the fastest rates of warming, with a loss of sea ice and retreat of coastal glaciers and ice shelves (IPCC 2018). The Antarctic Peninsula, in particular, is one of the areas with the fastest change over the last 50 years (Turner et al. 2009; Ducklow et al. 2013). Impacts of acute elevated seawater temperature on chemical interactions comprise the amount and the quality of chemical defenses, as well as predator's reactions to chemical cues in marine systems (Hay et al. 1994; McClintock and Baker 2001). Some studies investigated the direct effects of warming on Antarctic marine invertebrates determining that small increases in temperature can have significant impacts on aspects such as behavior, physiology, and growth rates in these largely stenothermal organisms. How the feeding preferences of an Antarctic, ecologically important mesograzer, amphipod (*Gondogeneia antarctica*), towards chemically deterrent macroalgae were affected by warming was recently investigated (Schram et al. 2015). Amphipods were exposed to 1.5 and 3.5 °C for 24 h and then used in choice feeding assays with artificial food containing chemical extracts from six sympatric macroalgae known to produce feeding deterrents. During exposure to elevated temperature, the amphipods lost their feeding preferences for several macroalgal extracts, suggesting that briefly increased temperature has the potential to alter feeding preferences in this common mesograzer. This effect may strongly influence these benthic communities. For herbivore–plant interactions, several theories have been postulated in relation to temperature increases. For example, as temperatures increase, enhanced positive or negative indirect effects on both the primary producer and the consumer may happen, depending on the strength of the interactions, such as the downstream influence of altered feeding preferences (O'Connor et al. 2009). Several models were developed to assess how food web dynamics might be influenced by seawater warming (O'Connor et al. 2011). One of the predictions is that both herbivore and plant abundances will change proportionally to a ratio of the temperature dependencies of the autotroph to the heterotroph

(O'Connor et al. 2011). However, in marine animal forest, we are still far from having this knowledge.

In tropical environments, where reef-building corals are succumbing to disease and environmental changes (pH, salinity, and temperature), sponges are becoming the dominant species (Puglisi et al. 2014). An example is the Caribbean reefs, where increasingly abundant sponges are chemically defended from predation and marine pathogens, either by the compounds they produce or those produced by symbionts or associated microorganisms (Pawlik 2011; Hentschel et al. 2012; Genta-Jouve and Thomas 2012). The Great Barrier Reef is the world's largest coral reef ecosystem, hosting very high biodiversity. Marine sponges are diverse, abundant, and ecologically important components of coral reefs, in both coastal and offshore environments. Due to their exceptionally high filtration rates, sponges also form a crucial coupling point between benthic and pelagic habitats. As mentioned above, sponges harbor extensive microbial communities, with many different taxa found exclusively within them, which are thought to contribute to the sponge's health and survival, and also producing chemical compounds. A study investigated the effects of sublethal thermal stress on the microbiome of the Great Barrier Reef sponge *Rhopaloeides odorabile* (Simister et al. 2012a). Sublethal thermal stress (31 °C) had no effect on the present and/or active portions of the *R. odorabile* bacterial community, but a shift in the bacterial assemblage was observed in necrotic sponges. A rapid decline in host health over a 1 °C temperature increment suggested that sponges such as *R. odorabile* may be highly vulnerable to the effects of global climate change. Bacterial communities in *R. odorabile* are highly stable between 27 and 31 °C, with bacterial community composition only shifting after the sponge tissue becomes necrotic. This demonstrated that sublethal temperatures do not affect the bacterial symbionts or the active fraction of the sponge-associated bacterial community and also confirmed a narrow (between 31 and 32 °C) thermal threshold for this species. Remarkably, this threshold is only ~2 °C above the current in situ mean maxima and represents a temperature that is expected to be exceeded by the end of this century. Thus, sponges such as *R. odorabile* could be highly vulnerable to the effects of global climate change as they undergo symbiont loss and a rapid decline in host health over a 1 °C temperature increment. Furthermore, coral reefs are under considerable pressure from global stressors, not only elevated sea surface temperature and ocean acidification but also local factors including eutrophication and poor water quality. The combined effects of water quality and elevated seawater temperature were investigated by exposing sponges to a range of elevated nutrient levels under ambient (27 °C) and sublethal (31 °C) seawater temperatures (Simister et al. 2012b). The highly stable microbial associations indicate that *R. odorabile* symbionts are capable of withstanding short-term exposure to elevated nutrient concentrations and sublethal temperatures. Nutrient enrichment levels have been shown to exacerbate the onset and severity of coral diseases, including black-band disease (Voss and Richardson 2006), aspergillosis, and yellow-band disease (Bruno et al. 2003). Although the mechanisms are still unknown, this may be due to an enhancement of microbial growth rates and/or increased pathogen virulence (Kim and Harvell 2002; Bruno et al. 2003; Kline et al. 2006; Simister et al. 2012b).

Another potentially huge impact for marine animal forests related to global change is the presence of invasive species. The success of alien species can often be attributed to the production of potent natural products. One example is the potential impact of the invasive Asian shore crab *Hemigrapsus sanguineus* on native marine species along the east coast of the USA. The larvae of this crab have shorter larval durations in response to water-soluble cues from conspecific adults, and research has tried to characterize this water-soluble cue that might affect its larval settlement (Anderson et al. 2010).

Moreover, the increase in seawater temperature caused by global change facilitates the spread of diseases in several coral species, and it is related to the massive bleaching of tropical corals (Weil et al. 2017; Rossi et al. 2017b). Indeed, emerging diseases are a very worrying issue that deserves particular attention. Chemical defenses of sponges against emerging diseases in the marine environment have become a topic of particular interest to biologists and chemical ecologists in recent years, raising questions regarding adaptability and survival of specific populations (Puglisi et al. 2014). Marine diseases can have dramatic influences in ecosystem structure, causing changes in species dominance, biodiversity, and function (Hewson et al. 2019). Sea stars in particular have been reported to suffer diseases for over a century, and they are ecologically significant constituents of benthic communities worldwide, where some species can exert significant influence on the population structure and composition of sympatric organisms (Hewson et al. 2019). Antarctic sea stars are no exception and have been reported to present an epidermal disease recently, which could be related to an event of environmental temperature increase (Núñez-Pons et al. 2018b). How chemical ecology may impact in these diseases is still unknown, but if the disease affecting the omnivorous macropredator *O. validus* becomes a cause of mass mortality, this would dramatically affect the benthic Antarctic ecosystems in an unpredictable way (Fig. 9).

Fig. 9 The Antarctic voracious, omnivorous macropredator sea star *Odontaster validus*, on top of different sponges at shallow waters of Deception Island (South Shetland Islands, Antarctica) at about 15 m depth. Right: *O. validus*, 10 cm diameter, with the recently reported epidermal disease (Núñez-Pons et al. 2018b)

7 Conclusions and Future Directions

Natural products are used by a wide variety of marine organisms as defenses against consumers, pathogens, and competitors having important complex or indirect effects that alter marine biodiversity at genetic, species, and ecosystem levels (Hay and Steinberg 1992; Paul 1992). In fact, most benthic marine organisms produce an array of natural products to be used as chemical defenses against large and small predators and competitors for space and resources, foulers, and pathogens, while some compounds may be also involved in reproduction, settlement, and metamorphosis, as well as habitat and prey location. All these relationships build up a diversified chemical network that can reach high levels of complexity, with many direct and indirect interactions, many of which are yet to be described in marine animal forests (Fig. 10). Chemical ecologists addressing questions in marine microbial chemical ecology are beginning to explore the role of chemical mediation of marine microorganisms and the role of natural products in preventing infection and large disease outbreaks (Paul and Puglisi 2004). Also, there is a good volume of research demonstrating qualitative and quantitative variation in natural compound production within and among populations, both temporally and spatially. However, while these studies describe patterns of variation, few studies sufficiently address the causes and consequences of this variability so far. Future studies on chemical variation are still needed to determine whether differences are due to local pressures by predators and competitors, environmental factors, symbionts, or genetic variation. In addition, as chemical ecologists continue to isolate active metabolites from crude extracts, we are gaining a better understanding of structure–activity relationships and the complexity of chemical defenses in marine organisms, which is crucial to understanding the

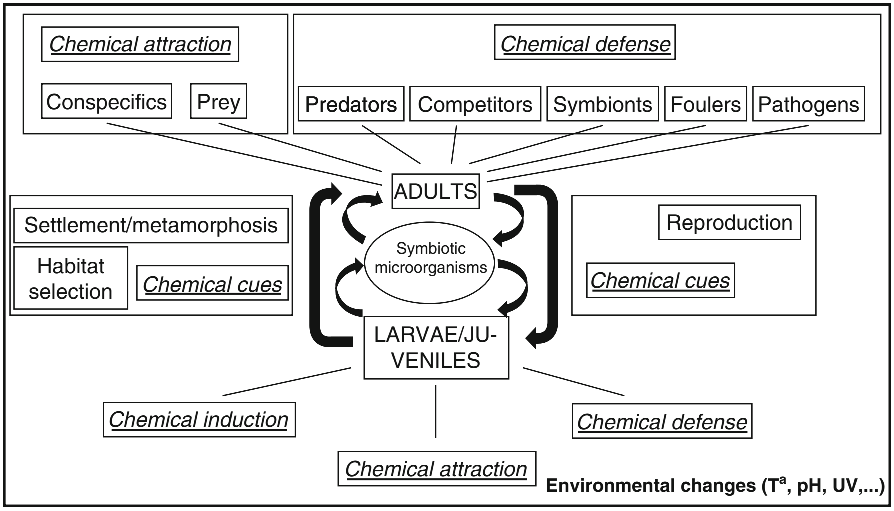


Fig. 10 Conceptual scheme of chemical relationships in marine animal forests

physiological effects of chemical defenses in predator–prey and pathogenic interactions (Paul and Puglisi 2004). Marine chemical ecology will continue to benefit greatly from collaborations between chemists and biologists, including natural product chemists, physiologists, biochemists, ecologists, molecular biologists, and microbiologists, as well as all the "omics." Moreover, given the concerns over environmental change, ocean acidification, and other effects, chemical and physical oceanographers are needed to collaborate to understand the roles that natural products are playing within ecological interactions, the mechanisms by which they are working, and the impacts of environmental changes on these interactions. Interdisciplinary approaches are thus the key to address complex questions in this field. Another key point is the need to extend the experiments to the field in polar areas, as it's more often done in tropical and temperate marine ecosystems, or, at least, to test the activity of the chemicals in natural conditions and ecologically meaningful interactions (Avila et al. 2008). Ecologically relevant assays using naturally co-occurring predators or competitors will greatly contribute to enhance our knowledge on chemical interactions. The ecological approach is particularly needed in the highly predictable Antarctic deepwater ecosystems, where community structure is ruled by biological factors (Dayton et al. 1974; Arntz et al. 1994). Identifying the natural products responsible for defensive activities but also for other roles that these compounds may play (Paul 1992), together with the increasing amount of autoecological and functional information of the species involved, will make possible to better understand the chemical processes affecting chemical interactions and will allow to establish proper comparisons with similar relationships occurring at other depths and latitudes. Since biodiversity is a key factor in all sort of ecological interactions (Margalef 1982), ultimately, high biodiversity and ecological interactions have driven chemical diversity, and therefore chemodiversity is intrinsically related to biodiversity (Núñez-Pons and Avila 2015).

Along with polar areas, the deep sea hosts a rich fauna still to be deeply studied. Whether deep-sea fauna is a richer source of bioactive metabolites than their shallow-water counterparts remains to be further investigated (Skropeta 2008). What it's true, however, is that the deep sea is an immense area, covering approximately 70% of the planet, and the relative amount of sampling done so far is very low (<5%); thus, it is a vast and relatively untapped reservoir of unique molecular, structural, and biological diversity waiting to be discovered (Skropeta 2008).

Once it has been well established that natural products play important roles in predator–prey interactions, symbioses, competition, reproduction, larval settlement, etc., we are now gaining greater insights not only into the presence of chemically mediated interactions but also into the compounds involved and the mechanisms by which they are being used (Puglisi et al. 2014). Advances in different techniques led to a greater understanding of the ecological importance of the microbiomes of many organisms, including the natural products produced by these microbes, and the ecological implications of chemically mediated alterations in the natural microbiome of some organisms (Puglisi et al. 2014).

Many complex relationships described in terrestrial forests probably also exist in marine animal forests, but we have not been able to study them yet. For example, mass attack by mountain pine beetles on a pine (*Pinus contorta*) produces white spots in the trunk, representing a beetle entry point at which resin has been secreted. This tree has survived the attack because turpentine production was sufficient to kill all of the bark beetles, which have been "pitched out" by resin outflow. On evaporation of the turpentine and exposure to air, the diterpenoid resin acids form a solid plug that seals the wound (Croteau et al. 2000). Whether similar sealing systems exist in marine benthic invertebrates is still unknown. Some butterflies obtain alkaloidal precursors from plants that are not their food sources and convert them into pheromones and defensive compounds (Croteau et al. 2000). Larvae of the cinnabar moth, *Tyria jacobaea*, continuously graze their plant host *Senecio jacobaea* until the plant is completely defoliated. The alkaloids obtained by the larvae are retained throughout metamorphosis. Male arctiid moths incorporate pyrrolizidine alkaloids into their reproductive biology by sequestering these alkaloids in abdominal scent organs, which are everted in the final stages of their courtship to release the pheromones necessary to gain acceptance by the female. The scent organs of a male arctiid moth (*Creatonotos transiens*) are directly proportional to the pyrrolizidine alkaloid content of its diet during the larval stage. The courtship success of these males, therefore, depends on the ingested alkaloids (Croteau et al. 2000). Similarly, the larvae of ithomiine butterflies feed on solanaceous plants and sequester their toxins, including tropane alkaloids and steroidal glycoalkaloids. However, adults do not contain these Solanaceae alkaloids but prefer to ingest plants that produce pyrrolizidine alkaloids, sequestering these bitter substances as N-oxides and monoesters. The pyrrolizidine alkaloid derivatives protect the butterflies from an abundant predator, the giant tropical orb spider. Mostly male butterflies are found feeding on the pyrrolizidine alkaloid-accumulating plants; however, up to 50% of the pyrrolizidine alkaloids present in these males is sequestered in the spermatophores and transferred to females at mating, giving them protection for life. In some butterfly species, the protective alkaloids are also transferred to the eggs (Croteau et al. 2000). It is highly probable that similar complex interactions exist in marine animal forests, although our knowledge is still very limited and further detailed studies are needed in this field of research.

Environmental change, however, is challenging marine animal forests, like the rest of ecosystems, in unpredictable and perhaps critical ways. Before anthropogenic impact produces irreversible changes, we need to understand the chemically mediated relationships regulating interactions in marine animal forests. Some particular areas, for example, the Antarctic Peninsula or some tropical islands, provide unique opportunities to study previously uninvestigated indirect effects of warming and acidification on marine benthic assemblages. Overall, it becomes necessary to establish a unifying framework for the role of chemical communication in ecosystem functioning and stability, to further decipher the universal chemical language of life, and to insist in the urgency to protect biodiversity, and thus chemodiversity, before it is too late.

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References

Affeld S, Kehraus S, Wägele H, König GM (2009) Dietary derived sesquiterpenes from *Phyllodesmium lizardensis*. J Nat Prod 72(2):298–300. https://doi.org/10.1021/np800583e

Ambrosio LJ, Brooks WR (2011) Recognition and use of ascidian hosts, and mate acquisition by the symbiotic pea crab *Tunicotheres moseri* (Rathbun, 1918): the role of chemical, visual and tactile cues. Symbiosis 53(2):53–61

Amsler CD (2001) Induced defenses in macroalgae: the herbivore makes a difference. J Phycol 37:353–356

Amsler CD, Fairhead VA (2006) Defensive and sensory chemical ecology of brown algae. Adv Bot Res 43:1–91

Amsler CD, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). J Phycol 34:53–59

Amsler CD, McClintock JB, Baker BJ (1999) An Antarctic feeding triangle: defensive interactions between macroalgae, sea urchins, and sea anemones. Mar Ecol Prog Ser 183:105–114

Amsler CD, McClintock JB, Baker BJ (2000) Chemical defenses of Antarctic marine organisms: a reevaluation of the latitudinal hypothesis. In: Davidson W, Howard-Williams C, Broady P (eds) Antarctic ecosystems: models for wider ecological understanding. 7th SCAR international biology symposium, Christchurch

Amsler CD, McClintock JB, Baker BJ (2001) Secondary metabolites as mediators of trophic interactions among Antarctic marine organisms. Am Zool 41:17–26

Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM, Furrow FB, Baker BJ (2005) Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. Mar Ecol Prog Ser 294:141–159

Amsler CD, McClintock JB, Baker BJ (2008) Macroalgal chemical defenses in polar marine communities. In: Amsler CD (ed) Algal chemical ecology. Springer, Berlin, pp 91–103

Amsler CD, Iken K, McClintock JB, Baker BJ (2009a) Defenses of polar macroalgae against herbivores and biofoulers. Bot Mar 52(6):535–546

Amsler MO, McClintock JB, Amsler CD, Angus RA, Baker BJ (2009b) An evaluation of sponge-associated amphipods from the Antarctic Peninsula. Ant Sci 21:579–589

Anderson JA, Valentine M, Epifanio CE (2010) Characterization of the conspecific metamorphic cue for *Hemigrapsus sanguineus* (De Haan). J Exp Mar Biol Ecol 382:139–144

Angulo-Preckler C, Cid C, Oliva F, Avila C (2015a) Antifouling activity in some benthic Antarctic invertebrates by “in situ” experiments at Deception Island, Antarctica. Mar Environ Res 105:30–38. https://doi.org/10.1016/j.marenvres.2015.02.001

Angulo-Preckler C, Spurkland T, Avila C, Iken K (2015b) Antimicrobial activity of selected benthic Arctic invertebrates. Polar Biol 38:1941–1948

Angulo-Preckler C, Tuya F, Avila C (2017a) Abundance and size patterns of echinoderms in coastal soft-bottoms at Deception Island (South Shetland Islands, Antarctica). Cont Shelf Res 137:131–141

Angulo-Preckler C, San Miguel O, García-Aljaro C, Avila C (2017b) Antibacterial defenses and palatability of some shallow-water Antarctic sponges. Hydrobiology 806(1):123–138

Anthoni U, Nielsen RH, Perieira M, Christophersen C (1990) Bryozoan secondary metabolites: a chemotaxonomical challenge. Comp Biochem Physiol 96B:431–437

Antonov AS, Avilov SA, Kalinovsky AI, Anastyuk SD, Dmitrenok PS, Evtushenko EV, Kalinin VI, Smirnov AV, Taboada S, Ballesteros M, Avila C, Stonik VA (2008) Triterpene glycosides from Antarctic Sea cucumbers I. Structure of liouvillosides A1, A2, A3, B1 and B2 from the sea cucumber *Staurocucumis liouvillei*: new procedure for separation of highly polar glycoside fractions and taxonomic revision. J Nat Prod 71(10):1677–1685

Antonov AS, Avilov SA, Kalinovsky AI, Anastyuk SD, Dmitrenok PS, Kalinin VI, Taboada S, Bosch A, Avila C, Stonik VA (2009) Triterpene glycosides from Antarctic Sea cucumbers II. Structure of Achlioniceosides A_1 (1), A_2 (2), A_3 (3), B_1 (4) from the sea cucumber *Achlionice violaecuspidata (=Rhipidothuria racowitzai)*. J Nat Prod 72(1):33–38

Antonov AS, Avilov SA, Kalinovsky AI, Dmitrenok PS, Kalinin VI, Taboada S, Ballesteros M, Avila C (2011) Triterpene glycosides from Antarctic Sea cucumbers III. Structures of liouvillosides A(4) and A(5), two minor disulphated tetraosides containing 3-O-methylquinovose as terminal monosaccharide units from the sea cucumber *Staurocucumis liouvillei* (Vaney). Nat Prod Res 25(14):1324–1333

Arntz WE, Brey T, Gallardo A (1994) Antarctic zoobenthos. Oceanogr Mar Biol 32:241–304

Aronson RB, Blake D (2001) Global climate change and the origin of modern benthic communities in Antarctica. Am Zool 41:27–39

Aumack CF, Amsler CD, McClintock JB, Baker BJ (2010) Chemically mediated resistance to mesoherbivory in finely branched macroalgae along the western Antarctic Peninsula. Eur J Phycol 45(1):19–26

Avila C (1992) A preliminary catalogue of natural substances of opisthobranch molluscs from Western Mediterranean and near Atlantic. Sci Mar 5(4):373–382

Avila C (1993) Sustancias naturales de moluscos opistobranquios: estudio de su estructura, origen y función en ecosistemas bentónicos. PhD Dissertation. Universitat de Barcelona, Barcelona, Catalonia

Avila C (1995) Natural products of opisthobranch molluscs: a biological review. Oceanogr Mar Biol Annu Rev 33:487–559

Avila C (2006) Molluscan natural products as biological models: chemical ecology, histology and laboratory culture. In: Cimino G, Gavagnin M (eds) Progress in molecular and subcellular biology. Subseries marine molecular biotechnology, vol 2. Springer, Berlin, pp 1–23

Avila C (2016) Biological and chemical diversity in Antarctica: from new species to new natural products. Biodiversity 17(1):1–7

Avila C, Durfort M (1996) Histology of epithelia and mantle glands of selected species of Doridacean molluscs with chemical defensive strategies. Veliger 39(2):148–163

Avila C, Paul VJ (1997) Chemical ecology of the nudibranch *Glossodoris pallida*: is the location of diet-derived metabolites important for defense? Mar Ecol Progr Ser 150:171–180

Avila C, Iken KB, Fontana A, Gimino G (2000) Chemical ecology of the Antarctic nudibranch *Bathydoris hodgsoni* Eliot, 1907: defensive role and origin of its natural products. J Exp Mar Biol Ecol 252:27–44

Avila C, Taboada S, Núñez-Pons L (2008) Antarctic marine chemical ecology: what is next? Mar Ecol 29:1–71

Avila C, Núñez-Pons L, Moles J (2018) From the tropics to the poles: chemical defensive strategies in sea slugs (Mollusca: Heterobranchia). In: Puglisi-Weening M, Becerro M (eds) Chemical ecology: the ecological impacts of marine natural products. CRC Press and Taylor and Francis, New York, pp 71–163

Bakus GJ, Green G (1974) Toxicity in sponges and holothurians: a geographic pattern. Science 185:951–953

Bane V, Lehane M, Dikshit M, O'Riordan A, Furey A (2014) Tetrodotoxin: chemistry, toxicity, source, distribution and detection. Toxins 6:693–755. https://doi.org/10.3390/toxins6020693

Bao J, Sun YL, Zhang XY, Han Z, Gao HC, He F, Qian PY, Qi SH (2013) Antifouling and antibacterial polyketides from marine gorgonian coral-associated fungus *Penicillium* sp. SCSGAF 0023. J Antibiot 66:219

Barnes DKA, Rothery P (1996) Competition in encrusting Antarctic bryozoan assemblages: outcomes, influences and implications. J Exp Mar Biol Ecol 196:267–284

Barthel D (1995) Tissue composition of sponges from the Weddell Sea, Antarctica—not much meat on the bones. Mar Ecol Prog Ser 123(1–3):149–153

Barthel D, Gutt J (1992) Sponge associations in the eastern Weddell Sea. Antarct Sci 4:137–150

Barthel D, Tendal OS (1994) Antarctic Hexactinellida. In: Wägele JW, Sieg J (eds) Synopses of Antarctic benthos. Koeltz Scientific Books, Champaing, IL, pp 9–135

Blackman AJ, Walls JT (1995) Bryozoan secondary metabolites and their chemical ecology. Stud Nat Prod Chem 17:73–112

Blumenberg M, Thiel V, Pape T, Michaelis W (2002) The steroids of hexactinellid sponges. Naturwissenschaften 89(9):415–419

Blunt JW, Carroll AR, Copp BR, Keyzers RA, Davis RA (2018) Marine natural products. Nat Prod Rep 35:8–53

Boal JG, Prosser KN, Holm JB, Simmons TL, Haas RE, Nagle GT (2010) Sexually mature cuttlefish are attracted to the eggs of conspecifics. J Chem Ecol 36:834–836

Bogdanov A, Kehraus S, Bleidissel S, Preisfeld G, Schillo D, Piel J, Brachmann AO, Wägele H, König GM (2014) Defense in the Aeolidoidean genus Phyllodesmium (Gastropoda). J Chem Ecol 40:1013–1024

Bosch TCG, McFall-Ngai MJ (2011) Metaorganisms as the new frontier. Zoology 114:185–190

Boucher DH, Jarnes S, Keeler KH (1982) The ecology of mutualism. Annu Rev Ecol Syst 13:315–347

Bourdeau PE (2010) Cue reliability, risk sensitivity and inducible morphological defense in a marine snail. Oecologia 162:987–994

Bowden DA (2005) Seasonality of recruitment in Antarctic sessile marine benthos. Mar Ecol Prog Ser 297:101–118

Bowden DA, Clarke A, Peck LS, Barnes DKA (2006) Antarctic sessile marine benthos: colonisation and growth on artificial substrata over 3 years. Mar Ecol Prog Ser 316:1–16

Brandt A, Gooday AJ, Brandaõ SN, Brix S, Brökeland W, Cedhagen T, Choudhury M, Cornelius N, Danis B, De Mesel I, Diaz RJ, Gillan DC, Ebbe B, Howe JA, Janussen D, Kaiser S, Linse K, Malyutina M, Pawlowski J, Raupach M, Vanreusel A (2007) First insights into the biodiversity and biogeography of the Southern Ocean deep sea. Nature 447 (7142):307–311

Brey T, Pearse J, Basch L, McClintock J, Slattery M (1995) Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. Mar Biol 124:279–292

Brodie ED (1999) Predator–prey arms races. Bioscience 49(7):557–568

Bronstein JL (1994) Our current understanding of mutualism. Q Rexi Biol 69:31–51

Bruno JF, Petes LE, Drew Harvell C, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. Ecol Lett 6:1056–1061

Bryan PJ, Yoshida WY, McClintock JB, Baker BJ (1995) Ecological role for pteroenone, a novel antifeedant from the conspicuous antarctic pteropod *Clione antarctica* (Gymnosomata: Gastropoda). Mar Biol 122:271–277

Bryan PJ, McClintock JB, Hopkins TS (1997) Structural and chemical defenses of echinoderms from the northern Gulf of Mexico. J Exp Mar Biol Ecol 210:173–186

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Bull AT, Ward AC, Goodfellow M (2000) Search and discovery strategies for biotechnology: the paradigm shift. Microbiol Mol Biol Rev 64:573–606

Burge CA, Eakin CM, Friedman CS, Froelich B, Hershberger PK, Hofmann EE, Petes LE, Prager KC, Weil E, Willis BL, Ford SE (2014) Climate change influences on marine infectious diseases: implications for management and society. Annu Rev Mar Sci 6:249

Callow JA, Callow ME (2006) Biofilms. In: Antifouling compounds. Springer, Berlin, pp 141–169

Campbell AH, Harder T, Nielsen S, Kjelleberg S, Steinberg PD (2011) Climate change and disease: bleaching of a chemically defended seaweed. Glob Chang Biol 17(9):2958–2970

Carbone M, Núñez Pons L, Castelluccio F, Avila C, Gavagnin M (2009) Illudalane sesquiterpenoids of the Alcyopterosin series from the Antarctic marine soft coral *Alcyonium grandis*. J Nat Prod 72(7):1357–1360

Carbone M, Núñez-Pons L, Paone M, Castelluccio F, Avila C, Gavagnin M (2012) Rossinone-related meroterpenes from the Antarctic tunicate *Aplidium fuegiense*. Tetrahedron 68:3541–3544

Carbone M, Gavagnin M, Haber M, Guo YW, Fontana A, Manzo E, Genta-Jouve G, Tsoukatou M, Rudman WB, Cimino G, Ghiselin MT, Mollo E (2013) Packaging and delivery of chemical weapons: a defensive Trojan horse stratagem in chromodorid nudibranchs. PLoS One 8:e62075

Cárdenas CA, González-Aravena M, Font A, Hestetun JT, Hajdu E, Trefault N, Malmberg M, Bongcam-Rudloff E (2018) High similarity in the microbiota of cold-water sponges of the genus *Mycale* from two different geographical areas. Peer J 6:e4935. https://doi.org/10.7717/peerj.4935

Castro P, Huber ME (2005) Marine biology, 5th edn. McGraw-Hill, Dubuque, IA

Cerrano C, Arillo A, Bavestrello G, Calcinai B, Cattaneo-Vietti R, Penna A, Sarà M, Totti C (2000) Diatom invasion in the antarctic hexactinellid sponge *Scolymastra joubini*. Polar Biol 23 (6):441–444

Cetrulo GL, Hay ME (2000) Activated chemical defenses in tropical versus temperate seaweeds. Mar Ecol Progr Ser 207:243–253

Cimino G, Ghiselin MT (2001) Marine natural products chemistry as an evolutionary narrative. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press LLC, pp 115–154

Clare AS, Rittschof D, Gerhart DJ, Maki JS (1992) Molecular approaches to nontoxic antifouling. Inv Repr Dev 22:67–76

Clark MS, Peck LS (2009a) HSP70 heat shock proteins and environmental stress in Antarctic marine organisms: a mini-review. Mar Gen 2:11–18

Clark MS, Peck LS (2009b) Triggers of the HSP70 stress response: environmental responses and laboratory manipulation in an Antarctic marine invertebrate (*Nacella concinna*). Cell Stress Chap 14:649–660

Clarke A, Aronson RB, Crame JA, Gili JM, Blake DB (2004) Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. Antarct Sci 16:559–568

Coley PD, Bryant JB, Chapin FS III (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Colin C, Leblanc C, Wagner E, Delage L, Leize-Wagner E, Van Dorsselaer A, Kloareg B, Potin P (2003) The brown algal kelp *Laminaria digitata* features distinct bromoperoxidase and iodoperoxidase activities. J Biol Chem 278:23545–23552

Colin C, Leblanc C, Wagner E, Delage L, Leize-Wagner E, Van Dorsselaer A, Potin P (2005) Vanadium-dependent iodoperoxidases in *Laminaria digitata*, a novel biochemical function diverging from brown algal bromoperoxidases. J Biol Inorg Chem 10:156–166

Cortesi F, Cheney KL (2010) Conspicuousness is correlated with toxicity in marine opisthobranchs. J Evol Biol 23(7):1509–1518

Costa Leal MC, Puga J, Serodio J, Gomes NCM, Calado R (2012) Trends in the discovery of new marine natural products from invertebrates over the last two decades – where and what are we bioprospecting? PLoS One 7(1):e30580. https://doi.org/10.1371/journal.pone.0030580

Cronin G (2001) Marine chemical ecology. In: McClintock JB, Baker BJ (eds). CRC Press, Boca Raton, p 325

Cronin G, Hay ME (1996a) Induction of seaweed chemical defenses by amphipod grazing. Ecology 77(8):2287–2301

Cronin G, Hay ME (1996b) Within plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth differentiation balance hypothesis. Oecologia 105:361–368

Croteau R, Kutchan TM, Lewis NG (2000) Natural products (secondary metabolites). In: Buchanan B, Gruissem W, Jones R (eds) Biochemistry & molecular biology of plants. American Society of Plant Physiologists

Cruz-Rivera E, Hay ME (2003) Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. Ecol Monogr 73(3):483–506

Cutignano A, Zhang W, Avila C, Cimino G, Fontana A (2011) Intrapopulation variability in the terpene metabolism of the Antarctic opisthobranch mollusc *Austrodoris kerguelenensis*. Eur J Org Chem 2011:5383–5389

Da Cruz JF, Gaspar H, Calado G (2012) Turning the game around: toxicity in a nudibranch-sponge predator-prey association. Chemoecology 22:47–53

Da Gama BAP, Pereira RC, Carvalho AGV, Coutinho R, Yoneshigue-Valentin Y (2002) The effects of seaweed secondary metabolites on biofouling. Biofouling 18:13–20

Davidson BS (1993) Ascidians: producers of amino acid-derived metabolites. Chem Rev 93 (5):1771–1791

Davidson SK (1999) The biology of bryostatins in the bryozoan *Bugula neritina*. Ph.D. dissertation, University of California San Diego, La Jolla

Davidson SK, Haygood MG (1999) Identification of sibling species of the bryozoan *Bugula neritina* that produce different anticancer bryostatins and harbor distinct strains of the bacterial symbiont "*Candidatus Endobugula sertula*". Biol Bull 196:273–280

Davidson SK, Allen SW, Um GE, Anderson CM, Haygood MG (2001) Evidence for the biosynthesis of bryostatins by the bacterial symbiont "*Candidatus Endobugula sertula*" of the bryozoan *Bugula neritina*. Appl Environ Microbiol 67:4531–4537

Dayton PK (1979) Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. In: Levi N, Bourny-Esnault (eds) Sponge biology. Centre de recherché Scientifique, Paris, pp 271–282

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecosyst 16:215–245

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44:105–128

Dayton PK, Mordida BJ, Bacon F (1994) Polar marine communities. Am Zool 34:90–99

De Broyer C, Jazdzewski K (1996) Biodiversity of the Southern Ocean: towards a new synthesis for the Amphipoda (Crustacea). Boll Mus Civ Stor Nat Verona 20:547–568

De Broyer C, Scailteur Y, Chapelle G, Rauschert M (2001) Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea. Polar Biol 24(10):744–753

De Broyer C, Lowry JK, Jazdzewski K, Robert H (2007) Part 1. Catalogue of the Gammaridean and Corophiidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. Bull Inst R Sci Nat Belg Biol 77(Suppl 1):1–325

De Bruyn C, De Ridder C, Rigaud T, David B (2011) Chemical host detection and differential attraction in a parasitic pea crab infecting two echinoids. J Exp Mar Biol Ecol 397:173–178

de la Haye KL, Spicer JI, Widdicombe S, Briffa M (2011) Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus*. Anim Behav 82:495–501

Dearborn JH (1977) Foods and feeding characteristics of Antarctic asteroids and ophiuroids. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, pp 293–326

Denno RF, McClure MS (1983) Variable plants and herbivores in natural and managed systems. Academic, New York

Dietl GP, Kelley PH (2002) The fossil record of predator–prey arms races: coevolution and escalation hypotheses. Paleontol Soc Pap 8:353–374

Dobretsov S, Qian PY (2002) Effect of bacteria associated with the green alga *Ulva reticulata* on marine micro-and macrofouling. Biofouling 18(3):217–228

Dobretsov S, Teplitski M, Paul V (2009) Mini-review: quorum sensing in the marine environment and its relationship to biofouling. Biofouling 25:413–427

Dobretsov S, Abed RM, Teplitski M (2013) Mini-review: inhibition of biofouling by marine microorganisms. Biofouling 29:423–441

Ducklow HW, Fraser WR, Meredith MP, Stammerjohn SE, Doney SC, Martinson DG, Sailley SF (2013) West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. Oceanography 26(3):190–203

Duckworth AR, Battershill CN (2001) Population dynamics and chemical ecology of New Zealand Demospongiae *Latrunculia* sp. nov. and *Polymastia croceus* (Poecilosclerida: Latrunculiidae: Polymastiidae). NZ J Mar Freshw Res 35:935–949

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72(4):1286–1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75(5):1304–1319

Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organization of a benthic community. Ecol Monogr 70(2):237–263

Dussourd DE, Denno RF (1991) Deactivation of plant defense: correspondence between insect behavior and secretory canal architecture. Ecology 72:1383–1396

Ebel R, Brenzinger M, Kunze A, Gross HJ, Proksch P (1997) Wound activation of protoxins in marine sponge *Aplysina aerophoba*. J Chem Ecol 23:1451–1462

Eisner T, Meinwald J (1995) Chemical ecology: the chemistry of biotic interaction. National Academy Press, Washington, DC

Elner RW, Vadas RL Jr (1990) Inference in ecology: the sea urchin phenomenon in the northwest Atlantic. Am Nat 136:108–125

Engel S, Jensen PR, Fenical W (2002) Chemical ecology of marine microbial defense. J Chem Ecol 28:1971–1985

Estes JA, Duggins DO (1995) Sea otter and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Farmer EE, Ryan CA (1990) Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proc Natl Acad Sci USA 87(19):7713–7716. https://doi.org/10.1073/pnas.87.19.7713

Farmer EE, Ryan CA (1992) Octadecanoid precursors of jasmonic acid activate the synthesis of wound-inducible proteinase inhibitors. Plant Cell 4:129–134. https://doi.org/10.1105/tpc.4.2.129

Faulkner DJ (1994) Marine natural products. Nat Prod Rep 11:355–394

Faulkner DJ (1998) Marine natural products. Nat Prod Rep 15:113–158

Faulkner DJ (2000) Highlights of marine natural products chemistry (1972–1999). ChemInform 31

Faulkner DJ, Ghiselin M (1983) Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. Mar Ecol Prog Ser 13:295–301

Ferretti C, Vacca S, De Ciucis C, Marengo B, Duckworth AR, Manconi R, Pronzato R, Domenicotti C (2009) Growth dynamics and bioactivity variation of the Mediterranean demosponges *Agelas oroides* (Agelasida, Agelasidae) and *Petrosia ficiformis* (Haplosclerida, Petrosiidae). Mar Ecol 30(3):1–10. https://doi.org/10.1111/j.1439-0485.2008.00278.x

Figuerola B, Núñez-Pons L, Vázquez J, Taboada S, Cristobo FJ, Ballesteros M, Avila C (2012) Chemical interactions in Antarctic marine benthic ecosystems. In: Cruzado A (ed) Marine ecosystems. InTech, Croatia, pp 105–126

Figuerola B, Núñez-Pons L, Moles J, Avila C (2013a) Feeding repellence in Antarctic bryozoans. Naturwiss 100:1069–1081. https://doi.org/10.1007/s00114-013-1112-8

Figuerola B, Taboada S, Monleón-Getino T, Vázquez J, Avila C (2013b) Cytotoxic activity of Antarctic benthic organisms against the common sea urchin *Sterechinus neumayeri*. Oceanography 1:107. https://doi.org/10.4172/2332-2632.1000107

Figuerola B, Núñez-Pons L, Monleón-Getino T, Avila C (2014) Chemo-ecological interactions in Antarctic bryozoans. Polar Biol 37(7):1017–1030

Firn RD, Jones CG (2009) A Darwinian view of metabolism: molecular properties determine fitness. J Exp Bot 60:719–726

Fleury BG, Lages BG, Barbosa JP, Kaiser CR, Pinto AC (2008) New hemiketal steroid from the introduced soft coral *Chromonephthea braziliensis* is a chemical defense against predatory fishes. J Chem Ecol 34:987–993

Frazao B, Vasconcelos V, Antunes A (2012) Sea Anemone (Cnidaria, Anthozoa, Actiniaria) toxins: an overview. Mar Drugs 10:1812–1851

Frederik JE, Snell HE, Haywood EK (1989) Solar ultraviolet radiation at the Earth's surface. Photochem Photobiol 50:443–450. https://doi.org/10.1111/j.1751-1097.1989.tb05548.x

Fuerst JA (2014) Diversity and biotechnological potential of microorganisms associated with marine sponges. Appl Microbiol Biotechnol 98(17):7331–7347

Furrow FB, Amsler CD, McClintock JB, Baker JB (2003) Surface sequestration of chemical feeding deterrents in the antarctic sponge *Latrunculia apicalis* as an optimal defense against sea star spongivory. Mar Biol 143(3):443–449

Gage JD (1996) Why are there so many species in deep-sea sediments? J Exp Mar Biol Ecol 200:257–286

Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms of the deep sea floor. Cambridge University Press, Cambridge

García-Arredondo A, Rojas-Molina A, Ibarra-Alvarado C, Iglesias-Prieto R (2011) Effects of bleaching on the pharmacological and toxicological activities elicited by the aqueous extracts prepared from two "fire corals" collected in the Mexican Caribbean. J Exp Mar Biol Ecol 396:171–176

Gavagnin M, de Napoli A, Cimino G, Iken K, Avila C, Garcia FJ (1999) Absolute configuration of diterpenoid diacylglycerols from the Antarctic nudibranch *Austrodoris kerguelenensis*. Tetr Asym 10:2647–2650

Genta-Jouve G, Thomas OP (2012) Sponge chemical diversity: from biosynthetic pathways to ecological roles. In: Becerro A, Uriz MJ, Maldonado M, Turon X (eds) Advances in sponge science, physiology, chemical and microbial diversity, pp 183–219

Gili JM, Arntz WE, Palanques A, Orejas C, Clarke A, Dayton PK, Isla E, Teixidó N, Rossi S, López-González PJ (2006) A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic. Deep-Sea Res II Top Stud Oceanogr 53:1029–1052. https://doi.org/10.1016/j.dsr2.2005.10.021

Goad LJ (1981) Sterol biosynthesis and metabolism in marine invertebrates. Pure Appl Chem 53 (4):837–852

Goecke F, Labes A, Wiese J, Imhoff JF (2010) Chemical interactions between marine macroalgae and bacteria. Mar Ecol Prog Ser 409:267–300

Göransson U, Jacobsson E, Strand M, Andersson HS (2019) The toxins of nemertean worms. Toxins 11(120):1–36. https://doi.org/10.3390/toxins11020120

Gordon BR, Leggat W (2010) *Symbiodinium*-invertebrate symbioses and the role of metabolomics. Mar Drugs 8:2546–2568

Grassle JF, Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. Am Nat 139:313–341

Gray J (2001) Marine diversity: the paradigms in patterns of species richness examined. Sci Mar 65:41–56

Green TR, Ryan CA (1972) Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. Science 175(4023):776–777

Hadfield MG, Paul VJ (2001) Natural chemical cues for settlement and metamorphosis of marine-invertebrate larvae. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, p 431

Hamilton PB, Poulin M, Yang J-R (1997) A new diatom genus *Porannulus* (Bacillariophyta), associated with marine sponges around King George Island, South Shetland Islands, Antarctica. Diat Res 12:229–242

Händeler K, Grzymbowski YP, Krug PJ, Wägele H (2009) Functional chloroplasts in metazoan cells—a unique evolutionary strategy in animal life. Front Zool 6:28

Harborne JB (2001) Twenty-five years of chemical ecology. Nat Prod Rep 18:361–379

Hardege JD, Bartels-Hardege HD, Fletcher N, Terschak JA, Harley M, Smith MA, Davidson L, Hayden D, Müller CU, Lorch M, Welham K, Walther T, Bublitz R (2011) Identification of a female sex pheromone in *Carcinus maenas*. Mar Ecol Prog Ser 436:177–189

Harder T, Lau SC, Dobretsov S, Fang TK, Qian PY (2003) A distinctive epibiotic bacterial community on the soft coral *Dendronephthya* sp. and antibacterial activity of coral tissue extracts suggest a chemical mechanism against bacterial epibiosis. FEMS Microbiol Ecol 43:337–347

Harder T, Tebben J, Möller M, Schupp PJ (2018) Chemical ecology of marine invertebrate larval settlement. In: Puglisi-Weening M, Becerro M (eds) Chemical ecology: the ecological impacts of marine natural products. CRC Press and Taylor and Francis, New York, pp 329–356

Harper MK, Bugni TS, Copp BR, James RD, Lindsay BS, Richardson AD, Schnabel PC, Tasdemir D, VanWagoner RM, Verbitseki SM, Ireland CM (2001) Introduction to the chemical ecology of marine natural products. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, pp 3–69

Harvell CD (1990) The ecology and evolution of inducible defenses. Q Rev Biol 65:323–340

Hay ME (1996) Marine chemical ecology: what's known and what's next? J Exp Mar Biol Ecol 200:103–134

Hay ME, Fenical W (1996) Chemical ecology and marine biodiversity: insights and products from the sea. Oceanography 9:10–20

Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites, vol II. Academic, New York

Hay ME, Duffy JE, Pfister CA, Fenical W (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68(6):1567–1580

Hay ME, Kappel QE, Fenical W (1994) Synergisms in plant defenses against herbivores: interactions of chemistry, calcification, and plant quality. Ecology 75:1714–1726

Haygood MG, Davidson SK (1997) Small subunit ribosomal RNA genes and in situ hybridization of the bacterial symbionts in the larvae of the bryozoan *Bugula neritina* and proposal of "*Candidatus Endobugula sertula*". Appl Env Microbiol 63:4612–4616

Heine JN, McClintock JB, Slattery M, Weston J (1991) Energetic composition, biomass, and chemical defense in the common Antarctic nemertean *Parborlasia corrugatus*. J Exp Mar Biol Ecol 153:15–25

Hemmi A, Honkanen T, Jormalainen V (2004) Inducible resistance to herbivory in *Fucus vesiculosus*–duration, spreading and variation with nutrient availability. Mar Ecol Progr Ser 273:109–120. https://doi.org/10.3354/meps273109

Henrikson AA, Pawlik JR (1995) A new antifouling assay method: results from field experiments using extracts of four marine organisms. J Exp Mar Biol Ecol 194:157–165

Hentschel U, Schmid M, Wagner M, Fieseler L, Gernert C, Hacker J (2001) Isolation and phylogenetic analysis of bacteria with antimicrobial activities from the Mediterranean sponges *Aplysina aerophoba* and *Aplysina cavernicola*. FEMS Microbiol Ecol 35(3):305–312

Hentschel U, Hopke J, Horn M, Friedrich AB, Wagner M, Hacker J, Moore BS (2002) Molecular evidence for a uniform microbial community in sponges from different oceans. Appl Environ Microbiol 68(9):4431–4440. https://doi.org/10.1128/AEM.68.9.4431-4440.2002

Hentschel U, Piel J, Degnan SM, Taylor MW (2012) Genomic insights into the marine sponge microbiome. Nat Rev Microbiol 10(9):641–654. https://doi.org/10.1038/nrmicro2839

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:285–335

Hewson I, Sullivan B, Jackson EW, Xu Q, Long H, Lin C, Quijano Cardé EM, Seymour J, Siboni N, Jones MRL, Sewell MA (2019) Perspective: something old, something new? Review of wasting and other mortality in Asteroidea (Echinodermata). Front Mar Sci 6:406. https://doi.org/10.3389/fmars.2019.00406

Hildebrand M, Waggoner LE, Liu H, Sudek S, Allen S, Anderson C, Sherman DH, Haygood M (2004a) *bry*A: an unusual modular polyketide synthase gene from the uncultivated bacterial symbiont of the marine bryozoan *Bugula neritina*. Chem Biol 11(11):1543–1552

Hildebrand M, Waggoner LE, Lim GE, Sharp KH, Ridley CP, Haygood M (2004b) Approaches to identify, clone, and express symbiont bioactive metabolite genes. Nat Prod Rep 21:122–142. https://doi.org/10.1039/B302336M

Hines DE, Pawlik JR (2012) Assessing the antipredatory defensive strategies of Caribbean non-scleractinian zoantharians (Cnidaria): is the sting the only thing? Mar Biol 159:389–398. https://doi.org/10.1007/s00227-011-1816-2

Huang YSM, McClintock JB, Amsler CD, Peters KJ, Baker BJ (2006) Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. J Exp Mar Biol Ecol 329:55–65

Huang YM, Amsler MO, McClintock JB, Amsler CD, Baker BJ (2007) Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula. Polar Biol 30:1417–1430

Hunting ER, van der Geest HG, Krieg AJ, van Mierlo ML, van Soest RWM (2010) Mangrove-sponge associations: a possible role for tannins. Aquat Ecol 44(4):679–684

Ianora A, Boersma M, Casotti R, Fontana A, Harder J, Hoffman F, Pavia H, Potin P, Poulet SA, Toth G (2006) The HT Odum synthesis essay. New trends in marine chemical ecology. Est Coasts 29:531–551

Iken K, Avila C, Ciavatta ML, Fontana A, Cimino G (1998) Hodgsonal, a new drimane sesquiterpene from the mantle of the Antarctic nudibranch *Bathydoris hodgsoni*. Tetr Lett 39:5635–5638

Iken K, Avila C, Fontana A, Gavagnin M (2002) Chemical ecology and origin of defensive compounds in the Antarctic nudibranch *Austrodoris kerguelenensis* (Opisthobranchia: Gastropoda). Mar Biol 141:101–109

IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner HO, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, 32 pp

Iyengar EV, Harvell CD (2001) Predator deterrence of early developmental stages of temperate lecithotrophic asteroids and holothuroids. J Exp Mar Biol Ecol 264:171–188

Jackson SA, Kennedy J, Morrissey JP, O'Gara F, Dobson AD (2012) Pyrosequencing reveals diverse and distinct sponge-specific microbial communities in sponges from a single geographical location in Irish waters. Microb Ecol 64(1):105–116

Jazdzewski K, Teodorczyk W, Siciński J, Kontek B (1991) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiology 223(1):105–117. https://doi.org/10.1007/BF00047632

Jormalainen V, Honkanen T, Koivikko R, Eränen J (2003) Induction of phlorotannin production in a brown alga: defense or resource dynamics? Oikos 103(3):640–650. https://doi.org/10.1034/j.1600-0706.2003.12635.x

Karban R, Meyers JH (1989) Induced plant responses to herbivory. Annu Rev Ecol Evol Syst 20:331–348

Karentz D (2001) Chemical defences of marine organisms against solar radiation exposure: UV-absorbing mycosporine-like amino acids and scytonemin. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, pp 481–520

Karentz D, Bosch I (2001) Influence of ozone-related increases in ultraviolet radiation on Antarctic marine organisms. Am Zool 41:3–16

Kelly SR, Jensen PR, Henkel TP, Fenical W, Pawlik JR (2003) Effects of Caribbean sponge extracts on bacterial attachment. Aquat Microb Ecol 31:175–182

Kelman D, Benayahu Y, Kashman Y (1999) Chemical defense of the soft coral *Parerythropadium fulvum fulvum* (Forskal) in the Red Sea against generalist reef fish. J Exp Mar Biol Ecol 238:127–137

Kessler A, Baldwin IT (2001) Defensive function of herbivore-induced plant volatile emissions in nature. Science 291(5511):2141–2144

Kicklighter CE, Kubanek J, Barsby T, Hay ME (2003) Palatability and defense of some tropical infaunal worms: alkylpyrrole sulfamates as deterrents to fish feeding. Mar Ecol Prog Ser 263:299–306

Kim K, Harvell CD (2002) Aspergillosis of sea fan corals: disease dynamics in the Florida keys. The everglades, Florida Bay, and coral reefs of the Florida keys: an ecosystem sourcebook, pp 813–824

Kline DI, Kuntz NM, Breitbart M, Knowlton N, Rohwer F (2006) Role of elevated organic carbon levels and microbial activity in coral mortality. Mar Ecol Prog Ser 314:119–125

Klöppel A, Brümmer F, Schwabe D, Morlock G (2013) Detection of bioactive compounds in the mucus nets of *Dendropoma maxima*, Sowerby 1825 (Prosobranch gastropod Vermetidae, Mollusca). J Mar Biol 283506:9. https://doi.org/10.1155/2013/283506

Knowlton N, Rohwer F (2003) Multispecies microbial mutualisms on coral reefs: the host as a habitat. Am Nat 162(S4):S51–S62

Kobayashi J, Ishibashi M (1993) Bioactive secondary metabolites from Okinawan sponges and tunicates. Stud Nat Prod Chem 23(2000):185–231

Koplovitz G, McClintock JB, Amsler CD, Baker BJ (2009) Palatability and chemical anti-predatory defenses in common ascidians from the Antarctic Peninsula. Aquat Biol 7:81–92

Koplovitz G, McClintock JB, Amsler CD, Baker BJ (2011) A comprehensive evaluation of the potential chemical defenses of Antarctic ascidians against sympatric fouling microorganisms. Mar Biol 158:2661–2671

Krediet CJ, Ritchie KB, Paul VJ, Teplitski MJ (2013) Coral-associated micro-organisms and their roles in promoting coral health and thwarting diseases. Proc R Soc B 280(1755):20122328. https://doi.org/10.1098/rspb.2012.2328

Krug PJ (2006) Defense of benthic invertebrates against surface colonization by larvae: a chemical arms race. In: Antifouling compounds. Springer, Berlin, pp 1–53

Kunzmann K (1996) Associated fauna of selected sponges (Hexactinellida and Demospongiae) from the Weddell Sea, Antarctica. Ber Polarforsch 210:1–93

Kwan JC, Donia MS, Han AW, Hirose E, Haygood MG, Schmidt EW (2012) Genome streamlining and chemical defense in a coral reef symbiosis. Proc Natl Acad Sci USA 109(50):20655–20660

Lasker HR (1985) Prey preferences and browsing pressure of the butterflyfish *Chaetodon capistratus* on Caribbean gorgonians. Mar Ecol Prog Ser 21:213–220

Lawrence JM (1975) On the relationships between marine plants and sea urchins. Oceanogr Mar Biol Annu Rev 13:213–286

Lebar MD, Heimbegner JL, Baker BJ (2007) Cold-water marine natural products. Nat Prod Rep 24:774–797

Lecchini D, Waqalevu VP, Parmetier E, Radford CA, Banaigs B (2013) Fish larvae prefer coral over algal water cues: implications of coral reef degradation. Mar Ecol Prog Ser 475:303–307

Lecchini D, Miura T, Lecellier G, Banaigs B, Nakamura Y (2014) Transmission distance of chemical cues from coral habitats: implications for marine larval settlement in context of reef degradation. Mar Biol 161:1677

Lee YK, Lee JH, Lee HK (2001) Microbial symbiosis in marine sponges. J Microbiol Seoul 39:254–264

Leong W, Pawlik JR (2011) Comparison of reproductive patterns among 7 Caribbean sponge species does not reveal a resource trade-off with chemical defenses. J Exp Mar Biol Ecol 401:80–84

Leys SP, Mackie GO, Reiswig HM (2007) The biology of glass sponges. Adv Mar Biol 52:1–145

Lim-Fong GE, Kabir R (2018) Chemical ecology of marine bryozoans. In: Puglisi-Weening M, Becerro M (eds) Chemical ecology: the ecological impacts of marine natural products. CRC Press, Taylor and Francis, pp 357–372

Lindquist N, Hay ME (1995) Can small rare prey be chemically defended? The case for marine larvae. Ecology 76(4):1347–1358

Lindquist N, Hay ME, Fenical W (1992) Defense of ascidians and their conspicuous larvae: adult vs larval chemical defenses. Ecol Monogr 62:547–568

Lippert H, Brinkmeyer R, Mulhaupt T, Iken K (2003) Antimicrobial activity in sub-Arctic marine invertebrates. Polar Biol 26:591–600

Lippert H, Iken K, Volk C, Köck M, Rachor E (2004) Chemical defence against predators in a sub-Arctic fjord. J Exp Mar Biol Ecol 310:131–146

Lo Giudice A, Azzaro M, Schiaparelli S (2019) Microbial symbionts of Antarctic marine benthic invertebrates. In: Castro-Sowinski S (ed) The ecological role of micro-organisms in the Antarctic environment. Springer Polar Sciences. https://doi.org/10.1073/978-3-030-02786-513

Lobban CS, Harrison PJ (1994) Seaweed ecology and physiology. Cambridge University Press, Cambridge

Lockhart SJ, Jones CD (2008) Biogeographic patterns of benthic invertebrate megafauna on shelf areas within the Southern Ocean Atlantic sector. CCAMLR Sci 15:167–192

Loh TL, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. Proc Natl Acad Sci USA 111:4151–4156. https://doi.org/10.1073/pnas.1321626111

Lopanik N, Lindquist N, Targett N (2004) Potent cytotoxins produced by a microbial symbiont protect host larvae from predation. Oecologia 139:131–139

López-Legentil S, Dieckmann R, Bontemps-Subielos N, Turon X, Banaigs B (2005) Qualitative variation of alkaloids in color morphs of Cystodytes (Ascidiacea). Biochem Syst Ecol 33:1107–1119. https://doi.org/10.1016/j.bse.2005.03.011

Luchner M (1984) Secondary metabolism in microorganisms, plants and animals. Springer, Berlin

Lyle M, Gibbs S, Moore TC, Rea DK (2007) Late Oligocene initiation of the Antarctic circumpolar current: evidence from the South Pacific. Geology 35:691–694

Macaya EC, Rothäusler E, Thiel M, Molis M, Wahl M (2005) Induction of defenses and within-alga variation of palatability in two brown algae from the northern-central coast of Chile: effects of mesograzers and UV radiation. J Exp Mar Biol Ecol 325(2):214–227

Mangano S, Michaud L, Caruso C, Brilli M, Bruni V, Fani R, Lo Giudice A (2009) Antagonistic interactions between psychrotrophic cultivable bacteria isolated from Antarctic sponges: a preliminary analysis. Res Microbiol 160(1):27–37. https://doi.org/10.1016/j.resmic.2008.09.013

Mangano S, Michaud L, Caruso C, Lo Giudice A (2014) Metal and antibiotic resistance in psychrotrophic bacteria associated with the Antarctic sponge *Hemigellius pilosus* (Kirkpatrick, 1907). Polar Biol 37:227–235. https://doi.org/10.1007/s00300-013-1426-1

Mangano S, Caruso C, Michaud L, Lo Giudice A (2018) First evidence of quorum sensing activity in bacteria associated with Antarctic sponges. Polar Biol 41:1435–1445. https://doi.org/10.1007/s00300-018-2296-3

Mann KH (1982) Ecology of coastal waters. A systems approach. University of California Press, Berkeley

Margalef R (1977) Comunicación y engaño. Aspectos e implicaciones de la cripsis, advertencia y mimetismo. Graellsia 31:341–356

Margalef R (1982) Ecologia. Ed. Omega, Barcelona, pp 1–951

MarinLit Database, John Blunt and Murray Munro at the University of Canterbury, New Zealand. http://pubs.rsc.org/marinlit

Martín Ledo R (2010) Simbiosis en ofiuroideos antárticos. Master Thesis, Máster Universitario en Investigación Biológica. Departamento de Anatomía, Biología Celular y Zoología, Facultad de Ciencias, Universidad de Extremadura, p 72

McClintock JB (1987) Investigation of the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctica. Mar Biol 94(3):479–487

McClintock JB (1994) Trophic biology of antarctic echinoderms. Mar Ecol Prog Ser 11(1):191–202

McClintock JB, Baker BJ (1997) A review of the chemical ecology of shallow-water antarctic marine invertebrates. Am Zool 37:329–342

McClintock JB, Baker BJ (1998) Chemical ecology in Antarctic seas. Am Sci 86:254–263

McClintock JB, Baker BJ (2001) Marine chemical ecology. CRC Marine Science Series Press, Boca Raton

McClintock JB, Janssen J (1990) Pteropod abduction as a chemical defense in a pelagic antarctic amphipod. Nature 346:424–426

McClintock JB, Heine J, Slattery M, Weston J (1990) Chemical bioactivity in common shallow-water Antarctic marine invertebrates. Antarct J US 25(5):204–206

McClintock JB, Slattery M, Heine J, Weston J (1992) Chemical defense, biochemical composition and energy content of three shallow-water Antarctic gastropods. Polar Biol 11:623–629

McClintock JB, Baker BJ, Baumiller TK, Messing CG (1999) Lack of chemical defense in two species of stalked crinoids: support for the predation hypothesis for mesozoic bathymetric restriction. J Exp Mar Biol Ecol 232(1):1–7

McClintock JB, Mahon AR, Peters KJ, Amsler CD, Baker BJ (2003) Chemical defenses in embryos and juveniles of two common Antarctic Sea stars and an isopod. Antarct Sci 15:339–344

McClintock JB, Amsler CD, Baker BJ, Van Soest R (2005) Ecology of Antarctic marine sponges: an overview. Integr Comp Biol 45:359–368

McClintock JB, Amsler MO, Koplovitz G, Amsler CD, Baker BJ (2009) Observations on an association between the dexaminid amphipod *Polycheria antarctica f. acanthopod*a and its ascidian host *Distaplia cylindrica*. J Crustac Biol 29:605–608

McClintock JB, Amsler CD, Baker BJ (2010) Overview of the chemical ecology of benthic marine invertebrates along the Western Antarctic Peninsula. Integr Comp Biol 50:967–980

McGovern TM, Hellberg ME (2003) Cryptic species, cryptic endosymbionts, and geographical variation in chemical defences in the bryozoan *Bugula neritina*. Mol Ecol 12(5):1207–1215

McKey D (1974) Adaptive patterns in alkaloid physiology. Am Nat 108:305–320

McKey D (1979) The distribution of secondary metabolites within plants. In: Rosenthal GA, Janzen DH (eds) Herbivores: their interactions with secondary plant metabolites. Academic, New York, pp 55–133

Menna M (2009) Antitumor potential of natural products from Mediterranean ascidians. Phytochem Rev 8(2):461–472

Menna M, Fattorusso E, Imperatore C (2011) Alkaloids from marine ascidians. Molecules 16 (10):8694–8732

Mercado JM, Carmona R, Niell FX (1998) Bryozoans increase available CO_2 for photosynthesis in *Gelidium sesquipedale* (Rhodophyceae). J Phycol 34:925–927

Meyer DL, Macurda DB (1977) Adaptive radiation of the comatulid crinoids. Paleobiology 3:74–82

Miyamoto T, Yamada K, Ikeda N, Komori T, Higuchi R (1994) Bioactive terpenoids from Octocorallia. 1. Bioactive diterpenoids – litophynol A and litophynol B from the mucus of the soft coral *Litophyton* sp. J Nat Prod 57:1212–1219

Moles J, Núñez-Pons L, Taboada S, Figuerola S, Cristobo J, Avila C (2015) Anti-predatory chemical defences in Antarctic benthic fauna. Mar Biol 162(9):1813–1821

Moon B, Park YC, McClintock JB, Baker BJ (2000) Structure and bioactivity of erebusinone, a pigment from the Antarctic sponge *Isodictya erinacea*. Tetrahedron 56:9057–9062. https://doi.org/10.1016/S0040-4020(00)00760-2

Moran Y, Genikhovich Y, Gordon D, Wienkoop S, Zenkert C, Özbek S, Technau U, Gurevitz M (2012) Neurotoxin localization to ectodermal gland cells uncovers an alternative mechanism of venom delivery in sea anemones. Proc R Soc B 279:1351–1358

Mouchka ME, Hewson I, Harvell CD (2010) Coral-associated bacterial assemblages: current knowledge and the potential for climate-driven impacts. Integr Comp Biol 50(4):662–674

Mutalipassi M, Mazzella V, Zupo V (2019) Ocean acidification influences plant-animal interactions: the effect of *Cocconeis scutellum parva* on the sex reversal of *Hippolyte inermis*. PLoS One 14(6):e0218238. https://doi.org/10.1371/journal.pone.0218238

Nappo M, Berkov S, Codina C, Avila C, Messina P, Zupo V, Bastida J (2009) Metabolite profiling of the benthic diatom *Cocconeis scutellum* by GC-MS. J Appl Phycol 21(3):295–306. https://doi.org/10.1007/s10811-008-9367-8

Nelson WG (1980) A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull Mar Sci 30:80–89

Núñez-Pons L, Avila C (2014) Deterrent activities in the crude lipophilic fractions of Antarctic benthic organisms: chemical defences against keystone predators. Polar Res 33(21624):1–12

Núñez-Pons L, Avila C (2015) Natural products mediating ecological interactions in Antarctic benthic communities: a mini-review of the known molecules. Nat Prod Rep 32:1114–1130. https://doi.org/10.1039/C4NP00150H

Núñez-Pons L, Forestieri R, Nieto RM, Varela M, Nappo M, Rodríguez J, Jiménez C, Castelluccio F, Carbone M, Ramos-Espla A, Gavagnin M, Avila C (2010) Chemical defenses of tunicates of the genus *Aplidium* from the Weddell Sea (Antarctica). Polar Biol 33:1319–1329

Núñez-Pons L, Carbone M, Vazquez J, Rodríguez J, Nieto RM, Varela MM, Gavagnin M, Avila C (2012a) Natural products from Antarctic colonial ascidians of the genera *Aplidium* and *Synoicum*: variability and defensive role. Mar Drugs 10:1741–1764

Núñez-Pons L, Rodríguez-Arias M, Gómez-Garreta A, Ribera-Siguán A, Avila C (2012b) Feeding deterrence in Antarctic marine organisms: bioassays with the omnivore amphipod *Cheirimedon femoratus*. Mar Ecol Prog Ser 462:163–174. https://doi.org/10.3354/meps09840

Núñez-Pons L, Carbone M, Paris D, Melck D, Ríos P, Cristobo J, Castelluccio F, Gavagnin M, Avila C (2012c) Chemo-ecological studies on hexactinellid sponges from the Southern Ocean. Naturwiss 99(5):353–368

Núñez-Pons L, Carbone M, Vázquez J, Gavagnin M, Avila C (2013) Lipophilic defenses from *Alcyonium* soft corals of Antarctica. J Chem Ecol 39(5):675–685

Núñez-Pons L, Avila C, Romano G, Verde C, Giordano D (2018a) UV-protective compounds in marine organisms from the Southern Ocean. Mar Drugs 16:336. https://doi.org/10.3390/md16090336

Núñez-Pons L, Work TM, Angulo-Preckler C, Moles J, Avila C (2018b) Exploring the pathology of an epidermal disease affecting a circum-Antarctic Sea star. Sci Rep 8:12. https://doi.org/10.1038/s41598-018-29684-0

O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. PLoS One 7:e1000178. https://doi.org/10.1371/journal.pbio.1000178

O'Connor MI, Gilbert B, Brown CJ (2011) Theoretical predictions for how temperature affects the dynamics of interacting herbivores and plants. Am Nat 178:626–638

Ohsawa N, Ogata Y, Okada N, Itoh N (2001) Physiological function of bromoperoxidase in the red marine alga, *Corallina pilulifera*: production of bromoform as an allochemical and the simultaneous elimination of hydrogen peroxide. Phytochemistry 58:683–692

Opitz SEW, Muller C (2009) Plant chemistry and insect sequestration. Chemoecology 19 (3):117–154. https://doi.org/10.1007/s00049-009-0018-6

Orejas C, Gili JM, Arntz WE, Ros JD, López PJ, Teixido N, Filipe P (2000) Benthic suspension feeders, key players in Antarctic marine ecosystems? Contrib Sci 1(3):299–311

Page JL, Dickman BD, Webster DR, Weissburg MJ (2011a) Getting ahead: context-dependent responses to odorant filaments drive along-stream progress during odor tracking in blue crabs. J Exp Biol 214:1498–1512

Page JL, Dickman BD, Webster DR, Weissburg MJ (2011b) Staying the course: chemical signal spatial properties and concentration mediate cross-stream motion in turbulent plumes. J Exp Biol 214:1513–1522

Papaleo MC, Fondi M, Maida I, Perrin E, Lo Giudice A, Michaud L, Mangano S, Bartolucci G, Romoli R, Fani R (2012) Sponge-associated microbial Antarctic communities exhibiting antimicrobial activity against *Burkholderia cepacia* complex bacteria. Biotechnol Adv 30 (1):272–293

Paré PW, Tumlinson JH (1999) Plant volatiles as a defense against insect herbivores. Plant Physiol 121(2):325–332. https://doi.org/10.1104/pp.121.2.325

Paul VJ (1992) Ecological roles of marine natural products. Cornell University Press and Comstock, Ithaca

Paul VJ, Puglisi MP (2004) Chemical mediation of interactions among marine organisms. Nat Prod Rep 21:189–209

Paul VJ, Van Alstyne KL (1992) Activation of chemical defenses in the tropical green algae *Halimeda* spp. J Exp Mar Biol Ecol 160:191–203

Paul VJ, Cruz-Rivera E, Thacker RW (2001) Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, pp 227–265

Paul VJ, Arthur KE, Ritson-Williams R, Ross C, Sharp K (2007) Chemical defenses: from compounds to communities. Biol Bull 213(3):226–251

Paul VJ, Ritson-Williams R, Sharp K (2011) Marine chemical ecology in benthic environments. Nat Prod Res 28:345–387

Pavia H, Brock E (2000) Extrinsic factors influencing phlorotannin production in the brown alga *Ascophyllum nodosum*. Mar Ecol Progr Ser 193:285–294. https://doi.org/10.3354/meps193285

Pavia H, Toth GB (2000) Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. Ecology 81:3212–3225

Pavia H, Cervin G, Lindgren A, Aberg P (1997) Effects of UV-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophyllum nodosum*. Mar Ecol Progr Ser 157:139–146. https://doi.org/10.3354/meps157139

Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

Pawlik JR (1993) Marine invertebrate chemical defenses. Chem Rev 93:1911–1922

Pawlik JR (2011) The chemical ecology of sponges on Caribbean reefs: natural products shape natural systems. BioScience 61:888–902. https://doi.org/10.1525/bio.2011.61.11.8

Pawlik JR, Chanas B, Toonen RJ, Fenical W (1995) Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrency. Mar Ecol Prog Ser 127:183–194

Pearse JS, Giese AC (1966) Food, reproduction and organic constitution of the common antarctic echinoid *Sterechinus neumayeri* (Meissner). Biol Bull 130:387–401

Peck LS (2018) Antarctic marine biodiversity: adaptations, environments and responses to change. Oceanogr Mar Biol: Annu Rev 56:105–236

Peckol P, Yates JL (1997) Inducible phlorotannins in brown algae from backreef sites. In: Lessios HA, Macintyre IG (eds) Proceedings of 8th international coral reef symposium, vol 2, pp 1259–1262

Peckol P, Krane JM, Yates JL (1996) Interactive effects of inducible defense and resource availability on phlorotannins in the North Atlantic brown alga *Fucus vesiculosus*. Mar Ecol Progr Ser 138:209–217

Peters L, Wright AD, Krick A, König GM (2004) Variation of brominated indoles and terpenoids within single and different colonies of the marine bryozoan *Flustra foliacea*. J Chem Ecol 30:1165–1182

Peters KJ, Amsler CD, McClintock JB, van Soest RWM, Baker BJ (2009) Palatability and chemical defenses of sponges from the western Antarctic Peninsula. Mar Ecol Prog Ser 385:77–85

Peters KJ, Amsler CD, McClintock JB, Baker BJ (2010) Potential chemical defenses of Antarctic sponges against sympatric microorganisms. Polar Biol 33:649–658

Pettit GR (1991) The bryostatins. In: Herz W, Kirby GW, Steglich W, Tamm C (eds) Fortschritte der Chemie organischer Naturstoffe/Progress in the chemistry of organic natural products, vol 57. Springer, Vienna. https://doi.org/10.1007/978-3-7091-9119-4_3

Pettit GR, Herald CL, Doubek DL, Herald DL, Arnold E, Clardy J (1982) Isolation and structure of bryostatin 1. J Am Chem Soc 104(24):6846–6848. https://doi.org/10.1021/ja00388a092

Piel J (2004) Metabolites from symbiotic bacteria. Nat Prod Rep 21:519–538

Piel J (2006) Bacteria symbionts: prospects for the sustainable production of invertebrate-derived pharmaceuticals. Curr Med Chem 13:39–50

Piepenburg D, Archambault P, Ambrose W, Blanchard A, Bluhm B (2011) Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. Mar Biodivers 41:51–70

Pietra F (2002) Biodiversity and natural product diversity. Pergamon, Oxford

Pohnert G, Boland W (2002) The oxylipin chemistry of attraction and defense in brown algae and diatoms. Nat Prod Rep 19(1):108–122

Puglisi MP, Sneed JM, Sharp KH, Ritson-Williams R, Paul VJ (2014) Marine chemical ecology in benthic environments. Nat Prod Rep 28:345–387. https://doi.org/10.1039/c0np00040j

Puglisi MP, Sneed JM, Ritson-Williams R, Young R (2018) Natural product reports marine chemical ecology in benthic environments. Nat Prod Rep 0:1–20

Putz A, König GM, Wägele H (2010) Defensive strategies of Cladobranchia (Gastropoda, Opisthobranchia). Nat Prod Rep 27:1386–1402

Rasch JA, O'Connor NJ (2012) Development and behavior of megalopae of the non-native crab *Hemigrapsus sanguineus* in response to chemical cues from coastal fishes. J Exp Mar Biol Ecol 416–417:196–201

Rasher DB, Hay ME (2014) Competition induces allelopathy but suppresses growth and anti-herbivore defense in a chemically rich seaweed. Proc R Soc B:281–20132615

Reshef L, Koren O, Loya Y, Zilber-Rosenberg I, Rosenberg E (2006) The coral probiotic hypothesis. Env Microbiol 8(12):2068–2073. https://doi.org/10.1111/j.1462-2920.2006.01148.x

Rhoades D (1979) Evolution of plant chemical defenses against herbivores. In: Rosenthal GA, Janzen DH (eds) Herbivores. Academic, New York, pp 4–54

Rhoades DF (1985) Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. Am Nat 125:205–238

Rhoades DF, Gates RG (1976) Toward a general theory of plant antiherbivore chemistry. Recent Adv Phytochem 10:168–213

Rhode S, Nietzer S, Schupp PJ (2015) Prevalence and mechanisms of dynamic chemical defenses in tropical sponges. PLoS One 10:e0132236

Ribeiro SM, Bianco EM, Rogers R, Teixeira VL, Pereira RC (2010) Chemical defense of *Hymeniacidon heliophila* (Porifera: Halichondrida) against tropical predators. Braz J Oceanogr 58:315–321

Richardson MG (1975) The dietary composition of some Antarctic fish. Br Antarct Surv Bull 41-42:113–120

Ricklefs RE (1990) Ecology, 3rd edn. WH Freeman, New York

Rideout JA, Smith NB, Sutherland MD (1979) Chemical defense of crinoids by polyketide sulphates. Experientia 35:1273–1274

Riguera R (1997) Isolating bioactive compounds from marine organisms. J Mar Biotechnol 5:187–193

Rittschof D (2001) Natural product antifoulants and coatings development. In: McClintock J, Baker P (eds) Marine chemical ecology. CRC Press, New York, pp 543–557

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312(5773):543–547

Robinson EM, Lunt J, Marshall CD, Smee DL (2014) Eastern oysters *Crassostrea virginica* deter crab predators by altering their morphology in response to crab cues. Aquat Biol 20:111

Rocha J, Peixe L, Gomes NCM, Calado R (2011) Cnidarians as a source of new marine bioactive compounds—an overview of the last decade and future steps for bioprospecting. Mar Drugs 9 (10):1860–1886

Rodríguez-Marconi S, De la Iglesia R, Díez B, Fonseca CA, Hajdu E, Trefault N (2015) Characterization of bacterial, archaeal and eukaryote symbionts from Antarctic sponges reveals a high diversity at a three-domain level and a particular signature for this ecosystem. PLoS One 10(9): e0138837. https://doi.org/10.1371/journal.pone.0138837

Roitberg BD, Isman MB (1992) Insect chemical ecology. Chapman & Hall, New York

Rosenberg E, Zilber-Rosenberg I (2016) Microbes drive evolution of animals and plants: the hologenome concept. mBio 7:e01395–e01315. https://doi.org/10.1128/mBio.01395-15

Rosenberg E, Zilber-Rosenberg I (2018) The hologenome concept of evolution after 10 years. Microbiome 6:78. https://doi.org/10.1186/s40168-018-0457-9

Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I (2007) The role of microorganisms in coral health, disease and evolution. Nat Rev Microbiol 5(5):355–362

Rossi S, Bramanti L, Gori A, Orejas C (2017a) An overview of the animal forests of the world. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer International, Berlin

Rossi S, Bramanti L, Gori A, Orejas C (eds) (2017b) Marine animal forests, the ecology of benthic biodiversity hotspots. Springer International, Berlin

Rowell-Rahier M, Pasteels JM (1990) Chemical specialization on toxic plants provides increased protection from natural enemies. Symp Biol Hung 39:343–347

Rowell-Rahier M, Pasteels JM (1992) Third trophic level influences of plant allelochemicals. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites. Academic, San Diego, pp 243–277

Ruzicka R, Gleason DF (2009) Sponge community structure and anti-predator defenses on temperate reefs of the South Atlantic Bight. J Exp Mar Biol Ecol 380(1–2):36–46

Ryan CA, Pearce G (1998) Systemin: a polypeptide signal for plant defensive genes. Annu Rev Cell Dev Biol 14:1–17

Sacristán-Soriano O, Angulo-Preckler C, Vázquez J, Avila C (2017) Potential chemical defenses of Antarctic benthic organisms against marine bacteria. Pol Res 36(1):1390385

Sagi A (1988) The androgenic gland in crustacea with emphasis on the cultured freshwater prawn *Macrobrachium rosenbergii* – a review. Israeli J Aquacult Bamidgeh 40:9–16

Scheuer PJ (1990) Some marine ecological phenomena: chemical basis and biochemical potential. Science 248:173–177

Schiaparelli S, Albertelli G, Cattaneo-Vietti R (2003) The epibiotic assembly on the sponge *Haliclona dancoi* (Topsent, 1901) at Terra Nova Bay (Antarctica, Ross Sea). Polar Biol 26 (5):342–347. https://doi.org/10.1007/s00300-003-0481-4

Schmidt EW, Nelson JT, Rasko DA, Sudek S, Eisen JA, Haygood MG, Ravel J (2005) Patellamide A and C biosynthesis by a microcin-like pathway in *Prochloron didemni*, the cyanobacterial symbiont of *Lissoclinum patella*. Proc Natl Acad Sci USA 102(20):7315–7320

Schmitt S, Weisz JB, Lindquist N, Hentschel U (2007) Vertical transmission of a phylogenetically complex microbial consortium in the viviparous sponge *Ircinia felix*. Appl Environ Microbiol 73:2067–2078

Schram JB, McClintock JB, Amsler CD, Baker BJ (2015) Impacts of acute elevated seawater temperature on the feeding preferences of an Antarctic amphipod toward chemically deterrent macroalgae. Mar Biol 162:425–433

Schubert N, Brown D, Rossi S (2017) Symbiotic versus non-symbiotic Octocorals: physiological and ecological implications. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests, the ecology of benthic biodiversity hotspots. Springer International, Berlin

Schultz JC (1992) Factoring natural enemies into plant tissue availability to herbivores. In: Hunter MD, Ohgushi T, Price PW (eds) Effects of resource distribution on animal plant interactions. Academic, San Diego

Schwab DB, Allen JD (2014) Size-specific maternal effects in response to predator cues in an intertidal snail. Mar Ecol Prog Ser 499:127

Sharp KH, Ritchie KB (2012) Multi-partner interactions in corals in the face of climate change. Biol Bull 223(1):66–77

Sharp JH, Winson MK, Porter JS (2007) Bryozoan metabolites: an ecological perspective. Nat Prod Rep 24:659–673

Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep Sea Res Part II (Top Stud Oceanogr) 45:517–567

Silchenko AS, Kalinovsky AI, Avilov SA, Andryjashchenko PV, Dmitrenok PS, Kalinin VI, Taboada S, Avila C (2013) Triterpene glycosides from Antarctic Sea cucumbers IV. Turquetoside A, a 3-O-methylquinovose containing disulfated tetraoside from the sea cucumber *Staurocucumis turqueti* (Vaney, 1906) (= *Cucumaria spatha*). Biochem Syst Ecol 51(1):45–49

Simister R, Taylor MW, Tsai P, Fan L, Bruxner TJ, Crowe ML, Webster N (2012a) Thermal stress responses in the bacterial biosphere of the great barrier reef sponge, *Rhopaloeides odorabile*. Environ Microbiol 14(12):3232–3246

Simister R, Taylor MW, Tsai P, Webster N (2012b) Sponge-microbe associations survive high nutrients and temperatures. PLoS One 7(12):e52220. https://doi.org/10.1371/journal.pone.0052220

Skropeta D (2008) Deep-sea natural products. Nat Prod Rep 25:1131–1166

Slattery M (2010) Bioactive compounds from echinoderms: ecological and evolutionary perspectives. In: Harris LG, Boettger SA, Walker CW, Lesser MP (eds) Echinoderms. CRC Press, London, pp 591–600

Slattery M, McClintock JB (1995) Population structure and feeding deterrence in three shallow-water Antarctic soft corals. Mar Biol 122:461–470

Slattery M, McClintock JB, Heine JN (1995) Chemical defenses in Antarctic soft corals: evidence for antifouling compounds. J Exp Mar Biol Ecol 190:61–77

Slattery M, Hamann MT, McClintock JB, Perry TL, Puglisi MP, Yoshida WY (1997) Ecological roles for water-borne metabolites from Antarctic soft corals. Mar Evol Prog Ser 161:133–144

Slattery M, Avila C, Starmer J, Paul VJ (1998) A sequestered soft coral diterpene in the aeolid nudibranch *Phyllodesmium guamensis*. J Exp Mar Biol Ecol 226:33–49

Sneed JM, Sharp KH, Ritchie KB, Paul VJ (2014) The chemical cue tetrabromopyrrole from a biofilm bacterium induces settlement of multiple Caribbean corals. Proc R Soc B 281:20133086

Snelgrove PVR, Smith CR (2002) A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanogr Mar Biol Ann Rev 40:311–342

Soldatou S, Baker BJ (2017) Cold-water marine natural products, 2006 to 2016. Nat Prod Rep 34 (6):585–626. https://doi.org/10.1039/c6np00127k

Sotka EE, Forbey J, Horn M, Poore AGB, Raubenheimer D, Whalen KE (2009) The emerging role of pharmacology in understanding consumer−prey interactions in marine and freshwater systems. Integr Comp Biol 49:291–313

Stachowicz JJ (2001) Chemical ecology of Mobile marine invertebrates: predators and prey, allies and competitors. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, pp p153–p190

Stachowicz JJ, Hay ME (1999) Reducing predation through chemically-mediated camouflage: indirect effects of plant defenses on herbivores. Ecology 80:495–509

Steinberg PD, de Nys R (2002) Chemical mediation of colonisation of seaweed surfaces. J Phycol 38:621–629

Steinberg PD, Schneider R, Kjelleberg S (1997) Chemical defenses of seaweeds against microbial colonization. Biodegradation 8:211–220

Steinberg PD, de Nys R, Kjelleberg S (2001) Chemical mediation of surface colonisation. In: McClintock JB, Baker BJ (eds) Marine chemical ecology. CRC Press, Boca Raton, FL, pp 355–387

Steinberg PD, De Nys R, Kjelleberg S (2002) Chemical cues for surface colonization. J Chem Ecol 28(10):1935–1951

Steinberg PD, Rice SA, Campbell AH, McDougald D, Harder T (2011) Interfaces between bacterial and eukaryotic "neuroecology". Integr Comp Biol 51:794–806

Sudek S, Lopanik NB, Waggoner LE, Hildebrand M, Anderson C, Liu H, Patel A, Sherman DH, Haygood MG (2007) Identification of the putative bryostatin polyketide synthase gene cluster from "*Candidatus Endobugula sertula*", the uncultivated microbial symbiont of the marine bryozoan *Bugula neritina*. J Nat Prod 70(1):67–74

Swanson RL, Byrne M, Prowse TAA, Mos B, Dworjanyn SA, Steinberg PD (2012) Dissolved histamine: a potential habitat marker promoting settlement and metamorphosis in sea urchin larvae. Mar Biol 159(4):915–925

Swearingen D III, Pawlik J (1998) Variability in the chemical defense of the sponge *Chondrilla nucula* against predatory reef fishes. Mar Biol 131:619–627

Taboada S, Núñez-Pons L, Avila C (2013) Feeding repellence of Antarctic and sub-Antarctic benthic invertebrates against the omnivorous sea star *Odontaster validus*. Polar Biol 36 (1):13–25

Tadesse M, Gulliksen B, Strom MB, Styrvold OB, Haug T (2008) Screening for antibacterial and antifungal activities in marine benthic invertebrates from northern Norway. J Invertebr Pathol 99:286–293

Taylor MW, Radax R, Steger D, Wagner M (2007) Sponge-associated microorganisms: evolution, ecology, and biotechnological potential. Microbiol Molec Biol Rev 71(2):295–347

Teeyapant B, Woerdenbag HJ, Gross HJ, Proksch P (1993) Biotransformation of the brominated compounds in the marine sponge *Verongia aerophoba*: evidence for an induced chemical defense? Planta Med 59(A):641

Thistle D (2003) The deep-sea floor: an overview. In: Tyler PA (ed) Ecosystems of the world: ecosystems of the deep oceans. Elsevier, Amsterdam

Thorton RS, Kerr R (2002) Induction of pseudopterosin biosynthesis in the gorgonian *Pseudopterogorgia elisabethae*. J Chem Ecol 28(10):2083–2090

Torssel KGB (1983) Natural product chemistry. A mechanistic and biosynthetic approach to secondary metabolism. Wiley, New York

Toth GB, Pavia H (2000) Lack of phlorotannin induction in the brown seaweed *Ascophyllum nodosum* in response to increasing copper concentrations. Mar Ecol Prog Ser 192:119–126

Toth GB, Karlsson M, Pavia H (2007) Mesoherbivores reduce net growth and induce chemical resistance in natural seaweed populations. Oecologia 152:245–255

Tremblay N, Abele D (2016) Response of three krill species to hypoxia and warming: an experimental approach to oxygen minimum zones expansion in coastal ecosystems. Mar Ecol 37:179–199

Tricaricoa E, Breithauptb T, Gherardia F (2011) Interpreting odours in hermit crabs: a comparative study. Estuar Coastal Shelf Sci 91:211–215

Tullrot A (1994) The evolution of unpalatability and warning coloration in soft-bodied marine invertebrates. Evolution 48(3):925–928

Tullrot A, Sundberg P (1991) The conspicuous nudibranch *Polycera quadrilineata*: aposematic coloration and individual selection. Anim Behav 41(1):175–176

Turner J, Bindschadler R, Convey P, di Prisco G, Fahrbach E, Gutt J, Hodgson D, Mayewsky P, Summerhayes C (2009) Antarctic climate change and the environment. Scientific Committee on Antarctic Research, Scott Polar Research Institute, Cambridge, p 526

Turon X, Becerro MA, Uriz MJ (1996) Seasonal patterns of toxicity in benthic invertebrates: the encrusting sponge *Crambe crambe* (Poecilosclerida). Oikos 75:33–40

Ueoka R, Uria AR, Reiter S, Mori T, Karbaum P, Peters EE, Helfrich EJ, Morinaka BI, Gugger M, Takeyama H, Matsunaga S, Piel J (2015) Metabolic and evolutionary origin of actin-binding polyketides from diverse organisms. Nat Chem Biol 11(9):705–712

Van Alstyne KL (1988) Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. Ecology 69(3):655–663. https://doi.org/10.2307/1941014

Van Alstyne KL, McCarthy JJ, Hustead CL, Kearns LJ (1999) Phlorotannin allocation among tissues of northeastern Pacific kelps and rockweeds. J Phycol 35:483–492

Van Dyck S, Caulier G, Todesco M, Gerbaux P, Fournier I, Wisztorski M, Flammang P (2011) The triterpene glycosides of *Holothuria forskali*: usefulness and efficiency as a chemical defense mechanism against predatory fish. J Exp Biol 214:1347–1356. https://doi.org/10.1242/jeb.050930

Vance RR (1978) A mutualistic interaction between a sessile marine clam and its epibionts. Ecology 59:679–685

Vaughn D (2010) Why run and hide when you can divide? Evidence for larval cloning and reduced larval size as an adaptive inducible defense. Mar Biol 157(6):1301–1312. https://doi.org/10.1007/s00227-010-1410-z

Vaughn D, Strathmann RR (2008) Predators induce cloning in echinoderm larvae. Science 319 (5869):1503. https://doi.org/10.1126/science.1151995

Venter JC, Remington K, Heidelberg JF, Halpern AL, Rusch D, Eisen JA, Wu DY, Paulsen I, Nelson KE, Nelson W, Fouts DE, Levy S, Knap AH, Lomas MW, Nealson K, White O, Peterson J, Hoffman J, Parsons R, Baden-Tillson H, Pfannkoch C, Rogers YH, Smith HO (2004) Environmental genome shotgun sequencing of the Sargasso Sea. Science 304 (5667):66–74. https://doi.org/10.1126/science.1093857

Vermeij GJ (1987) Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, NJ

Vermeij GJ (1994) The evolutionary interaction among species: selection, escalation, and coevolution. Annu Rev Ecol Syst 25:219–236

von Salm JL, Schoenrock KM, McClintock JB, Amsler CD, Baker BJ (2018) The status of marine chemical ecology in Antarctica. Form and function of unique high-latitude chemistry. In: Puglisi MP, Becerro MA (eds) Chemical ecology: the ecological impacts of marine natural products. CRC Press, Taylor and Francis, pp 27–69

Voss J, Richardson L (2006) Nutrient enrichment enhances black band disease progression in corals. Coral Reefs 25:569–576

Vrolijk NH, Targett NM (1992) Biotransformation enzymes in *Cyphoma gibbosum* (Gastropoda: Ovulidae): implications for detoxification of gorgonian allelochemicals. Mar Ecol Prog Ser 88:237–246

Wägele H (2004) Potential key characters in Opisthobranchia (Gastropoda, Mollusca) enhancing adaptive radiation. Org Divers Evol 4(3):175–188. https://doi.org/10.1016/j.ode.2004.03.002

Wagele H, Ballesteros M, Avila C (2006) Defensive glandular structures in opisthobranch molluscs: from histology to ecology. Oceanogr Mar Biol 44:197–276

Wahl M (1989) Marine epibiosis. I. Fouling and antifouling: some basic aspects. Mar Ecol Prog Ser 58:175–189

Wahl M, Mark O (1999) The predominantly facultative nature of epibiosis: experimental and observational evidence. Mar Ecol Prog Ser 187:59–66

Wahl M, Goecke F, Labes A, Dobretsov S, Weinberger F (2012) The second skin: ecological role of epibiotic biofilms of marine organisms. Front Microbiol 3:1–21

Walls J, Ritz D, Blackman A (1993) Fouling, surface bacteria and antibacterial agents of four bryozoan species found in Tasmania, Australia. J Exp Mar Biol Ecol 169:1–13

Wang W, Namikoshi M (2007) Bioactive nitrogenous metabolites from ascidians. Heterocycles 74:53–88

Wang C, Liu H, Shao C, Wang Y, Li L, Guan H (2008) Chemical defensive substances of soft corals and gorgonians. Acta Ecol Sinica 28:2320–2328

Webster NS, Bourne D (2007) Bacterial community structure associated with the Antarctic soft coral, *Alcyonium antarcticum*. FEMS Microbiol Ecol 59(1):81–94

Webster NS, Negri AP, Munro MMHG, Battershill CN (2004) Diverse microbial communities inhabit Antarctic sponges. Environ Microbiol 6:288–300

Weidner K, Lages BG, da Gama BAP, Molis M, Wahl M, Pereira RC (2004) Effect of mesograzers and nutrient levels on induction of defenses in several Brazilian macroalgae. Mar Ecol Progr Ser 283:113–125. https://doi.org/10.3354/meps283113

Weil E, Rogers CS, Croquer A (2017) Octocoral diseases in a changing ocean. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests, the ecology of benthic biodiversity hotspots. Springer International, Berlin

Weiss B, Ebel R, Elbrächter M, Kirchner M, Proksch P (1996) Defense metabolites from the marine sponge *Verongia aerophoba*. Biochem Syst Ecol 24:1–12

Weissburg M, Atkins L, Berkenkamp K, Mankin D (2012) Dine or dash? Turbulence inhibits blue crab navigation in attractive–aversive odor plumes by altering signal structure encoded by the olfactory pathway. J Exp Biol 215:4175–4182

Whalan S, Webster NS, Negri AP (2012) Crustose coralline algae and a cnidarian neuropeptide trigger larval settlement in two coral reef sponges. PLoS One 7:e30386

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105

Wiebring A, Helmholz H, Sötje I, Lassen S, Prange A, Tiemann H (2010) A new method for the separation of different types of nematocysts from Scyphozoa and investigation of proteinaceous toxins utilizing laser catapulting and subsequent mass spectrometry. J Mar Biotechnol 12:308–317. https://doi.org/10.1007/s10126-010-9261-7

Wilkinson CR (1978) Microbial associations in sponges. I. Ecology, physiology and microbial populations of coral reef sponges. Mar Biol 49(2):161–167

Williamson JE, Gleeson C, Bell JE, Vaïtilingon D (2012) The role of visual and chemical cues in host detection by the symbiotic shrimp *Gnathophylloides mineri*. J Exp Mar Biol Ecol 414 (415):38–43

Wilson NG, Schrödl M, Halanych KM (2009) Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic Sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). Mol Ecol 18(5):965–984. https://doi.org/10.1111/j.1365-294X.2008.04071.x

Wilson NG, Maschek JA, Baker BJ (2013) A species flock driven by predation? Secondary metabolites support diversification of slugs in Antarctica. PLoS One 8:e80277. https://doi.org/10.1371/journal.pone.0080277

Woollacott RM (1981) Association of bacteria with bryozoan larvae. Mar Biol 65:155–158

Woollacott RM, Zimmer RL (1975) A simplified placenta-like system for the transport of extra-embryonic nutrients during embryogenesis of *Bugula neritina* (Bryozoa). J Morphol 147:355–377. https://doi.org/10.1002/jmor.1051470308

Woollacott RM, Zimmer RL (eds) (1977) The biology of bryozoans. Academic, New York, pp 57–89

Wright PC, Westacott RE, Burja AM (2003) Piezotolerance as a metabolic engineering tool for the biosynthesis of natural products. Biomol Eng 20(4–6):325–331

Xiong Y, Liu Y (2010) Biological control of microbial attachment: a promising alternative for mitigating membrane biofouling. Appl Microbiol Biotechnol 86:825–837

Yates JL, Peckol P (1993) Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus*. Ecology 74(6):1757–1766. https://doi.org/10.2307/1939934

Yoshida W, Bryan P, Baker BJ, McClintock JB (1995) Pteroenone: a defensive metabolite of the abducted antarctic pteropod *Clione antarctica*. J Org Chem 60:780–782

Zhang D, Terschak JA, Harley MA, Lin J, Hardege JD (2011) Simultaneously hermaphroditic shrimp use lipophilic cuticular hydrocarbons as contact sex pheromones. PLoS One 6:e17720. https://doi.org/10.1371/journal.pone.0017720

Zimmer RK, Butman CA (2000) Chemical signaling processes in the marine environment. Biol Bull 198:168–187

Zubía E, Ortega MJ, Salvá J (2005) Natural products chemistry in marine ascidians of the genus *Aplidium*. Mini Rev Org Chem 2:389–399

Zupo V, Messina P (2007) How do dietary diatoms cause the sex reversal of the shrimp *Hippolyte inermis* Leach (Crustacea, Decapoda). Mar Biol 151:907–917

Zupo V, Messina P, Buttino I, Sagi A, Avila C, Nappo M, Bastida J, Codina C, Zupo S (2007) Do benthic and planktonic diatoms produce equivalent effects in crustaceans? Mar Fresh Behav Physiol 40(3):169–181

The Nursery Role of Marine Animal Forests

A. Cau, A. Mercier, D. Moccia, and P. J. Auster

Abstract Marine animal forests (MAFs) are constituted by dense aggregations of epibenthic and emergent animals, chiefly members of Porifera (sponges), Cnidaria (hydrozoans and anthozoans, including corals), and Bryozoa. Their three-dimensional structure and collective spatial complexity provide a diversity of habitats for associated fauna.

Dispersed throughout the ecological literature are examples of the functional role that MAFs play in terms of nursery functions for vagile species of ecological and economic importance. However, a holistic approach for identifying the time and space domains for the ecological role of MAFs is not a trivial task. MAFs are biodiversity hotspots, with juvenile life-history stages of a diversity of species co-occurring in such habitats. Unfortunately, co-occurrence is not enough to discriminate a functional linkage between species and thus properly define the function and role of these biogenic habitats as nurseries. Applying ecological theory based on habitat selection models for different species is the first step toward this discrimination, with subsequent field sampling to test and refine models based on patterns of survivorship, density, and fitness (e.g., size, weight). Such fieldwork aims to define important elements for delineating MAFs as nursery habitats and developing conservation alternatives in a conservation and fisheries context.

Overfishing and habitat degradation have profoundly altered populations of taxa that form MAFs. Currently, a great portion of species subject to exploitation across the globe is overfished. In this negative context, however, the good news is that humanity holds the power to attenuate or even reverse this trend. Fundamentally, this goal relies on a more holistic approach that conserves habitats designated as

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“essential” for, at least, a crucial part of marine organisms’ life cycles. In this regard, nursery habitats enhance populations of some species through adjacent habitats; hence, their conservation becomes a buffer against overexploitation.

The aim of this chapter is to present a synthesis of the role of the nursery functions of MAFs, link MAF species to patterns of use as nurseries, describe approaches and tools to identify such habitats, and provide guidance for future research and conservation planning.

Keywords Black coral · Cold water coral · Nursery role · Spawning ground · Nursery concept · Habitat selection theory · Density model · Hydroid · Soft coral · Scleractinian coral

1 Structured Habitats and the Nursery Role

> What is the ecological role of a tree in a forest? Way more than providing food!

This concise and oversimplistic answer was given by Jones et al. (1994) when they investigated the ecological role of ecosystem engineers in terrestrial ecosystems.

Ecological theories report that interactions between organisms are a major determinant of the distribution and abundance of species, which are macroscopically generalized as intra- and interspecific competition for biotic and abiotic resources. This definition, however, fails to consider a whole set of interactions that often play a crucial role in enhancing diversity and changing patterns of species composition and dominance at different spatial scales, despite not being direct or trophic-related. The nursery effect falls within these interactions and is specifically referred to juveniles of any taxon that can grow and mature within the structured complexity provided by abovementioned engineers.

Similar to terrestrial forests, marine animal forests (MAFs) are constituted of organisms that are considered “engineers” or “structuring” since their complex three-dimensional shape enhances the otherwise two-dimensional unstructured habitats, such as sand and mud, which provide only a relatively flat surface. Structured habitats like MAFs are ecologically and economically important since they directly or indirectly provide a variety of ecosystem services.

These habitats indeed act as a shelter that reduces the foraging efficiency of consumers (Bartholomew et al. 2000), thus providing refuge for a multitude of species (Guizien and Ghisalberti 2017), strongly influencing population dynamics through the enhancement of recruitment into adult populations.

Field studies on nurseries started across those habitats that were more accessible to marine scientists such as estuaries, mangroves, seagrass meadows, and coral reefs. Those initial attempts were essentially focused on defining which estuarine and coastal habitats do or do not function as nurseries, providing an important and fundamental basis for the forthcoming researches on the topic.

The use of the term “nursery” was common in the marine scientific literature (e.g., back to the 1980s), and it simply referred to those habitats hosting high densities of juvenile individuals, but a formal definition with explicit criteria began with Beck et al. (2001). While the recognition of spots where juveniles were more abundant was somehow immediate, the establishment of a unique definition of "nursery habitat," on the contrary, was not, even though it was restricted to coastal habitats. Beck et al. (2001) greatly improved the simplistic definition by arguing that a habitat could be defined as a nursery if juveniles of various taxa (1) occur at higher densities, (2) avoid predation more successfully, or (3) grow faster than in other habitats.

The underlying premise of the nursery role, besides recognizing the abovementioned benefits, is quantifying the contribution of certain habitats to the production of individuals that recruit to adult populations. First, this estimation implicitly relies on the presence of two none (or partially) overlapping habitats, since for a species where juvenile and adult habitats overlap, the nursery would simply be known as its habitat (Beck et al. 2001; Dahlgren et al. 2006). Second, nurseries should be classified as such according to a 'per-unit-area' contribution, in comparison to other habitats used by juveniles. Dahlgren et al. (2006) argued that such a definition might omit habitats with relatively small per-unit-area contributions to adult populations that, however, could significantly contribute in sustaining adult populations.

Over the last 10 years, it was also recognized how species with complex life cycles might not benefit from the protection of a single static "nursery habitat unit" without considering the sequence of sub-habitats that are used throughout ontogeny. In addition, other aspects of nursery habitats (e.g., movement corridors, density hotspots) should be considered to conserve the most productive and important habitat patches within nursery habitats (Nagelkerken et al. 2015). These observations led to the most developed concept of the nursery: the "seascape nursery," which combines seascape ecology and the nursery function (Lefcheck et al. 2019; Nagelkerken et al. 2015), while previous approaches underestimated effective linkages among habitats that affect the critical growth and survival of juveniles.

The seascape nursery concept, in brief, emphasizes the fact that multiple components of nursery areas should be conserved. Without the whole mosaic of habitats and ecological elements that facilitate connectivity and recruitment, the "nursery" function would be compromised. These components can be briefly summarized as follows:

1. Transient settlement habitats, which are defined as those habitats that may be occupied only briefly, yet may form population bottlenecks for early post-settlement stages (Fodrie et al. 2009)
2. Habitats constrained by animal home ranges, which consequently attract higher densities of mobile organisms and which are more productive than other areas
3. Successive essential life stage habitats
4. Migration routes, which connect different abundance hotpots during ontogeny or just facilitate movement from nurseries to offshore populations

While interactions among MAFs and multiple species are extensively documented in tropical coral reef ecosystems (Nagelkerken et al. 2000), this research subject is still in its early stages when talking about deep-sea habitats (i.e., outer shelf, slope, bathyal zones, and abyssal plains). As a premise, the study of MAFs dwelling in the deeper portions of the oceans grew besides a number of issues related to (1) the development of efficient technologies to sample and survey (e.g., multibeam sonar to map habitats, high-resolution video for faunal surveys) at depths at which MAFs are commonly found; (2) the consequent elevated costs related to surveys in the deep sea; and (3) funding priorities.

In recent decades, improvements in technologies such as occupied submersibles and remotely operated vehicles (ROVs) provided scientists with the opportunity to carry out accurate, quantitative in situ investigations at depths that were out of reach of autonomous divers.

Studies on deepwater MAFs have increased dramatically over the last decades, greatly expanding our knowledge on these important and vulnerable ecosystems. In addition, evidence of their role as habitat providers for abundant and diverse fauna has been shown in several studies (Buhl-Mortensen et al. 2010; Buhl-Mortensen and Mortensen 2005). MAFs, indeed, may house large assemblages of fishes, crustaceans, mollusks and ophiuroids (Baillon et al. 2014), and elasmobranchs (Etnoyer and Warrenchuk 2007).

It was immediately recognized how all the components of deep-dwelling MAFs could host or drive a variety of ecological interactions like those documented for shallow coastal environments such as mangroves, estuaries, and shallow tropical corals reefs. However, as mentioned above, the proper discrimination of effective linkages between fauna and MAFs, particularly the nursery role that MAFs may provide to such fauna, is not so immediate (Auster 2007). Similar to what was observed in shallower habitats, the preference for structured habitats exhibited by certain species does not necessarily involve a functional interaction among species (Auster 2005). Also, constraints of the "nursery role" definition imply that time-series surveys should be performed before acquiring the necessary information to determine whether or when a particular habitat acts as a nursery. With all these caveats, it is not surprising that not many nursery habitats dwelling in deep-sea MAFs have been properly identified, and we are quite far from applying a more developed concept, such as the seascape nursery, to outer shelf and deep-sea habitats at the spatial scale of biogenic features. Surveys conducted by means of ROVs or autonomous underwater vehicles (AUVs) do provide snapshots of a more complex perspective that is not easily linked to population-level dynamics of species observed using MAFs and thus requires considerable effort.

Over the last decades, identifying nursery habitats has emerged as an area of interest both for research and for environmental agencies and policymakers in light of the decline and poor recovery of many fish stocks (Pauly et al. 1998; Pauly and Zeller 2016). Indeed, the tool that humanity holds to stop and possibly revert this trend relies on the identification of habitats that are essential for marine organisms to spawn, breed, feed, and grow to maturity (Guidetti and Danovaro 2018; Rosenberg and Bigford 2000).

The aim of this chapter is to present a synthesis of the role of the nursery functions of MAFs; link impacts, recovery, and resilience of MAF species to patterns of use as nurseries; identify reliable approaches and tools to identify such habitats properly; and provide guidance for future research and conservation planning.

2 Approaches for the Study of MAF Nurseries

The challenge to address the nursery function of MAFs arises in the spatial disconnect between observation approaches of MAFs (i.e., small-habitat-patch scale, image-based) and those of the populations that use such habitats (i.e., large-geographic scale, often trawl-based or similar towed sampling device although large-spatial-scale surveys with fixed gears have been implemented). Indeed, the objective of defining nursery function of MAFs is to demonstrate that such habitats create a population bottleneck and influence adult population size. While manipulative experiments may be possible for species with low movement rates in coastal ecosystems (e.g., hermit crab and shell habitat; Halpern 2004), natural experiments will be necessary in deeper waters, to take advantage of patterns in fisheries exploitation (i.e., variation in size/stage-structured populations) and variations in the state of MAFs (e.g., variations in the density and rugosity of structure-forming organisms) and other habitats, so time-series of data to elucidate ecological roles will be required.

Habitat selection theory provides a useful construct to interpret patterns of recruitment, growth, and mortality (or survivorship) of populations hypothesized to use MAFs as nursery habitat. That is, we need to determine how variation in density and abundance of the species of interest within MAF habitats varies and the response at the scale of the population. Such local-scale variation will depend on overall population responses to variation in local and regional population size. In brief there are three general conceptual models that describe the variation in the spatial patterns of species distributions and related variation in population size (Petitgas 1997; Shepherd and Litvak 2004). These are the proportional density model (Houghton 1987; Myers and Stokes 1989; Hilborn and Walters 1992; Petitgas 1997), constant density model (Iles and Sinclair 1982; Hilborn and Walters 1992; Rodenhouse et al. 1997; McPeek et al. 2001), and the basin model (MacCall 1990). The basin model is based on the ideal-free distribution model of Fretwell and Lucas (1970) that serves as the foundational mechanism. Table 1 summarizes the relevant properties of each model as they relate to approaches for understanding patterns of habitat use with MAFs and linking to larger population responses based on numbers and individual fitness (see Pereira et al. 2012). Patterns of movement by mobile organisms emigrating from, or expanding from, MAFs can also be interpreted in the context of habitat selection theory. While these types of models were originally developed to address distributions of mobile animals, there has been validation that such models are useful constructs for examining processes that mediate the distribution of sessile organisms, such as those that compose MAFs, as well (e.g., Gersani et al. 1998; Li and Wang 2006). Scaling sampling to address variation in patterns of habitat use, in this case MAFs, will be a key constraint on developing survey approaches and matching sampling technologies across spatial scales to ecological questions at hand.

Table 1 Properties of populations based on three different habitat use models (modified from Pereira et al. 2012)

	Proportional density model	Constant density model	Basin model
Density	Local density increases and decreases within MAFs in phase with population size	Local density within MAFs constant	Local density increases and decreases within MAFs in phase with population size
Geographic range	Range is constant	Range expands and contracts in phase with variation in population size	Range expands and contracts in phase with variation in population size
Population responses	Local fitness constant over population changes	Local fitness constant over population changes	Local fitness decreases with population increase with response across all habitats
Local- versus regional-scale processes	MAFs provide local refugia from predators as a potential mechanism to explain local variation in density and size	Local competition for resources within MAFs but individuals in adjacent patches have no population-wide effect on density and size	Optimal habitats, inclusive of MAFs, fill first. Range expands to suboptimal habitats as habitat value decreases with increased density

3 Nurseries Across Space and Time

3.1 An Overview on the Nursery Role of Short-Lived Taxa of Marine Animal Forests

Multiple species of relatively short-lived structure-forming taxa (i.e., months to several years) occur as MAFs and have been observed to function in a manner consistent with the concept of nurseries for both fish and other vagile fauna. The scope of taxonomic affinities of ephemeral MAFs is diverse and includes, for example, dense patches of hydrozoans, bryozoans, emergent amphipod tubes, polychaete worm tubes, and attached bivalves as well as aggregates of shell from deceased mollusks. Such taxa increase the spatial complexity of seafloor habitats at micro- and meso-spatial scales (e.g., Greene et al. 1999; Auster et al. 1995) and are components of the mosaic of habitats nested within large-scale landscapes (Caddy 2008). There are multiple examples of differential use of these relatively ephemeral habitats composed of short-lived structure-forming fauna.

Marine bryozoans that are heavily calcified and become relatively large (three-dimensional size $\geq$50 mm) generate complex habitats that may play various roles, including that of nursery ground. In a recent review, such habitat-forming bryozoans were shown to occur from about 59° N to 77° S, predominantly in temperate continental shelf environments (Wood et al. 2012). Based on fishery data, habitat-forming bryozoans are suggested to be of nursery importance for juvenile finfish (Vooren 1975; Saxton 1980), which formed the basis of a successful campaign to have power-fishing methods banned in the bryozoan beds of Separation Point (Abel

Tasman National Park, New Zealand) since 1980 (Mace 1981). However, it is estimated that this evidence might not meet empirical data standards required today to show a nursery function (Morrison et al. 2014).

In experimental work comparing responses to substrates that are naturally used by red king crab in Alaska, small crabs predominantly associated with bryozoans, followed by hydroids (Pirtle and Stoner 2010). These results are in line with the fact that early post-settlement stages of red king crab have been found exclusively in MAFs composed of bryozoans, hydroids, polychaetes, or mussels (McMurray et al. 1986; Stevens and MacIntosh 1991). In the north-central Gulf of Mexico, ephemeral bryozoans that occur annually along a muddy bottom play a role as a nursery habitat to young fish (Franks and VanderKooy 2000; Peterson et al. 2000) and provide a dispersal mechanism similar to habitats like *Sargassum* and drift algae (Pederson and Peterson 2002).

Aggregates of shell from bivalves (Auster et al. 1995; Langton et al. 1995; Stoner and Titgen 2003), solitary and colonial hydroids (Auster et al. 1996; Auster, unpublished observations), sabellariid worm reefs (Gore et al. 1978), amphipod tubes (Auster et al. 1997), pen shells (Kuhlmann 1998), cerianthid anemones (Auster et al. 2003; Langton et al. 1995), and polychaete tubes (Diaz et al. 2003; Stoner et al. 2007) have demonstrated use by diverse crustaceans and juvenile demersal-stage fishes. Such habitats (Fig. 1) are both shelter from predators and flow (i.e., the later

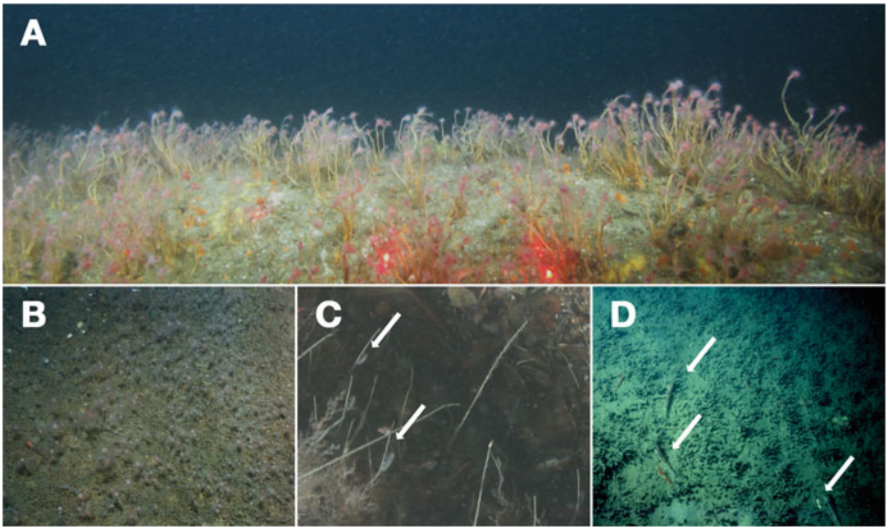

Fig. 1 Exemplars of MAFs formed by short-lived species (NW Atlantic). (**a**) Forest of the hydroid *Ectopleura crocea* on boulder surface (30 m, Long Island Sound, Mid-Atlantic); (**b**) dense forest of the hydroid *Corymorpha pendula* in sand wave habitat with *Crangon* and *Dichelopandalus* decapod shrimp, which are important prey for crustacean-eating fishes (40 m, Stellwagen Bank, Gulf of Maine); (**c**) crustacean and molluscan prey (white arrows) associated with stalked hydroid tests (Long Island Sound); and (**d**) silver hake *Merluccius bilinearis* (white arrows) in a dense amphipod tube habitat (55 m, mid-shelf, Southern New England shelf, see Auster et al. 1997 for details). The figure was created ex-novo, using images belonging to authors' private collection

for minimizing bioenergetic costs) and focal sites for finding prey (i.e., for minimizing search costs in search of prey).

3.2 Nurseries in Long-Lasting Marine Animal Forests

3.2.1 Cold Water Corals

Although CWCs may occur in subtidal areas at higher latitudes, they generate some of the most complex biogenic habitats in the deep sea, where they offer diverse microhabitats that serve as feeding, hiding, and nursery grounds to other species (Baillon et al. 2012; Buhl-Mortensen and Mortensen 2005; Longo et al. 2005; Murillo et al. 2011). Like all corals, they may occur as unitary or colonial forms, the latter being the most commonly associated with nursery roles, especially when they form thickets, fields, or reefs (Buhl-Mortensen and Mortensen 2005; Roberts et al. 2006). CWCs of the deep can be broadly divided into stony corals of subclass Hexacorallia (represented by orders Antipatharia and Scleractinia) and soft corals of subclass Octocorallia (represented by orders Alcyonacea, formerly known as Gorgonacea, and order Pennatulacea). The nursery roles of the main groups are presented separately below.

Scleractinia

Scleractinian framework-forming species are widespread throughout the world oceans from shallow depth of 40 m in the mid-Norway sea to the deep waters (3383 m) in the New England Seamount chain (Zibrowius 1980), mostly in areas characterized by precise combinations of hydrologic, sedimentological, and geomorphic characteristics (Freiwald et al. 2004; Buhl-Mortensen et al. 2015; Cau et al. 2015, 2017a; De Clippele et al. 2019). These habitat engineers enhance the heterogeneity of both hard and soft bottom, influencing the surrounding environmental processes and generating microhabitats with ideal conditions for thousands of animal species (Buhl-Mortensen et al. 2010; D'Onghia et al. 2016; Roberts et al. 2006). While the co-occurrence of a broad diversity of species associated with these deep-sea habitats has been demonstrated by numerous studies (Costello et al. 2006; Henry and Roberts 2017), the functional ecological role as nursery areas is still a major focus of the scientific community's research efforts (Auster 2005, 2007).

In the northeast Atlantic continental shelves is located one of the most spectacular *Lophelia pertusa* reefs (Fosså et al. 2002; Husebo et al. 2002). The functional role of such biogenic habitat as nursery area was firstly hypothesized by Fosså et al. (2002), who documented high density of gravid redfish (*Sebastes viviparous*) individuals within *L. pertusa* branches. The same association was documented by Costello et al. (2006), who observed the presence of gravid redfish as well as egg cases of skate (*Raja* sp.) at Sula Ridge off the coast of Norway. Foley et al. (2010) further corroborated this hypothesis using a production function approach model that demonstrated the functional values provided by the Norwegian *L. pertusa* extensive reef in influencing both the carrying capacity and the intrinsic growth rate of the redfish stocks. More recently, the association between gravid *Sebastes* sp. and CWC reefs was reported in another part of the northeast Atlantic sea, at Rockall Bank off the coast of Ireland (Milligan et al. 2016). In the opposite side of the Atlantic Ocean, habitat-fishery model has been used by Koenig et al. (2000) to speculate the role of another important CWC reef made by the stony coral *Oculina varicosa* off the coast of Florida. The authors described this deep-sea reef as important breeding and spawning areas for gag grouper (*Mycteroperca microlepis*) and scamp (*Mycteroperca phenax*), highlighting their importance on the conservation of main fish stocks (Gilmore and Jones 1992; Koenig et al. 2000). In the northwest Atlantic Ocean, *O. varicosa* reef was proposed as nursery grounds, also for the snowy grouper *Hyporthodus niveatus*, the calico grouper *Epinephelus drummondhayi*, the black sea bass *Centropristis striata*, and the red barbier (*Baldwinella vivanus*) (Coleman et al. 1996; Koenig et al. 2005; Reed 2002). More recently, video documentations, using ROVs and towed cameras, and noninvasive longline surveys, were used to hypothesize the nursery and spawning role of several deepwater scleractinian corals. Along the Apulian margin (eastern-central Mediterranean Sea) is located a belt of CWC sites, mostly composed by the scleractinian species *M. oculata* and *L. pertusa* colonies, known to be an important habitat for a large variety of marine species and a potential “renewal network” for the fish populations (Angeletti et al. 2014; Capezzuto et al. 2018; D’Onghia et al. 2016). Within this CWC network, the significant abundance of large reproductive and juvenile individuals of demersal species, i.e. *Etmopterus spinax*, *Galeus melastomus*, *Merluccius merluccius*, *Micromesistius poutassou*, *Phycis blennoides*, and *Helicolenus dactylopterus*, led the authors to hypothesize their role as nursery area for these deepwater species (Capezzuto et al. 2018; D’Onghia et al. 2010). Furthermore, the water mass circulation that connects these CWC sites might favor the transport of the pelagic eggs and larvae, making them an important network of stock renewal areas (D’Onghia et al. 2016). Juvenile and recruits of *H. dactylopterus* were also documented among the Cabliers Coral Mound Province in the Alboran sea (western Mediterranean) confirming the use of CWC assemblages as nursery grounds by a commercially valuable species (Corbera et al. 2019).

The presence of high abundance of juveniles, mature, and post-reproductive individuals, estimated both through image analyses and direct sampling, has been considered the first proxy for evaluating the scleractinian three-dimensional framework as fish nursery areas (Fig. 2). However, as mentioned before, it does not provide evidence of direct functional links (Auster 2005, 2007). Further and more direct evidence of a close relationship between fish and CWC communities as nursery areas has been provided by the documentation of egg cases nested among CWC branches. The egg cases of commercially important species of deep-sea shark *G. melastomus* were found nested in live colonies of *L. pertusa* in the Mingulay Reef Complex (northeast Atlantic) (Henry et al. 2013). A similar scenario was recently discovered in the same geographic area, 200 miles from the west coast of Ireland, by

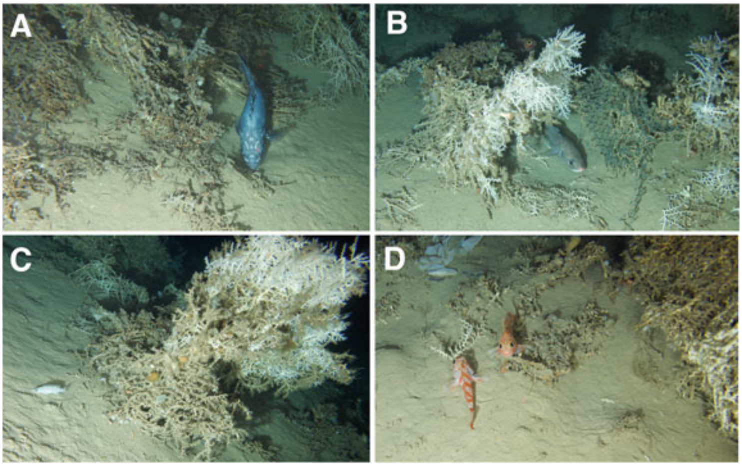

Fig. 2 (**a**) A juvenile of *Polyprion americanus* swimming within collapsed *M. oculata* branches; (**b**) individual of *Phycis blennoides* finding shelter below *M. oculata* and *Desmophyllum dianthus* colonies, with a small individual of *H. dactylopterus* covering behind the scleractinian framework; (**c**) a small individual of *Acantholabrus palloni* swimming in and out a *M. oculata* arborescent bush; (**d**) two small exemplars of *H. dactylopterus* swimming among live and dead *M. oculata* branches. The figure was created ex-novo, using images belonging to authors' private collection

the Marine Institute's Sea Rover program. A remote-operated vehicle surveyed a CWC reef, mostly formed of dead skeleton rubbles, upon which numerous individuals of the blackmouth shark (*G. melastomus*) deposited thousands of eggs. In the same video, young individuals of *H. dactylopterus* and fish larval were recorded along with several other species (Marine Institute's Sea Rover program, unpublished data). In the opposite geographic area, a *L. pertusa* coral bank located off Cape Lookout (northwest Atlantic) has been suggested to represent an important egg-laying area for skate species after egg cases, and hatched juveniles of Pluto skate *Fenestraja plutonia* were collected near the deep coral banks (Quattrini et al. 2009). The presence of egg cases lying on scleractinian corals is also reported in the Mediterranean Sea. An egg case of *S. canicula* was recorded along the northern part of the Sardinian CWC province (western Mediterranean; Taviani et al. 2017) on the branches of *M. oculata* colony by Moccia et al. (2019). Deep-sea sharks seem to choose these particularly biogenic habitats for laying their eggs due to the complex three-dimensional structures that they can provide. In fact, these hard colonial skeletons help to keep the egg cases safe by reducing the risk of drifting away, protect them from egg predators, and expose them to water currents so they don't get covered by sedimentation (Henry et al. 2013).

To date, the evidence presented within the scarce literature suggests that deep-water fish species do utilize the hard calcium-based reef provided by scleractinian coral structure as nursery areas, indicating the importance such habitats to fish and shark populations. However, the level of their association and dependence still needs more spatial and temporal investigation, in order to enable a full evaluation of the ecological roles of CWC habitat as nursery areas.

Antipatharia

When focusing on nursery areas across space and time, a case that deserves attention is that of black corals of the order Antipatharia. Black corals are spread across all oceans over a wide bathymetric range (Carreiro-Silva et al. 2013; Komugabe et al. 2014; Kregting and Gibbs 2006; Warner 2005) and comprise the most long-living organisms on our planet, with a life span that can exceed thousands of years in some cases (Bo et al. 2015; Lartaud et al. 2017; Roark et al. 2009). Because of this, they represent one of the most durable and stable MAFs of the worlds' oceans.

These organisms do form dense aggregations over a variety of geological settings such as seamounts, submarine canyons, ledges, and rocky outcrops, among others (Bo et al. 2013, 2015; Cau et al. 2015, 2017b; Opresko and Sánchez 2005), constituting some of the oldest living MAFs in the worlds' oceans.

Despite many bioecological traits of black corals still have to be assessed, a common feature is the arborescent shape and the preference for sites with considerable hydrodynamic since their flexible organic skeleton allows them to counteract the potential negative effects of turbulent conditions (Lartaud et al. 2017). Such ecological feature renders these habitats useful for a variety of species that take advantage of the ventilated habitat colonized by these corals. Over the last decade, several black coral forests dwelling in the deep sea have been discovered and described for their bioecological features (Etnoyer et al. 2017; Roark et al. 2006, 2009; Ruiz-Ramos et al. 2015). However, when close and functional association with benthic fauna has to be described and ecologically discriminated, the spectrum becomes very narrow with very few investigations conducted (Angeletti et al. 2014; Bo et al. 2015; D'Onghia et al. 2016; De Matos et al. 2014; Deidun et al. 2010; Massi et al. 2018). Among these studies, the Carloforte Shoal (Sardinia, Italy, central western Mediterranean; Bo et al. 2015) documented a nursery area for the small spotted catshark *Scyliorhinus canicula* (Cau et al. 2017a) (Fig. 3). Taking advantage of the very slow population dynamics of *L. glaberrima* that provide a stable environment across time, the study demonstrated the continuous use across years of the black coral forest, showing the presence of both degraded egg capsule and others with living embryos inside, which is an essential requirement to properly identify a nursery ground for elasmobranches (Heupel et al. 2007). The presence of deep-sea shark egg cases attached on colonies *Anthipathes speciosa* was also documented off the southern coast of Chile (southeastern Pacific Ocean; Concha et al. 2010).

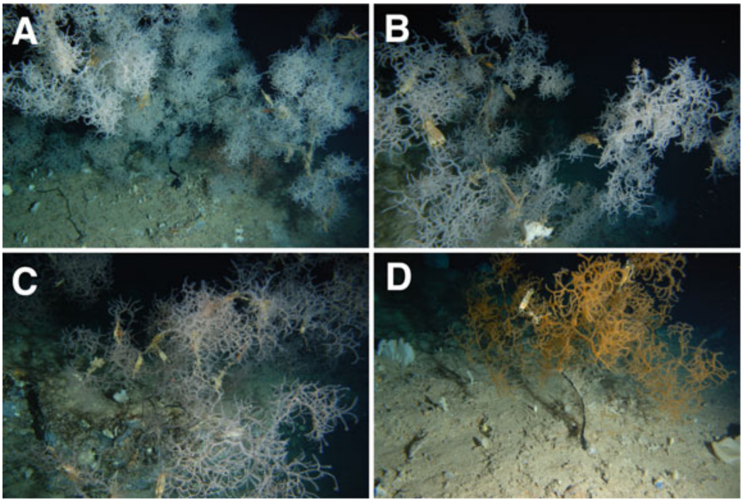

Fig. 3 Images from the ROV survey conducted on the Carloforte Shoal in Sardinia, Italy, central western Mediterranean. (**a**–**d**) Egg cases of the spotted catshark *Scyliorhinus canicula* showing different stages of degradation or embryos' development, providing evidence on the fact that this spot has been used across years as spawning ground for this species. The panel figure was created ex-novo, using images belonging to authors' private collection

Alcyonacea and Pennatulacea (Octocorallia)

Order Alcyonacea comprises the true soft corals (mainly Alcyoniina) and so-called horny corals, commonly known as gorgonians or sea fans, which have a semirigid proteinous skeleton (e.g., Calcaxonia, Holaxonia, Scleraxonia). Also included in the Octocorallia subclass is order Pennatulacea (sea pens), which has not received as much attention as other groups of CWCs (Baillon et al. 2012; Watling et al. 2011), but are still considered structural species due to their extension above the seafloor and their ability to create complex biohabitats.

Deep-sea octocorals are increasingly well demonstrated to offer nursery grounds to a variety of fish species. Complementing a string of anecdotal observations, a gorgonian field was clearly identified as a spawning ground for scyliorhinid catshark, from the presence of 296 egg cases attached to 117 colonies of the primnoid *Callogorgia delta* (as *Callogorgia americana delta*) at 533 m in the Mississippi Canyon (Gulf of Mexico) (Etnoyer and Warrenchuk 2007). Also, egg capsules of *Scyliorhinus* sp. were observed to be attached to the branches of the Isididae *Isidella elongata* in Mediterranean waters (Mastrototaro et al. 2017). Early evidence of the importance of octocorals for mackerel and redfish/rockfish (*Sebastes* spp.) came from their apparent association (Buhl-Mortensen et al. 2010), including the increased occurrence of large individuals among gorgonian colonies (*Primnoa* spp.) on the continental shelf (160–365 m) of the Gulf of Alaska (Krieger and Wing 2002). Larvae of *Sebastes* spp. were eventually found to be closely associated with three species of deep-sea alcyonaceans and five species of deep-sea pennatulaceans during spring months of multiyear surveys (2005–2010) conducted between 100 and 700 m off the coast of eastern Canada (Baillon et al. 2012).

For the many symbiotic (parasitic, commensal, or mutualistic) species that associate with octocorals (Baillon et al. 2014; Buhl-Mortensen et al. 2010), the latter almost certainly offer a nursery ground, although definitive evidence is not always available. Several species of sea anemones, polychaetes, crustaceans, and ophiuroid echinoderms (Mosher and Watling 2009) are classified as obligate symbionts of deepwater octocorals. The brittle star *Ophiocreas oedipus* was found on the chrysogorgiid octocoral *Metallogorgia melanotrichos* at various depths on New England seamounts, with evidence suggesting that the brittle star settles directly on a young octocoral colony and the two species then grow, mature, and senesce together. A number of other presumably obligatory associations between brittle stars and gorgonian octocorals have been documented from seamounts of the northwest Atlantic (Cho and Shank 2010). Close relationships with pennatulacean octocorals include a copepod parasite that spends its whole life in *Anthoptilum grandiflorum* (Baillon et al. 2014; Fig. 4) along the continental slope of eastern Canada (to 1350 m depth) and a polychaete living on *Funiculina quadrangularis* (Nygren and Pleijel 2010) along the Swedish coast (300 m depth). The sea pen *F. quadrangularis* is additionally suspected of hosting the brittle star *Asteronyx loveni* (Buhl-Mortensen et al. 2010).

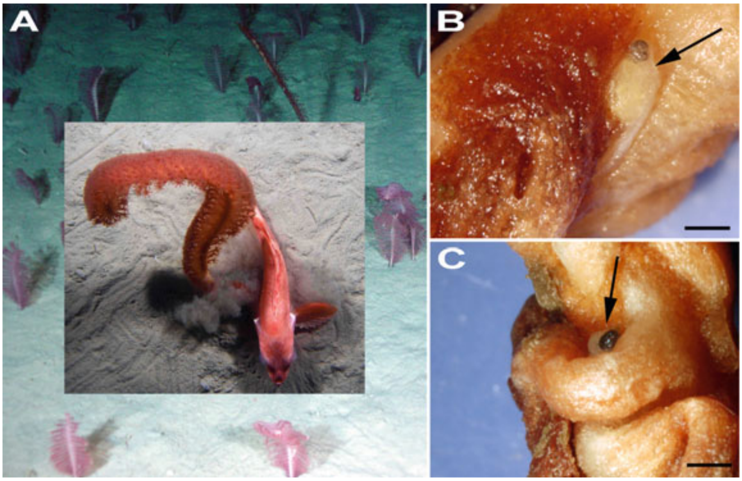

Fig. 4 (**a**) Fields of pennatulacean corals (shown here) and other deep-sea corals have been shown to serve a nursery function for rockfish (*Sebastes* sp., insert). (**b** and **c**) Fish larvae (arrows) tucked among polyps of the deep-sea pennatulacean coral *Anthoptilum grandiflorum* (shown in **a**, insert). Photos in (**a**) courtesy of the Department of Fisheries and Oceans Canada. (**b**) and (**c**) adapted from Baillon et al. (2012). Scale bars in (**b**) and (**c**) represent 1 mm

3.2.2 Porifera

Organisms belonging to the phylum Porifera are widely distributed in world's oceans and can be found over a wide geographical and bathymetric range: from tropical coral reefs to the poles and from the intertidal zone to abyssal plains (Maldonado 2017). In benthic communities they act as ecosystem engineers that can alter the three-dimensional complexity of the environment. In peculiar geomorphological and hydrodynamical conditions, sponges can form dense aggregation called "sponge grounds," where they do dominate in terms of size and biomass, constituting up to 90% of benthic biomass (excluding fishes; Bo et al. 2011; Hawkes et al. 2019). Conspicuous sponges are reported to be constituents of the more mature MAFs, where they can alter major current flows and particle retention, thus concentrating more biodiversity in their surroundings (Murillo et al. 2012).

Knowledge on the distribution and the ecological role of sponge-dominated habitats constantly increased in the last decades, especially for deepwater habitats, besides technological development. Before this, knowledge on sponge grounds was based on sea bottom fishery bycatch, which still represents one of the major threats to these environments, and thus skewed toward soft bottoms which are more easily accessible to these gears rather than submarine canyons or rocky outcrops (Bo et al. 2011). Ecological research on these habitats emphasized the importance of sponge grounds in the benthic-pelagic coupling, cycling of nutrients, and their role in affecting near-bottom layer hydrodynamic.

Some interesting insights on the nursery role of these habitats come from cold waters of British Columbia, where sponge grounds are abundant and widely distributed. As already mentioned in this chapter, most of the studies conducted on the nursery role rely on the comparison of "structured" versus "unstructured" habitats; in the case of sponges, Marliave et al. (2009) compared cloud sponge (*Aphrocallistes vastus*) grounds growing over rocky bottoms, to more simple habitats called *bioherms*, where sponges keep on growing on the dead portion of older colonies, that may even date centuries. When comparing these habitats, bioherms appeared to host higher abundance of organisms than unstructured habitats, but up to an order of magnitude less biodiversity. Interestingly, while adult and subadult rockfishes of the genus *Sebastes* (*S. maliger*, *S. ruberrimus*, *S. proriger*, and *S. elongatus*) were present on bioherms, only the sponge garden provided nursery for high densities of newly recruited *S. maliger*, possibly because of the combination of both refuge and feeding opportunities. A recent survey along the Nova Scotia shelf, Canada (Hawkes et al. 2019), documented through a combination of trawl survey and in situ observations higher species density and abundance on hard substrates covered by the glass sponge *Vazella pourtalesi* compared to less-structured habitats; however, in this case, the "presence" of glass sponges included all the states combined (both living and dead sponges), and the specific role of sponges could not be discriminated from the effect provided by more complex rocky habitat. Another study on temperate sponge grounds based on trawl surveys at depths comprised between 500 and 1500 identified three species strongly associated with sponge grounds: shortnose snipe eel

Serrivomer beanie, deep-sea catshark *Apristurus profundorum*, and eelpout *Lycodes* spp. (Kenchington et al. 2013), which showed increasing abundance besides sponge grounds.

4 Conclusion and Perspectives

Great abundance and, in general, positive effects on vagile fauna related to the presence of MAFs have been recorded across the world's oceans. The nursery role, however, as mentioned in the introduction, is a more complex paradigm that is not easy to disentangle from co-occurrence of species.

The three-dimensional framework typical of MAFs can provide habitats that otherwise could not be present in the surrounding areas. At the same time, the topography and hydrography of the sites where MAFs occur can enhance food supply for planktivorous fishes, suspension and deposit feeders, and scavengers.

All the case studies described in the present chapter emphasize quite often that the use of MAFs by mobile fauna does not necessarily imply their importance from a demographic perspective but do provide however insights that are consistent with the nursery paradigm.

Indeed, the occurrence of gravid individuals frequently caught and observed within the coral habitats, as well as the presence of egg cases attached to corals or found nested in coral colonies or egg masses found deposited on coral stalks, can be seen as evidence of the role of MAFs as critical habitats for spawning and nursery areas.

All proposed examples further confirm how research focused on the nursery role in MAFs dwelling at great depths is quite far from detailed and the development of a more complex and thoughtful nursery concept still has to be developed.

As mentioned in Sect. 2, available typologies of data (images or trawls) do provide only snapshots of a complex story. Recruitment of vagile fauna is often addressed at geographically comprehensive spatial scales using trawls, which can be implemented through frequently visited multiple sampling sites. On the contrary, data on associations of such fauna at small spatial scales requires specialized technologies such as underwater still and video imaging. The role of MAFs is nested within the multi-scale elements of the environment that drive recruitment and survival. Clearly juveniles, as well as adults, of many species select habitats or exhibit differential survival in the matrix of habitats, available within a landscape (Auster et al. 1995, 1997). Such story appears to be tightly related to the temporal component, which is an intrinsic feature of the structuring species of MAFs, and biological traits of involved species as well. Indeed, species that display ontogenetic migration (D'Onghia et al. 2010, 2016; Milligan et al. 2016), as well as those that cover larger areas during foraging activity (Kutti et al. 2014; Mastrototaro et al. 2017), may frequent MAFs by chance and not by necessity.

Another interesting aspect that must be considered is the changes in use of habitat over time by some species. For example, even though deep-sea skates and rays are not tightly associated with corals (Costello et al. 2006; Ross and Quattrini 2007; Sulak et al. 2007), their egg cases co-occur with these benthic organisms (e.g. Costello et al. 2006; Etnoyer and Morgan 2005; Quattrini et al. 2009; Buhl-Mortensen et al. 2017).

In this regard, future research on the topic should rely on time-series of data that can possibly elucidate the ecological roles of different habitats and effectively discriminate their use over time and the effective contribution to adult populations. Indeed, while specific attributes of habitat structure are critical for juvenile survival in some species, how this dependence translates into population-level responses is more difficult to demonstrate (but see Caley et al. 1996 for shallow tropical systems). The main challenge for future work is in both demonstrating nursery function through a comprehensive set of criteria described in the introduction for coastal environments and applying such knowledge to effective conservation and management measures for marine resources.

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References

Angeletti L, Taviani M, Canese S, Foglini F, Mastrototaro F, Argnani A, Trincardi F, Bakran-Petricioli T, Ceregato A, Chimienti G, Mačić V, Poliseno A (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 15:263–273

Auster PJ (2005) Are deep-water corals important fish habitats for fishes? In: Freiwald A, Roberts J (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 747–760. https://doi.org/10.1007/3-540-27673-4_39

Auster PJ (2007) Linking deep-water corals and fish populations. Bull Mar Sci 81:93–99

Auster PJ, Malatesta RJ, LaRosa SC (1995) Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Mar Ecol Prog Ser 127:77–85

Auster PJ, Malatesta RJ, Langton RW, Watting L, Valentine PC, Donaldson CLS, Langton EW, Shepard AN, Babb WG (1996) The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. Rev Fish Sci 4(2):185–202

Auster PJ, Malatesta RJ, Donaldson CLS (1997) Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. Environ Biol Fishes 50:195–200

Auster PJ, Lindholm J, Valentine PC (2003) Variation in habitat use by juvenile Acadian redfish, *Sebastes fasciatus*. Environ Biol Fishes 68:381–389. https://doi.org/10.1023/B:EBFI.0000005751.30906.d5

Baillon S, Hamel J-F, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ 10:351–356. https://doi.org/10.1890/120022

Baillon S, Hamel J-F, Mercier A (2014) Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. PLoS One 9:e111519. https://doi.org/10.1371/journal.pone.0111519

Bartholomew A, Diaz RJ, Cicchetti G (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. Mar Ecol Prog Ser 206:45–58. https://doi.org/10.3354/meps206045

Beck MW, Heck KLJ, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 22:521–533. https://doi.org/10.1641/0006-3568(2001)051

Bo M, Bertolino M, Bavestrello G, Canese S, Giusti M, Angiolillo M, Pansini M, Taviani M (2011) Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. Hydrobiologia 687:163–177. https://doi.org/10.1007/s10750-011-0964-1

Bo M, Cerrano C, Canese S, Salvati E, Angiolillo M, Santangelo G, Bavestrello G (2013) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 1–11:332. https://doi.org/10.1111/maec.12089

Bo M, Bavestrello G, Angiolillo M, Calcagnile L, Canese S, Cannas R, Cau A, Elia MD, Oriano FD, Follesa MC, Quarta G, Cau A (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS One 10:1–21. https://doi.org/10.1371/journal.pone.0119393

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonain corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 849–879. https://doi.org/10.1007/3-540-27673-4_44

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50. https://doi.org/10.1111/j.1439-0485.2010.00359.x

Buhl-Mortensen L, Olafsdottir SH, Buhl-Mortensen P, Burgos JM, Ragnarsson SA (2015) Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: effects of bathymetry and hydrography. Hydrobiol 759(1):39–61. https://doi.org/10.1007/s10750-014-2116-x

Buhl-Mortensen, P., Buhl-Mortensen, L., & Purser, A. (2017). Trophic ecology and habitat provision in cold-water coral ecosystems. In Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots (pp. 919–944). https://doi.org/10.1007/978-3-319-21012-4_20

Caddy JF (2008) The importance of "cover" in the life histories of demersal and benthic marine resources: a neglected issue in fisheries assessment and management. Bull Mar Sci 83:7–52

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477–500. https://doi.org/10.1146/annurev.ecolsys.27.1.477

Capezzuto F, Sion L, Ancona F, Carlucci R, Carluccio A, Cornacchia L, Maiorano P, Ricci P, Tursi A, D'Onghia G (2018) Cold-water coral habitats and canyons as essential fish habitats in the southern Adriatic and northern Ionian Sea (Central Mediterranean). Ecol Quest 29:9. https://doi.org/10.12775/eq.2018.019

Carreiro-Silva M, Andrews AH, Braga-Henriques A, De Matos V, Porteiro FM, Santos RS (2013) Variability in growth rates of long-lived black coral Leiopathes sp. from the Azores. Mar Ecol Prog Ser 473:189–199. https://doi.org/10.3354/meps10052

Cau A, Follesa MC, Moccia D, Alvito A, Bo M, Angiolillo M, Canese S, Paliaga EM, Orrù PE, Sacco F, Cannas R (2015) Deepwater corals biodiversity along roche du large ecosystems with different habitat complexity along the South Sardinia continental margin (CW Mediterranean Sea). Mar Biol 162:1865–1878. https://doi.org/10.1007/s00227-015-2718-5

Cau A, Follesa MCMC, Moccia D, Bellodi A, Mulas A, Bo M, Canese S, Angiolillo M, Cannas R (2017a) *Leiopathes glaberrima* millennial forest from SW Sardinia as nursery ground for the small spotted catshark *Scyliorhinus canicula*. Aquat Conserv Mar Freshw Ecosyst 27:731–735. https://doi.org/10.1002/aqc.2717

Cau A, Moccia D, Follesa MC, Alvito A, Canese S, Angiolillo M, Cuccu D, Bo M, Cannas R (2017b) Coral forests diversity in the outer shelf of the south Sardinian continental margin. Deep Sea Res Part I Oceanogr Res Pap 122:60–70. https://doi.org/10.1016/j.dsr.2017.01.016

Cho W, Shank TM (2010) Incongruent patterns of genetic connectivity among four ophiuroid species with differing coral host specificity on North Atlantic seamounts. Mar Ecol 31:121–143. https://doi.org/10.1111/j.1439-0485.2010.00395.x

Coleman FC, Koenig CC, Collins LA (1996) Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environ Biol Fish 47:129–141. https://doi.org/10.1007/BF00005035

Concha F, Bustamante C, Oddone MC, Hernández S, Lamilla J (2010) Egg capsules of the dusky catshark Bythaelurus canescens (Carcharhiniformes, Scyliorhinidae) from the South-Eastern Pacific Ocean. J Fish Biol 77:963–971. https://doi.org/10.1111/j.1095-8649.2010.02736.x

Corbera G, Lo Iacono C, Gràcia E, Grinyó J, Pierdomenico M, Huvenne VAI, Aguilar R, Gili JM (2019) Ecological characterisation of a Mediterranean cold-water coral reef: Cabliers coral Mound Province (Alboran Sea, western Mediterranean). Prog Oceanogr 175:245–262. https://doi.org/10.1016/j.pocean.2019.04.010

Costello MJ, McCrea M, Freiwald A, Lundälv T, Jonsson L, Bett BJ, van Weering TCE, de Haas H, Roberts JM, Allen D (2006) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer, Berlin, pp 771–805. https://doi.org/10.1007/3-540-27673-4_41

D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, Tursi A, D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, Tursi A, D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, Tursi A (2010) Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep Sea Res Part II Top Stud Oceanogr 57:397–411. https://doi.org/10.1016/j.dsr2.2009.08.022

D'Onghia G, Calculli C, Capezzuto F, Carlucci R, Carluccio A, Maiorano P, Pollice A, Ricci P, Sion L, Tursi A (2016) New records of cold-water coral sites and fish fauna characterization of a potential network existing in the Mediterranean Sea. Mar Ecol 37:1398–1422. https://doi.org/10.1111/maec.12356

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Mar Ecol Prog Ser 312:291–295. https://doi.org/10.3354/meps312291

De Clippele LH, Huvenne VAI, Molodtsova TN, Roberts JM (2019) The Diversity and ecological role of non-scleractinian corals (Antipatharia and Alcyonacea) on Scleractinian Cold-Water Coral Mounds. Front Mar Sci 6. https://doi.org/10.3389/fmars.2019.00184

De Matos V, Gomes-Pereira JN, Tempera F, Ribeiro P a, Braga-Henriques A, Porteiro F (2014) First record of Antipathella subpinnata (Anthozoa, Antipatharia) in the Azores (NE Atlantic), with description of the first monotypic garden for this species. Deep Res Part II Top Stud Oceanogr 99:113–121. https://doi.org/10.1016/j.dsr2.2013.07.003

Deidun A, Tsounis G, Balzan F, Micallef A (2010) Records of black coral (Antipatharia) and red coral (*Corallium rubrum*) fishing activities in the Maltese Islands. Mar Biodivers Rec 3:e90–e90. https://doi.org/10.1017/s1755267210000709

Diaz RJ, Cutter GRJ, Able KW (2003) The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26:12–20. https://doi.org/10.1007/BF02691689

Etnoyer P, Morgan LE (2005) Habitat forming deep-sea corals in the northeast Pacific Ocean. In: Freiwald A, Roberts JM (eds) Cold-water corals and ecosystems. Springer-Verlag, Heidelberg, pp 331–343

Etnoyer P, Warrenchuk J (2007) A catshark nursery in a deep gorgonian field in the Mississippi Canyon, Gulf of Mexico. Bull Mar Sci 81:553–559

Etnoyer PJ, Wagner D, Fowle HA, Poti M, Kinlan B, Georgian SE, Cordes EE (2017) Models of habitat suitability, size, and age-class structure for the deep-sea black coral *Leiopathes glaberrima* in the Gulf of Mexico. Deep Res Part II Top Stud Oceanogr 0–1. https://doi.org/10.1016/j.dsr2.2017.10.008

Fodrie FJ, Levin LA, Lucas AJ (2009) Use of population fitness to evaluate the nursery function of juvenile habitats. Mar Ecol Prog Ser 385:39–49. https://doi.org/10.3354/meps08069

Foley NS, Kahui V, Armstrong CW, van Rensburg TM (2010) Estimating linkages between redfish and cold water coral on the Norwegian coast. Mar Resour Econ 25(1):105–120. https://doi.org/10.5950/0738-1360-25.1.105

Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471:1–12. https://doi.org/10.1023/A:1016504430684

Franks JS, VanderKooy KE (2000) Feeding habits of juvenile lane snapper *Lutjanus synagris* from Mississippi coastal waters, with comments on the diet of gray snapper *Lutjanus griseus*. Gulf Caribb Res 12:11–17. https://doi.org/10.18785/gcr.1201.02

Freiwald A, Fosså JH, Grehan A et al (2004) Cold-water coral reefs. UNEP-WCMC, Cambridge, 86 pp

Fretwell SD, Lucas HL Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. Acta Biotheor 19:16–36

Gersani M, Abramsky Z, Falik O (1998) Density-dependent habitat selection in plants. Evol Ecol 12:223–234. https://doi.org/10.1023/A:1006587813950

Gilmore RG, Jones RS (1992) Color variation and associated behavior in the epihepheline groupers, Mycteroperca microlepis (Goode and Bean) and M. phenax Jordan Swain. Bull Mar Sci 51:83–103

Gore RH, Scotto LE, Becker LJ (1978) Community composition, stability, and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellariid worm reefs studies on decapod crustacea from the Indian River region of Florida. Bull Mar Sci 28(2):221–248

Greene HG, Yoklavich MM, Starr RM, O'Connell VM, Wakefield WW, Sullivan DE, McRea JE Jr, Cailliet GM (1999) A classification scheme for deep seafloor habitats. Oceanol Acta 22:663–678

Guidetti P, Danovaro R (2018) Global ocean conservation under the magnifying glass. Aquat Conserv Mar Freshw Ecosyst 28:259–260. https://doi.org/10.1002/aqc.2854

Guizien K, Ghisalberti M (2017) Living in the canopy of the animal forest: physical and biogeochemical aspects. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer International, Cham, pp 507–528. https://doi.org/10.1007/978-3-319-17001-5

Halpern BS (2004) Habitat bottlenecks in stage-structured species: hermit crabs as a model system. Mar Ecol Prog Ser 276:197–207. https://doi.org/10.3354/meps276197

Hawkes N, Korabik M, Beazley L, Rapp HT, Xavier JR, Kenchington E (2019) Glass sponge grounds on the Scotian shelf and their associated biodiversity. Mar Ecol Prog Ser 614:91–109. https://doi.org/10.3354/meps12903

Henry LA, Navas JM, Hennige SJ, Wicks LC, Vad J, Murray Roberts J (2013) Cold-water coral reef habitats benefit recreationally valuable sharks. Biol Conserv 161:67–70. https://doi.org/10.1016/j.biocon.2013.03.002

Henry LA, Roberts JM (2017) Global biodiversity in cold-water coral reefs. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer, Netherlands, pp 235–256

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment: choice dynamics and uncertainty. Chapman and Hall, New York, 570 p

Houghton RG (1987) The consistency of the spatial distributions of young gadoids with time. ICES CM1987/D:15, International Council for Exploration of the Sea, 7 p

Husebo A, Nottestand L, Fossa JH, Furevik DM, Jorgensen SB (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471:91–99

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215:627–633

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kenchington E, Power D, Koen-Alonso M (2013) Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. Mar Ecol Prog Ser 477:217–230. https://doi.org/10.3354/meps10127

Koenig CC, Coleman FC, Grimes CB, Fitzhugh GR, Scanlon KM, Gledhill CT, Grace M (2000) Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. Bull Mar Sci 66(3):593–616

Koenig CC, Shepard AN, Reed JK, Coleman FC, Brooke SD, Brusher J, Scanlon KM (2005) Habitat and fish populations in the deep-sea fish populations Oculina coral ecosystem of the Western Atlantic. Am Fish Soc Symp 41:795–805

Komugabe AF, Fallon SJ, Thresher RE, Eggins SM (2014) Modern Tasman Sea surface reservoir ages from deep-sea black corals. Deep Res Part II Top Stud Oceanogr 99:207–212. https://doi.org/10.1016/j.dsr2.2013.05.024

Kregting LT, Gibbs MT (2006) Salinity controls the upper depth limit of black corals in doubtful sound. N Z J Mar Freshw Res 40:43–52. https://doi.org/10.1080/00288330.2006.9517402

Krieger KJ, Wing BL (2002) Megafauna associations with deepwater corals (Primnoa spp.) in the Gulf of Alaska. Hydrobiologia 471:83–90. https://doi.org/10.1023/A:1016597119297

Kuhlmann ML (1998) Spatial and temporal patterns in the dynamics and use of pen shells (*Atrina rigida*) as shelters in St. Joseph Bay, Florida. Bull Mar Sci 62:157–179

Kutti T, Bergstad OA, Fosså JH, Helle K (2014) Cold-water coral mounds and sponge-beds as habitats for demersal fish on the Norwegian shelf. Deep Res Part II Top Stud Oceanogr 99:122–133. https://doi.org/10.1016/j.dsr2.2013.07.021

Langton RW, Auster PJ, Schneider DC (1995) A spatial and temporal perspective on research and management of groundfish in the Northwest Atlantic. Rev Fish Sci 3:201–229. https://doi.org/10.1080/10641269509388572

Lartaud F, Galli G, Raza A, Priori C, Benedetti MC, Cau A, Santangelo G, Iannelli M, Solidoro C, Bramanti L (2017) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer International, Cham, pp 595–626. https://doi.org/10.1007/978-3-319-17001-5

Lefcheck JS, Hughes BB, Johnson AJ, Pfirrman BW, Rasher DB, Smyth AR, Williams BL, Beck MW, Orth RJ (2019) Are coastal habitats important nurseries? A meta-analysis. Conserv Lett e12645. https://doi.org/10.1111/conl.12645

Li L, Wang G (2006) The ideal free distribution of clonal plant's ramets among patches in a heterogeneous environment. Bull Math Biol 68:1837–1850. https://doi.org/10.1007/s11538-005-9011-6

Longo C, Mastrototaro F, Corriero G (2005) Sponge fauna associated with a Mediterranean deep-sea coral bank. J Mar Biol Assoc UK 85:1341–1352. https://doi.org/10.1017/S0025315405012518

MacCall AD (1990) Dynamic geography of marine fish populations. University of Washington Press, Seattle 153 p

Mace J (1981) Separation point closed. Catch 8:15–16

Maldonado M (2017) Marine animal forests: the ecology of benthic biodiversity hotspots. https://doi.org/10.1007/978-3-319-21012-4

Marliave JB, Conway KW, Gibbs DM, Lamb A, Gibbs C (2009) Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. Mar Biol 156:2247–2254. https://doi.org/10.1007/s00227-009-1252-8

Massi D, Vitale S, Titone A, Milisenda G, Gristina M, Fiorentino F, Vitale S, Titone A, Milisenda G, Gristina M, Fiorentino F (2018) Spatial distribution of the black coral *Leiopathes glaberrima* (Esper, 1788) (Antipatharia: Leiopathidae) in the Mediterranean: a prerequisite for protection of Vulnerable Marine Ecosystems (VMEs). Eur Zool J 85:170–179. https://doi.org/10.1080/24750263.2018.1452990

Mastrototaro F, Chimienti G, Acosta J, Blanco J, Garcia S, Rivera J, Aguilar R (2017) *Isidella elongata* (Cnidaria: Alcyonacea) facies in the western Mediterranean Sea: visual surveys and descriptions of its ecological role. Eur Zool J 84:209–225. https://doi.org/10.1080/24750263.2017.1315745

McMurray G, Vogel AH, Fishman PA, Armstrong DA, Jewett SC (1986) Distribution of larval and juvenile red king crabs (*Paralithodes camtschatica*) in Bristol Bay. Outer Continental Shelf Environmental Assessment Program 53, pp 267–477

McPeek MA, Rodenhouse NL, Holmes RT, Sherry TW (2001) A general model of site-dependent population regulation: population-level regulation without individual-level interactions. Oikos 94:417–424

Milligan RJ, Spence G, Roberts JM, Bailey DM (2016) Fish communities associated with cold-water corals vary with depth and substratum type. Deep Res Part I Oceanogr Res Pap 114:43–54. https://doi.org/10.1016/j.dsr.2016.04.011

Moccia D, Cannas R, Cau A, Alvito A, Follesa MC (2019) New sites expanding the "Sardinian cold – water coral province" extension: a new potential cold – water coral network? Aquat Conserv Mar Freshw Ecosyst 153–160. https://doi.org/10.1002/aqc.2975

Morrison M, Jones EG, Consalvey M, Berkenbusch K (2014) Linking marine fisheries species to biogenic habitats in New Zealand: a review and synthesis of knowledge. Ministry for Primary Industries

Mosher CV, Watling L (2009) Partners for life: a brittle star and its octocoral host. Mar Ecol Prog Ser 397:81–88. https://doi.org/10.3354/meps08113

Murillo FJ, Duran Munoz P, Altuna Á, Serrano A (2011) Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. ICES J Mar Sci 68:319–332. https://doi.org/10.1093/icesjms/fsq071

Murillo FJ, Muñoz PD, Cristobo J, Ríos P, González C, Kenchington E, Serrano A (2012) Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): distribution and species composition. Mar Biol Res 8:842–854. https://doi.org/10.1080/17451000.2012.682583

Myers RA, Stokes K (1989) Density-dependent habitat utilization of groundfish and the improvement of research surveys. ICES CM1989/D:15, International Council for Exploration of the Sea, 17 p

Nagelkerken I, Van Der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, Den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51:31–44. https://doi.org/10.1006/ecss.2000.0617

Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish 16:362–371. https://doi.org/10.1111/faf.12057

Nygren A, Pleijel F (2010) Redescription of Imajimaea draculai—a rare syllid polychaete associated with the sea pen *Funiculina quadrangularis*. J Mar Biol Assoc UK 90:1441–1448

Opresko DM, Sánchez JA (2005) Caribbean shallow-water black corals (Cnidaria: Anthozoa: Antipatharia). Carribean J Sci 41:492–507

Pauly D, Zeller D (2016) Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nat Commun 7:10244. https://doi.org/10.1038/ncomms10244

Pauly D, Christensen V, Dalsgaard J, Froese R Jr, Torres F (1998) Fishing down marine food webs. Science 279:860–863. https://doi.org/10.1126/science.279.5352.860

Pederson EJ, Peterson MS (2002) Bryozoans as ephemeral estuarine habitat and a larval transport mechanism for mobile benthos and young fishes in the north-central Gulf of Mexico. Mar Biol 140:935–947. https://doi.org/10.1007/s00227-001-0766-5

Pereira JJ, Schultz ET, Auster PJ (2012) Geospatial analysis of habitat use in yellowtail flounder *Limanda ferruginea* on Georges bank. Mar Ecol Prog Ser 468:279–290. https://doi.org/10.3354/meps10035

Peterson MS, Comyns BH, Hendon JR, Bond PJ, Duffy GA (2000) Habitat use by early life-history stages of fishes and crustaceans along a changing estuarine landscape: differences between natural and altered shoreline sites. Wetl Ecol Manag 8:209–219. https://doi.org/10.1023/A:1008452805584

Petitgas P (1997) Sole egg distributions in space and time characterised by a geostatistical model and its estimation variance. ICES J Mar Sci 54:213–225. https://doi.org/10.1006/jmsc.1996.0184

Pirtle JL, Stoner AW (2010) Red king crab (Paralithodes camtschaticus) early post-settlement habitat choice: structure, food, and ontogeny. J Exp Mar Biol Ecol 393(1–2):130–137

Quattrini AM, Partyka ML, Ross SW (2009) Aspects of the reproductive biology of the skate *Fenestraja plutonia* (Garman) off North Carolina. Southeast Nat 8:55–70. https://doi.org/10.1656/058.008.0106

Reed JK (2002) Deep-water Oculina coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471:43–55

Roark EB, Guilderson TP, Dunbar RB, Ingram BL, Pen O, Roark EB, Guilderson TP, Dunbar RB, Ingram BL (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Prog Ser 327:1–14. https://doi.org/10.3354/meps327001

Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. Proc Natl Acad Sci USA 106:5204–5208. https://doi.org/10.1073/pnas.0810875106

Roberts JM, Wheeler AJ, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312:543–547. https://doi.org/10.1126/science.1119861

Rodenhouse NL, Sherry TW, Holmes RT (1997) Site-dependent regulation of population size: a new synthesis. Ecology 78:2025–2042

Rosenberg A, Bigford T (2000) Ecosystem approaches to fishery management through essential fish habitat. Bull Mar 66:535–542

Ross SW, Quattrini AM (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Res I: Oceanogr Res Pap 54(6):975–1007

Ruiz-Ramos DV, Saunders M, Fisher CR, Baums IB (2015) Home bodies and wanderers: sympatric lineages of the deep-sea black coral *Leiopathes glaberrima*. PLoS One 10:e0138989. https://doi.org/10.1371/journal.pone.0138989

Saxton F (1980) Coral loss could deplete fish stocks. Catch 7:12–13

Shepherd TD, Litvak MK (2004) Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. Fish Fish 5:141–152. https://doi.org/10.1111/j.1467-2979.2004.00143.x

Stevens B. G., MacIntosh R. A. 1991. Cruise results supplement, cruise 91-1 Ocean Hope 3: 1991 Eastern Bering Sea juvenile red king crab survey, May 24–June 3, 1991. National Marine Fisheries Service, Alaska Fisheries Science Center, Kodiak Fisheries Research Center, 301

Stoner AW, Titgen RH (2003) Biological structures and bottom type influence habitat choices made by Alaska flatfishes. J Exp Mar Biol Ecol 292(1):43–59

Stoner AW, Spencer ML, Ryer CH (2007) Flatfish-habitat associations in Alaska nursery grounds: use of continuous video records for multi-scale spatial analysis. J Sea Res 57:137–150. https://doi.org/10.1016/j.seares.2006.08.005

Sulak KJ, Brooks RA, Luke KE, Norem AD, Randall M, Quaid AJ, Yeargin GE, Miller JM, Harden WM, Caruso JH, Ross SW (2007) Demersal fishes associated with *Lophelia pertusa* coral and hard-substrate biotopes on the continental slope, northern Gulf of Mexico. Bull Mar Sci 81(3):65–92

Taviani M, Angeletti L, Canese S, Cannas R, Cardone F, Cau A, Al C, Follesa MC, Marchese F, Montagna P, Tessarolo C (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep-Sea Res Part II 145:61–78

Vooren CM (1975) Nursery grounds of tarakihi (Teleostei:Cheilodactylidae) around New Zealand. N Z J Mar Freshw Res 9:121–158

Warner GF (2005) The occurrence of black corals in Jamaican reef environments, with special reference to *Stichopathes lutkeni* (Antipatharia: Antipathidae). Rev Biol Trop 53:61–66

Watling L, France SC, Pante E, Simpson A (2011) Biology of deep-water octocorals. Adv Mar Biol 60:41–122

Wood ACL, Probert PK, Rowden AA, Smith AM (2012) Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. Aquat Conserv Mar Freshw Ecosyst 22:547–563. https://doi.org/10.1002/aqc.2236

Zibrowius H (1980) Les scleractiniaires de la Mediter - ranée et de l'Atlantique nord-oriental.Mem Inst Oceanogr Monaco 11: 1−284

Marine Animal Forests as Carbon Immobilizers or Why We Should Preserve These Three-Dimensional Alive Structures

S. Rossi and L. Rizzo

Abstract Marine ecosystems continue to be transformed by human activities. Among them, benthic ecosystems are perhaps one of the most affected, because of bottom trawling, urban or agricultural development, climate change, and other stressors. Benthic communities that are dominated by structuring species, the marine animal forests (MAF), are among the most threatened ecosystems. MAFs are generally composed of benthic suspension feeders (e.g., sponges, corals) that form living three-dimensional structures. Besides the paramount structuring role these communities play, MAF also acts as carbon immobilizers. Estimates of carbon amount retained by terrestrial forests, seagrasses, mangroves, crops, and soils are available; however, there is scarce information on the amount of carbon retained by MAF. Here, we address the potential role of MAF as carbon immobilizers, highlighting the importance of their preservation and active restoration.

Keywords Carbon cycle · Carbon sinks · Anthropogenic impacts · Climate change · Bottom trawling · Marine restoration · Coral reef · Artificial reef · Habitat-forming species · Blue carbon

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1 Introduction

In the 1970s, we began to be conscious about the problems of deforestation in the Amazon tropical forest. In that moment, we identified the lung of the Earth with this complex and biodiverse ecosystem. However, the time passed, and researchers identified the real lung of the Earth: the oceans and the coastal areas. It is not that tropical forests are not important for the oxygen production through photosynthesis but that tiny humble cells were responsible for the at least half of the oxygen production on the Earth (Duarte and Cebrián 1996; Friend et al. 2009). It is not the first time that, because of the bias between ocean and land perspectives, we pay more attention to the terrestrial areas with respect to the aquatic ones. During the last decades, research programs, private enterprise entrepreneurs, politics, and the society claimed for a higher relevance of the ocean's role in our lives. However, the truth is that there is a vast unknown set of topics that we still do not dominate about the role of the seas in Earth's functioning.

For example, we have precise maps of the Earth's surface, not only of the topography but also of the different ecosystems and, within these ecosystems, the population structure of the vegetation that inhabits very large areas. It is roughly calculated that only 5% of the ocean's floor is properly mapped from the biocenotic point of view (Rossi et al. 2017a). In this context, we have precise numbers about carbon that is retained by trees (Le Quéré et al. 2013, 2015), bushes, and other vegetation on land, and we may also have numbers about the soil retention of this element (Lal 2004; Smith 2004). We can even calculate the numbers of how much of the human-produced carbon (from industry, transport, or agriculture/farming) is retained in long-lived structures and how these terrestrial ecosystems contribute to the carbon sink (Luyssaert et al. 2008; Pan et al. 2011; Carlson and Pfeiffenberger 2015). In the sea and coastal areas, we have reliable numbers about the carbon retained in coastal systems like mangroves (Alongi 2014) and seagrasses (Duarte et al. 2010; Fourqurean et al. 2012). We do have some approximation about tropical shallow coral reef carbon immobilization, even though it is still controversial if these ecosystems are in fact true carbon sinks (Kinsey and Hopley 1991; Gattuso et al. 1996). What about the rest of the benthic communities? Do they immobilize and/or sequester significant amounts of carbon?

The knowledge in benthic ecosystems in which suspension feeding animals (those depending on the suspended captured particles to live) are present is very scarce with respect to the abovementioned habitats. Below 50–100 m depth, when the light is not the direct driver of productivity, the marine animal forest (MAF), i.e., three-dimensional alive structures composed of sponges, gorgonians, corals, etc. (Rossi 2013; Rossi et al. 2017a), completely dominates the seascape in the world's oceans. In the overall C equation, Schmitz et al. (2014) claimed for the role of animals as carbon sinks, but we do not have a reliable number (in most cases, we do not even have a number) of the role of these MAFs as carbon sinks. Are they important? Which is their real extension? Are these ecosystems a key factor for the so-called missed or hidden carbon (Schlesinger 1999) in the overall biogeochemical cycle of the planet? There is no answer to this question because we simply do not know its extension, distribution, basic biological knowledge (in some cases), and importance in the overall context.

The idea of a forest is obviously associated with a terrestrial community dominated by trees. Forests are complex three-dimensional habitats that support high biodiversity, giving many other sessile and mobile organism structures to live, food, nursery areas, and shelter, establishing 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., some boreal forests) or by several species (e.g., tropical rain forest), depending on the environmental constraints. In the oceans and seas, megabenthic communities dominated by sessile suspension feeders are capable of growing three-dimensional frameworks with high structural complexity that offer similar advantages with respect to the terrestrial ones for hundreds of associated species (Rossi et al. 2017a). These communities have structural and functional similarities with terrestrial forests, but they are dominated by animals instead of plants. These animal-structured ecosystems can be described as "animal forests" highlighting the similarities with their terrestrial counterparts (Rossi 2013). As terrestrial vegetal forests, animal forests can also be monospecific (e.g., mussel beds or some sea pen assemblages) or be formed by different species with variable morphologies and trophic needs (e.g., tropical coral reefs or the Mediterranean coralligenous habitat). Thus, the definition of marine animal forest includes all these alive three-dimensional communities in which the structuring organisms are benthic suspension feeders (Fig. 1).

In this chapter, we want to explore the role of MAFs as carbon immobilizers, highlighting the importance of the human threats to such complex systems, the past ecosystem structures, and how and why should we preserve this (and other) global role in the ongoing Anthropocene (Crutzen 2006).

2 Calculation of C Immobilization: Extrapolations and Limitations

To clarify the concepts, carbon immobilization is the path in which the organism retains, for an elapsed time, carbon from the water column in their structures. Carbon sink is the almost permanent immobilization of the organic carbon in sediments and, to be considered as such, has to be over 10% of the organic carbon (Buddemeier 1996; Barnes 2018). We are on our way to understand better, step-by-step, the role of the MAFs as carbon immobilizers or sequesters, but the question remains the same: How much carbon is retained by the complex structures of the marine animal forests? What's the role as a carbon immobilizer of anthropogenic and non-anthropogenic origin? We are simply running out of time to answer this question. This lack of knowledge represents a huge deficit in our comprehension of the global carbon cycle, and specifically the process of removing carbon from the atmosphere of the planet.

Fig. 1 Different types of marine animal forest. (**a**) *Corallium rubrum* patch, Mediterranean Sea (© ADOBE STOCK), (**b**) mussel bed from North Atlantic waters (© ADOBE STOCK); (**c**) Gorgonian forest in Antarctic waters (© AWI-Julian Gutt); (**d**) deep coral assemblage in a Mediterranean underwater canyon (© ICMGEOMAR); (**e**) gorgonian from Indonesian waters (Irian-Java) (© ADOBE STOCK); (**f**) Bryozoan *Chartella* sp. in the Mediterranean Sea (© ADOBE STOCK); (**g**) coral reef in the Caribbean sea (© ADOBE STOCK); (**h**) hydrocoral *Errina antarctica*, Southern Ocean (© AWI-Julian Gutt)

2.1 The Carbon Sink Polemic: Coral Reefs

One of the most extended (and well-studied) marine animal forests are tropical coral reefs. Even if they occupy only 0.17% of the world's oceans, it has been roughly calculated that 15% of the coastal area between 0 and 30 m depth are tropical coral reefs. This area is larger if we consider also Mesophotic coral ecosystems (representing possibly up to 80% of the coral reef extension all over the world) and marginal reefs (Pyle and Copus 2019; Soares et al. 2020). Cold water corals, which have even a larger extension (Hoegh-Guldberg et al. 2017), have to be also considered. The shallow coral reefs are considered in most cases carbon sources (Frankignoulle et al. 1995; Gattuso et al. 1996, 1999; Suzuki and Kawahata 2003).

The $CaCO_3$ precipitation releases CO_2:

$$Ca^{2+} + 2HCO^{-3} \rightarrow CaCO_3 + CO_2H_2O$$

An increase of a carbon pool does not necessarily lead to a reduction of atmospheric CO_2 concentrations. When inorganic carbonates are produced by calcification, CO_2 is also formed as a by-product of the chemical reaction (Tokoro et al. 2019; Watanabe and Nakamura 2019). Therefore, as carbonates are formed, the partial pressure of CO_2 in the water increases, and this increase may lead to an efflux of CO_2 into the atmosphere by diffusive exchanges at the air-water interface. This CO_2 release apparently is not compensated by the symbiotic relationship (photosynthesis) with the microalgae:

$$CO_2 + H_2O \rightleftarrows CH_2O + O_2$$

The contribution of coral reef ecosystems to global carbon balance primarily results from the dominant metabolic processes on coral reefs, which are the organic metabolic pulse (balance between photosynthesis and respiration) and inorganic metabolic pulse (balance between $CaCO_3$ precipitation and dissolution) (Gattuso et al. 1999; Cyronak et al. 2018). As the main coral reef ecosystems present oversaturation of CO_2 compared to the atmosphere equilibrium, they are considered as sources of CO_2 reflecting their low net CO_2 uptake by photosynthetic processes (Gattuso et al. 1999 and references therein). This suggests that the net community production is close to zero, whereas the net community calcification is higher and prevalent in reef ecosystems (Gattuso et al. 1999). An important part of the CO_2 consumed in the photosynthetic process is produced by respiration (Cyronak et al. 2018; Gattuso et al. 1999), and the rest do not compensate the amount of CO_2 released by the $CaCO_3$ precipitation (Andersson and Mackenzie 2004). Other metabolic processes of scleractinians and the reef system related with photosynthesis involving N, P, and Si are also considered, but the whole balance is, in many cases, a net release of CO_2 in the short term (Watanabe and Nakamura 2019).

When you consider the system as a whole or the seasonal variability, conditions may lead to different results. For example, the presence of macroalgae may, during the year cycle and in certain conditions, compensate the CO_2 released by the scleractinian structural growth (Bates 2002; Suzuki and Kawahata 2004), because of the net assimilation of CO_2 of these algae. Studies have documented a shift from coral-dominated to algal-dominated states (Smith and Buddemeier 1992; Hughes 1994; McClanahan and Muthiga 1998). Hydrodynamics and the exchange of water masses with the open ocean make it difficult to make an accurate calculation, sometimes, of the role of coral reefs as C sinks or sources (Suzuki and Kawahata 2004). The role of other systems connected with the reef system (e.g., mangroves) has to be also considered, in a moment when we understand that all these systems are connected and act balancing each other (Macreadie et al. 2017a). This article of Saderne et al. (2019) states that "Calcium carbonates ($CaCO_3$) often accumulate in mangrove and seagrass sediments. A mass balance assessment highlights that the C inorg burial is mainly supported by inputs from adjacent ecosystems rather than by local calcification, and that blue carbon ecosystems are sites of net $CaCO_3$ dissolution." In this way, if the $CaCO_3$ is autochthonous-derived (produced in the ecosystem itself), they could partially offset the CO_2 sink; however, if the $CaCO_3$ is allochthonous, they effectively contributes with the carbon sink.

In fact, there are many factors to consider in this complex equation. The first is the role of photosynthesis. Part of the photosynthetic activity fuels the $CaCO_3$ precipitation (Andersson and Mackenzie 2004). The precipitation of this $CaCO_3$ is an active process, not a passive one (Allemand et al. 2010). In this framework, we still have, for example, to understand how much of the organic matter produced by the Symbiodiniaceae (sensu LaJeunesse et al. 2018) in different moments of the seasonal cycle balances the CO_2 release in the $CaCO_3$ process. The process of calcification is an extracellular process controlled by the symbiotic relationship (Allemand et al. 2010), being the light a promoter of such calcification (González-Guerreo 2015). One recent hypothesis suggests that synthesis of photosynthates (oxygen and glycerol) of Symbiodiniaceae is required for light enhancement calcification, where dissolved inorganic carbon in the form of bicarbonate is taken from the water column and is converted into CO_2 by the carbonic anhydrase. The CO_2 is fixed by photosynthesis, is translocated as glycerol to the host, and then is respired generating the ATP necessary for the transport of ions and organic matrix synthesis, and again using a carbonic anhydrase, the CO_2 product of respiration is placed in the form of HCO_3 at the calcification site (González-Guerreo 2015; Iglesias-Prieto personal communication). This could make scleractinians a net sink, not a source, but further research is needed also to understand the role of the dark respiration in the whole process (Gattuso et al. 1999). In this sense, there is still a lot of work to do, especially in the interface between geochemistry, ecophysiology, and biochemistry. Another factor to consider is the organic matrix (rings, Cuif and Dauphin 2005) that has to be accounted possibly not as carbon sink but at least as immobilized carbon. It has been showed that the heterotrophic input and the autotrophic input may be a non-neglectable part of the C fixed in the skeleton of scleractinians (Houlbrèque and Ferrier-Pagès 2009). Heterotrophy accounts for between 0 and 66% of the fixed carbon incorporated into coral skeletons and can meet from 15 to 35% of daily metabolic requirements in healthy corals and up to 100% in bleached corals

(Houlbrèque and Ferrier-Pagès 2009). The zooplankton partly fuels the whole process (Houlbréque 2004), being an essential part to understand skeleton formation (organic matter rings between the calcified structures, Houlbrèque et al. 2003). The question is: How much organic carbon is fixed in this way? This carbon will be hardly degraded even if the corals are consumed by fishes, for example, and in most cases will be in the structure for millennia or even more time. All these considerations must be taken into consideration when we think about shallow coral reefs as carbon sinks or sources. In general, the oceanic $CaCO_3$-mediated CO_2 pump is an oscillating pump. The magnitude and oscillation of the pump depend upon (1) temporal variations in the absolute and relative rates of planktonic and benthic $CaCO_3$ production and dissolution, (2) temporal variations in atmospheric pCO_2, and (3) vertical and temporal variations in pCO_2 (Smith 2013).

In deep waters, where heterotrophy is the dominant source of food, cold water corals (scleractinians) have even more questions to answer. Another central question is: Which proportion of the calcium carbonate pool is made up of geogenic Ca carbonate (fossil) and biogenic Ca carbonate (recent) (Zamanian et al. 2016; Macreadie et al. 2017a)? Probably the whole system acts as a carbon immobilizer in many ways and as a source of C in others. We have to figure out these questions to assess the real role of these extensive ecosystems. Barnes (2018), in a very interesting work, highlights the possibility to distinguish between carbon immobilization and C sink. Following Fig. 2 (transformed from Barnes 2018), we can understand better the proposed concept. In Antarctic waters, complex and highly biodiverse megabenthic communities are present (Gutt and Starmans 1998; Gili et al. 2006; Barnes et al. 2018). Huge algal blooms produced in late spring to summer time will fuel sediments (Smith et al. 2006; Isla et al. 2011), forming green carpets rich in

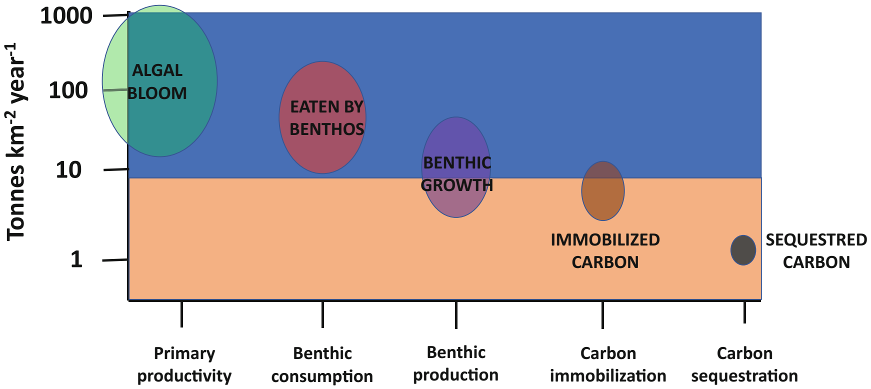

Fig. 2 From an algal bloom in surface waters to the final carbon sequestration in the sediments. Only a small fraction of the total carbon captured from the atmosphere will last for millennia or millions of years in the benthic sediments. However, in the meanwhile, an important fraction will be immobilized as blue carbon in the marine animal forests after having been consumed and retained in pluriannual structures (in some cases up to centuries, depending on the sessile organism) (transformed from Barnes 2018)

organic matter. These green carpets, once resuspended, will feed suspension feeding organisms and their associate fauna (Isla et al. 2006; Gili et al. 2009). Part of the heterotrophic input (coming from the primary and secondary productivity of the water column) is assimilated and converted in respiration and reproduction, but another part will be fixed as structural molecules (growth) (Fig. 2). The carbon represented by these molecules is immobilized, and only a smaller fraction will finally part of the sunk carbon (Barnes et al. 2018). The important concept is how much and how long C is immobilized in these three-dimensional alive structures. In the very long term, for example, coral reefs (shallow or deep) are carbon sinks (Howard et al. 2017); the C immobilized in the structures may stand for very long periods without entering again in the general C cycle. The question is what we really consider a carbon sink: Is it a matter of geological time? Or we may have different perspectives about the carbon sequestration rates?.

2.2 How Much Time Immobilized or Sequestered?

Due to the long life cycles of the habitat-forming species in these animal-dominated ecosystems, they might accumulate elevated quantities of C as biomass (Barnes 2018; Rossi et al. 2019a). This C might last for decades, centuries, or millennia and might be accumulated in the body structures of these species (Roark et al. 2006). An interesting paper by Howard et al. (2017) tries to clarify which ecosystems or communities are efficient carbon sequesters or not. The conclusion is that only wetlands, mangroves, and seagrasses in coastal areas are real carbon sinks. Here the question that we have to bear in our minds is the time scale considered. Let us make an example. Phytoplankton may be considered a carbon sink only for hours or weeks (Buitenhuis et al. 2013). Once consumed and respired, only a low fraction (but not negatable as a whole, 0.1%) reaches the seafloor and remains unaltered for millennia (Falkowski 2012). This phytoplankton is processed by upper trophic levels, including benthic suspension feeding organisms (Gili and Coma 1998). The days or weeks in which the carbon is processed in the phytoplankton may be partially transformed in decades or centuries or even millennia in these three-dimensional long-lived structures. Macroalgae like kelp also act as C immobilizers. The carbon stored in kelp biomass ranges from 37 to 54 Mg C ha^{-1} (Muraoka 2004), but the short life span of individual kelp plants (~1 year) and their lack of long-term carbon storage mean that they cannot act as effective long-term carbon sinks (Spalding et al. 2003; Muraoka 2004). However, once the algae is fragmented and degraded, a non-neglectable part may be grazed by secondary production. Some animals will have ephemeral life cycles, while others may last for decades and accumulate part of the organic matter in their structures. It is the case of heterotrophic gorgonians or ascidians, which partly take this detritus, incorporating in their budget (and structures) the organic matter originated from photosynthetic metabolism (Coma et al. 2001). The same calculation has to be made for microzooplankton; the whole seston is a source of material coming directly or indirectly from photosynthesis (Rossi and Gili 2009) that will be partly fixed in the organic structures of benthic suspension feeders. In many cases, the elapsed time of sequestration will be short, like on the hydrozoans (Rossi et al. 2012), but in other cases may last for very long periods of time (Rossi 2013; Mallo et al. 2019). Other systems should be considered, beside the previously studied C sink communities, like most of the marine animal forests. There are no broad-scale studies for animal-dominated ecosystems calculating its importance as carbon retainers, except possibly for tropical coral reefs. And, as previously stated, there is still an open debate.

It is important thus to understand the life cycle and permanence of these organisms and account how much CO_2 is produced (community respiration) and compare to the amount of carbon that is net buried for the carbon sink equation. Immobilization and sink have to be clearly identified and studied in depth for each community. In addition, we cannot forget that CO_2 sink is not consistent with reef sediment geochemistry. The sink behavior have been detected in studies carried out mostly on fringing reefs, which are more likely subject to anthropogenic stresses. There is increasing number of reefs shifting from coral-dominated to algal-dominated states (Done 1992). This could lead to changes in coral reef metabolism, from net sources to net sinks. The effect of these changes on the ecosystem function is poorly known, and we have also to understand how effects of climate change will affect such balances. For example, there is the increasing effects of ocean acidification, which must be addressed to understand what the future of such balances will be (Comeau and Cornwall 2017).

2.3 Methods to Extrapolate C Immobilization

To calculate the immobilized carbon, we must see the organic matter inputs and outputs (Coppari et al. 2019). Measuring the carbon input through a set of seasonal observations and experiments will be essential to quantify the potential heterotrophic contribution (which could be the only one or shared with the autotrophic one, Coppari et al. 2016; Schubert et al. 2017; Rossi et al. 2020). Knowing the C output will be the next step, paying attention in the immobilized carbon (growth, Coma et al. 1998; Rossi et al. 2011; Coppari et al. 2019). Once we have made the calculation of how much C can be immobilized, we have to make extrapolations similar to those made for seagrasses, mangroves, or tropical rain forests. In the past few decades, the development of remotely operated vehicles (ROVs) and their decreased operational cost have provided the opportunity to perform detailed sampling of benthic species at broad spatial and bathymetric scale, from shallow to deep waters (Rossi et al. 2008; Gori et al. 2011a, b; Chimienti et al. 2018). The analysis of ROV video transects provides both qualitative and quantitative data distribution and size class of species populations (Rossi et al. 2008; Gori et al. 2011a, b; Coppari et al. 2014). These broad-scale data of size and spatial and bathymetrical distribution of benthic species, coupled with experimental and observational results of feeding, reproduction, respiration, and growth, will allow the large-scale calculation of the impact of benthic suspension feeders on benthic-pelagic coupling processes and consequently their importance as carbon immobilizers (Rossi et al. 2017b; Coppari et al. 2019). Crossing the experimental field data with the seascape methodology of the ROV will make possible this approach for the first time, giving the real importance of these three-dimensional structures as carbon sinks and retainers of part of the carbon emitted by humans. The improved understanding of the global role of the MAFs as carbon sink is urgently required to develop knowledge-based management strategies to support conservation actions and policies.

Large-scale spatial comparison is essential to consider different MAF composition, especially because ecological processes will be different depending on different environmental and biological features. In fact, several animal forests have to be considered, as there are very different systems depending on temperature, light incidence, depth, primary productivity, available carbon, current regime, etc. Therefore, several places, with different animal forests, will give reliable numbers that will be essential to conservation plans and make more relevant the role of these ecosystems in the overall C world budget.

In order to understand how much carbon is captured (and retained), we need to know how much carbon is available in the near bottom water layers. The primary production, epibenthic zooplankton and seston available carbon (sediment traps and filtered seawater) will be possible applying know protocols (water seston Rossi and Gili 2005; zooplankton Rossi et al. 2004; Sediment traps Rossi et al. 2003; temperature, currents and other environmental parameters Rossi et al. 2019b; Gori et al. 2012).

A comparison of the three-dimensional structure diversity and complexity has to be made between the systems. This point is crucial in understanding the complexity patterns, and how they influence the optimization of carbon input in the animal forest, in the frame of the optimal foraging theory (Hughes 1980). This is also essential for better understanding of how the different structures are able to retain part of the carbon in their structures. For example, the structure of Caribbean coral reefs is very different from the fjord animal forests of Chile, both in patch distribution and three-dimensional structuration of the communities; this step has to be done prior to the application of the model of C retention in the different areas.

To calculate how much carbon is retained by the MAF, the models that are currently available for the precious coral *Corallium rubrum* can be adapted (Galli et al. 2016). Thus, the seafloor cartography (especially the extension of the different communities, as per Sardá et al. 2012) and biomass and population structure data with the seasonal carbon flux (inputs and outputs) of selected species could be combined, considering the potential available carbon (Coppari et al. 2016, 2019). The available seston C is also calculated, considering the environmental seasonal parameters (temperature, salinity, currents, etc.), to know how much is really captured. The biomass and population structure of other suspension feeders is thus evaluated, making taxonomic and functional group extrapolations (approximate numbers based on a large-scale approach) from the numbers obtained by case studies on selected species (Fig. 3). A projection considering different heterotrophic and

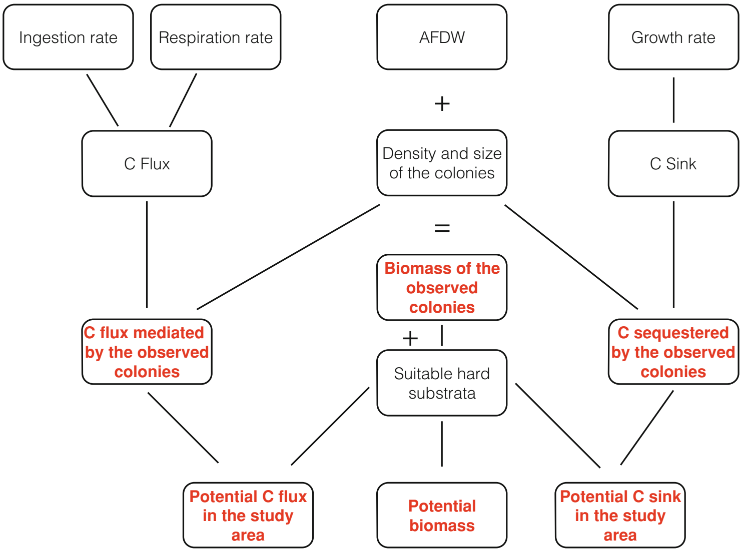

Fig. 3 Diagram summarizing the steps to be performed to calculate C flux and C immobilization in benthic suspension feeders (from Coppari et al. 2019)

autotrophic inputs can be made, making a broad extrapolation and comparison (Rossi et al. 2017b).

2.4 Seasonality and C Immobilization

One of the most important targets in studying the possibility to retain carbon by MAFs is to consider seasonality (Rossi et al. 2012; Coppari et al. 2019). Heterotrophy and autotrophy vary through the annual cycle, being the carbon budget very different when we consider different seasons (Coppari et al. 2014, 2016). There is clear favorable season (e.g., the spring in the Mediterranean Sea) in which the benthic suspension feeding organisms have a net entrance of C in their system (Coppari et al. 2016). This is valid for all MAFs, even those which may seem stable such as tropical shallow water coral reefs (Rossi et al. 2020). Climate patterns will be a key point to understand the variability of carbon immobilization, so we need to make careful approaches following temporal fluctuations that will depend on the latitude and particular habitat features (Coppari et al. 2016). Such seasonality is especially relevant in ephemeral organisms, where the combination of population structure and density is optimized to maximize the C entry (Rossi et al. 2012).

For the autotrophic C input (carbon translocation and fixation in permanent structures) of autotrophic suspension feeders, the photobiological performance has to be assessed (Ramsby et al. 2014; Rossi et al. 2018). For the heterotrophic C input,

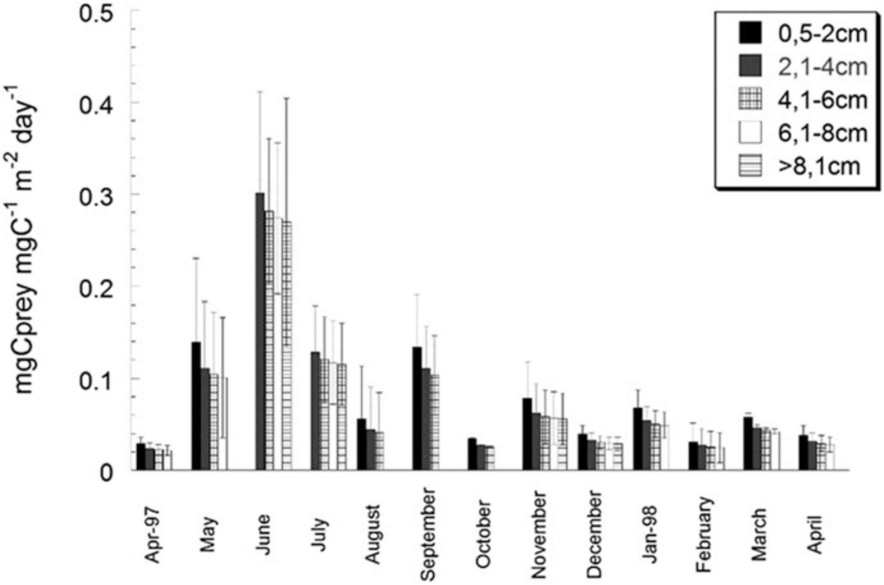

Fig. 4 The hydrozoan *Eudendrium racemosum* as an example of carbon immobilization in ephemeral organisms. During most of the year, this hydrozoan has a high-density low-size colonies growing in the shallow rocky bottoms. In the reproductive period (from May to late July, 1997–-1998 year cycle shown) the colonies are less dense but taller. Such colonies concentrate more biomass and are also capable to capture more food due to the fact that they possess more polyps. In long-lived sessile species (including trees), this is also the case, following the self-thinning role (transformed from Rossi et al. 2012)

the methodologies used may combine incubation chambers (Ribes et al. 2003; Tsounis et al. 2006; Coppari et al. 2016), the gut contents (Rossi et al. 2004, 2012; Tsounis et al. 2006), and the stable isotope-fatty acid approach (Gori et al. 2012; Elias-Piera et al. 2013). These protocols have been tested with different species and give reliable numbers about the quantity of carbon entering in the suspension feeder structures (Fig. 4). Transformation of C units will be contrasted with the abovementioned energy input approach and corrected with the available information about the activity of the organisms. Growth (which is the final number that you need to evaluate how much C is definitively sunk as a structural part of the animal) can be calculated directly with photographs using plane pictures for lineal growth (Coma et al. 1998; Rossi et al. 2011) or photogrammetry methods (Koopmans and Wijffels 2008). The diameter growth (and the C seasonally retained) in organisms in which this approach is feasible and reliable (e.g., scleractinians and octocorals) can be made with known methodologies (Bramanti et al. 2014).

3 How Much C Is Stored?

3.1 Comparison with Other Species/Ecosystems

Most of the global carbon is set in the geosphere as carbonates or sequestered in sedimentary organic carbon, and only a small fraction circulates in the biosphere (Miyajima and Hamaguchi 2019). The quantification of carbon captured and stored by several species or by complex ecosystems is a challenge since it varies with a wide range of environmental and biological features, including geography, life history, type of substratum, etc. In general, the term blue carbon is used for this sequestered carbon, especially in coastal areas where most of the studies have been done (Krause-Jensen et al. 2018). The understanding of sequestration and storage processes of blue carbon appears to be enough complex, complicated by the selection of key criteria to calculate the efficacy of carbon sequestration in marine ecosystems. Nowadays, sequestration of CO_2 has been estimated mainly for terrestrial ecosystems, taking into account land-based sequestered green carbon (Table 1). The UNEP report underlines the importance of the blue carbon ecosystem, in terms of macrophytes and sediments; however, other blue carbon ecosystems should be evaluated in the ocean. Scientific researches highlighted the contribution of benthic organisms on rock substrates to carbon storage (Duarte and Krause-Jensen 2017; Barnes et al. 2019). Understanding the connection between sources and sinks of blue carbon in order to attribute the contribution of each marine ecosystem to the blue carbon sink is crucial.

Recently, the blue carbon report has revealed that more than 50% of the CO_2 absorbed by the plants is principally cycled into the marine ecosystems; moreover, half of the carbon stored in the ocean has been sequestered by coastal ecosystems, accounting for 0.5% of the marine surface (Kuwae and Hori 2019). The annual rates of absorption by terrestrial vegetation and the ocean are estimated to be 2.3 billion tons of C per year and 2.4 billion tons of C per year, respectively. Recent emissions from anthropogenic activities have reported approximatively 9.4 billion tons of C per year and the residual amount 4.7 billion tons of C per year in the atmosphere (Kuwae et al. 2019). Although the total surface of marine ecosystems considered is less than 2% that of tropical rain forests, the carbon storage rates of blue carbon ecosystems and tropical rain forests appear to be similar (Kuwae and Hori 2019). The numbers that start to be clear in land systems and appear to be consistent are the plant-structured coastal and marine ones. However, the MAFs are pending to be quantitatively assessed in this overall picture.

The only example of carbon immobilization and efficiency in benthic-pelagic coupling processes in these three-dimensional structures is represented by coralligenous gorgonians. These Anthozoa are long-lived, slow-growing organisms with a life span that can succeed more than 100 years, being particularly sensitive to environmental and human-induced disturbances (Bramanti et al. 2014). In a recent study, the amount of C retained by three Mediterranean gorgonian species with different distribution and trophic strategy was calculated as the difference between

Table 1 Examples of annual carbon sequestration in different ecosystems or by key species per unit area (hectare)

Ecosystem/taxonomic group	Quantification of C sink ($t\ C\ ha^{-1}$)	References
Amazonian forest	1.02	Grace et al. (1995)
Boreal forests	0.046	Kuwae and Hori (2019)
Cereal straw	0.69	Rees et al. (2005)
Continental shelf area	0.2	Kuwae and Hori (2019)
Convert cropland to grassland	1.2–1.69	Rees et al. (2005)
Convert cropland to woodland	0.62	Rees et al. (2005)
Coral reefs ($CaCO_3$)	1.19	Kinsey and Hopley (1991)
Deciduous forest	2.4	Pryor et al. (2001)
Deep sea	0.00018	Kuwae and Hori (2019)
Deep rooting crops	0.62	Rees et al. (2005)
Deserts	0.008	Kuwae and Hori (2019)
Estuaries (sediment)	0.45	Duarte et al. (2005)
Estuary/inner bay/outside bay	0.5	Kuwae and Hori (2019)
Howland Forest Spruce Fir Site	2.1	Pryor et al. (2001)
Mangroves salt marshes (sediment)	0.21	Chmura et al. (2003)
Mangrove forests	2.9	Estrada and Soares (2017)
Microphytobenthos temperate intertidal	1.11	Cahoon (1999)
Peatlands	0.11	Kuwae and Hori (2019)
Permanent crops	0.62	Rees et al. (2005)
Phytoplankton	2.18	Tada et al. (1998)
Primary forest (peat swamp forests)	5.32	Suzuki et al. (1999)
Saltmarsh	1.51	Kuwae and Hori (2019)
Seagrass	6.70	Duarte et al. (2010)
Secondary forest (peat swamp forests)	5.22	Suzuki et al. (1999)
Spruce plantations	3.36	Kilbride et al. (1999)
Temperate forests	0.051	Kuwae and Hori (2019)
Temperate grasslands	0.022	Kuwae and Hori (2019)
Tidal flat (sediment)	0.10–1.05	Widdows et al. (2004)
Tropical forests	0.04	Kuwae and Hori (2019)
Tundra	0.012	Kuwae and Hori (2019)
Arcuatula senhousia (shell)	0.46	Mistri and Munari (2013)
Cerastoderma edule	0.114	Sauriau and Kang (2000)
Corallium rubrum	0.0000071	Mallo et al. (2019)
Cyperus papyrus	10	Saunders et al. (2012)
Enteromorpha spp.	11.10	Pregnall and Rudy (1985)
Genista sp., *Stipa* spp.	0.76	Padilla et al. (2010)
Olea europaea	2.80	Testi et al. (2008)

(continued)

Table 1 (continued)

Ecosystem/taxonomic group	Quantification of C sink (t C ha^{-1})	References
Phragmites australis	26.10	González-Alcaraz et al. (2012)
Pinus halepensis	0.99	Grünzweig et al. (2007)
Pinus nigra	1.57	Padilla et al. (2010)
Pinus pinaster	5.7	Padilla et al. (2010)
Pinus sylvestris	1.58	Zha et al. (2004)
Pinus sylvestris	1.48	Padilla et al. (2010)
Populus spp.	0.632–1.061	Lafleur et al. (2012)
Potamocorbula amurensis (shell)	0.265	Chauvaud et al. (2003)
Prunus dulcis	7	Esparza et al. (1999)
Quercus ilex	2.78	Allard et al. (2008)
Ruditapes philippinarum	0.965	Komorita et al. (2014)
Sarcocornia fruticosa	12.98	Sousa et al. (2010)
Spartina alterniflora	2.16	Liao et al. (2007)
Triticum aestivum	1.85–2.45	Anthoni et al. (2004)
Ulva rigida	1.32–3.58	Sfriso et al. (1993)
Vitis vinifera	−2.27	Padilla et al. (2010)
Zostera marina	0.052–0.491	Röhr et al. (2016)
Flesh coral reef algae	7.30	Larkum (1983)
Coralline algae	3.29	Van der Heijden and Kamenos (2015)
Mediterranean gorgonians	0.014	Coppari et al. (2019)
Ecosystem/taxonomic group	**C sequestration (t C ha^{-1})**	**References**
Boreal forests	117	Bridgham (2014), Kuwae and Hori (2019)
Cropland	150	Bridgham (2014), Kuwae and Hori (2019)
Deserts	91	Bridgham (2014), Kuwae and Hori (2019)
Extreme desert, rock, ice	1	Bridgham (2014), Kuwae and Hori (2019)
Mangrove forests (soil organic carbon pools)	864	Bridgham (2014), Kuwae and Hori (2019)
Mangrove forests (aboveground)	78	Estrada and Soares (2017)
Peatlands	1497	Bridgham (2014), Kuwae and Hori (2019)
Salt marsh (1 m of sediment)	165.41	Macreadie et al. (2017b)
Seagrass beds	140	Bridgham (2014), Kuwae and Hori (2019)

(continued)

Table 1 (continued)

Ecosystem/taxonomic group	Quantification of C sink (t C ha^{-1})	References
Shrublands	122	Bridgham (2014), Kuwae and Hori (2019)
Temperate forests	196	Bridgham (2014), Kuwae and Hori (2019)
Temperate grasslands	159	Bridgham (2014), Kuwae and Hori (2019)
Tidal flat (1 m of sediment)	29.5–35.7	Kokubu et al. (2017)
Tropical forests	238	Bridgham (2014), Kuwae and Hori (2019)
Tropical savannah/grasslands	187	Bridgham (2014), Kuwae and Hori (2019)
Tundra	166	Bridgham (2014), Kuwae and Hori (2019)
Ecosystem/taxonomic group	**C biomass (g C m^{-2})**	**References**
Laminaria (standing crop)	220–720	Reed and Brzezinski (2009)
Ecklonia (standing crop)	270–610	Reed and Brzezinski (2009)
Macrocystis (standing crop)	120–273	Reed and Brzezinski (2009)
Nematoda (shallow subtidal environments)	0.2–0.5	Vranken and Heip (1986)
Calanus finmarchicus	2	Wassmann et al. (2006)
Calanus glacialis	2.5	Wassmann et al. (2006)
Nereis succinea	2.1	Cammen (1980)
Cavity-dwelling sponges	21.1	Richter et al. (2001)
Mobile epifauna (*Crangon*, *Carcinus*, *Pleuronectes*, *Platichthys*, *Pomatoschistus*)	6.3	Pihl (1985)
Sediment macrofauna (140–1850 m)	0.06–0.91	Woulds et al. (2009)
Sediment foraminifera (140–1850 m)	0.04–0.38	Woulds et al. (2009)
Tube-dwelling Amphipoda	10.7	Grebmeier (1987)
Zostera marina	627–6005	Röhr et al. (2016)
Corbicula japonica shell	12–176	Kuwae and Hori (2019)

ingested and respired C and was as high as 1.4×10^{-2} t C ha^{-1} (Coppari et al. 2019). We have information on the amount of carbon retained by key species or habitats, including terrestrial systems such as forests (Le Quéré et al. 2015), crops, and soils (Serrano-Ortiz et al. 2010) and marine systems such as seaweeds (Smale et al. 2016; Krause-Jensen and Duarte 2016), mangroves, and seagrasses (Macreadie et al. 2019). In these calculations, the carbon storage rate of mangrove forests and seagrass beds appears to be high, followed by saltmarshes and other coastal areas such as estuaries, continental shelves, and the deep-sea sediments. At first sight, the C retained by the three gorgonians species appears to be thus two orders of magnitude lower than other terrestrial (forests) and coastal (mangroves and seagrasses) ecosystems (Table 1) (Coppari et al. 2019). Nevertheless, we have to consider that the coralligenous habitat is made by several habitat-forming species: only three species were considered in that study, so it's difficult to compare it with the terrestrial counterpart where the habitats are represented by monospecific dominant engineers.

Among marine habitats, *Posidonia oceanica* seagrass is the most typical photophilic Mediterranean habitat type. It has similar features of terrestrial habitats, since they are made by main monospecific organisms. In the case of bioconstructions, made up of multispecific organisms, such as coralline algae, bryozoans, Cnidaria, serpulids, and many others, the constituents of the "physical" component of the habitat are represented by dead bodies of several perennial habitat-forming species, which create permanent concretions available for other live organisms. The main difference between bioconstructions (coralligenous and maërl habitats) and *Posidonia* meadows (and terrestrial habitats too) is that one is made of multispecific engineers while the other is made of a monospecific engineer. The list of habitat-forming species and of bioconstructors, in particular, represents an informative tool to assess the real capability to store carbon and on priorities for protection.

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. An impediment to the understanding of the dynamics of pelagic-benthic coupling and their energy transfer at local and wider scales (Rossi et al. 2017b) is represented by the wide variability in types of habitat-forming marine benthos, so there is a lack of general information about the distribution, life cycle, phenology, and ecophysiology of key species (Rossi et al. 2017a). Despite MAFs occurrence from coastal areas to the deep ocean, from polar to tropical latitudes, and from hard to soft bottoms (Rossi et al. 2017a; Paoli et al. 2017; Crocetta et al. 2020), their capability to sequester carbon in the form of long-lived structures, also known as blue carbon (Barnes 2018; Macreadie et al. 2019), remains poorly known. Then, underestimated amount of sequestered carbon by MAF may be a key to understand the "hidden carbon" in the global cycle (Serrano-Ortiz et al. 2010; Li et al. 2015; Belcher et al. 2019).

3.2 Future of C Sinks Due to Changes in Food Availability and Climate Change

MAFs are among the most vulnerable systems in front to global environmental change (Martin et al. 2014; Roberts et al. 2016; Rocha et al. 2018; Rossi et al. 2019a, c; Soares et al. 2020), and progress in understanding ecosystem processes has been slower than the fragmentation and destruction of these marine habitats caused by pollution, anthropic activities, and climate change. In this framework, climate change co-occurs together with the transformation of the seascapes of oceans and in turn by changing the energy availability and the metabolic rates of the organisms. Combined effects of environmental changes and anthropic impacts could modify the resistance or resilience of MAFs. Active and passive suspension feeding organisms could abruptly have to face severe changes in energy budgets and related consequences phenology, larval nutritional condition, and population viability. Loss of these habitat-forming species also would lead to loss of their role as an essential part of the biogeochemical cycles. The knock-on effects are multiple: we can think of the effects on soft sediments impacted by trawling where a decrease of 52% of organic matter content is accompanied by a reduction of the organic C turnover rates as well as reduction of meiofaunal biodiversity, abundance, and biomass (Pusceddu et al. 2014). These insights suggest that cumulative impacts will decrease the energy transfer and lead to benthic communities made by small organisms (Keil 2017).

We have to keep in mind that MAFs are composed of sessile filter feeders and then depend on primary and secondary productivity coming from currents (Steinacher et al. 2010; Bopp et al. 2013; Rossi et al. 2017b), being thus forced to face changes of food availability (Jones et al. 2014). Climate change, indeed, will affect their capability to capture particles. In the last decades, the decline of phytoplankton productivity has already been observed in relation with climate change, with seasonal shifts in several areas (Henson et al. 2013; Laufkötter et al. 2015; D'Alelio et al. 2016). Indeed if, on the hand, the high temperatures favor the growth of phytoplankton, on the other hand, nutrient availability depends on the appropriate mixing of the water layers. Primary productivity is affected by prolonged periods of water column stratification and reduced upwelling due to ocean warming; this modifies plankton migrations, and the benthic animals could not be able to store the adequate energy coming in discontinue ways (Curry et al. 2003; Doney 2006). In the next decades, some areas will have an increased productivity, whereas other areas will have a declined productivity (up to 20%) (Roxy et al. 2016). In the last areas, we will expect dramatic effects on marine animal forests, since the associated energy will be lower and will have consequences on their ability of recruitment. The pelagic secondary productivity will be affected by changes in phytoplankton productivity and environmental conditions provoked by climate change (Howes et al. 2015). As in benthic sediments, zooplankton communities are expected to constitute individuals characterized by smaller sizes (Richardson and Schoeman 2004; Daufresne et al. 2009). Zooplankton has a key position in marine ecosystems, transferring energy from primary productivity to higher trophic levels, such as sessile filter feeders (Gili and Coma 1998). Shifts in benthic-pelagic coupling (Griffiths et al. 2017; Rossi et al. 2017b) and changes in trophic efficiency of pelagic food webs (Fanelli et al. 2013) will profoundly influence benthic seascapes. All these changes could easily affect the capability to grow for the different MAFs around the world (Fig. 5). The C immobilization can be thus compromised (Rossi et al. 2019a).

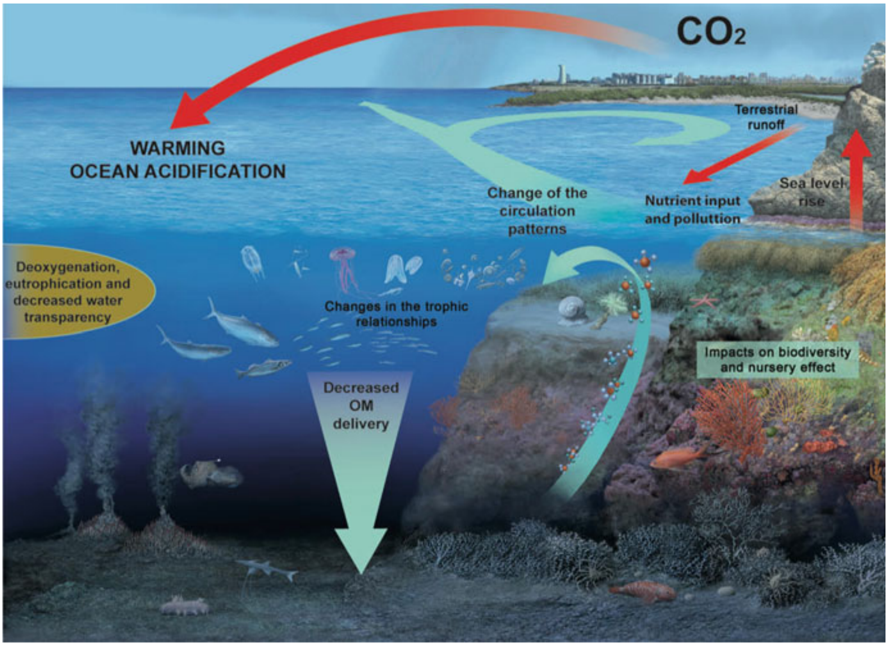

Fig. 5 Climate change will significatively transform seascapes and their capability to immobilize carbon. Sea warming and acidification will affect the water column not only transforming the primary and secondary productivity but also changing the biogeochemical cycles due to the direct impacts on deoxygenation. This will change trophic chains and the availability of food for benthic suspension feeders. Changes in circulation patterns will also transform the dispersive properties of the water column and the recruitment processes, impacting populations and also the community balance and biodiversity. The change in rain patterns and the sea level rise will also affect productivity and the potential light harvesting of key species (transformed from Rossi et al. 2019a; artwork by Alberto Gennari with some modifications from Gianmarco Ingrosso)

4 How We Transformed C Immobilization Through the Time: Some Interesting Stories

The optimization of resource capture by suspension feeders constituting MAFs pass through an increase of complexity of the living structures. In Octocorallia and Hexacorallia, as well as in Bryozoa, the bigger the colony, the higher the number of polyps or active lophophores; in Ascidiacea and Porifera, increasing the size of the specimens increases the captured organic material as well; in Bivalvia, the larger the individuals and the patch size, the higher the pumped water volume. This clearly demonstrates that larger and complex colonies/individuals/patches have a prominent role in benthic-pelagic coupling processes, in biogeochemical cycles, as well as in the carbon immobilization than in flattened and smaller three-dimensional alive structures. It is clear that the bigger the colony, the more we have also to consider the respiration but is also evident that the carbon immobilized will be higher compared with smaller (and denser) colonies (Cau et al. 2016). During centuries, but especially during the last 200 years, MAFs drastically changed due to the direct or indirect impacts and so their capability to sequester carbon in their structures (Thurstan et al. 2017). Knowing the forests of the past may give us clues about future predictions and how to apply tools for conservation.

4.1 Terrestrial Forests

Before we give some examples of how MAFs changed through the time and thus their capability to retain C, we may look at the terrestrial forests as C sink to better understand the extent of the change. Terrestrial forests cover 30% of the land (4.7×10^7 km^2). While in the atmosphere there are 810 Pg of C, terrestrial systems hold between 500 and 1500 Pg C, 60% on the above-mentioned forests (Whitehead 2011). Thus, terrestrial forests have an essential role in C retention, being responsible of an important part of the 3.0 Pg C retained per year (in comparison with 2.3 Pg C retained each year in the oceans, Whitehead 2011). Approximate calculations give a general number of 20% of the CO_2 emitted by burning fossil fuels sequestered each year by the living land biosphere (Pan et al. 2011; Le Quéré et al. 2018).

These terrestrial forests are always changing. In the beginning of the Holocene, the rapid regression of the glaciers gave the opportunity to different tree species to retrieve space, in some cases making displacements of the populations at a rate of 100 m per year (Petit et al. 2008). Climate change pushed the tree populations, increasing their capability as C sinks all over the planet. An unstable climate threats some tree species, uncapable to withstand with the new conditions such as water, wind, nutrient, etc. (Petit et al. 2008).

Thus, the change for these forests relates to changing conditions. As the terrestrial forests nowadays also are rapidly changing, their capability to store C is also in a transition phase. For example, from 1990 to 2015, an equivalent area of South Africa (129×10^6 ha) has been lost all over the world (0.13% of the total surface cover) (FAO 2015), and from 1920 to 1957, 8.8 Pg C were released to the atmosphere because of the transformation of forests to crops (Canadell et al. 2007). Climate change and bad forest management positive feedback are now increasing their impacts in several areas like Australia or the Amazon rain forest, diminishing the ecosystem functioning at a large scale (Barlow et al. 2020; Jager and Coutant 2020). These changes have a significant impact in the overall C cycle that depends on the biosphere. Global change and deforestation may unbalance the equation of carbon sinks and sources, with a positive feedback that may stimulate more and more sources and saturate sinks (Canadell et al. 2007). Such actions entail stewardship of the entire Earth system—biosphere, climate, and societies—and could include decarbonization of the global economy and enhancement of biosphere carbon sinks (Steffen et al. 2018).

However, it is very important to understand that the forest demography and composition are the key to understand if they are sinks or became sources of

C. Old forests (more than 140 years old) can retain 0.85 Pg C per year, while young forests retain 1.3 Pg C per year, with very different trends depending if we are talking about mid-high latitude or tropical forests (Pugh et al. 2019). An important part of the C retained everywhere is thus in transition, with only decades of retention until it is released again or is no longer capable to be immobilized for long times in the living structures.

4.2 Coral Reef Stories

Historical information of marine ecosystems can help us to document and interpret long-term change (Lotze and Worm 2009). Historical data sources could provide a picture of species and communities existed in our oceans in the past and furnish insights about the drivers of environmental shifts over the time (Jackson 2001). These studies furnish precious data of the decline degree and how the mechanisms of regime shift and alternate stable states induce loss of capabilities as C sink in coral communities.

In the Caribbean, elkhorn (*Acropora palmata*) and staghorn (*A. cervicornis*) corals were once dominant species; nevertheless in the 1980s, community composition has been subjected to large fluctuations and a series of episodic mortality events of corals has been observed. Declines in dominance from prehuman values first occurred in the 1950s for *Acropora palmata* and the 1960s for *Acropora cervicornis*, decades before outbreaks of acroporid disease or bleaching (Cramer et al. 2020). For hundreds of thousands of years, these species exhibited a remarkable dominance in Caribbean shallow coral reefs, as confirmed by fossil records, suggesting an important impact due to cumulative effects of several anthropic impacts (Pandolfi and Jackson 2006). These episodes have led to a shift in community structure now dominated by seaweed communities. Indeed, in the Caribbean, reefs near areas heavy stressed by long-term anthropogenic stressors such as fishing and declining water quality (Bocas del Toro, Panama) (Cramer et al. 2012; Pandolfi et al. 2003; Hughes et al. 2003) were affected by bleaching and diseases (Cramer et al. 2012).

Australian coral reef communities represent another example of strong decline of a once dominant coral in the central Great Barrier Reef (Roff et al. 2013; Thurstan et al. 2017) and in a coastal embayment south of the Great Barrier Reef (Lybolt et al. 2011) associated with European colonization. Although current and historical comparisons are difficult because of different approaches, the changes observed in these coral communities are unquestionable and without parallels in the historical record. It is hard to understand how these damaged ecosystems will change. Many Scleractinia-dominated assemblages are transitioning away toward non-Scleractinia communities. In the south coast of St. John, US Virgin Islands Scleractinia have experienced a decadal-scale density decline leaving space to other important benthic taxa. Some researchers demonstrated that the whole Octocorallia density increases occurred, especially after 2002 (Lenz et al. 2015). This finding suggests that scleractinian communities could be partially replaced by octocoral species (Lasker et al. 2020). Also in the Florida Keys, following the mass mortality associated with the 1997/1998 El Niño, abundance of reef taxa and stony coral species were evaluated from 1999 to 2009 in order to verify eventual shift in community structure. The authors reported that stony corals showed little recovery and continued to be a dwindling part of the benthic assemblage at deep and shallow forereefs. The cold water mortality event in 2010 could have increased the Octocorallia cover at the expense of Scleractinia and hence with a following persistent loss of the dominant, framework-building *Orbicella annularis*. The mass bleaching events together with other factors, such as disease, predation, and thermal stress, prevented the recovery of Scleractinia species in this Florida Keys reefs (Ruzicka et al. 2013).

It is well-known that Scleractinia have a greater ability as carbon sink due to the structure of their skeleton. This state of transition of coral reefs indicates not only changes in benthic composition but also losses of ecosystem capabilities to store carbon.

4.3 Emperor Sea Mountain Story

We don't know the extent of the MAFs all over the world. We don't have the notion of how they have been transformed and which is the potential capability to retain C. More dramatic is the fact that we do have an idea of how terrestrial forests changed through the time (FAO 2015), but we have no idea of how MAFs did. We can only guess a bit of what happened through some examples.

One of the most spectacular underwater mountain ranges on the planet lies in the middle of the Pacific, north of the Hawaiian Islands, the Emperor Sea Mountains, stretching more than 5800 km from the Aleutian Arc to Kure Atoll (Tsao and Morgan 2005). The particularity of this existence area is that this vast region is mostly submerged, the skirts of the mountains distributed in several thousand meters under the sea. There are gorges which climb from 1000 to 400 m, and their unique position allows them to host almost unknown wildlife. In 1965, the Japanese fleet, harvesters of precious corals, discovered vast populations of these and other cnidarians of great value and began systematic plunder. For this purpose, in areas such as the banks of Milwaukee on the seamounts of Koko, around 100 boats were equipped with special gears consisting of nets hung with heavy weights to drag all the organisms found at these depths. They caught up to 200 tons of *Corallium* sp. per year during several years (Koslow 2000; Tsao and Morgan 2005). The Russians and Taiwanese also exploited these deep banks area in the midst of international waters, following the example of the Japanese. In 1966, the catch was 375 tons of precious corals, especially *Corallium* spp. In just 3 years (1965–1967; Koslow 2000), more than a thousand tons of very long-lived coral were harvested, and some parts might have been centuries old. The catch in the area felt sharply, not only because the coral was taken from many places but because the price suddenly dropped due to the large volume of the product distributed on the market. During peak production, more than a hundred large tonnage boats swiped banks that had remained undisturbed for thousands of years. Grigg (2002) found, using ROV surveys, that in a non-trawled area of this zone, the colony mean density of *Corallium secundum* may be 0.3 colonies m^{-2}. In the area surveyed (4.3 km^2), this means a potential presence of 1.26×10^6 colonies only of this species. Due to the fact that the richness of the mega-epibenthic fauna (especially Gorgoniacea and Scleractinia) in non-trawled zones is very high (Miyamoto et al. 2017), the potential C stored in these MAFs may be really high.

In 2006, a Japanese expedition made several transects in the area using a special robot able to descend to more than 400 m in an Emperor Sea mountain trawled area (Rossi 2019). The report mentions sparse fauna, just a gorgonian or coral branch here and there. We will never know about the complexity, density, and population structure of the different species in these high-canopy coral forests in that area prior to the looting, because the systematic removal of all sessile organisms has done so much damage that their distribution and numbers are unclear. Some places were probably beautiful, filled with all kinds of organisms taking advantage of the currents and the shelter of this lush marine forest in areas where no one would have imagined so much exuberance. It will be hundreds, if not thousands, of years in the future before the area recovers from this devastation for the sake of items of jewelry.

4.4 Red Coral Story

We definitively lost the red coral forests, gorgonians that shaped like a small vermilion tree at the bottoms of different areas of the Mediterranean. This is perhaps one of the least known and saddest phenomena to have taken place in our seas (Tsounis et al. 2010a). Precious corals have been traded since the earliest times (Tescione 1968). In particular, the exploitation of red coral (*Corallium rubrum*) has a long history, from the Paleolithic period. Remains of objects made of red coral have been classified from more than 25,000 years ago, and in the Neolithic age, it was already being traded by the Minoan and Mycenaean civilizations (Jiménez and Orejas 2017). Whole branches of this coral were found after strong easterly storms: even in the twentieth century, until a few decades ago, it could be found in some places of northern Catalan Coast after gales (author's personal observation). It became an important material of the Mediterranean culture, being later on exported to places such as Nepal, China, Japan, Yemen, Persia, and Jordan (Tsounis et al. 2010b; Jiménez and Orejas 2017). We have found engravings from that time showing people extracting large branches of red coral by free diving, so it must have been at shallow depths. After the proliferation of amulets in the Roman Empire, the use did not decline with the arrival of Christianity, which used it, especially in the beginning, as a protection against Satan (Jiménez and Orejas 2017; Price and Narchi 2015). Extraction spread, gradually becoming industrialized and no longer from shallow depths by free diving, because the red coral that could be reached that way had probably been exhausted in accessible places (Tsounis et al. 2010b). Deeper and deeper extraction was the norm, and more and more men and boats were being used to obtain the precious "red gold." The exploitation, more mining than fishing, consisted of finding a coral bank and extracting coral until it was exhausted and then moving to the next patch. The *coralline* (boats dedicated to coral extraction) reached their maximum numbers in the nineteenth century, when the craft and market were gathered in Torre del Greco, near Naples. In 1862, there were about 350 ships, and in just 2 years, these increased to more than 1200 for the systematic plunder of the known banks (Tescione 1968).

One of the most spectacular and valuable source of *C. rubrum* was discovered at that time in the legendary Capo Caccia Cavern in Sardinia at a depth of 37 m (Liverino 1983). Liverino (1983) reports that in 1956, divers worked at 30–35 m, but only in few years later, in 1958, they worked at 40–45 m. By 1964, an ever-growing group of divers was working at depths below 70 m, and inevitably, a long list of accidents were the result of the spreading "coral fever" among the younger divers (Liverino 1983). Leonardo Fusco reported that in 1955, he harvested at 60 m in the Gulf of Naples but in 1964 he had to descend to 90 m. Similarly, pioneer Fausto Zoboli is reported to have said that he worked as one of the first at 60 m in 1964 (near Rome), while in 1971, he was forced to work at 100 m in Alghero, Sardinia (Liverino 1983). Others similarly documented that by the late 1950s, divers in France and Italy already had to descend to depths of 80 m, and at times to even more than 100 m, to find coral (Galasso 2000). In 1974, helium-based mixed gas diving techniques developed by the French ocean engineering company COMEX started to spread among coral divers, permitting them to work at 120 m for 20 min without the dangers of nitrogen narcosis (Liverino 1983). Step-by-step, red coral large branches disappeared, and divers had to go deeper and deeper (Tsounis et al. 2010b). This was not a new thing; long before (100–150 years before), the industrial dredging completely transformed the red coral (and the coralligenous) populations with intensive harvest that was prolonged until the 1980s (Tsounis et al. 2010b). The transformation of such *Corallium rubrum* populations was so huge that cannot be even recognized (Tsounis et al. 2013).

Red coral began to disappear from certain areas, from where it would never recover, and in others, it was then exploited until the forest of red "trees" of about 20–30 cm in height (branches up to 50 cm and trunks of over 3 cm in diameter are known) was reduced to a field of mere blades of grass just 4–8 cm in height and a few mm at the base (Tsounis et al. 2013). The last major bank to be exploited was Alborán in the 1980s, where *corallines*, especially from Sicily, plundered the unspoiled resource without control (Tsounis et al. 2010b). The arrival of scuba diving in the 1950s and 1960s was the final blow, because divers could penetrate the coral reefs where the bars and beams of the St Andrew's cross-style gear and nets could not: caves, cracks, ceilings of large rocks, and walls. In the Medes Islands (Girona), in the 1960s and 1970s, the Cow Tunnel was an underwater cathedral, its walls almost entirely lined with crimson forest. Within a few weeks, divers had destroyed the red trees, removing everything. Today there is hardly any coral—here

Fig. 6 Red coral harvested in the shallow waters off the Sicily coast, in the eighteenth century. We can observe the precious coral (large colonies) collected by freediving activity, nowadays impossible (From Giovanni Tescione 1973)

and there, in the tunnel, twigs of a few centimeters in length try to survive and grow (Boavida et al. 2016).

A few millennia ago, the hard substrate, the rock of Mediterranean coasts, must have been widely populated by this red forest, a living stone paradise formed by the slow-growing organism, red coral (Fig. 6). As an eco-engineering species, its three-dimensional structure added a great deal of complexity to the system (Rossi et al. 2008). It served to retain particles and transform currents, had a great impact on the recycling of matter, and was a refuge for countless organisms. In a recent long-term study, it has been shown that red coral populations have been drastically changed and only in marine protected areas they recovered (Tsounis et al. 2006; Linares et al. 2011; Garrabou et al. 2017; Mallo et al. 2019). The carbon retained nowadays (one of the very few numbers that are available about the potential C sequestration by the MAFs) is quite ridiculous, but this is mainly due to the fact that the data available (data in which you may trust, Mallo et al. 2019) are very recent and belong to populations already transformed. The vermilion forest has disappeared, and we shall probably never see the like of this splendor again. We can only guess how much carbon was retained by the red forests of the past, just few centuries ago.

4.5 Oyster Beds

Oysters (Mollusca Bivalvia of the family Ostreidae) were systematically exploited from 1800 until they were removed by mechanical means (excavators) in 1870, cleaning the channels of these mollusks. Little by little, the regression of the oysters had unexpected effects. These animals are active filter feeders, captured particles from the water column to the benthos, increasing water clarity and hence acting as the kidneys of the system (Jackson 2001). Before 1850, they were able to filter all the water in the bay in a week. Recent estimates of the density and distribution of these creatures put the time needed to do the same task between 46 and 50 weeks (Officer et al. 1984; Jackson 2001).

Using fishery data together with other historical sources, fishery collapse has been reconstructed as firstly started in estuaries nearest to developing urban centers and widely spread along the coast of North America and eastern and south Australia (Kirby 2014; Alleway and Connell 2015). Along the Gulf of Mexico Coast, several estuaries were individuated as historically having been dominated by oysters, while now oyster population cannot filter and clean appropriately the volume of water in most estuaries (zu Ermgassen et al. 2013). Only occasionally punctual data contain quantitative estimates of what has been lost, so we can calculate the areal extent and density of historical oyster reefs (zu Ermgassen et al. 2012), showing 88% decline in oyster biomass and a 64% decline in the spatial extent during the last century. Unfortunately, nowadays, oyster beds are destructed throughout much of their original range (Beck et al. 2011). We have lost oyster habitat before understanding the historical extent of these habitats, their natural density, size distribution, and population dynamics and composition of the community associated with it. Oyster beds were thus once rich (Thurstan et al. 2017), probably capable to immobilize huge amounts of C.

5 Who Is Destroying the MAF C Sinks?

In terrestrial forests, the human impact is huge, but the human impact on the ocean is even more rapidly increasing, with largely unknown consequences (Halpern et al. 2008, 2019). During the last decades, there has been an increasing evidence of important changes in these marine ecosystems due to human-induced disturbances, which are dramatically reducing biodiversity, biomass, and resilience of the animal forests all over the world (Rossi et al. 2017a). Most of these impacts are in the benthic ecosystems, being those below the twilight zone and in deeper regions especially problematic to quantify and solve. There is a combined effect due to many stressors acting at the same time (Rossi 2013).

5.1 Bottom Trawling in the Continental Shelf and Deep-Sea Habitats

We are destroying at an unknown rate the seafloor communities (but all the experts confirm that at a higher rate than in the land), affecting wide areas in which the animal forests are dominant elements of the ecosystems. For example, it has been calculated that 1/3 of the continental platform of the world is bottom trawled each year (Thrush and Dayton 2002), not even considering deep bottom trawling that has been dramatically increased in submarine canyons or sea mountains where deep-water corals structure the habitats (Clark et al. 2010). A forest being dragged away by a net is an outrage on land, but this is what happens underwater when a trawler drags the seabed's complex system: the MAFs. Bottom trawling is one of the main causes of disturbance to the balance of species and ecosystem energy flows, if not the chief culprit. Among all the methods of resource extraction, trawling has definitely been the most damaging in the past century and continues to inflict damage (Thrush and Dayton 2002). Why? Trawling scrapes the bottom, clearing wide areas not only of mobile fauna (fish, cephalopods, crustaceans, etc.) but sessile fauna and flora (sponges, gorgonians, corals, marine spermatophytes) that provide complexity in the marine system (Aguilar et al. 2017). The impact of fishing gear on the seafloor depends on its mass, the degree of contact, and the speed at which it moves. In some places, such as California, the average trawl is 1.5 times per year and in some areas up to three times per year. Near Hong Kong, there may be trawling up to three times a day, and elsewhere are areas that have seven trawls per year (there are plots where the same area can be trawled 400 times a year) (Thrush and Dayton 2002) (Fig. 7).

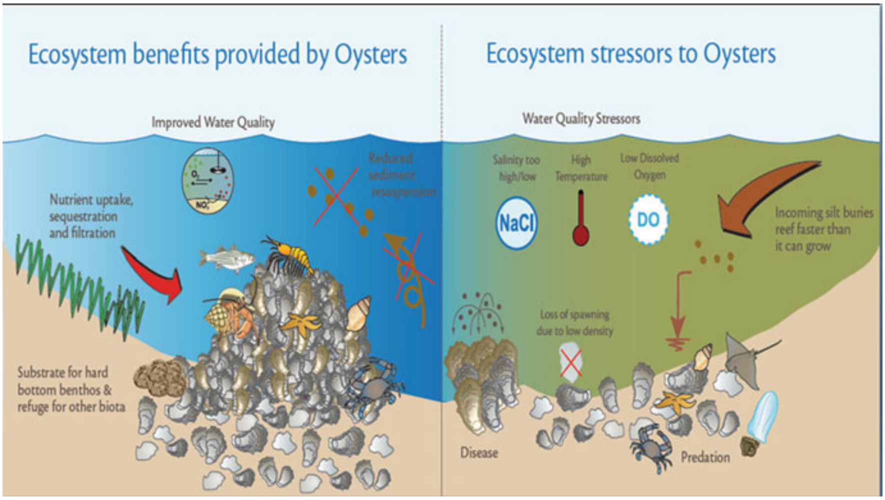

Fig. 7 Oyster beds provide different ecosystem services; one of the most important is the capability to actively filter particles such as detritus and phytoplankton, transforming part of such organic material in immobilized carbon. The depletion of these organisms has a direct impact on the overall system and also is net loss for the carbon immobilization (with the permission of https://estuarychesapeake.wordpress.com/tag/oyster-reefs/)

Even if is a very rough approximation, we can make some numbers. If we have 12,000 trawler ships (well below the true, FAO Report 2018) with a net mouth of 25 m wide, operating at about 5 km per hour for 6 h on 175 days a year, the swept area will be about 1575 million km^2. Spain has around 505,000 km^2, so it will be as much as three times the area of this country. If we count on the world's continental shelves, an equivalent of 5.6% of this area of the planet is trawled every year. But there are many more boats that undertake dragging in other areas, so this estimate falls far short. Some specialists estimate that about 15 million km^2 are trawled each year, more than half of the area of the continental shelf (Thrush and Dayton 2002). As an intermediate approximation (20%), the bottom of the entire global continental shelf is being disturbed once every 5 years (Thrush and Dayton 2002). There are some almost undisturbed areas and other places where dragging is carried out extremely frequently. The area affected by trawling is estimated to be about 150 times that of the forests cut down on land, which is 0.1% per year. Unfortunately, no one exactly knows how much of the planet we have been disturbing by dragging. While in shallow areas the impact is well studied, in deep areas of our oceans, it is practically unknown (Hinz 2017).

The deep ocean, related to sea bottoms deeper than 1000 m, is estimated to be 62% of the planet surface. Despite over 150 years of deep-sea researches, it remains largely unexplored. These huge areas are intensively impacted by bottom trawling and mining (see below), and a recent work suggests that industrial fishing occurs in >55% of ocean area and has a spatial extent more than four times that of agriculture (Kroodsma et al. 2018). Dramatic impacts on the seamount benthos off Tasmania (Australia) have been documented where fragile biogenic habitats constituted by stony corals have been declined until two orders of magnitude and diversity and density richness of benthic communities reduced threefold with scarce evidence of recovery in areas where bottom trawling had been strongly reduced a decade ago (Roberts 2002). Due to slow growth rates and fragility of the deep-water corals, the closure of fishing could not be enough to restore C sink capacity of complex habitat (Fig. 8).

5.2 *Deep-Sea Mining*

The exploitation of the sea in terms of minerals is not new, but we are increasingly prospecting and exploring deeper and deeper. There are many areas susceptible to systematic exploitation, and the few companies capable of doing so already see real benefits in this. There is an increasing pressure on science and technology to find new resources and extract them profitably from the seabed (Morgan et al. 1999; Murton 2013). Currently, of more than 200 areas of underwater exploration, 10 have ores to exploit profitably, each concentrating a deposit of potentially more than 100 million tons of ore (Murton 2013). There are more than 100,000 seamounts around the world (Wessel et al. 2010), so, in fact, more than 155 countries could benefit directly from this beneficial business, which will soon be systematic. Also, in

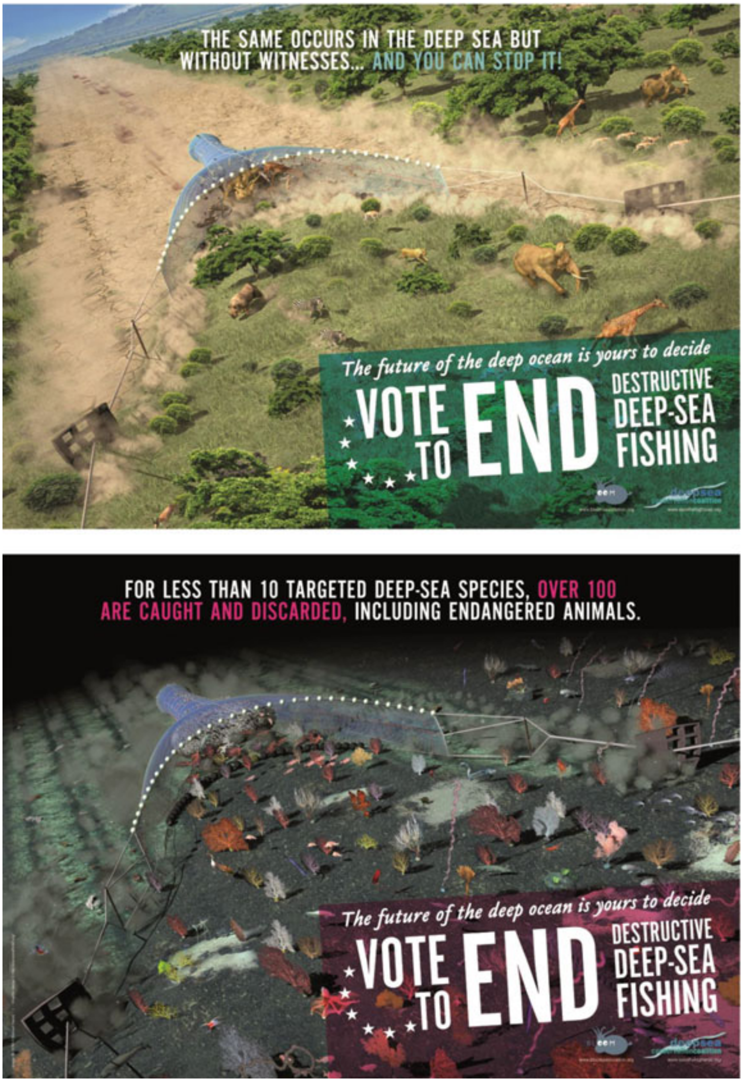

Fig. 8 Outreach campaign by Bloom Association (https://www.bloomassociation.org) to sensibilize people about what is happening in the seafloor, especially on the continental shelf, due to the intensive bottom trawling all over the world (from Rossi et al. 2017a; Images courtesy of Bloom Association)

many cases, no one needs to be asked for permission, because many of them are located in international waters, and as we have already seen with precious corals or trawling, the question is who comes first and takes the spoils. Some 400 sites have already been successfully explored, 165 of which have exploitable material that could be exploited for profit (Murton 2013; Clark et al. 2020).

Oil platforms, polymetallic nodules, carbon dioxide sinks—there are very few information written on how to conduct environmental impact studies (Clark et al. 2020), their consequences for deep-water communities, or the degree of susceptibility of areas being prospected, exploited, or used. Little work that has been done to understand how communities function at those depths and how it would affect them if minery began to move huge amounts of rock and resuspend sediments, being possibly even worse than that of trawling (Clark et al. 2010; Washburn et al. 2019). The direct impact of mining will be, in a near future, a cause of concern for the MAFs. Once the action is a large-scale operation, the destruction of the long-lived structures may be irreversible. It has been shown that, once impacted, these deep-sea MAFs do not easily recover (or don't recover at all, Boschen et al. 2013).

5.3 Coastal Transformations

One of the biggest problems for the MAFs is that more than half of the world's population lives less than 200 km from the coast, and all this activity, all that movement, has a direct impact on the sea. Coastal areas are, undoubtedly, one of the more pressured and threatened ecosystems on the planet (IPCC 2018). Let's explore a part of the planet in full development to give an example: the sea of the Persian Gulf. Due to the uncontrolled growth, every shore in Qatar, United Arab Emirates, and Kuwait is undergoing a rapid degradation of its ecosystems (Sheppard et al. 2010). We must bear in mind that the waters of this sea, mostly off the Arabian peninsula, are very shallow and some areas have been flooded for only 3000 or 4000 years, due to the ingress of the sea caused by the melting of glaciers and polar ice caps after the last ice age about 15,000 years ago (Haq and Milliman 1985). We are therefore facing coral reefs, mangroves, seagrass beds, and quite recent macroalgae (Sheppard et al. 2010; Fabbrizzi et al. 2020). Coastal ecosystems are areas where the sheets of shallow waters are very large. Since the beginning of the 1990s, when pressure began to be exerted for industrialization, the creation of ports, airports, canals, or desalination plants, as well as residential complexes or luxury business centers, there is no more than 40% of the coastal area left. In some cases, there has been such drastic alteration that it has led to changes in currents and areas of increased evaporation of water in the world where the sea is already more saline, due to its hydrography.

In certain areas, such as the famous artificial islands off Dubai, the coastline has been increased by 11% (more than 90 km^2), gaining ground on the sea and degrading the surrounding areas by adding sand (Sheppard et al. 2010). More than 150 km^2 have been lost, where the turbidity, the addition of nutrients, and changes in currents already reflect the drastic changes in the dynamics of systems. Such is the lack of an appropriate management in the region that there are already recurrent eutrophy and algal blooms and an absence of hydrodynamics (Saunders et al. 2007; Ali et al. 2015).

There are two other examples of nefarious coastal management: Cancun and the Riviera Maya, Mexico. Tourist expansion here has been the fastest and least planned ever known. Cancun alone has about four million tourists every year, spending more than 4000 million dollars. Beaches have been transformed and mangrove swamps destroyed, and there has been strong eutrophication and erosion of the reef, which has gone from 40% live coral cover in the 1980s to less than 5% in 2010 (Arias-González et al. 2017). There is no control, and the resident population, without proper services, has grown from about 60,000 inhabitants to almost 800,000 in just two decades (Clancy 2001). Everything has changed, the chemical flows, availability of drinking water, biodiversity, and the complexity of ecosystems (Arias-González et al. 2017) The *Sargassum* blooms only worsen the situation (Langin 2018). These algae are now rotting under the sand and leaving a worrying stench. But the worst thing is that they are also out on the reef, which is lethally poisoned by pollution from uncontrolled nutrients and stifled by the lack of fish that had controlled both them and the feast of phosphates, nitrites, and nitrates released by faulty hotel control system (Arias-González et al. 2017).

With no doubt, the coastal development has been a key factor in coastal areas to understand the loss of C sink capacities of marine forests, including the MAFs (Rossi 2013). These anthropic stressors influence coastal ecosystems directly or indirectly, modifying ecosystem health and living resources. A very interesting yet not well-understood stressor for MAFs are the intensive aquaculture facilities. Let’s take the case of the Chilean fjords: they are recognized as a biodiversity hotspot (Häussermann and Försterra 2007), a unique, highly vulnerable and fragile ecosystem (Iriarte et al. 2010) that extends over 240,000 km^2 and has more than 80,000 km of coastline and hosts, among the various species living are several MAF species. Despite the ecological importance, the Chilean fjords were characterized by a fast-economic development from high-impact industry-scale salmonid farming, infrastructure, and industrialization projects up to growing extractive activities with no sustainability plans in the exploitation of the marine resources. In particular, 3058 aquaculture (1493 fish farms) concessions were registered for Chilean Patagonia in 2013, and salmonid farming reaches US$2–2.5 billion in export market and a production of 1 million tons of salmonids by year. When we compare the density of farms in these areas with those of Norway, we find much higher values, up to 40 other concessions in a radius of 15 km; Proctor et al. 2009). This growth of aquaculture sector leads to elevated sedimentation (Wlodarska-Kowalczuk and Weslawski 2001), eutrophication (Mayr et al. 2014) and hypoxia, with consequent profound changes in the benthic communities and death of marine animal forests directly under the farms. Due to the anthropogenic transformation at large scale of the region caused by the salmon farming industry, once the communities of fragile and long-living species of these organisms decrease, their recovery might occur in a long term or not able to fully cope with them (Haya et al. 2005). The magnitudes and rate of degradation of MAFs in Chilean Patagonia are worrying, especially in the south part where there are pristine areas (Niklitschek et al. 2013). The anthropic activities are radically influencing the structures, functioning, and processes of the coastal areas where densities of aquaculture installations are extreme, threating Patagonia to lose numerous ecosystem services irredeemably (Outeiro et al. 2015).

5.4 Climate Change

The impacts of climate change exceed the capacity of many stressed organisms. The species have a highly rapid onset, but animals and plants, even if they can adapt to environmental and biological changes and acclimatize to specific situations, face fast-changing conditions rarely found in other critical moments of the planet, and this phenomenon is also true for the components of the MAFs (Hughes 2003). Even if these impacts are not the main target of the present chapter, a brief explanation must be included, because their additive effects also affect the MAF health and future adaptation.

Briefly, there are three main effects of climate change on the animal forest: warming, ocean acidification, and sea level rise. All these impacts act synergically. For example, coral bleaching has been related to a seawater temperature shifts in coral reefs all over the world. Over the coming decades, coral mortality may reach up to 60% in the areas where corals are present as a fundamental part of the benthic structure of the marine animal forests (Grottoli et al. 2006). The bleaching phenomena have increased in frequency and strength, and another phenomenon related to sea warming is already ongoing: the increase of the intensity of hurricanes (Veron et al. 2009) (Fig. 9). The bleaching phenomena and the impact of hurricanes are patchy, due to the wide biogeographic differences in the response to climate change, depending on the species composition, the topography and main current regime, as

Fig. 9 Bleaching in Pacific coral reefs. Before and after the bleaching. If the bleaching effect is too long, the reef loses the capacity to withstand, the biodiversity is lost, the productivity drops, and the massive phenomenon of bleaching is more and more intense and frequent, as the temperature of our seas rises (Source: https://desdemonadespair.net/2016/04/coral-crisis-great-barrier-reef.html)

well as the health status of the environment (Bellwood et al. 2004). Together with these two phenomena, ocean acidification is also affecting the organisms in different ways, especially those based on the $CaCO_3$ precipitation. Thus, the animal forests based on hermatypic corals (which seem to be the most affected, Hoegh-Guldberg et al. 2007) are now the most sensitive to the synergic effects of warming, hurricane destruction, and ocean acidification, changing their abundance and distribution because of the effects of these climate changes.

We argue that the MAFs in the oceans are thus in a transition state, shifting from the natural range of variation, found prior to the industrial revolution, to an unpredictable state that may or may not stabilize during decades or centuries (Rossi et al. 2019a). As previously mentioned, in our oceans the energy availability and the metabolic rates of the organisms are changing under the effects of climate change. The fast-ongoing environmental changes are modifying energy fluxes, acting in synergy with increasing anthropic pressures on MAFs (Rossi et al. 2019a). Warming and changes in ocean acidification operate at multiple spatial and temporal scales: they cause rising temperature, acidification, sea level rise at large scale, and heat waves, tropical cyclones, and strong storms at local scale. The decrease of the oxygen concentrations caused by greenhouse gases and ocean warming affects the microbial loop with effects on marine food webs and the dynamics of organic carbon transfer (Howes et al. 2015; Keil 2017; Breitburg et al. 2018). Sea level rise contributes to increment of coastal erosion and turbidity, mixing, and circulation and in turn to decrement of light availability (Storlazzi et al. 2011) for MAFs composed of mostly symbiotic corals. Moreover, the increasing salinity due to the increases in seawater temperature associated with evaporation rates (Rixen et al. 2005; Vargas-Yanez et al. 2010; Borghini et al. 2014) is crucial for current circulation and ocean mixing depth and, once again, for the efficiency of nutrient transfer.

Climate change is altering the complex dynamics of extreme habitat leading to large blue carbon losses. According to Barnes et al. (2018), an ice shelf calving a 5000 km^2 iceberg actually is estimated to contain approximately 106 tons of immobilized zoobenthic carbon per year ($t\ C\ year^{-1}$); consequently, giant iceberg formation represents a severe negative feedback of climate change (Barnes et al. 2018). Many factors worldwide are thus eroding the capability to maintain the C in long-lived structures, and we have to understand that possibly part of the positive feedback that is seen in the increase of greenhouse gases in the atmosphere may be due to the loss of terrestrial and ocean forests' capability to immobilize the carbon.

5.5 *Are We Losing an Ally?*

We have seen how the co-occurrence of anthropic impacts and climate change can lead to rapid changes and discontinuities in energy availability that have repercussions on the carbon immobilization capability of the organisms. Profound bounces in energy budgets of marine animal forests prolonged in time are expected to cause alterations in the biogeochemical cycles.

The loss of the capability to store C in marine animal forests will contribute to an intense and unknown degradation of fragile, biodiverse ecosystems in large areas. When they are impacted, the retention of organic matter and benthic-pelagic coupling processes are altered. Since MAFs lose their typical three-dimensional structure, their sizes become smaller, the branch number decrease, and their biomass is reduced. We know that benthic communities of shallow rocky reef affected by ocean acidification meet a decrease of the variability of communities. This led to homogenization and loss of the functional diversity at a landscape scale (Kroeker et al. 2013). Degradation processes accelerate simplification process toward more immature and less diverse three-dimensional structures. This confirms that soon the ecosystem will be simplified through environmentally mediated changes in community dynamics, with cascading impacts on functional diversity and ecosystem function (Kroeker et al. 2013). The simplification of MAF systems and their complex interactions pushes toward a bidimensional system without a solid base of adaptation (Jackson 2008), eliminating top predators and other key species able to structure the habitats.

Nowadays we do not have the tools to avoid the collapse of the animal forests and the ongoing oversimplification process of marine systems, since there is a poor understanding of the MAF distribution, processes, and patterns, and we do not know the metabolic, physiological, reproductive models. A holistic and ecosystem-based view is needed to cope with the loss of the system functioning and to guarantee the survivorship and the recovery of the animal forests (Rossi 2019).

6 Preservation and Restoration: Challenges and Some New Ideas

Once it has been demonstrated the gap of knowledge about the potential global role of the MAFs as carbon sinks (or as carbon immobilizers) and the fragility of these systems, we have to understand how to protect them and what are the tools to restore the complex systems they constitute. It is clear that at least an important part of the CO_2 is trapped in these structures, sometimes (e.g., in coral reefs or Antarctic megabenthic communities) for very long periods of time (Barnes et al. 2018; Macreadie et al. 2019).

Because seascapes are fast changing especially due to climate change (Rossi et al. 2019a), we need to act now to preserve and enhance their role as carbon sequesters (among other things). We observe such changes almost “in real time,” seeing that several species, for example, move poleward due to climate change forcing or deeply change their phenology (Rossi et al. 2019c; Sanford et al. 2019). In a world where 59% of the ocean areas accumulate different impacts (especially coastal areas, but also offshore zones, Halpern et al. 2019), we must take action as soon as possible with ambitious plans.

As previously mentioned, MAFs may be our allies in mitigation policies against climate change impacts. It has been suggested that tropical rain forests of Africa and South America may be on their limit to uptake CO_2, due to climatological (because of climate change) and management factors (Hubau et al. 2020). This means that carbon sequestration (these forests are responsible of the 50% of the CO_2 uptake in terrestrial areas, and 15% of the greenhouse gases is captured by these complex habitats) may be saturated or even declining (Hubau et al. 2020).

The blue carbon is, with no doubt, one of the most challenging issues to understand, having an important role in carbon sequestration (Howard et al. 2017; Lovelock and Duarte 2019; Macreadie et al. 2019). If the terrestrial areas suffer because climate change (and mismanagement) is transforming the capability to capture CO_2 (fires, droughts, desertification, etc.), possibly marine animal forests may partially be the solution to make mitigation plans. We know that the quantity of sequestered carbon is underestimated, possibly by orders of magnitude, in these habitats. It is clear that the carbon sequestration rate per unit surface area will never be as high as in terrestrial or transitional (coastal) habitats but may be a key to understand the "hidden carbon" in the global cycle (Serrano-Ortiz et al. 2010; Li et al. 2015; Wang et al. 2016; Belcher et al. 2019). Protecting and making ambitious restoration plans may be the key for the immobilization of the excess of CO_2 produced by humans, waiting for the clear response needed to transform our carbon-dependent society.

6.1 Conservation Measures for Marine Animal Forest Carbon Sinks

Conservation of MAFs is the necessary step that must be considered to enhance the possibility to immobilize and store part of the primary productivity of the oceans, helping the mitigation of climate change. Bottom trawling is, as previously mentioned, the most destructive method with direct impact of eroding the complex structures of MAFs in continental platforms and deep-sea habitats (Rossi 2013; Hinz 2017). Bottom trawling has been claimed as the most devastating practice in the benthos since long time ago (Jones 1992; Thrush and Dayton 2002). As far as 1376 A.D., the Britain Parliament made a curious statement, in which the fishermen claimed that the "algae" of the sea were swept out and the fish yield was drastically reduced by the trawling impacts (Jones 1992). The fishermen in that moment made a cause-effect relationship of this fishery with the impoverishment of the area. More rigorous was Garstang in 1900, probably the first paper in which this kind of biodiversity and biomass impoverishment was quantified (Garstang 1900). The evidence of those impacts nowadays has been quantified in MAFs (Thrush and Dayton 2002; Aguilar et al. 2017; Gori et al. 2017). To seriously preserve MAFs, bottom trawling must be banned in all the areas of the world, avoiding the destruction of a potential C immobilizer (and biodiversity promoter) (Rossi 2013; Rossi et al. 2017a).

Deep-sea mining is also envisaged as an impact that will be more frequent in several areas of the planet (Clark et al. 2010; Boschen et al. 2013). This practice has a devastating effect. After 26 years, a deep-sea area monitored after a deep-mining experience demonstrated that sessile suspension feeding organisms have not recovered, being present mostly detritivores, deposit feeding, and scavengers in the impacted zone (Simon-Lledó et al. 2019). Heterogeneity was drastically reduced, and the authors claimed that some species were irreversibly damaged. The question raised is what can be considered "serious harm" and how it can be quantified (Levin et al. 2016). In a marine habitat, any effect from a specific activity that promotes a significant adverse change in the biota (biodiversity and functioning) is considered a serious harm (Levin et al. 2016). We suggest here to include in such "significant adverse change" the capability to sequester C in the complex structures of MAFs. In deep areas, such as submarine mountains, canyons, or continental slopes, MAFs are particularly abundant and fragile (Jiménez and Orejas 2017), so this "serious harm" concept has to be a priority in the conservation and management plans, especially because we still don't know how much C can be immobilized by these suspension feeding organisms and the associated fauna.

Other impacts have to be considered, as previously stated, but the mechanical action that devastates the benthic habitats is a priority. The concept that we have to consider making a proper management and conservation plan is wider than the one developed during the last decades. We have to see the conservation areas as a whole, connected cells as described by Boero (2015). The "cells of ecosystem functioning" concept describe a set of ecological processes that affect not only the local fauna and flora but also the biota in far zones that are connected by oceanographic processes (Boero 2015; Boero et al. 2019). The concept is interesting because the relationship between planktion and benthos is considered, relationship between plankton and benthos, a neglected path that helps in the understanding of the system as a whole (Boero et al. 1996). Boero (2015) insists in the importance of properly describing, managing, and protecting also the water column biodiversity, biomass, and associated processes to make a good conservation practice of the benthic habitats, including MAFs (Fig. 10).

In the carbon sink-carbon immobilization processes of the MAFs, the study and preservation of the water column represent a crucial step. As suggested by Rossi et al. (2019a), changes in the water column productivity and biodiversity due to climate change will have consequences in the seascape performance, in the distribution, and in the survivorship of many benthic suspension feeders. According to "cells of ecosystem functioning" concept, the study of all the components is needed to understand the potential impacts even in areas placed at long distances (Boero et al. 2019). For example, it has been suggested that in areas like the Northern Adriatic Sea and the Gulf of Lions (Mediterranean Sea), dry extreme cold winds (the main driver of cold water cascade, bringing sediments, oxygen, and food to the MAFs) may be reduced, producing a direct effect on the viability of deep-water

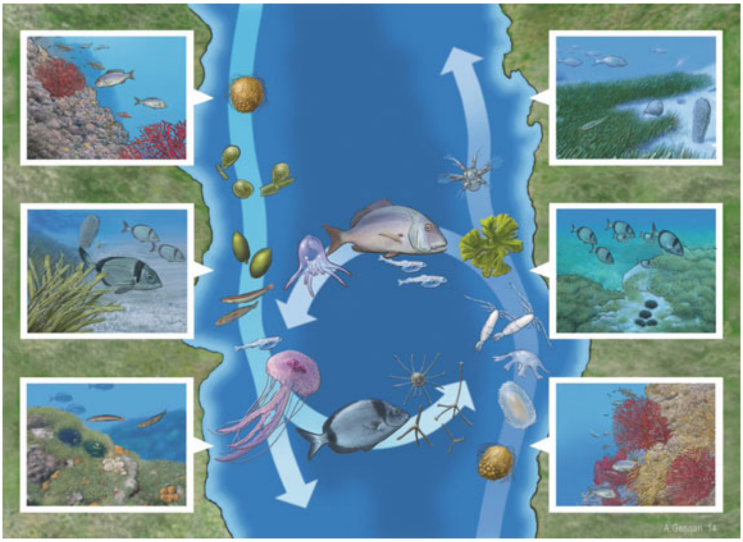

Fig. 10 Cells of ecosystem functioning. To perform marine conservation plans, we should consider the whole connectivity of the different communities, including the plankton. Mature benthic communities will store more carbon, but maintaining such population dynamics depends on the capability to have a supply from different sources, not only a punctual benthic community. The study of such metapopulations, their trophic interactions beyond local processes, and large-scale preservation has to be seriously considered in future management plans of the marine animal forests (from Boero et al. 2019, artwork by Alberto Gennari)

populations (Taviani et al. 2016; De Clippele et al. 2018; Boero et al. 2019). Hypoxia can also have dramatic consequences for their metabolism, altering the input-output equilibrium, which will be reflected in their survivorship (Gooday et al. 2010). Reducing the deep-sea MAFs will consequently reduce the capability to immobilize C, thus acting against the mitigation effect of these biodiversity hotspots.

The protection of the cells of ecosystem functioning has also another important task: protecting the capability to restore damaged populations through the connectivity of the system. The biophysical models and the genetic approaches help to understand that distant coral populations may be almost isolated or highly connected (Jones et al. 2009). Such connection may be a key point to maintain or enhance the possibility to immobilize C, allowing the growth of new generations and increasing the complexity of the structures. The Great Barrier Reef in Australia, for example, is more than 25,000 km^2, and more than 3000 reefs are identified to be large as 500 km^2 or small as less than 1 km^2 (Almany et al. 2009). The connectivity of these reefs is one of the keys to understand the recovery after a recurrent mass bleaching (Hughes et al. 2018), but we have to understand the potential connectivity of the single species and the different habitats as a whole (Miller and Ayre 2008). Depending on the reproductive strategy, we will have a different genetic flow (Nunes et al. 2011; Martinez-Quintana et al. 2014) and thus a different recovery potential. It is important to understand which benthic suspension feeder species have the capability to restore the associated community (Jones et al. 2009) also because their growth potential and settlement strategies will be different, affecting the capability to make more or less complex structures that will store more or less C.

In all the MAF management and protection guidelines, we have to seriously think about the possibility to improve the marine restoration processes, concentrating our efforts in enhancing the biodiversity and C immobilization possibilities in this fast-changing panorama.

6.2 May MAF Restoration Be Part of the Solution for C Immobilization and Biodiversity Enhancement?

To restore or enhance the capability of MAFs to immobilize C, an active restoration plan has to be applied. Duarte et al. (2020) suggest that the proper conservation and restoration actions may recover ocean ecosystems by 2050, but serious efforts have to be considered for making this 2–10% of annual improvement of biomass and biodiversity. In most of the cases, the action has to be at the ecosystem level, with a clear effort, in many cases, of an active restoration plan.

In MAFs, restoration plans have been greatly improved during the last two decades. The ecosystem engineering approach (Rinkevich 2020) in MAFs is essential if we want to stimulate the potential sequestration of C in the three-dimensional alive structures. An ambitious plan has been elaborated based on not single species, but different suspension feeders and plants gathered conforming a true ecosystem (Horoszowski-Fridman and Rinkevich 2017) that may trap the C in organic or inorganic structures. This approach is a key factor because you are enhancing the resilience, the gene flow, and the possibility to face possible perturbations (Rinkevich 2020). Restoring specific nurseries (floating or land-based, Rinkevich 2020; Golomb et al. 2020) that could feed the ongoing restoring populations is an effective yet not expanded possibility to make serious restoration plans in coral reefs, a solution that, well-managed, may easily have economic benefits at the local level reinforcing the ecosystem services (Rinkevich 2015a, b).

The problem, up to now, is that large-scale restoration plans have not been seriously considered (Rinkevich 2015a, b; Gordon et al. 2020; Duarte et al. 2020) also due to the lack of appropriate experimentation. In a recent paper, Van Oppen et al. (2017) claim that the recovery of large areas has to consider the possibility to select and enhance certain Scleractinia (eco-engineering species) that will be more resistant both to global (e.g., climate change and acidification) or local (e.g., eutrophication or chemical pollution) threats. In this sense, also Rinkevich (2015a, b) claims for a paradigm shift, suggesting that we do not have to concentrate in what was the structure of tropical coral reefs to make restoration plans, but what can they be from a realistic point of view.

Keeping in mid-tropical coral reef restoration future plans to partly immobilize a large set of C in their three-dimensional structures, we may propose ideas in which the combination of biology, sociology, and economy give an equilibrated panorama that may be even stimulating for local economies (France 2016). For example, only the biological approach in which you save the coral community through an efficient plan of coral reimplantation with Symbiodiniaceae well adapted to temperature shifts (Van Oppen et al. 2017) may be not enough to make our C storage plans. In this context, laboratory evolution of cultured *Symbiodinium* under the elevated temperature and pCO_2 selection followed by inoculation in coral hosts with the evolved algal cultures as suggested by Van Oppen et al. (2017) may be a good idea, but you need an available pool of these algae at hand to reimplant the microalgae after the bleaching event. Microalgae are suitable organisms to create biofuel (Santos-Ballardo et al. 2016), and an increase in biodiesel and biogas rentability is possible in monocultures (Fuentes-Grünewald et al. 2011). The needed biomass for an innoculation may thus come from outdoor bioreactors (Fuentes-Grünewald et al. 2012) that will be continuously producing biofuel in optimized conditions (Itoiz et al. 2012) (Fig. 11a). The combination of a rescue plan for coral reefs and a blue growth project to partially subministrate fuel to the local economical promoters could be an optimal solution in the complex framework of a restoration plan (Fig. 11b). Taking into account the distribution of tropical coral reefs around the world and their importance for the local economies, this complementary solution (i.e., saving the reefs and its potential C retention and the availability of energy in remote and poor areas) may be a good plan.

6.3 *What If We Engage People for Active Restoration Plans? The Role of Artificial Reefs and Active Restoration in C Immobilization*

Up to now, many solutions related to the preservation of MAFs have been not only sparse but also disconnected from stakeholder collaboration. We need to collate three different points to successfully implement a set of trusted and workable solutions for MAFs: (1) implement restoration (and mariculture) innovations related to MAFs, considering all the previous efforts done up to now, (2) embed citizen participation from the beginning of these processes, and (3) create monitoring and restoration protocols that are replicable under surveillance across different coastal regions and ecosystems. The solutions related to climate change impacts have to consider the potential of MAFs as carbon sinks, biodiversity hotspots, and a testable source of blue growth and sustainable tourism enhancement. New concepts of conservation, management, mariculture, and restoration, going far beyond the already well-structured know-how that we have gathered during the last decades (Rinkevich 2015a, b; Horoszowski-Fridman and Rinkevich 2017), have to be applied to effective scaling up with wide integration and participation. The fundamental part of successful large-scale restoration is education and citizen engagement (Page and Vaughan 2014).

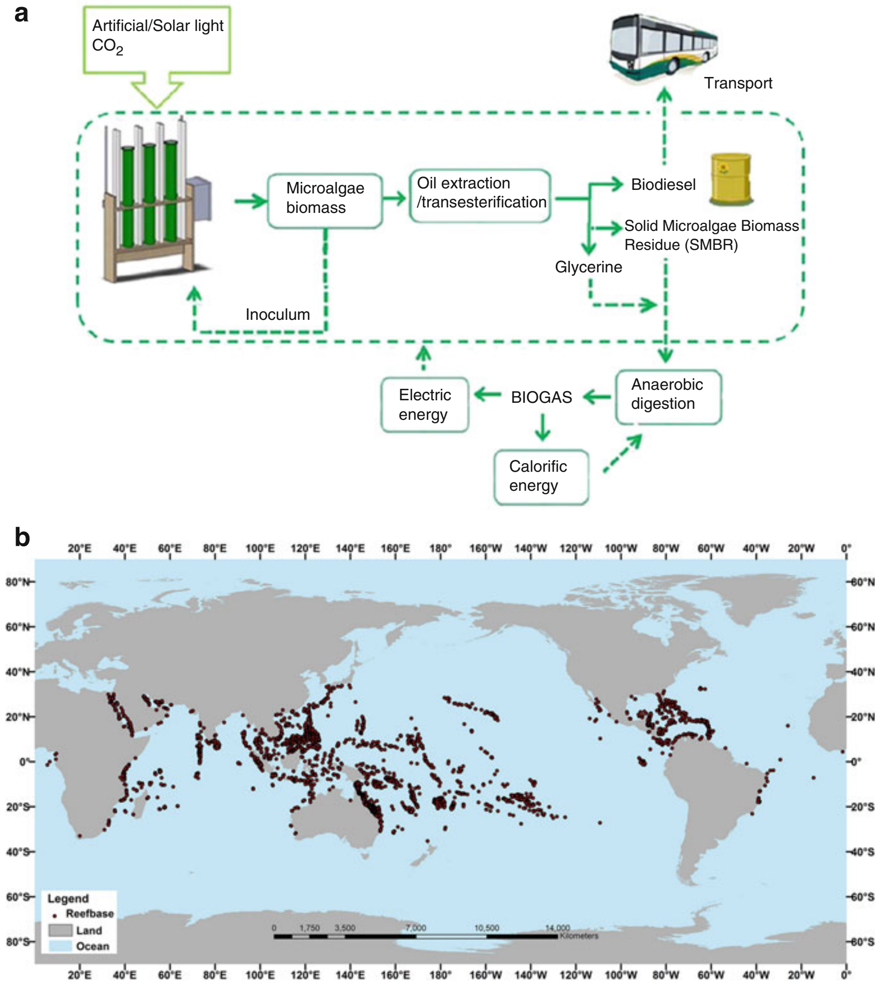

Fig. 11 Producing biofuels or other by-products with *Symbiodiniaceae*. (**a**) Schematic process of biofuel (biodiesel and biogas) production from microalgae biomass; the bioreactors will permanently generate energetic products (or other substances) that can be used in local economies; when a bleaching event occurs, the local government, with the help of the local population, may use part of the production to restore the before bleaching conditions of the scleractinians (drawing from Santos-Ballardo et al. 2015). (**b**) Map of the potential use of this methodology, highlighting the importance of the biofuel production in tropical areas where the energetic crisis will be much harder in future decades (map from NOAA Service of Education https://aamboceanservice.blob.core.windows.net/oceanservice-prod/education/kits/corals/media/coralreefmap.jpg)

The first step is changing the concept of artificial reefs (AR), up to now based on structures not designed to satisfy the biota particular needs. We need to develop symbiotic enhanced reefs (SERs) according to the biological, environmental, and touristic needs of any location (Fig. 12). This model could be a worldwide reference

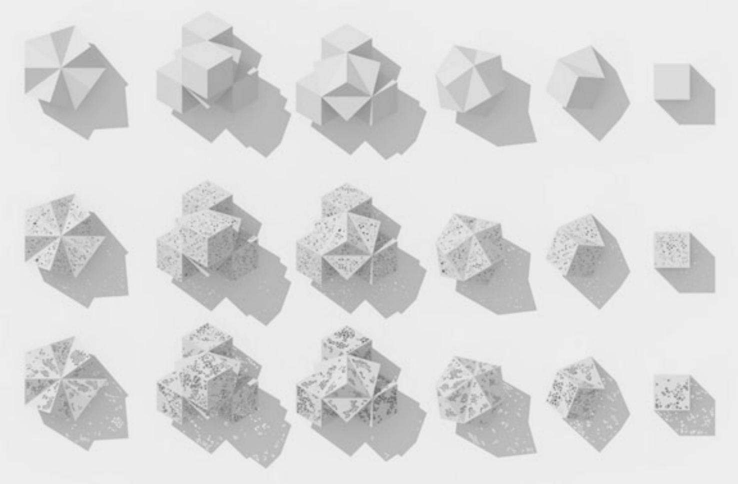

Fig. 12 The symbiotic enhanced reef (SER) is designed to adapt morphology, texture, and substrate material, and orientation to the sessile or vagile species will colonize the structure or will be actively transplanted. Architects, engineers, and marine biologists work together to create the algorithms that will "enhance" life in these reefs. The software creates a form that is more and more complex, following information like currents, light incidence, sediment transport, orientation, size of the organisms, feeding preferences, etc. (image courtesy of Underwater Gardens International, https://www.underwatergardens.com, *Artwork by the Underwater Gardens Team*)

with regard to the designing of AR. There is a current and urgent need to involve professionals from different areas (biologists, geologists, environmentalists, engineers, policy-makers, etc.) when developing actions and strategies in new AR areas. We have to consider the possibility of developing a software design protocol, powered by Parametric Intelligence (PI). The software considers and combines multiple aspects, such as engineering, environmental and monitoring needs, and biological and spatial characteristics. The inclusion of all these constraints and the adoption of new materials in the SER construction ensure that the resulting structure designs are appropriately adapted to surrounding biotic and abiotic variables. Not only the restoration per se is important, but also a set of clear participation protocols in transplanting and monitoring by nonprofessional divers, in order to develop SERs as ecotourism destinations. These types of SERs could potentially increase and promote the local economy while promoting the local biodiversity restoration and decongesting natural reefs from massive tourism.

The second step is to improve and standardize the restoration methods of MF components. For example, standard coral restoration methods suggest the fragmentation of fast-growing branching corals or massive corals (in the size of coral nubbins) in field (in situ) nurseries and then, when they reach large 3D shapes, outplantings of the farmed corals into denuded areas, as is done in terrestrial forestation (Rinkevich 2019). New technologies now include land (ex situ)-based and floating field nurseries and even hatcheries to augment the yield of coral aquaculture. Improved culture systems have already yielded the successful transplantation of more than 100 coral species, including branching, massive, and encrusting species, for the formation of complex 3D MAFs, where microfragmentation (using coral nubbins) and the use of already broken coral fragments that otherwise will die (the "corals of opportunity") allow the development of considerable (tens of thousands and more) coral colonies available for transplantation and become not only very effective but also environmentally friendly since the use of such fragments minimizes impacts on donor colonies. An additional option for restoration is the transplantation of sexually gravid coral colonies to augment sexual reproduction in transplantation areas and to recover genetic diversity of naturally resilient species and genotypes (Horoszowski-Fridman and Rinkevich 2017). By the addition and utilization of a land-based nursery or hatchery and multiple nursery functions of even the final field outplantings, a full brigade of culture tools and technologies could allow restoration to be done at proper space scale (Rinkevich 2014). The employment of these technologies can not only restore impacted reefs back to function (Morse 2000) but can also become a vital tool to colonize coral colonies onto artificial structures (AR) to produce a carbon-functioning living reef in a fraction of the time. Thus the deployment of the above-combined tools is one of the best approaches to (a) augment reefs' carbon sequestering through photosynthesis; (b) store carbon captured in all living matter, as performed in established terrestrial forests; and (c) ensure the rapid development of MF habitats for reef-dwelling species (Rinkevich 2014, 2019).

Floating reefs (FRs) are proved to be complementary to traditional bottom ARs (Rinkevich 2015a, b). Not only that their situation at mid-water provides endless opportunities for spaces and uses; they are healthier as subjected to enhanced water flow that brings more nutrients while removing sediments. FRs can be positioned at different depths and be customized for any MF organisms' specific needs, allowing for the gradual acclimatization of the growing MF organisms to conditions of depth and radiation and also for designated transplantation sites. They serve as one of the best tools for carbon sequestering, through photosynthesis and the stored carbon captured from the alive matter. Other benefits are their use as repositories for MF and reef-dwelling species, the development of novel biodiversity offsets/credits and banking credits associated with ecological engineering practices, enhanced levels of MF reproduction as ecological and market-based incentive tools (e.g., Horoszowski-Fridman et al. 2011), their association with novel ecotourism concepts, the use of MF organisms farmed in FRs (algae, Porifera, Cnidaria, Tunicata), and drug development (e.g., Molinski et al. (2009), Leal et al. (2013)). The restoration activities are associated with the development of various AR types, based on the "gardening" tenet (Rinkevich 2015a, b). We have the opportunity to reshape MF in such a way that novel reef ecosystems with novel functionalities. Using the "gardening" approach as a CC mediator, several novel ecosystem engineering management approaches were raised and discussed (Rinkevich 2015a, b). These AR will provide new substrate for species that will act as carbon sink, biodiversity hotspots, and nursery grounds (Fig. 13).

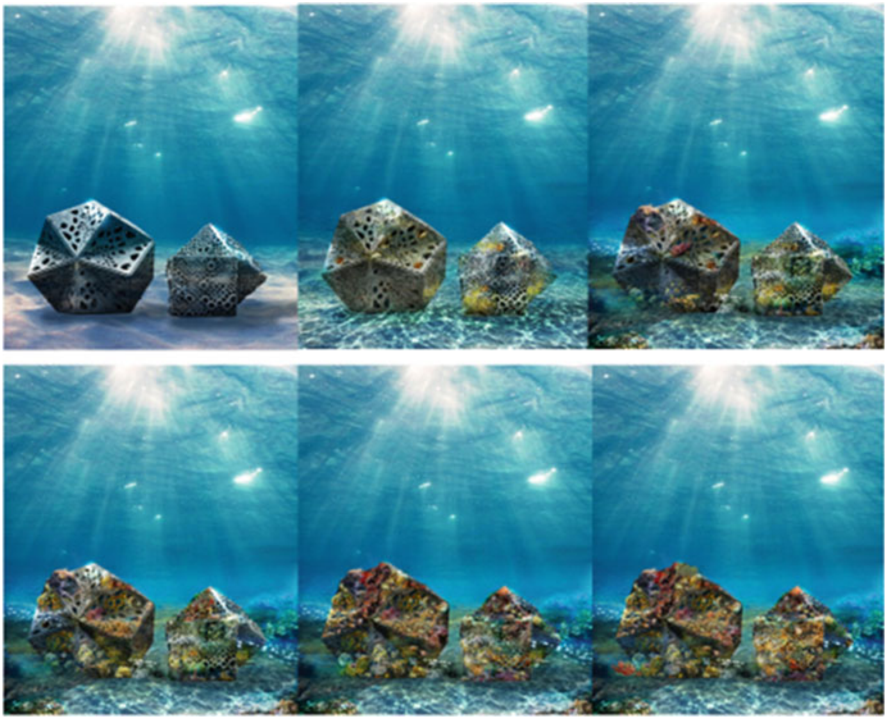

Fig. 13 (**a**–**e**) Succession paths. Passive or active colonization will enhance complexity. The elapsed time of the ecosystem engineering species settlement and growth will depend on the specific programs made in each restored area. The active transplantation will follow specific protocols based on the ideal patch structure and size of ecosystem engineering organisms, animal or vegetal (image courtesy of Underwater Gardens International, https://www.underwatergardens.com, *Artwork by the Underwater Gardens Team*)

However, we have to keep in mind that also marine vegetated ecosystems are essential carbon sinks, having a key role as biodiversity enhancers. Both seagrass and seaweed habitats provide also refuge against ocean acidification (Koch et al. 2013). Seagrasses also prevent coastal erosion and facilitate sediment accretion and thus seafloor rising. Activities to restore marine vegetation, and the associated provision of ecosystem services, encompass implementation of policy regulations to cease the drivers of habitat loss and reinforce habitat conservation toward facilitating natural recovery (e.g., EU Water Framework Directive, EU Habitat Directive) as well as planting initiatives to catalyze the recovery process.

To date, restoration of marine vegetation is recognized among the actions delivering ocean-based solutions aiming to reduce global and local climate change impacts while restoring other important ecosystem services (e.g., food provision, nutrient removal) at local and regional scale (Gattuso et al. 2018). Seagrass planting projects are being conducted worldwide since 1970, while those for seaweed are starting to be implemented more recently and, generally, can be considered at a development stage. Effective planting projects aimed to recover the vegetation (Paulo et al. 2019), enhance carbon sequestration (Greiner et al. 2013; Marbà et al. 2015), and prevent emissions from historic carbon accumulated by the lost meadow (Marbà et al. 2015). The success of seagrass planting efforts can be improved, regarding the anchoring techniques of propagules, by the choice of suitable substrates and the development of methodologies that allow the use of seeds and seedlings in restoration programs.

It will be of great importance to test and produce innovative tools to improve propagules anchoring in restoration programs and to facilitate natural recolonization of seagrasses. The best methodologies for seaweed restoration should be identified: self-seeding from reproductive thallus, artificial release of propagules, development of substrate or substrate preparation and laboratory seeded field placed substrates. Because the development of a seagrass and seaweed meadows, as well as animal MFs, requires decadal time scales after the onset of implementation of conservation and environmental quality polices as well as planting effort finishes, modelling exercises will be also useful to examine projected trajectories of provision of ecosystem services for CC mitigation and adaptation delivered by restoration efforts. These models will represent a key to identify the best restoration strategies (Saunders et al. 2017) to be selected depending on initial conditions of areal extent of remaining MF species.

It will be thus interesting to implement ARs to enhance biomass and biodiversity in these areas, coupled with fishing management plans, in order not just to restore but also to maintain the restored habitats. Circular economy models can be developed and tested, in order to provide local communities with sustainable, and Blue Growth-based, development opportunities (Fig. 14). Several vegetal and animal species can contribute significantly as bioremediators of eutrophicated and acidified coastal waters, and the harvested biomass can be used as human food, as animal feed, or as a substitute for fossil oil to produce different valuable products (e.g., biomaterials, biofuel, fertilizers, etc.) (Duarte et al. 2017). The three-dimensional structure created by mariculture farms may increase biodiversity and function as nursing grounds for wild fish and crustacean populations, but few studies have tested this hypothesis. In general, however, present mariculture practice using monocultures where all biomass and parts of the infrastructure are removed at harvest create ephemeral habitats with little potential to function as attractive and persistent biotopes. Solutions to this are multi-trophic integrated aquaculture (IMTA), based on the cocultivation of several low impacting species (e.g., macroalgae, suspension feeders, etc.) and/or practicing rotation in order to more closely replicate a marine forest and to increase the duration of the three-dimensional habitat. While some methods have already been developed and successfully implemented, new perspectives and protocols have to be developed to improve productivity as to maintain restored habitats in a climate change scenario (e.g., bioremediation (Stabili et al. 2019)).

Fig. 14 The restoration activities are associated with the development of various SER types, based on the "gardening" concept, further approved in a number of sites worldwide. This will be an opportunity to reshape marine forests in such a way that novel reef ecosystems—with novel functionalities—are developed, based on the previous experiences and the features of the habitats. Using the "gardening" approach as a climate change mediator, several novel ecosystem engineering management approaches were raised and discussed. These *underwater sea gardens* (© Underwater Gardens International) will provide new substrate for species that will act as carbon sink, biodiversity hotspots, and nursery grounds. People will be engaged from the beginning in the transplant and monitoring activities (image courtesy of Underwater Gardens International, https://www.underwatergardens.com, *Artwork by the Underwater Gardens Team*)

6.4 Climate Change Mitigation Using Deep MAF Restoration

In this restoration panorama, the continental platform and the deep sea are further important components to be considered (Van Dover et al. 2014). Among habitats impacted by several abovementioned stressor (including bottom trawling, artisanal fisheries, land-ocean interactions, and climate change), the deeper habitats (continental shelf) are almost neglected when we want to apply restoration measures (Montseny et al. 2019, 2020). As a first example, an integrated plan of deep artificial reefs for ecological restoration combined with sustainable artisanal fishery can be envisaged to protect these biodiversity hotspots, enhancing the potential C storage (Montseny et al. 2019, 2020). The deeper MAFs composed of Octocorallia, Porifera, Bryozoa, Bivalvia, Polychaeta, Tunicata, or similar other suspension feeders are also carbon immobilizers. The structural complexity of these ecosystems results in a high heterogeneity in the main environmental features (e.g., current flow, sedimentation rates, food availability), allowing for an abundant and diverse associated vagile and/or swimming fauna, comprising fish, mollusks, and crustaceans of commercial interest (Gori et al. 2017). For this reason, MAFs at 50–200 m depth are the main target of bottom trawling and artisanal fisheries using bottom contact gears (i.e., longlines, trammel nets) (Hinz 2017). Consequently, Octocorallia and Porifera are among the most abundant bycatch in artisanal fishery (Montseny et al. 2019, 2020). Today, the impacts induced by fishing acting on Octocorallia and Porifera populations are already weakened by the ongoing climate change (deep seawater warming and acidification, reduced oxygen, and surface productivity), with consequences on the long-term viability and ecosystem functioning of these paramount deep-sea ecosystems still to be quantified.

More interesting could be, however, to make a very large-scale restoration plan not only in the continental platform but also in the sea mountain slope with ARs. The idea of stimulating phytoplankton production adding essential micronutrients for the microalgal growth (e.g., iron, Boyd et al. 2000) is well-known. Few years ago, the idea of fixing C stimulating phytoplankton growth in the Southern Ocean was proved in an experimental approach (LOAFEX project, Smetacek and Naqvi 2008; Smetacek et al. 2012). The main idea was promoting a bloom that will partly sink in deep sediments, which are already known to be a non-neglectable C sink (Smetacek and Naqvi 2008). The main problem was that an important part of this production was not only grazed by copepods but also respired once degraded in the microbial loop (Boyd et al. 2007). What if we promote the same blooms but we place suspension feeders in strategic areas to consume the primary and secondary production? The carrying capacity of the environment must be considered to regulate the quantity of suspension feeders. In this approach, you can't have more suspension feeders than the local environment can sustain. In the continental platform, where there are huge areas of soft bottom, the SERs could be the hard bottom needed to support the three-dimensional organisms that will take an important part of the productivity, fixing a non-neglectable part in their long-lived structures (Gori et al. 2017). We can't deny, however, the importance soft bottom and the associated biodiversity (Ellingsen 2002). Whenever we put an SER, we will cover an important surface of soft bottom with all the related consequences. We also have to carefully consider the possibility to explore the consequences of the facilitation of the connectivity of alien species (Airoldi and Bulleri 2011; Miranda et al. 2020; Pusceddu et al. 2016) and the effects on the transformation of biogeochemical cycles promoted by some of these species (Rizzo et al. 2016a, b, 2017, 2020; Stabili et al. 2017). However, if you make appropriate plans to avoid these problems, the gain may be huge. Promoting specific nurseries (floating or land-based) for corals, gorgonians, corals, etc. (specific of the target areas) in a very large-scale project, will have huge benefits (a) promoting the C immobilization and (b) adding a complex habitat (hard substrate) that will be enhanced with eco-engineering species harboring a high biodiversity and high biomass, and (c) we will definitively stop bottom trawling in the area. In sea mountains, the effect could be even more evident. The existence of particular hydrodynamic features in these submarine promontories (Genin 2004) will promote the sinking of the bloom to the benthos, enhancing the capture rates of the transplanted fauna (Mueller et al. 2014; Orejas et al. 2016). Long-lived species demonstrated to have a higher success in transplantation

(Montero-Serra et al. 2017), but surely optimized methods can be used to promote the clonal organism proliferation (Bowden-Kerby 2001; Meesters et al. 2015; Rinkevich 2015a, b, 2020). The huge number of sea mountains over the world (around 100,000 (Wessel et al. 2010)) and the huge extension of the continental shelf (in some areas, like Siberia, the continental shelf may be as wide as 1500 km (Harris et al. 2014)) will be crucial to make this action significant in terms of immobilized C. The stable water temperature in these areas will not be a constraint like in surface waters (Pinet 2003), where massive mortalities are present and have huge impact on MAFs (Galli et al. 2017).

To construct the SARs, the same protocol presented above (SER approaches) could be followed, but with some significant implementations. The ARs should mimic the natural outcropping rocky bottoms present in the target areas. The structure surface will have a morphology specifically designed to be suitable for the settlement of corals, gorgonians, and sponges and will present plenty of cavities of different size and shape to enhance the presence of vagile species (i.e., fishes, mollusks, and crustaceans). The SERs could be deployed following a well-defined design with each structure separated from the others, in order to enhance the movement of fishes, mollusk, and crustacean among them, considering also the reef-scale restoration process, which is important to be successful (Hein et al. 2020). Remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) and photogrammetric methods (Koopmans and Wijffels 2008) could be used throughout all the study for the regular monitoring of the state of the animal MFs on the artificial reefs after deployment. Transplanted gorgonians and sponges should be monitored to quantify their individual survival, growth, and population dynamics. Macrophotographs could be analyzed to quantify species recruitment rate and recruit survival, according to well-established methodology used in shallow waters (e.g., Bramanti et al. (2005), Santangelo et al. (2012)). The amount of C included in the deep reefs by the growth of the gorgonian and sponge populations could be quantified with photogrammetry and 2D pictures, obtained during the regular monitorings (Koopmans and Wijffels 2008). Additionally, samples of transplanted gorgonians and sponges could be collected with the ROV after 1.5 years from deployment and analyzed for C content and its isotopic composition, depending on the tissue (i.e., living tissue, sclerite, axis), to explore its trophic condition. The combination of these data could allow quantifying the total amount of C included by the animal MFs in the deep reefs (Fig. 15).

Banning of bottom trawling, suppression all over the world creating artificial structures that enhance connectivity, biomass production, and biodiversity could be a good side effect, but also the creation of a large-scale connectivity areas for sessile and vagile organisms may be a good effort to restore marine habitats and their ecosystem services.

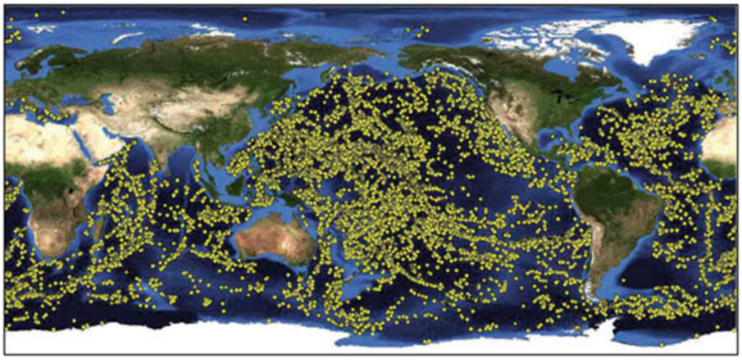

Fig. 15 More than 100,000 sea mountains have been numbered in different areas of the world. These sea mountains may be the perfect match, with part of the continental shelf, for a large restoration program to enhance carbon immobilization by the marine animal forests (http://jupiterfoundation.org/current/2018/3/7/mountains-in-the-deep-sea)

7 The Whole Concept: Toward a Recovery of C Immobilization in the Sea

The development of C sequestration estimates across large scales in marine habitats will contribute to the development of adequate policy, as well as to the implementation of management and conservation actions and the recognition of blue carbon benefits from MAFs. Prioritizing conservation actions would then lead to the identification of candidate areas for active restoration where MAFs have been removed or modified by physical disturbance or other local-scale perturbations. Fishing and dredging activities have removed or disturbed many of the large slow growth colonial animals from deep-sea habitats (Clark and Dunn 2012), reducing the global capacity for immobilizing carbon. Where environmental conditions preclude effective restoration, preemptive conservation measures (e.g., prohibition of bottom trawling at Mesophotic and deep-sea habitats) should be considered to maintain the integrity of representative MAFs. Protection measures are not enough even if they are essential (Claudet et al. 2020), so we must take some decisive action to change the restoration measures. Such measures, if implemented, need to be realistic but ambitious. Without prompt action, we will continue to lose yet another set of habitats that may help to mitigate biodiversity loss and climate change effects. Such restoration actions have to be more practical, jumping from the academic world to a more integrative and transversal approach (Fig. 16), in which a direct citizen commitment is seriously considered, thanks also to an interface between social and natural sciences (McKinley et al. 2020). Moreno-Mateos et al. (2020) claim that we have to “focus restoration science on the long-term (centuries to millennia) re-assembly of degraded ecosystem complexity integrating interaction network and evolutionary potential approaches.” This vision is correct, only with challenging and brave ideas,

Fig. 16 The loss of complexity and biodiversity is an unquestionable fact that has an uneasy resolution. On the one hand, one of the main problems is the lack of empathy with the marine ecosystems because we don't see them and we think that the oceans can absorb the multiple impacts to which they are exposed. On the other hand, a serious restoration plan for the benthic communities, a "reforestation" approach, does not exist in the different countries. We need to introduce the "gardening" concept. What we need is making a mix between ocean literacy and direct citizen action to make an ambitious restoration plan. An applied solution for marine restoration in which the protagonist is the citizen may be one of the possible solutions, at a large scale. Families, individuals, leisure collectives, children, and teenagers, everybody is directly involved, with the aid of a professional team, to restore damaged coastal ecosystems. Circular Economy and Blue Growth (mariculture with integrated multi-trophic aquaculture protocols, reintroduction of vulnerable species, bycatch restoration plans, biomass enhancement of economic important species, education and leisure facilities, etc.) are implemented in a complex but realistic program, adapting the project to the local needs with the direct implication of the academic world. Sociology and economic features of the restoration areas are part of our bottom-up plan, involving fishermen, tourist operators, SCUBA divers, etc. from the beginning (Image courtesy of Underwater Gardens International, https://www.underwatergardens.com, *Artwork by the Underwater Gardens Team*)

always based on the scientific tools that we have, we may indeed solve the multiple problems that we have provoked. Considering large conservation and restoration programs to protect marine animal forests (and all the forests of the sea), promoting among other things the biodiversity and the carbon immobilization, has to be a priority in future ocean management plans.

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References

Aguilar R, Perry AL, López J (2017) Conservation and management of vulnerable marine benthic ecosystems. In: Marine animal forests. Springer International, Cham, pp 1165–1207. https://doi.org/10.1007/978-3-319-21012-4_34

Airoldi L, Bulleri F (2011) Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. PLoS One 6:e22985. https://doi.org/10.1371/journal.pone.0022985

Ali TA, Mortula M, Atabay S, Navadeh E (2015) A GIS-based spatiotemporal study of the variability of water quality in the Dubai Creek, UAE. Water Qual Res J 51:219–232. https://doi.org/10.2166/wqrjc.2015.020

Allard V, Ourcival JM, Rambal S, Joffre R, Rocheteau A (2008) Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. Glob Chang Biol 14:714–725. https://doi.org/10.1111/j.1365-2486.2008.01539.x

Allemand D, Tambutté É, Zoccola D, Tambutté S (2010) Coral calcification, cells to reefs. In: Coral reefs: an ecosystem in transition. Springer, Cham, pp 119–150. https://doi.org/10.1007/978-94-007-0114-4_9

Alleway HK, Connell SD (2015) Loss of an ecological baseline through the eradication of oyster reefs from coastal ecosystems and human memory. Conserv Biol 29(3):795–804

Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ et al (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28:339–351. https://doi.org/10.1007/s00338-009-0484-x

Alongi DM (2014) Carbon cycling and storage in mangrove forests. Annu Rev Mar Sci 6:195–219. https://doi.org/10.1146/annurev-marine-010213-135020

Andersson AJ, Mackenzie FT (2004) Shallow-water oceans: a source or sink of atmospheric CO_2? Front Ecol Environ 2(7):348–353

Anthoni PM, Freibauer A, Kolle O, Schulze E-D (2004) Winter wheat carbon exchange in Thuringia, Germany. Agric Forest Meteorol 121:55–67. https://doi.org/10.1016/s0168-1923(03)00162-x

Arias-González JE, Rivera-Sosa A, Zaldivar-Rae J, Alva-Basurto C, Cortés-Useche C (2017) The animal forest and its socio-ecological connections to land and coastal ecosystems. In: Marine animal forests. Springer International, Cham, pp 1209–1240. https://doi.org/10.1007/978-3-319-21012-4_33

Barlow J, Berenguer E, Carmenta R, França F (2020) Clarifying Amazonia's burning crisis. Glob Chang Biol 26:319–321. https://doi.org/10.1111/gcb.14872

Barnes DKA (2018) Blue carbon on polar and subpolar seabeds. In: Carbon capture, utilization and sequestration. InTech. https://doi.org/10.5772/intechopen.78237

Barnes DKA, Fleming A, Sands CJ, Quartino ML, Deregibus D (2018) Icebergs, sea ice, blue carbon and Antarctic climate feedbacks. Philos Trans R Soc A Math Phys Eng Sci 376:20170176. https://doi.org/10.1098/rsta.2017.0176

Barnes DKA, Sands CJ, Richardson A, Smith N (2019) Extremes in benthic ecosystem services blue carbon natural capital shallower than 1000 m in isolated, small, and young Ascension Island's EEZ. Front Mar Sci 6. https://doi.org/10.3389/fmars.2019.00663

Bates NR (2002) Seasonal variability of the effect of coral reefs on seawater CO_2 and air-sea CO_2 exchange. Limnol Oceanogr 47:43–52. https://doi.org/10.4319/lo.2002.47.1.0043

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C et al (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61 (2):107–116

Belcher A, Henson SA, Manno C, Hill SL, Atkinson A, Thorpe SE et al (2019) Krill faecal pellets drive hidden pulses of particulate organic carbon in the marginal ice zone. Nat Commun 10:889. https://doi.org/10.1038/s41467-019-08847-1

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833. https://doi.org/10.1038/nature02691

Boavida J, Paulo D, Aurelle D, Arnaud-Haond S, Marschal C, Reed J et al (2016) A well-kept treasure at depth: precious red coral rediscovered in Atlantic deep coral gardens (SW Portugal) after 300 years. PLoS One 11:e0147228. https://doi.org/10.1371/journal.pone.0147228

Boero F (2015) The future of the Mediterranean Sea ecosystem: towards a different tomorrow. Rend Lincei 26:3–12. https://doi.org/10.1007/s12210-014-0340-y

Boero F, Belmonte G, Fanelli G, Piraino S, Rubino F (1996) The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? Trends Ecol Evol. 11:177–180. https://doi.org/10.1016/0169-5347(96)20007-2

Boero F, Leo F De, Fraschetti S, Ingrosso G (2019) The cells of ecosystem functioning: towards a holistic vision of marine space. In: Advances in marine biology. Elsevier, pp 129–153. https://doi.org/10.1016/bs.amb.2019.03.001

Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M et al (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10:6225–6245. https://doi.org/10.5194/bg-10-6225-2013

Borghini M, Bryden H, Schroeder K, Sparnocchia S, Vetrano A (2014) The Mediterranean is becoming saltier. Ocean Sci 10:693–700

Boschen RE, Rowden AA, Clark MR, Gardner JPA (2013) Mining of deep-sea seafloor massive sulfides: a review of the deposits, their benthic communities, impacts from mining, regulatory frameworks and management strategies. Ocean Coast Manag. 84:54–67. https://doi.org/10.1016/j.ocecoaman.2013.07.005

Bowden-Kerby A (2001) Low-tech coral reef restoration methods modeled after natural fragmentation processes. Bull Mar Sci 69(2):915–931

Boyd PW, Watson AJ, Law CS, Abraham ER, Trull T, Murdoch R et al (2000) A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. Nature 407:695–702. https://doi.org/10.1038/35037500

Boyd PW, Jickells T, Law CS, Blain S, Boyle EA, Buesseler KO et al (2007) Mesoscale Iron enrichment experiments 1993-2005: synthesis and future directions. Science 315:612–617. https://doi.org/10.1126/science.1131669

Bramanti L, Magagnini G, De Maio L, Santangelo G (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L 1758), a 4-year study. J Exp Mar Biol Ecol 314(1):69–78

Bramanti L, Vielmini I, Rossi S, Tsounis G, Iannelli M, Cattaneo-Vietti R et al (2014) Demographic parameters of two populations of red coral (*Corallium rubrum* L. 1758) in the North Western Mediterranean. Mar Biol 161:1015–1026. https://doi.org/10.1007/s00227-013-2383-5

Breitburg D, Levin LA, Oschlies A, Gregoire M, Chavez FP, Conley DJ, Garcon V (2018) Declining oxygen in the global ocean and coastal waters. Science 359:eaam7240

Bridgham SD, Ye R, DeLaune RD, Reddy KR, Richardson CJ, Megonigal JP (2014) Carbon dynamics and ecosystem processes. In: Organic matter mineralization and decomposition, pp 185–202

Buddemeier RW (1996) Coral reefs and carbon dioxide. Science 271:1298b–1299b. https://doi.org/10.1126/science.271.5253.1298b

Buitenhuis ET, Vogt M, Moriarty R, Bednaršek N, Doney SC, Leblanc K et al (2013) MAREDAT: towards a world atlas of MARine Ecosystem DATa. Earth Syst Sci Data 5:227–239. https://doi.org/10.5194/essd-5-227-2013

Cahoon LB (1999) The role of benthic microalgae in neritic ecosystems. Oceanogr Mar Biol Annu Rev 37:47–86

Cammen LM (1980) The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. Mar Biol 61:9–20. https://doi.org/10.1007/bf00410337

Canadell JG, Pataki DE, Gifford R, Houghton RA, Luo Y, Raupach MR et al (2007) Saturation of the terrestrial carbon sink. In: Terrestrial ecosystems in a changing world. Springer, Berlin, pp 59–78. https://doi.org/10.1007/978-3-540-32730-1_6

Carlson D, Pfeiffenberger H (2015) Global carbon budget 2015. Earth Syst Sci Data Discuss 8:859–861. https://doi.org/10.5194/essdd-8-859-2015

Cau A, Bramanti L, Cannas R, Follesa MC, Angiolillo M, Canese S et al (2016) Habitat constraints and self-thinning shape Mediterranean red coral deep population structure: implications for conservation practice. Sci Rep 6:23322

Chauvaud L, Thompson JK, Cloern JE, Thouzeau G (2003) Clams as CO_2 generators: the *Potamocorbula amurensis* example in San Francisco Bay. Limnol Oceanogr 48:2086–2092. https://doi.org/10.4319/lo.2003.48.6.2086

Chimienti G, Angeletti L, Rizzo L, Tursi A, Mastrototaro F (2018) ROV vs trawling approaches in the study of benthic communities: the case of *Pennatula rubra* (Cnidaria: Pennatulacea). J Mar Biol Assoc UK 98:1859–1869. https://doi.org/10.1017/s0025315418000851

Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003) Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem Cycles 17. https://doi.org/10.1029/2002gb001917

Clancy M (2001) Mexican tourism: export growth and structural change since 1970. Lat Am Res Rev 36(1):128–150

Clark MR, Dunn MR (2012) Spatial management of deep-sea seamount fisheries: balancing sustainable exploitation and habitat conservation. Environ Conserv 39:204–214. https://doi.org/10.1017/s0376892912000021

Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI et al (2010) The ecology of seamounts: structure, function, and human impacts. Annu Rev Mar Sci 2:253–278. https://doi.org/10.1146/annurev-marine-120308-081109

Clark MR, Durden JM, Christiansen S (2020) Environmental impact assessments for deep-sea mining: can we improve their future effectiveness? Mar Policy 114. https://doi.org/10.1016/j.marpol.2018.11.026

Claudet J, Loiseau C, Sostres M, Zupan M (2020) Underprotected marine protected areas in a global biodiversity hotspot. One Earth 2:380–384. https://doi.org/10.1016/j.oneear.2020.03.008

Coma R, Ribes M, Zabala M, Gili J-M (1998) Growth in a modular colonial marine invertebrate. Estuar Coast Shelf Sci 47:459–470. https://doi.org/10.1006/ecss.1998.0375

Coma R, Ribes M, Gili JM, Hughes RN (2001) The ultimate opportunists: consumers of seston. Mar Ecol Prog Ser 219:305–308. https://doi.org/10.3354/meps219305

Comeau S, Cornwall CE (2017) Contrasting effects of ocean acidification on coral reef animal forests versus seaweed kelp forests. In: Marine animal forests. Springer International, Cham, pp 1083–1107. https://doi.org/10.1007/978-3-319-21012-4_29

Coppari M, Gori A, Rossi S (2014) Size, spatial, and bathymetrical distribution of the ascidian Halocynthia papillosa in Mediterranean coastal bottoms: benthic pelagic coupling implications. Mar Biol 161:2079–2095. https://doi.org/10.1007/s00227-014-2488-5

Coppari M, Gori A, Viladrich N, Saponari L, Canepa A, Grinyó J et al (2016) The role of Mediterranean sponges in benthic pelagic coupling processes: *Aplysina aerophoba* and *Axinella polypoides* case studies. J Exp Mar Bio Ecol. 477:57–68. https://doi.org/10.1016/j.jembe.2016.01.004

Coppari M, Zanella C, Rossi S (2019) The importance of coastal gorgonians in the blue carbon budget. Sci Rep 9. https://doi.org/10.1038/s41598-019-49797-4

Cramer KL, Jackson JB, Angioletti CV, Leonard-Pingel J, Guilderson TP (2012) Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. Ecol Lett 15 (6):561–567

Cramer KL, Jackson JBC, Donovan MK, Greenstein BJ, Korpanty CA, Cook GM et al (2020) Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. Sci Adv 6:eaax9395. https://doi.org/10.1126/sciadv.aax9395

Crocetta F, Riginella E, Lezzi M, Tanduo V, Balestrieri L, Rizzo L (2020) Bottom-trawl catch composition in a highly polluted coastal area reveals multifaceted native biodiversity and complex communities of fouling organisms on litter discharge. Mar Environ Res 155:104875

Crutzen PJ (2006) The anthropocene. In: Earth system science in the anthropocene. Springer, New York, pp 13–8. https://doi.org/10.1007/3-540-26590-2_3

Cuif J-P, Dauphin Y (2005) The two-step mode of growth in the scleractinian coral skeletons from the micrometre to the overall scale. J Struct Biol 150:319–331. https://doi.org/10.1016/j.jsb.2005.03.004

Curry R, Dickson B, Yashayaev I (2003) A change in the freshwater balance of the Atlantic Ocean over the past four decades. Nature 426:826–829. https://doi.org/10.1038/nature02206

Cyronak T, Andersson AJ, Langdon C, Albright R, Bates NR, Caldeira K et al (2018) Taking the metabolic pulse of the world's coral reefs. PLoS One 13:e0190872. https://doi.org/10.1371/journal.pone.0190872

D'Alelio D, Libralato S, Wyatt T, d'Alcalà MR (2016) Ecological-network models link diversity, structure and function in the plankton food-web. Sci Rep 6. https://doi.org/10.1038/srep21806

Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. Proc Natl Acad Sci 106:12788–12793. https://doi.org/10.1073/pnas.0902080106

De Clippele LH, Huvenne VAI, Orejas C, Lundälv T, Fox A, Hennige SJ et al (2018) The effect of local hydrodynamics on the spatial extent and morphology of cold-water coral habitats at Tisler reef, Norway. Coral Reefs 37:253–266. https://doi.org/10.1007/s00338-017-1653-y

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132. https://doi.org/10.1007/bf00008211

Doney SC (2006) Plankton in a warmer world. Nature 444:695–696. https://doi.org/10.1038/444695a

Duarte CM, Cebrián J (1996) The fate of marine autotrophic production. Limnol Oceanogr 41:1758–1766. https://doi.org/10.4319/lo.1996.41.8.1758

Duarte CM, Krause-Jensen D (2017) Export from seagrass meadows contributes to marine carbon sequestration. Front Mar Sci 4. https://doi.org/10.3389/fmars.2017.00013

Duarte CM, Middelburg JJ, Caraco N (2005) Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2:1–8. https://doi.org/10.5194/bg-2-1-2005

Duarte CM, Marbà N, Gacia E, Fourqurean JW, Beggins J, Barrón C et al (2010) Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. Global Biogeochem Cycles 24. https://doi.org/10.1029/2010gb003793

Duarte CM, Wu J, Xiao X, Bruhn A, Krause-Jensen D (2017) Can seaweed farming play a role in climate change mitigation and adaptation? Front Mar Sci 4:100

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso J-P et al (2020) Rebuilding marine life. Nature 580:39–51. https://doi.org/10.1038/s41586-020-2146-7

Elias-Piera F, Rossi S, Gili JM, Orejas C (2013) Trophic ecology of seven Antarctic gorgonian species. Mar Ecol Prog Ser 477:93–106. https://doi.org/10.3354/meps10152

Ellingsen KE (2002) Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Mar Ecol Prog Ser 232:15–27. https://doi.org/10.3354/meps232015

Esparza G, DeJong TM, Grossman YL (1999) Modifying 'peach' to model the vegetative and reproductive growth of almonds. Acta Hortic 91–98. https://doi.org/10.17660/actahortic.1999.499.8

Estrada GCD, Soares MLG (2017) Global patterns of aboveground carbon stock and sequestration in mangroves. An Acad Bras Cienc 89:973–989. https://doi.org/10.1590/0001-3765201720160357

Fabbrizzi E, Scardi M, Ballesteros E, Benedetti-Cecchi L, Cebrian E, Ceccherelli G et al (2020) Modeling macroalgal forest distribution at Mediterranean scale: present status, drivers of changes and insights for conservation and management. Front Mar Sci 7:20

Falkowski P (2012) Ocean science: the power of plankton. Nature 483:S17–S20. https://doi.org/10.1038/483s17a

Fanelli E, Cartes JE, Papiol V, López-Pérez C (2013) Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). Deep Sea Res Part I Oceanogr Res Pap 78:79–94. https://doi.org/10.1016/j.dsr.2013.04.009

FAO Food and Agriculture Organization (2015) Global forest resources assessment 2015. How are the world's forests changing?. http://www.fao.org/3/a-i4793e.pdf

FAO Food and Agriculture Organization (2018) The state of world fisheries and aquaculture 2018. UN. https://doi.org/10.18356/8d6ea4b6-en

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA et al (2012) Seagrass ecosystems as a globally significant carbon stock. Nat Geosci 5:505–509. https://doi.org/10.1038/ngeo1477

France RL (2016) From land to sea: governance-management lessons from terrestrial restoration research useful for developing and expanding social-ecological marine restoration. Ocean Coast Manag 133:64–71. https://doi.org/10.1016/j.ocecoaman.2016.08.022

Frankignoulle M, Pichon M, Gattuso J-P (1995) Aquatic calcification as a source of carbon dioxide. In: Carbon sequestration in the biosphere. Springer, Berlin, pp 265–271. https://doi.org/10.1007/978-3-642-79943-3_18

Friend AD, Geider RJ, Behrenfeld MJ, Still CJ (2009) Photosynthesis in global-scale models. In: Photosynthesis in silico. Springer, Cham, pp 465–497. https://doi.org/10.1007/978-1-4020-9237-4_20

Fuentes-Grünewald C, Garcés E, Alacid E, Sampedro N, Rossi S, Camp J (2011) Improvement of lipid production in the marine strains Alexandrium minutum and Heterosigma akashiwo by utilizing abiotic parameters. J Ind Microbiol Biotechnol 39:207–216. https://doi.org/10.1007/s10295-011-1016-6

Fuentes-Grünewald C, Garcés E, Alacid E, Rossi S, Camp J (2012) Biomass and lipid production of Dinoflagellates and Raphidophytes in indoor and outdoor photobioreactors. Mar Biotechnol 15:37–47. https://doi.org/10.1007/s10126-012-9450-7

Galasso M (2000) Pesca del *Corallium rubrum* in Sardegna nell'antichita attraverso l'indagine archeologica, cartografica e I rilevamenti in mare. In: Khanoussi M et al (eds) L'Africa Romana. Atti del XIV Convegno di Studi. Carocci editore, Rome, pp 1159–1200

Galli G, Bramanti L, Priori C, Rossi S, Santangelo G, Tsounis G et al (2016) Modelling red coral (*Corallium rubrum*) growth in response to temperature and nutrition. Ecol Model 337:137–148. https://doi.org/10.1016/j.ecolmodel.2016.06.010

Galli G, Solidoro C, Lovato T (2017) Marine heat waves Hazard 3D maps and the risk for low motility organisms in a warming Mediterranean Sea. Front Mar Sci 4. https://doi.org/10.3389/fmars.2017.00136

Garrabou J, Sala E, Linares C, Ledoux JB, Montero-Serra I, Dominici JM et al (2017) Re-shifting the ecological baseline for the overexploited Mediterranean red coral. Sci Rep 7. https://doi.org/10.1038/srep42404

Garstang W (1900) The impoverishment of the sea. A critical summary of the experimental and statistical evidence bearing upon the alleged depletion of the trawling grounds. J Mar Biol Assoc UK 6:1–69. https://doi.org/10.1017/s0025315400072374

Gattuso J-P, Frankignoulle M, Smith SV, Ware JR, Wollast R (1996) Coral reefs and carbon dioxide. Science 271(5253):1298–1298

Gattuso J-P, Frankignoulle M, Smith SV (1999) Measurement of community metabolism and significance in the coral reef CO_2 source-sink debate. Proc Natl Acad Sci 96:13017–13022. https://doi.org/10.1073/pnas.96.23.13017

Gattuso JP, Magnan AK, Bopp L, Cheung WW, Duarte CM, Hinkel J et al (2018) Ocean solutions to address climate change and its effects on marine ecosystems. Front Mar Sci 5:337

Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J Mar Syst 50:3–20. https://doi.org/10.1016/j.jmarsys.2003.10.008

Gili J-M, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321. https://doi.org/10.1016/s0169-5347(98)01365-2

Gili J-M, Arntz WE, Palanques A, Orejas C, Clarke A, Dayton PK et al (2006) A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic. Deep Sea Res Part II Top Stud Oceanogr 53:1029–1052. https://doi.org/10.1016/j.dsr2.2005.10.021

Gili JM, Orejas C, Isla E, Rossi S, Arntz WE (2009) Seasonality on the high Antarctic benthic shelf communities?. In: Antarctic climate change and the environment. ACCE report, Cambridge University Press, Cambridge, pp 276–278

Golomb D, Shashar N, Rinkevich B (2020) Coral carpets- a novel ecological engineering tool aimed at constructing coral communities on soft sand bottoms. Ecol Eng 145:105743. https://doi.org/10.1016/j.ecoleng.2020.105743

González-Alcaraz MN, Egea C, Jiménez-Cárceles FJ, Párraga I, Maria-Cervantes A, Delgado MJ et al (2012) Storage of organic carbon, nitrogen and phosphorus in the soil plant system of *Phragmites australis* stands from a eutrophicated Mediterranean salt marsh. Geoderma 185–186:61–72. https://doi.org/10.1016/j.geoderma.2012.03.019

González-Guerreo L (2015) Corales del Orden Scleractinia: sumideros de carbono. Master Thesis of the Universidad Nacional Autónoma de México pp 1–89

Gooday AJ, Bett BJ, Escobar E, Ingole B, Levin LA, Neira C et al (2010) Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Mar Ecol 31:125–147. https://doi.org/10.1111/j.1439-0485.2009.00348.x

Gordon TAC, Radford AN, Simpson SD, Meekan MG (2020) Marine restoration projects are undervalued. Science 367:635–636. https://doi.org/10.1126/science.aba9141

Gori A, Rossi S, Berganzo E, Pretus JL, Dale MRT, Gili J-M (2011a) Spatial distribution patterns of the gorgonians *Eunicella singularis*, *Paramuricea clavata*, and *Leptogorgia sarmentosa* (Cape of Creus, Northwestern Mediterranean Sea). Mar Biol 158:143–158. https://doi.org/10.1007/s00227-010-1548-8

Gori A, Rossi S, Linares C, Berganzo E, Orejas C, Dale MRT et al (2011b) Size and spatial structure in deep versus shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). Mar Biol 158:1721–1732. https://doi.org/10.1007/s00227-011-1686-7

Gori A, Viladrich N, Gili J-M, Kotta M, Cucio C, Magni L et al (2012) Reproductive cycle and trophic ecology in deep versus shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). Coral Reefs 31:823–837. https://doi.org/10.1007/s00338-012-0904-1

Gori A, Bavestrello G, Grinyó J, Dominguez-Carrió C, Ambroso S, Bo M (2017) Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. In: Marine animal forests: the ecology of benthic biodiversity hotspots, pp 207–233

Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS et al (1995) Carbon dioxide uptake by an undisturbed tropical rain Forest in Southwest Amazonia, 1992 to 1993. Science 270:778–780. https://doi.org/10.1126/science.270.5237.778

Grebmeier JM (1987) The ecology of benthic Carbon cycling in the northern Bering and Chukchi Seas. Ph.D. dissertation, University of Alaska, Fairbanks

Greiner JT, McGlathery KJ, Gunnell J, McKee BA (2013) Seagrass restoration enhances "blue carbon" sequestration in coastal waters. PLoS One 8(8):e72469

Griffiths JR, Kadin M, Nascimento FJA, Tamelander T, Törnroos A, Bonaglia S et al (2017) The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. Glob Chang Biol 23:2179–2196. https://doi.org/10.1111/gcb.13642

Grigg RW (2002) Precious corals in Hawaii: discovery of a new bed and revised management measures for existing beds. Mar Fish Rev 64(1):13–20

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189. https://doi.org/10.1038/nature04565

Grünzweig JM, Gelfand I, Fried Y, Yakir D (2007) Biogeochemical factors contributing to enhanced carbon storage following afforestation of a semi-arid shrubland. Biogeosciences 4:891–904. https://doi.org/10.5194/bg-4-891-2007

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev seas (Antarctica): ecological role of physical parameters and biological interactions. Polar Biol 20:229–247. https://doi.org/10.1007/s003000050300

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C et al (2008) A global map of human impact on marine ecosystems. Science 319:948–952. https://doi.org/10.1126/science.1149345

Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C et al (2019) Recent pace of change in human impact on the world's ocean. Sci Rep 9. https://doi.org/10.1038/s41598-019-47201-9

Haq BU, Milliman JD (1985) Marine geology and oceanography of Arabian Sea and coastal Pakistan. New York

Harris PT, Macmillan-Lawler M, Rupp J, Baker EK (2014) Geomorphology of the oceans. Mar Geol 352:4–24. https://doi.org/10.1016/j.margeo.2014.01.011

Häussermann V, Försterra G (2007) Large assemblages of cold-water corals in Chile: a summary of recent findings and potential impacts. Bull Mar Sci 81:195e208

Haya K, Burridge LE, Davies IM, Ervik A (2005) A review and assessment of environmental risk of chemicals used for the treatment of sea lice infestations of cultured salmon. Environ Chem 5 (M):305–340

Hein MY, Beeden R, Birtles A, Gardiner NM, Le BT, Levy J et al (2020) Coral restoration effectiveness: multiregional snapshots of the long-term responses of coral assemblages to restoration. Diversity 12:153. https://doi.org/10.3390/d12040153

Henson S, Cole H, Beaulieu C, Yool A (2013) The impact of global warming on seasonality of ocean primary production. Biogeosciences 10:4357–4369. https://doi.org/10.5194/bg-10-4357-2013

Hinz H (2017) Impact of bottom fishing on animal forests: science, conservation, and fisheries management. In: Marine animal forests. Springer International, Cham, pp 1041–1059. https://doi.org/10.1007/978-3-319-21012-4_37

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E et al (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742. https://doi.org/10.1126/science.1152509

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci 4:158. https://doi.org/10.3389/fmars.2017.00158

Horoszowski-Fridman YB, Rinkevich B (2017) Restoration of the animal forests: harnessing Silviculture biodiversity concepts for coral transplantation. In: Marine animal forests. Springer International, Cham, pp 1313–1335. https://doi.org/10.1007/978-3-319-21012-4_36

Horoszowski-Fridman YB, Izhaki I, Rinkevich B (2011) Engineering of coral reef larval supply through transplantation of nursery-farmed gravid colonies. J Exp Mar Biol Ecol 399(2):162–166

Houlbrèque F (2004) Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. J Exp Biol 207:1461–1469. https://doi.org/10.1242/jeb.00911

Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical Scleractinian corals. Biol Rev 84:1–17. https://doi.org/10.1111/j.1469-185x.2008.00058.x

Houlbrèque F, Tambutté E, Ferrier-Pagès C (2003) Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata*. J Exp Mar Bio Ecol. 296:145–166. https://doi.org/10.1016/s0022-0981(03)00259-4

Howard J, Sutton-Grier A, Herr D, Kleypas J, Landis E, Mcleod E et al (2017) Clarifying the role of coastal and marine systems in climate mitigation. Front Ecol Environ 15:42–50. https://doi.org/10.1002/fee.1451

Howes EL, Joos F, Eakin CM, Gattuso J-P (2015) An updated synthesis of the observed and projected impacts of climate change on the chemical, physical and biological processes in the oceans. Front Mar Sci 2:36. https://doi.org/10.3389/fmars.2015.00036

Hubau W, Lewis SL, Phillips OL, Affum-Baffoe K, Beeckman H, Cuní-Sanchez A et al (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature 579:80–87. https://doi.org/10.1038/s41586-020-2035-0

Hughes RN (1980) Optimal foraging theory in the marine context. Ocenogr Mar Biol Ann Rev 18:423–481

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551. https://doi.org/10.1126/science.265.5178.1547

Hughes TP (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933. https://doi.org/10.1126/science.1085046

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C et al (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635):929–933

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF et al (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

IPCC (2018) Summary for policymakers. In: Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, p 32

Iriarte JL, González HE, Nahuelhual L (2010) Patagonian fjord ecosystems in southern Chile as a highly vulnerable region: problems and needs. Ambio 39:463e466

Isla E, Rossi S, Palanques A, Gili J-M, Gerdes D, Arntz W (2006) Biochemical composition of marine sediment from the eastern Weddell Sea (Antarctica): high nutritive value in a high benthic-biomass environment. J Mar Syst 60:255–267. https://doi.org/10.1016/j.jmarsys.2006.01.006

Isla E, Gerdes D, Rossi S, Fiorillo I, Sañé E, Gili J-M et al (2011) Biochemical characteristics of surface sediments on the eastern Weddell Sea continental shelf, Antarctica: is there any evidence of seasonal patterns? Polar Biol 34:1125–1133. https://doi.org/10.1007/s00300-011-0973-6

Itoiz ES, Fuentes-Grünewald C, Gasol CM, Garcés E, Alacid E, Rossi S et al (2012) Energy balance and environmental impact analysis of marine microalgal biomass production for biodiesel generation in a photobioreactor pilot plant. Biomass Bioenergy 39:324–335. https://doi.org/10.1016/j.biombioe.2012.01.026

Jackson JBC (2001) What was natural in the coastal oceans? Proc Natl Acad Sci 98:5411–5418. https://doi.org/10.1073/pnas.091092898

Jackson JBC (2008) Ecological extinction and evolution in the brave new ocean. Proc Natl Acad Sci 105(Suppl 1):11458–11465. https://doi.org/10.1073/pnas.0802812105

Jager HI, Coutant CC (2020) Knitting while Australia burns. Nat Clim Chang 10:170. https://doi.org/10.1038/s41558-020-0710-7

Jiménez C, Orejas C (2017) The builders of the oceans part II: corals from the past to the present (the stone from the sea). In: Marine animal forests. Springer International, Cham, pp 1–41. https://doi.org/10.1007/978-3-319-17001-5_56-2

Jones JB (1992) Environmental impact of trawling on the seabed: a review. N Z J Mar Freshw Res 26:59–67. https://doi.org/10.1080/00288330.1992.9516500

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH et al (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325. https://doi.org/10.1007/s00338-009-0469-9

Jones DOB, Yool A, Wei C-L, Henson SA, Ruhl HA, Watson RA et al (2014) Global reductions in seafloor biomass in response to climate change. Glob Chang Biol 20:1861–1872. https://doi.org/10.1111/gcb.12480

Keil R (2017) Anthropogenic forcing of carbonate and organic carbon preservation in marine sediments. Annu Rev Mar Sci 9:151–172. https://doi.org/10.1146/annurev-marine-010816-060724

Kilbride CM, Byrne KA, Gardiner JJ (1999) Carbon sequestration and Irish forests. COFORD, Dublin

Kinsey DW, Hopley D (1991) The significance of coral reefs as global carbon sinks response to greenhouse. Palaeogeogr Palaeoclimatol Palaeoecol 89:363–377. https://doi.org/10.1016/0031-0182(91)90172-n

Kirby MX (2014) Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. PNAS 101(35):13096–13099

Koch M, Bowes G, Ross C, Zhang XH (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob Change Biol 19(1):103–132

Kokubu H, Ishii Y, Miyazaki H, Yabe T (2017) Estimation of carbon storage in tidal flat and *Zostera marina* bed in Ise bay, toward a blue carbon evaluation. J Jpn Soc Civ Eng Ser B Coast Eng 73:1261–1266. https://doi.org/10.2208/kaigan.73.i_1261

Komorita T, Kajihara R, Tsutsumi H, Shibanuma S, Yamada T, Montani S (2014) Food sources for *Ruditapes philippinarum* in a coastal lagoon determined by mass balance and stable isotope approaches. PLoS One 9:e86732. https://doi.org/10.1371/journal.pone.0086732

Koopmans M, Wijffels RH (2008) Seasonal growth rate of the sponge *Haliclona oculata* (Demospongiae: Haplosclerida). Mar Biotechnol 10:502–510. https://doi.org/10.1007/s10126-008-9086-9

Koslow J (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES J Mar Sci 57:548–557. https://doi.org/10.1006/jmsc.2000.0722

Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. Nat Geosci 9:737–742. https://doi.org/10.1038/ngeo2790

Krause-Jensen D, Lavery P, Serrano O, Marbà N, Masque P, Duarte CM (2018) Sequestration of macroalgal carbon: the elephant in the blue carbon room. Biol Lett 14:20180236. https://doi.org/10.1098/rsbl.2018.0236

Kroeker KJ, Gambi MC, Micheli F (2013) Community dynamics and ecosystem simplification in a high-CO_2 ocean. Proc Natl Acad Sci 110:12721–12726. https://doi.org/10.1073/pnas.1216464110

Kroodsma DA, Mayorga J, Hochberg T, Miller NA, Boerder K, Ferretti F et al (2018) Tracking the global footprint of fisheries. Science 359:904–908. https://doi.org/10.1126/science.aao5646

Kuwae T, Hori M (eds) (2019) Blue carbon in shallow coastal ecosystems. Springer, Singapore. https://doi.org/10.1007/978-981-13-1295-3

Kuwae T, Kanda J, Kubo A, Nakajima F, Ogawa H, Sohma A et al (2019) CO_2 uptake in the shallow coastal ecosystems affected by anthropogenic impacts. In: Blue carbon in shallow coastal ecosystems. Springer, Singapore, pp 295–319. https://doi.org/10.1007/978-981-13-1295-3_11

Lafleur B, Thiffault E, Paré D, Camiré C, Bernier-Cardou M, Masse S (2012) Effects of hog manure application on the nutrition and growth of hybrid poplar (*Populus* spp.) and on soil solution chemistry in short-rotation woody crops. Agric Ecosyst Environ 155:95–104. https://doi.org/10.1016/j.agee.2012.04.002

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR et al (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol 28:2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008

Lal R (2004) Soil carbon sequestration impacts on global climate change and food security. Science 304:1623–1627. https://doi.org/10.1126/science.1097396

Langin K (2018) Seaweed masses assault Caribbean islands. Science 360:1157–1158. https://doi.org/10.1126/science.360.6394.1157

Larkum AWD (1983) The primary productivity of plant communities on coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science, Townsville, pp 221–230

Lasker HR, Martinez-Quintana Á, Bramanti L, Edmunds PJ (2020) Resilience of Octocoral forests to catastrophic storms. Sci Rep 10. https://doi.org/10.1038/s41598-020-61238-1

Laufkötter C, Vogt M, Gruber N, Aita-Noguchi M, Aumont O, Bopp L et al (2015) Drivers and uncertainties of future global marine primary production in marine ecosystem models. Biogeosciences 12:6955–6984. https://doi.org/10.5194/bg-12-6955-2015

Le Quéré C, Andres RJ, Boden T, Conway T, Houghton RA, House JI et al (2013) The global carbon budget 1959-2011. Earth Syst Sci Data 5:165–185. https://doi.org/10.5194/essd-5-165-2013

Le Quéré C, Moriarty R, Andrew RM, Peters GP, Ciais P, Friedlingstein P et al (2015) Global carbon budget 2014. Earth Syst Sci Data 7(1):47–85

Le Quéré C, Andrew RM, Friedlingstein P, Sitch S, Pongratz J, Manning AC et al (2018) Global carbon budget 2017. Earth Syst Sci Data 10(1):405–448

Leal MC, Calado R, Sheridan C, Alimonti A, Osinga R (2013) Coral aquaculture to support drug discovery. Trends Biotechnol 31(10):555–561

Lenz EA, Bramanti L, Lasker HR, Edmunds PJ (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34(4):1099–1109

Levin LA, Mengerink K, Gjerde KM, Rowden AA, Van Dover CL, Clark MR et al (2016) Defining serious harm to the marine environment in the context of deep-seabed mining. Mar Policy 74:245–259. https://doi.org/10.1016/j.marpol.2016.09.032

Li Y, Wang Y-G, Houghton RA, Tang L-S (2015) Hidden carbon sink beneath desert. Geophys Res Lett 42:5880–5887. https://doi.org/10.1002/2015gl064222

Liao C, Luo Y, Jiang L, Zhou X, Wu X, Fang C et al (2007) Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen Stocks in the Yangtze Estuary, China. Ecosystems 10:1351–1361. https://doi.org/10.1007/s10021-007-9103-2

Linares C, Garrabou J, Hereu B, Diaz D, Marschal C, Sala E et al (2011) Assessing the effectiveness of marine reserves on unsustainably harvested long-lived sessile invertebrates. Conserv Biol 26:88–96. https://doi.org/10.1111/j.1523-1739.2011.01795.x

Liverino B (1983) Il Corallo—Esperienze e ricordi di un corallaro. Banca di credito populare Torre del Greco. Torre del Greco, Li Causi Editore

Lotze HK, Worm B (2009) Historical baselines for large marine animals. Trends Ecol Evol 24 (5):254–262

Lovelock CE, Duarte CM (2019) Dimensions of blue carbon and emerging perspectives. Biol Lett 15:20180781. https://doi.org/10.1098/rsbl.2018.0781

Luyssaert S, Schulze E-D, Börner A, Knohl A, Hessenmöller D, Law BE et al (2008) Old-growth forests as global carbon sinks. Nature 455:213–215. https://doi.org/10.1038/nature07276

Lybolt M, Neil D, Zhao J, Feng Y, Yu KF, Pandolfi J (2011) Instability in a marginal coral reef: the shift from natural variability to a human-dominated seascape. Front Ecol Environ 9(3):154–160

Macreadie PI, Serrano O, Maher DT, Duarte CM, Beardall J (2017a) Addressing calcium carbonate cycling in blue carbon accounting. Limnol Oceanogr Lett 2:195–201. https://doi.org/10.1002/lol2.10052

Macreadie PI, Ollivier QR, Kelleway JJ, Serrano O, Carnell PE, Lewis CJE et al (2017b) Carbon sequestration by Australian tidal marshes. Sci Rep 7:44071. https://doi.org/10.1038/srep44071

Macreadie PI, Anton A, Raven JA, Beaumont N, Connolly RM, Friess DA et al (2019) The future of blue carbon science. Nat Commun 10. https://doi.org/10.1038/s41467-019-11693-w

Mallo M, Ziveri P, Reyes-Garcia V, Rossi S (2019) Historical record of *Corallium rubrum* and its changing carbon sequestration capacity: a meta-analysis from the North Western Mediterranean. PLoS One 14:e0223802. https://doi.org/10.1371/journal.pone.0223802

Marbà N, Arias-Ortiz A, Masqué P, Kendrick GA, Mazarrasa I, Bastyan GR et al (2015) Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. J Ecol 103 (2):296–302

Martin CS, Giannoulaki M, Leo F De, Scardi M, Salomidi M, Knittweis L et al (2014) Coralligenous and maërl habitats: predictive modelling to identify their spatial distributions across the Mediterranean Sea. Sci Rep 4. https://doi.org/10.1038/srep05073

Martinez-Quintana A, Bramanti L, Viladrich N, Rossi S, Guizien K (2014) Quantification of larval traits driving connectivity: the case of *Corallium rubrum* (L. 1758). Mar Biol 162:309–318. https://doi.org/10.1007/s00227-014-2599-z

Mayr C, Rebolledo L, Schulte K, Schuster A, Zolitschka B, Försterra G, Häussermann V (2014) Responses of nitrogen and carbon deposition rates in Comau Fjord (42°S, Southern Chile) to natural and anthropogenic impacts during the last century. Cont Shelf Res 78:29–38

Mcclanahan TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. Environ Conserv 25:122–130. https://doi.org/10.1017/s0376892998000174

McKinley E, Acott T, Yates KL (2020) Marine social sciences: looking towards a sustainable future. Environ Sci Policy 108:85–92. https://doi.org/10.1016/j.envsci.2020.03.015

Meesters HWG, Smith SR, Becking LE (2015) A review of coral reef restoration techniques (No. C028/14). IMARES

Miller KJ, Ayre DJ (2008) Population structure is not a simple function of reproductive mode and larval type: insights from tropical corals. J Anim Ecol 77:713–724. https://doi.org/10.1111/j.1365-2656.2008.01387.x

Miranda RJ, Nunes JACC, Creed JC, Barros F, Macieira RM, Santos RG et al (2020) Brazil policy invites marine invasive species. Science 368:481. https://doi.org/10.1126/science.abb7255

Mistri M, Munari C (2013) The invasive bag mussel *Arcuatula senhousia* is a CO_2 generator in near-shore coastal ecosystems. J Exp Mar Bio Ecol 440:164–168. https://doi.org/10.1016/j.jembe.2012.11.019

Miyajima T, Hamaguchi M (2019) Carbon sequestration in sediment as an ecosystem function of seagrass meadows. In: Blue carbon in shallow coastal ecosystems. Springer, Singapore, pp 33–71. https://doi.org/10.1007/978-981-13-1295-3_2

Miyamoto M, Kiyota M, Hayashibara T, Nonaka M, Imahara Y, Tachikawa H (2017) Megafaunal composition of cold-water corals and other deep-sea benthos in the southern Emperor Seamounts area, North Pacific Ocean. Galaxea, J Coral Reef Stud 19:19–30. https://doi.org/10.3755/galaxea.19.1_19

Molinski TF, Dalisay DS, Lievens SL, Saludes JP (2009) Drug development from marine natural products. Nat Rev Drug Discov 8(1):69–85

Montero-Serra I, Garrabou J, Doak DF, Figuerola L, Hereu B, Ledoux J-B et al (2017) Accounting for life-history strategies and timescales in marine restoration. Conserv Lett 11:e12341. https://doi.org/10.1111/conl.12341

Montseny M, Linares C, Viladrich N, Olariaga A, Carreras M, Palomeras N et al (2019) First attempts towards the restoration of gorgonian populations on the Mediterranean continental shelf. Aquat Conserv Mar Freshw Ecosyst 29:1278–1284. https://doi.org/10.1002/aqc.3118

Montseny M, Linares C, Viladrich N, Capdevila P, Ambroso S, Diaz D et al (2020) A new large-scale and cost-effective restoration method for cold-water coral gardens. Aquat Conserv Mar Freshw Ecosyst. 30:977–987. https://doi.org/10.1002/aqc.3303

Moreno-Mateos D, Alberdi A, Morriën E, van der Putten WH, Rodriguez-Uña A, Montoya D (2020) The long-term restoration of ecosystem complexity. Nat Ecol Evol 4:676–685. https://doi.org/10.1038/s41559-020-1154-1

Morgan CL, Odunton NA, Jones AT (1999) Synthesis of environmental impacts of deep seabed mining. Mar Georesour & Geotechnol 17:307–356. https://doi.org/10.1080/106411999273666

Morse AN (2000) Opportunities for biotechnology for coral and reef restoration. In: Opportunities for environmental applications of marine biotechnology: proceedings of the October 5–6, 1999, Workshop. National Academies Press, p 74

Mueller CE, Larsson AI, Veuger B, Middelburg JJ, van Oevelen D (2014) Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. Biogeosciences 11:123–133. https://doi.org/10.5194/bg-11-123-2014

Muraoka D (2004) Seaweed resources as a source of carbon fixation. Bull Fish Res Agen Jpn 1:59–64

Murton B (2013) Seafloor mining: the future or just another pipe dream? Int J Soc Underwat Tech 31:53–54

Niklitschek E, Soto D, Lafon A, Molinet C, Toledo P (2013) Southward expansion of the Chilean salmon industry in the Patagonian fjords: main environmental challenges. Rev Aquac 5 (3):172–195

Nunes FLD, Norris RD, Knowlton N (2011) Long distance dispersal and connectivity in Amphi-Atlantic corals at regional and basin scales. PLoS One 6:e22298. https://doi.org/10.1371/journal.pone.0022298

Officer CB, Biggs RB, Taft JL, Cronin LE, Tyler MA, Boynton WR (1984) Chesapeake Bay anoxia: origin, development, and significance. Science 223:22–27. https://doi.org/10.1126/science.223.4631.22

Orejas C, Gori A, Rad-Menéndez C, Last KS, Davies AJ, Beveridge CM et al (2016) The effect of flow speed and food size on the capture efficiency and feeding behaviour of the cold-water coral *Lophelia pertusa*. J Exp Mar Bio Ecol 481:34–40. https://doi.org/10.1016/j.jembe.2016.04.002

Outeiro L, Häussermann V, Viddi F, Hucke-Gaete R, Försterra G, Oyarzo H, Kosiel K, Villasante S (2015) Using ecosystem services mapping for marine spatial planning in southern Chile under scenario assessment. Ecosyst Serv 16:341–353

Padilla FM, Vidal B, Sánchez J, Pugnaire FI (2010) Land-use changes and carbon sequestration through the twentieth century in a Mediterranean mountain ecosystem: implications for land management. J Environ Manag 91:2688–2695. https://doi.org/10.1016/j.jenvman.2010.07.031

Page CA, Vaughan DE (2014) The cultivation of massive corals using "micro-fragmentation" for the "reskinning" of degraded coral reefs

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA et al (2011) A large and persistent carbon sink in the worlds forests. Science 333:988–993. https://doi.org/10.1126/science.1201609

Pandolfi JM, Jackson JB (2006) Ecological persistence interrupted in Caribbean coral reefs. Ecol Lett 9(7):818–826

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG et al (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301(5635):955–958

Paoli C, Montefalcone M, Morri C, Vassallo P, Bianchi CN (2017) Ecosystem functions and services of the marine animal forests. In: Marine animal forests. Springer International, Cham, pp 1271–1312. https://doi.org/10.1007/978-3-319-21012-4_38

Paulo D, Cunha AH, Boavida, J, Serrao E, Gonçalves EJ, Fonseca M (2019) Open coast seagrass restoration. Can we do it? Large scale seagrass transplants. Front Mar Sci 6:UNSP-52

Petit RJ, Hu FS, Dick CW (2008) Forests of the past: a window to future changes. Science 320:1450–1452. https://doi.org/10.1126/science.1155457

Pihl L (1985) Food selection and consumption of mobile epibenthic fauna in shallow marine areas. Mar Ecol Prog Ser 22:169–179. https://doi.org/10.3354/meps022169

Pinet PR (2003) Invitation to oceanography. Jones & Bartlett Learning, Boston. ISBN: 978-0-7637-2136-7

Pregnall AM, Rudy PP (1985) Contribution of green macroalgal mats (Enteromorpha spp.) to seasonal production in an estuary. Mar Ecol Prog Ser 24:167–176. https://doi.org/10.3354/meps024167

Price LL, Narchi NE (2015) Ethnobiology of *Corallium rubrum*: protection, healing, medicine, and magic. In: Ethnobiology of corals and coral reefs. Springer International, Cham, pp 73–86. https://doi.org/10.1007/978-3-319-23763-3_5

Proctor J, Bennett J, Steiner E, Gerhart A (2009) CESTA (Spatial History Project) [Internet]. [cited 2016 Apr 26]. Available from: https://web.stanford.edu/group/spatialhistory/media/visualizations/ChileNorway12.swf

Pryor SC, Barthelmie RJ, Carreiro M, Davis ML, Hartley A, Jensen B et al (2001) Nitrogen deposition to and cycling in a deciduous forest. Sci World J 1:245–254. https://doi.org/10.1100/tsw.2001.372

Pugh TAM, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V et al (2019) Role of forest regrowth in global carbon sink dynamics. Proc Natl Acad Sci 116:4382–4387. https://doi.org/10.1073/pnas.1810512116

Pusceddu A, Bianchelli S, Martin J, Puig P, Palanques A, Masque P et al (2014) Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proc Natl Acad Sci 111:8861–8866. https://doi.org/10.1073/pnas.1405454111

Pusceddu A, Fraschetti S, Scopa M, Rizzo L, Danovaro R (2016) Meiofauna communities, nematode diversity and C degradation rates in seagrass (*Posidonia oceanica* L.) and unvegetated sediments invaded by the algae *Caulerpa cylindracea* (Sonder). Mar Environ Res 119:88–99

Pyle RL, Copus JM (2019) Mesophotic coral ecosystems: introduction and overview. In: Coral reefs of the world. Springer International, Cham, pp 3–27. https://doi.org/10.1007/978-3-319-92735-0_1

Ramsby BD, Shirur KP, Iglesias-Prieto R, Goulet TL (2014) *Symbiodinium* photosynthesis in Caribbean octocorals. PLoS One 9:e106419. https://doi.org/10.1371/journal.pone.0106419

Reed D C, Brzezinski MA (2009) Kelp forests. In: Laffoley Dd'A, Grimsditch G (eds) The management of natural coastal carbon sinks, 31

Rees RM, Bingham IJ, Baddeley JA, Watson CA (2005) The role of plants and land management in sequestering soil carbon in temperate arable and grassland ecosystems. Geoderma 128:130–154. https://doi.org/10.1016/j.geoderma.2004.12.020

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar Ecol Prog Ser 254:141–150. https://doi.org/10.3354/meps254141

Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305:1609–1612. https://doi.org/10.1126/science.1100958

Richter C, Wunsch M, Rasheed M, Kötter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413:726–730. https://doi.org/10.1038/35099547

Rinkevich B (2014) Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? Curr Opin Environ Sustain 7:28–36

Rinkevich B (2015a) Climate change and active reef restoration—ways of constructing the "reefs of tomorrow". J Mar Sci Eng 3(1):111–127

Rinkevich B (2015b) Novel tradable instruments in the conservation of coral reefs, based on the coral gardening concept for reef restoration. J Environ Manag 162:199–205. https://doi.org/10.1016/j.jenvman.2015.07.028

Rinkevich B (2019) The active reef restoration toolbox is a vehicle for coral resilience and adaptation in a changing world. J Mar Sci Eng. 7(7):201

Rinkevich B (2020) Ecological engineering approaches in coral reef restoration. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsaa022

Rixen M, Beckers J-M, Levitus S, Antonov J, Boyer T, Maillard C, Fichaut M et al (2005) The Western Mediterranean deep water: a proxy for climate change. Geophys Res Lett 32:1–4

Rizzo L, Fraschetti S, Alifano P, Pizzolante G, Stabili L (2016a) The alien species *Caulerpa cylindracea* and its associated bacteria in the Mediterranean Sea. Mar Biol 163(1):4

Rizzo L, Fraschetti S, Alifano P, Tredici MS, Stabili L (2016b) Association of *Vibrio* community with the Atlantic Mediterranean invasive alga *Caulerpa cylindracea*. J Exp Mar Biol Ecol 475:129–136. https://doi.org/10.1016/j.jembe.2015.11.013

Rizzo L, Pusceddu A, Stabili L, Alifano P, Fraschetti S (2017) Potential effects of an invasive seaweed (*Caulerpa cylindracea*, Sonder) on sedimentary organic matter and microbial metabolic activities. Sci Rep 7(1):1–10. https://doi.org/10.1038/s41598-017-12556-4

Rizzo L, Pusceddu A, Bianchelli S, Fraschetti S (2020) Potentially combined effect of the invasive seaweed *Caulerpa cylindracea* (Sonder) and sediment deposition rates on organic matter and meiofaunal assemblages. Mar Environ Res 104966. https://doi.org/10.1016/j.marenvres.2020.104966

Roark EB, Guilderson TP, Dunbar RB, Ingram BL (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. Mar Ecol Prog Ser 327:1–14. https://doi.org/10.3354/meps327001

Roberts CM (2002) Deep impact: the rising toll of fishing in the deep sea. Trends Ecol Evol 17:242–245. https://doi.org/10.1016/s0169-5347(02)02492-8

Roberts JM, Murray F, Anagnostou E, Hennige S, Gori A, Henry L-A et al (2016) Cold-water corals in an era of rapid global change: are these the deep ocean's most vulnerable ecosystems? In: The Cnidaria, past, present and future. Springer International, Cham, pp 593–606. https://doi.org/10.1007/978-3-319-31305-4_36

Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL et al (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science 361:281–284. https://doi.org/10.1126/science.aaq1614

Roff G, Clark TR, Reymond CE, Zhao JX, Feng Y, McCook LJ et al (2013) Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore great barrier reef, following European settlement. Proc R Soc B-Biol Sci 280(1750):20122100

Röhr ME, Boström C, Canal-Vergés P, Holmer M (2016) Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. Biogeosciences 13:6139–6153. https://doi.org/10.5194/bg-13-6139-2016

Rossi S (2013) The destruction of the 'animal forests' in the oceans: towards an over-simplification of the benthic ecosystems. Ocean Coast Manag. 84:77–85. https://doi.org/10.1016/j.ocecoaman.2013.07.004

Rossi S (2019) Oceans in decline. Copernicus Books, Springer-Nature, Cham, pp 1–349. ISBN: 978-3-030-02513-7

Rossi S, Gili J-M (2005) Composition and temporal variation of the near-bottom seston in a Mediterranean coastal area. Estuar Coast Shelf Sci 65:385–395. https://doi.org/10.1016/j.ecss.2005.05.024

Rossi S, Gili JM (2009) Near bottom phytoplankton and seston: importance in the pelagicbenthic coupling processes. In: Marine phytoplankton. Nova Science, New York, pp 45–85. ISBN: 978-1-60741-087-4

Rossi S, Grémare A, Gili J-M, Amouroux J-M, Jordana E, Vétion G (2003) Biochemical characteristics of settling particulate organic matter at two north-western Mediterranean sites: a seasonal comparison. Estuar Coast Shelf Sci 58:423–434. https://doi.org/10.1016/s0272-7714(03)00108-2

Rossi S, Ribes M, Coma R, Gili J-M (2004) Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study. Mar Biol 144:89–99. https://doi.org/10.1007/s00227-003-1168-7

Rossi S, Tsounis G, Orejas C, Padrón T, Gili J-M, Bramanti L et al (2008) Survey of deep-dwelling red coral (*Corallium rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154:533–545. https://doi.org/10.1007/s00227-008-0947-6

Rossi S, Gili J-M, Garrofé X (2011) Net negative growth detected in a population of *Leptogorgia sarmentosa*: quantifying the biomass loss in a benthic soft bottom-gravel gorgonian. Mar Biol 158:1631–1643. https://doi.org/10.1007/s00227-011-1675-x

Rossi S, Bramanti L, Broglio E, Gili JM (2012) Trophic impact of long-lived species indicated by population dynamics in the short-lived hydrozoan *Eudendrium racemosum*. Mar Ecol Prog Ser 467:97–111. https://doi.org/10.3354/meps09848

Rossi S, Bramanti L, Gori A, Orejas C (2017a) An overview of the animal forests of the world. In: Marine animal forests. Springer International, Cham, pp 1–26. https://doi.org/10.1007/978-3-319-17001-5_1-1

Rossi S, Coppari M, Viladrich N (2017b) Benthic-pelagic coupling: new perspectives in the animal forests. In: Marine animal forests. Springer International, Cham, pp 855–885. https://doi.org/10.1007/978-3-319-21012-4_23

Rossi S, Schubert N, Brown D, de Oliveira Soares M, Grosso V, Rangel-Huerta E et al (2018) Linking host morphology and symbiont performance in octocorals. Sci Rep 8. https://doi.org/10.1038/s41598-018-31262-3

Rossi S, Isla E, Bosch-Belmar M, Galli G, Gori A, Gristina M et al (2019a) Changes of energy fluxes in marine animal forests of the Anthropocene: factors shaping the future seascape. ICES J Mar Sci 76:2008–2019. https://doi.org/10.1093/icesjms/fsz147

Rossi S, Rizzo L, Duchêne J-C (2019b) Polyp expansion of passive suspension feeders: a red coral case study. PeerJ 7:e7076. https://doi.org/10.7717/peerj.7076

Rossi S, Gravili C, Milisenda G, Bosch-Belmar M, De Vito D, Piraino S (2019c) Effects of global warming on reproduction and potential dispersal of Mediterranean cnidarians. Eur Zool J 86:255–271. https://doi.org/10.1080/24750263.2019.1631893

Rossi S, Schubert N, Brown D, Gonzalez-Posada A, Soares MO (2020) Trophic ecology of Caribbean octocorals: autotrophic and heterotrophic seasonal trends. Coral Reefs 39:433–449. https://doi.org/10.1007/s00338-020-01906-w

Roxy MK, Modi A, Murtugudde R, Valsala V, Panickal S, Kumar SP et al (2016) A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean. Geophys Res Lett 43:826–833. https://doi.org/10.1002/2015gl066979

Ruzicka RR, Colella MA, Porter JW, Morrison JM, Kidney JA, Brinkhuis V et al (2013) Temporal changes in benthic assemblages on Florida keys reefs 11 years after the 1997/1998 El Niño. Mar Ecol Prog Ser 489:125–141

Saderne V, Geraldi NR, Macreadie PI, Maher DT, Middelburg JJ, Serrano O et al (2019) Role of carbonate burial in blue carbon budgets. Nat Commun 10:1106. https://doi.org/10.1038/s41467-019-08842-6

Sanford E, Sones JL, Garcia-Reyes M, Goddard JHR, Largier JL (2019) Widespread shifts in the coastal biota of northern California during the 2014-2016 marine heatwaves. Sci Rep 9. https://doi.org/10.1038/s41598-019-40784-3

Santangelo G, Bramanti L, Rossi S, Tsounis G, Vielmini I, Lott C, Gili JM (2012) Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. J Exp Mar Biol Ecol 411:7–13

Santos-Ballardo DU, Rossi S, Reyes-Moreno C, Valdez-Ortiz A (2016) Microalgae potential as a biogas source: current status, restraints and future trends. Rev Environ Sci Bio/Technol 15:243–264. https://doi.org/10.1007/s11157-016-9392-z

Sardá R, Rossi S, Marti X, Gili JM (2012) Marine benthic cartography of the Cap de Creus (NE Catalan Coast, Mediterranean Sea). Sci Mar 76:159–171. https://doi.org/10.3989/scimar.03101.18d

Sasaki N, Putz FE (2009) Critical need for new definitions of forest and forest degradation in global climate change agreements. Conserv Lett 2:226–232. https://doi.org/10.1111/j.1755-263x.2009.00067.x

Saunders JE, Zahed KMA, Paterson DM (2007) The impact of organic pollution on the macrobenthic fauna of Dubai Creek (UAE). Mar Pollut Bull 54:1715–1723. https://doi.org/10.1016/j.marpolbul.2007.07.002

Saunders MJ, Kansiime F, Jones MB (2012) Agricultural encroachment: implications for carbon sequestration in tropical African wetlands. Glob Chang Biol 18:1312–1321. https://doi.org/10.1111/j.1365-2486.2011.02633.x

Saunders MI, Bode M, Atkinson S, Klein CJ, Metaxas A, Beher J et al (2017) Simple rules can guide whether land-or ocean-based conservation will best benefit marine ecosystems. PLoS Biol 15(9):e2001886

Sauriau P-G, Kang C-K (2000) Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder Cerastoderma edule (Mollusca, Bivalvia) in the Marennes-Oléron Bay. In: Island, ocean and deep-sea biology. Springer, Cham, pp 317–329. https://doi.org/10.1007/978-94-017-1982-7_29

Schlesinger WH (1999) Carbon and agriculture: carbon sequestration in soils. Science 284:2095. https://doi.org/10.1126/science.284.5423.2095

Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, Ritchie ME et al (2014) Animating the carbon cycle. Ecosystems 17:344–359. https://doi.org/10.1007/s10021-013-9715-7

Schubert N, Brown D, Rossi S (2017) Symbiotic versus nonsymbiotic octocorals: physiological and ecological implications. In: Marine animal forests. Springer International, Cham, pp 887–918. https://doi.org/10.1007/978-3-319-21012-4_54

Serrano-Ortiz P, Roland M, Sanchez-Moral S, Janssens IA, Domingo F, Goddéris Y et al (2010) Hidden, abiotic CO_2 flows and gaseous reservoirs in the terrestrial carbon cycle: review and perspectives. Agric For Meteorol 150:321–329. https://doi.org/10.1016/j.agrformet.2010.01.002

Sfriso A, Marcomini A, Pavoni B, Orio AA (1993) Species composition, biomass, and net primary production in shallow coastal waters: the Venice lagoon. Bioresour Technol 44:235–249. https://doi.org/10.1016/0960-8524(93)90158-8

Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J et al (2010) The Gulf: a young sea in decline. Mar Pollut Bull 60:13–38. https://doi.org/10.1016/j.marpolbul.2009.10.017

Simon-Lledó E, Bett BJ, Huvenne VAI, Köser K, Schoening T, Greinert J et al (2019) Biological effects 26 years after simulated deep-sea mining. Sci Rep 9. https://doi.org/10.1038/s41598-019-44492-w

Smale DA, Burrows MT, Evans AJ, King N, Sayer MDJ, Yunnie ALE et al (2016) Linking environmental variables with regional- scale variability in ecological structure and standing stock of carbon within UK kelp forests. Mar Ecol Prog Ser 542:79–95. https://doi.org/10.3354/meps11544

Smetacek V, Naqvi SWA (2008) The next generation of iron fertilization experiments in the Southern Ocean. Philos Trans R Soc A Math Phys Eng Sci 366:3947–3967. https://doi.org/10.1098/rsta.2008.0144

Smetacek V, Klaas C, Strass VH, Assmy P, Montresor M, Cisewski B et al (2012) Deep carbon export from a Southern Ocean iron-fertilized diatom bloom. Nature 487:313–319. https://doi.org/10.1038/nature11229

Smith P (2004) Soils as carbon sinks: the global context. Soil Use Manag 20:212–218. https://doi.org/10.1079/sum2004233

Smith SV (2013) Parsing the oceanic calcium carbonate cycle: a net atmospheric carbon dioxide source, or a sink? Association for the Sciences of Limnology and Oceanography

Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. Annu Rev Ecol Syst 23:89–118. https://doi.org/10.1146/annurev.es.23.110192.000513

Smith CR, Mincks S, DeMaster DJ (2006) A synthesis of bentho-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. Deep Sea Res Part II Top Stud Oceanogr. 53:875–894. https://doi.org/10.1016/j.dsr2.2006.02.001

Soares de Oliveira M (2020) Marginal reef paradox: a possible refuge from environmental changes? Ocean Coast Manag 185:105063. https://doi.org/10.1016/j.ocecoaman.2019.105063

Soares de Oliveira M, de Araújo JT, Ferreira SMC, Santos BA, Boavida JRH, Costantini F et al (2020) Why do mesophotic coral ecosystems have to be protected? Sci Total Environ 138456. https://doi.org/10.1016/j.scitotenv.2020.138456

Sousa AI, Pardal AILMA, Caçador I (2010) Productivity and nutrient cycling in salt marshes: contribution to ecosystem health. Estuar Coast Shelf Sci 87:640–646. https://doi.org/10.1016/j.ecss.2010.03.007

Spalding H, Foster MS, Heine JN (2003) Composition, distribution, and abundance of deep-water macroalgae in Central California. J Phycol 39:273–284. https://doi.org/10.1046/j.1529-8817.2003.02010.x

Stabili L, Rizzo L, Pizzolante G, Alifano P, Fraschetti S (2017) Spatial distribution of the culturable bacterial community associated with the invasive alga *Caulerpa cylindracea* in the Mediterranean Sea. Mar Environ Res 125:90–98

Stabili L, Cecere E, Licciano M, Petrocelli A, Sicuro B, Giangrande A (2019) Integrated multitrophic aquaculture by-products with added value: the Polychaete *Sabella spallanzanii* and the seaweed *Chaetomorpha linum* as potential dietary ingredients. Mar Drugs 17:677. https://doi.org/10.3390/md17120677

Steffen W, Rockström J, Richardson K, Lenton TM, Folke C, Liverman D et al (2018) Trajectories of the earth system in the Anthropocene. Proc Natl Acad Sci 115:8252–8259. https://doi.org/10.1073/pnas.1810141115

Steinacher M, Joos F, Frölicher TL, Bopp L, Cadule P, Cocco V et al (2010) Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences 7:979–1005. https://doi.org/10.5194/bg-7-979-2010

Storlazzi CD, Elias E, Field ME, Presto MK (2011) Numerical modeling of the impact of sea-level rise on fringing coral reef hydrodynamics and sediment transport. Coral Reefs 30:83–96

Suzuki A, Kawahata H (2003) Carbon budget of coral reef systems: an overview of observations in fringing reefs, barrier reefs and atolls in the Indo-Pacific regions. Tellus B 55:428–444. https://doi.org/10.1034/j.1600-0889.2003.01442.x

Suzuki A, Kawahata H (2004) Reef water CO_2 system and carbon production of coral reefs: topographic control of system level performance. In: Global environmental change in the ocean and on land, pp 229–248

Suzuki S, Ishida T, Nagano T, Waijaroen S (1999) Influences of deforestation on carbon balance in a natural tropical peat swamp forest in Thailand. Environ Control Biol 37:115–128. https://doi.org/10.2525/ecb1963.37.115

Tada K, Monaka K, Morishita M, Hashimoto T (1998) Standing stocks and production rates of phytoplankton and abundance of bacteria in the Seto Inland Sea. Jpn J Oceanogr 54:285–295. https://doi.org/10.1007/bf02742613

Taviani M, Angeletti L, Beuck L, Campiani E, Canese S, Foglini F et al (2016) Reprint of On and off the beaten track: megafaunal sessile life and Adriatic cascading processes. Mar Geol 375:146–160. https://doi.org/10.1016/j.margeo.2015.10.003

Tescione G (1968) The Italians and their coral fishing. Fausto Fiorentino (ed) Napoli, Italia, p 490

Testi L, Orgaz F, Villalobos F (2008) Carbon exchange and water use efficiency of a growing, irrigated olive orchard. Environ Exp Bot 63:168–177. https://doi.org/10.1016/j.envexpbot.2007.11.006

Thrush SF, Dayton PK (2002) Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annu Rev Ecol Syst 33:449–473. https://doi.org/10.1146/annurev.ecolsys.33.010802.150515

Thurstan RH, Pandolfi JM, zu Ermgassen PSE (2017) Animal forests through time: historical data to understand present changes in marine ecosystems. In: Marine animal forests. Springer International, Cham, pp 947–963. https://doi.org/10.1007/978-3-319-21012-4_31

Tokoro T, Watanabe K, Tada K, Kuwae T (2019) Air-water CO_2 flux in shallow coastal waters: theory, methods, and empirical studies. In: Kuwae T, Hori M (eds) Blue carbon in shallow coastal ecosystems. Springer, Singapore, pp 153–184. https://doi.org/10.1007/978-981-13-1295-3_6

Tsao F, Morgan LE (2005) Corals that live on mountaintops. J Mar Educ 21(4):9–11

Tsounis G, Rossi S, Gili J-M, Arntz W (2006) Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). Mar Biol 149:1059–1070. https://doi.org/10.1007/s00227-006-0302-8

Tsounis G, Rossi S, Gili JM (2010a) Identifying population decline in *Corallium rubrum* by using historical information. In: Bussoletti E, Cottingham D, Bruckner A, Roberts G (eds) Proceedings of the international workshop on red coral science, management, and trade: lessons from the Mediterranean. Napoli, September 23–26, 2009, pp 33–39

Tsounis G, Rossi S, Grigg R, Santangelo G, Bramanti L, Gili J-M (2010b) The exploitation and conservation of precious corals. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) Oceanography and marine biology. Chapman and Hall/CRC, London, pp 161–212. https://doi.org/10.1201/ebk1439821169-3

Tsounis G, Rossi S, Bramanti L, Santangelo G (2013) Management hurdles for sustainable harvesting of *Corallium rubrum*. Mar Policy 39:361–364. https://doi.org/10.1016/j.marpol.2012.12.010

van der Heijden LH, Kamenos NA (2015) Reviews and syntheses: calculating the global contribution of coralline algae to total carbon burial. Biogeosciences 12:6429–6441. https://doi.org/10.5194/bg-12-6429-2015

Van Dover CL, Aronson J, Pendleton L, Smith S, Arnaud-Haond S, Moreno-Mateos D et al (2014) Ecological restoration in the deep sea: desiderata. Mar Policy 44:98–106. https://doi.org/10.1016/j.marpol.2013.07.006

Van Oppen MJH, Gates RD, Blackall LL, Cantin N, Chakravarti LJ, Chan WY et al (2017) Shifting paradigms in restoration of the worlds coral reefs. Glob Chang Biol 23:3437–3448. https://doi.org/10.1111/gcb.13647

Vargas-Yanez M, Moya F, Garcia-Martınez MC, Tel E, Zunino P, Plaza F, Salat J et al (2010) Climate change in the Western Mediterranean Sea 1900–2008. J Mar Syst 82:171–176

Veron JEN, Hoegh-Guldberg O, Lenton TM, Lough JM, Obura DO, Pearce-Kelly P et al (2009) The coral reef crisis: the critical importance of 350ppm CO_2. Mar Pollut Bull 58:1428–1436. https://doi.org/10.1016/j.marpolbul.2009.09.009

Vranken G, Heip C (1986) The productivity of marine nematodes. Ophelia 26:429–442. https://doi.org/10.1080/00785326.1986.10422004

Wang W, Chen X, Wang L, Zhang H, Yin G, Zhang Y (2016) Approaching the truth of the missing carbon sink. Polish J Environ Stud 25:1799–1802. https://doi.org/10.15244/pjoes/62357

Washburn TW, Turner PJ, Durden JM, Jones DOB, Weaver P, Van Dover CL (2019) Ecological risk assessment for deep-sea mining. Ocean Coast Manag. 176:24–39. https://doi.org/10.1016/j.ocecoaman.2019.04.014

Wassmann P, Slagstad D, Riser CW, Reigstad M (2006) Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone. J Mar Syst 59:1–24. https://doi.org/10.1016/j.jmarsys.2005.05.006

Watanabe A, Nakamura T (2019) Carbon dynamics in coral reefs. In: Kuwae T, Hori M (eds) Blue carbon in shallow coastal ecosystems. Springer, Singapore, pp 273–293. https://doi.org/10.1007/978-981-13-1295-3_10

Wessel P, Sandwell D, Kim S-S (2010) The global seamount census. Oceanography 23:24–33. https://doi.org/10.5670/oceanog.2010.60

Whitehead D (2011) Forests as carbon sinks—benefits and consequences. Tree Physiol 31:893–902. https://doi.org/10.1093/treephys/tpr063

Widdows J, Blauw A, Heip CHR, Herman PMJ, Lucas CH, Middelburg JJ et al (2004) Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. Mar Ecol Prog Ser 274:41–56. https://doi.org/10.3354/meps274041

Wlodarska-Kowalczuk M, Weslawski JM (2001) Impact of climate warming on Arctic benthic biodiversity: a case study of two Arctic glacial bays. Clim Res 18(1–2):127–132

Woulds C, Andersson JH, Cowie GL, Middelburg JJ, Levin LA (2009) The short-term fate of organic carbon in marine sediments: comparing the Pakistan margin to other regions. Deep Sea Res Part II Top Stud Oceanogr. 56:393–402. https://doi.org/10.1016/j.dsr2.2008.10.008

Zamanian K, Pustovoytov K, Kuzyakov Y (2016) Pedogenic carbonates: forms and formation processes. Earth-Sci Rev 157:1–17. https://doi.org/10.1016/j.earscirev.2016.03.003

Zha T, Kellomaki S, Wang K-Y, Rouvinen I (2004) Carbon sequestration and ecosystem respiration for 4 years in a Scots pine forest. Glob Chang Biol 10:1492–1503. https://doi.org/10.1111/j.1365-2486.2004.00835.x

Zu Ermgassen PS, Spalding MD, Blake B, Coen LD, Dumbauld B, Geiger S et al (2012) Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. Proc R Soc B-Biol Sci 279(1742):3393–3400

Zu Ermgassen PS, Spalding MD, Grizzle RE, Brumbaugh RD (2013) Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. Estuar Coast 36 (1):36–43

From Trees to Octocorals: The Role of Self-Thinning and Shading in Underwater Animal Forests

H. Nelson and L. Bramanti

Abstract While it is known that octocorals and trees share many similarities in form and function due to their sessile modular nature, and octocoral communities create dense canopies termed "animal forests," there has been little quantification of whether these similarities derive from the same ecological and evolutionary processes. Nowadays, octocoral forests constitute the "new normal" for several shallow Caribbean reefs. Unlike scleractinians, they do not build hard, wave-resistant structures, but they provide some of the ecosystem services formerly supported by scleractinians. The parallel between trees and gorgonian forests can help in strengthening marine conservation awareness, focusing on the perception people have about conservation issues of terrestrial forests. Apart communication purposes, the tree/octocoral parallelism allow transferring to marine environment, theoretical instruments developed for terrestrial ecology. In the present chapter, we explore classic concepts developed in the terrestrial plant literature (e.g., self-thinning and shading) and discuss their application to octocoral communities.

Keywords Octocorals · Marine animal forest · Self-thinning · Shading · Gorgonians

1 Octocorals and the Future of Coral Reefs

Since the onset of the Anthropocene, humans have dramatically altered the face of coral reefs worldwide (Hoegh-Guldberg 2014). Many reefs previously dominated by large, structurally complex reef-building corals have been dramatically degraded due

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to a combination of global and local stressors, such as climate change, ocean acidification, overfishing, and pollution (Hoegh-Guldberg et al. 2007; Hughes et al. 2017). The chronic and accelerated nature of these anthropogenic threats has offered reefs scant opportunities for recovery (Pandolfi et al. 2011; Osborne et al. 2017), and in some cases multiple disturbances can further reduce coral health and prevent reefs from returning to coral-dominated states (van de Leemput et al. 2016).

As stony corals continue to decline in abundance, there is potential for other benthic macroinvertebrates, such as soft corals, sponges, urchins, anemones, ascidians, and corallimorpharians, to play a larger role in the structure and function of future reefs (Norström et al. 2009; Bell et al. 2013). Transitions from coral assemblages to alternative assemblages dominated by these other macroinvertebrates, following a disturbance or change in environmental conditions, have already been documented in several reef locations (Norström et al. 2009). Although historically the focus of coral reef phase shifts has been on macroalgae (Bruno et al. 2009), one taxonomic group that is likely to occupy a larger portion of the benthic assemblage on some future reefs is the octocorals.

In the Caribbean, long-term studies in the US Virgin Islands (Lenz et al. 2015; Tsounis and Edmunds 2017), southwestern Caribbean (Ruzicka et al. 2013; Sánchez et al. 2019), and Florida Keys (Ruzicka et al. 2013) have demonstrated that octocorals have increased in abundance at multiple sites over the past couple decades. The long-term nature of these studies suggests that transitions from stony coral- to octocoral-dominated communities may represent more than temporary fluctuations in benthic community cover (Edmunds and Lasker 2016; Lasker et al. 2020). Octocoral-dominated communities (Fig. 1) have already been reported for many Caribbean (Goldberg 1973) and Indo-Pacific reefs (Nishihira 1974; Dinesen 1983; Fox et al. 2003; Stobart et al. 2005).

Unlike stony corals, which depend on aragonite saturation for their skeletal calcification, most octocorals accrete protein-based skeletons with calcium carbonate retained only in their sclerites (Fig. 2) (Bayer 1961). This key difference have been considered one of the mechanisms which could explain why octocorals may be more resistant than stony corals to the threats posed by global climate change and ocean acidification (Ateweberhan et al. 2013; Gabay et al. 2014; Gómez et al. 2015; Enochs et al. 2016). Moreover, field and laboratory observations have demonstrated that some octocorals appear more resilient than stony corals to bleaching

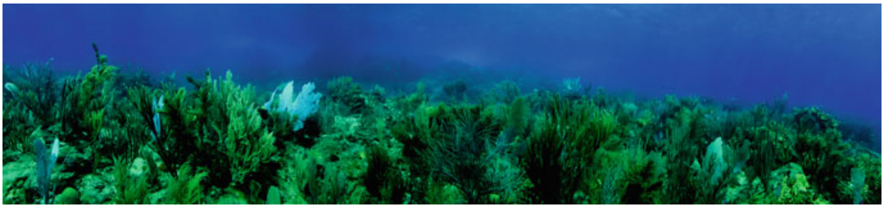

Fig. 1 Octocoral dominated community in St John (US Virgin Islands). (Photo credits: L. Bramanti)

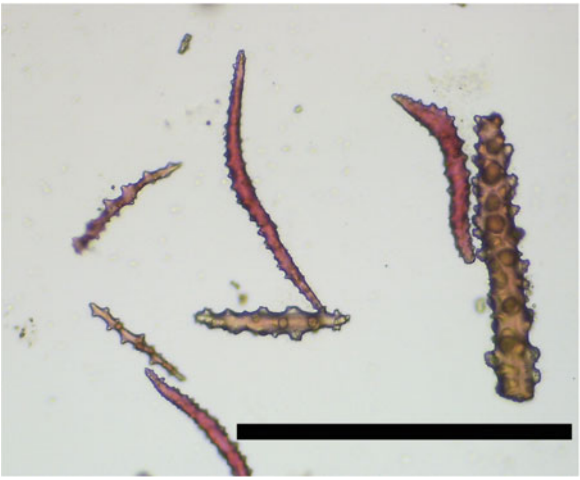

Fig. 2 Octocoral sclerites. Black bar = 1 mm. (Photo credits: L. Bramanti)

(Ateweberhan et al. 2013; Goulet et al. 2017; McClanahan et al. 2018) and nutrient enrichment (McCauley and Goulet 2019) and less affected by Peyssonnelid algal crust threats (Edmunds et al. 2019). Though increased seawater temperatures can lead to direct necrosis of octocorals in extreme cases (Fig. 3) (Cerrano et al. 2000; Lasker 2005; Sammarco and Strychar 2013), many warm-water anomalies don't seem to elicit the same mass bleaching response in octocorals that is observed in stony corals (Prada et al. 2010).

The higher resistance of octocorals to bleaching has still not been completely explained, and it is probably the result of concurrent factors. In fact, even if scleractinians are more efficient in light capture (Enríquez et al. 2005, 2017), octocorals can better manage their energy budget (Rossi et al. 2020) and are more adaptable to changing environmental conditions (Rossi et al. 2018). In the Caribbean, this thermal tolerance has been hypothesized to be a consequence of most octocoral species exclusively hosting clade B zooxanthellae (Goulet and Coffroth 2003). Recent studies in the Caribbean have also shown a resilience capacity of octocorals after the effects of hurricanes (Lasker et al. 2020) and the effects of long exposure to cold temperatures (Bartlett et al. 2018). Octocorals might not only be replacing stony corals but also accelerating their decline (Ateweberhan et al. 2013). As direct spatial competitors with stony corals, octocorals, once they form dense forests, can reduce stony corals settlement through allelopathic mechanisms, shading, and larval predation (Maida et al. 1995, 2001; Fabricius and Metzner 2004). The current onslaught of threats facing modern reefs and higher resilience of octocorals to anthropogenic stress relative to stony corals suggest that any competitive advantage octocorals already possess over stony corals is likely only to increase. Given the opportunistic and resilient nature of octocorals and mounting historical evidence of transitions from stony coral- to octocoral-dominated states, it is possible, under certain environmental and biotic conditions (e.g., the ones prevailing on present-

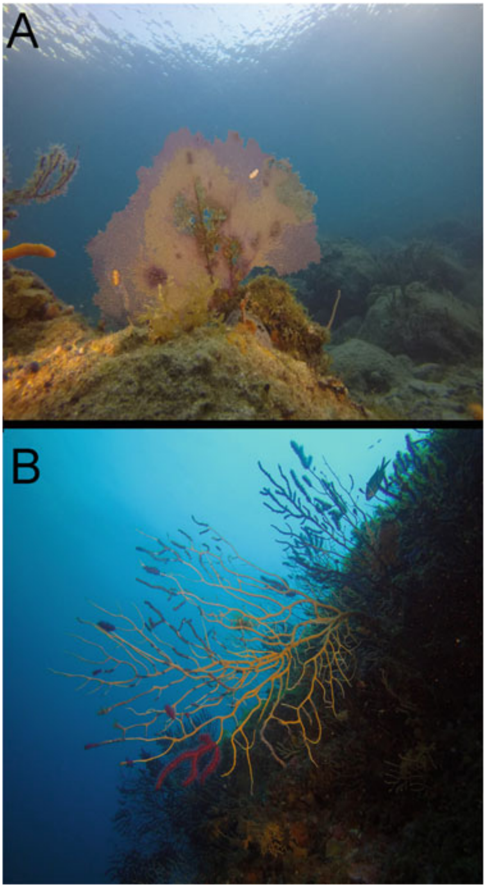

Fig. 3 Gorgonians affected by disease. (**a**) Necrosis due to fungal infection in *Gorgonia ventalina*. (**b**) Necrosis due to bacterial infection in *Paramuricea clavata*. (Photo credits: L. Bramanti)

day shallow Caribbean reefs), that octocorals might come to dominate more reefs in the future (Lasker et al. 2020). However, the resilience exhibited by octocorals is not unlimited, and it may decline with the intensification of disturbances.

2 Bridging the Gap: From Trees to Octocorals

Despite their conspicuous presence on reefs and ecological relevance, most coral reef scientists have historically ignored octocorals, choosing instead to focus on scleractinian corals and macroalgae. Given the unprecedented pace at which some reefs are changing (Graham et al. 2014) and the trend of increasing octocoral abundance on many Caribbean reefs (Ruzicka et al. 2013; Lenz et al. 2015; Sánchez et al. 2019), this "gap" in knowledge could hinder our ability to understand and preserve some future Caribbean reefs.

A group of organisms that is prime to yield insights and offer a deeper understanding of the ecology and evolution of octocorals is higher plants, such as trees. Although there are many consistent differences between marine and terrestrial ecosystems (reviewed in Carr et al. 2003), there is a growing body of literature demonstrating that cross-fertilization of ideas between terrestrial and marine ecology has been fruitful, and ecological theory can cross the land-sea boundary (Steele 1991; Menge et al. 2009).

One strategy that has been suggested to overcome some of the barriers preventing integrating the two domains is to make targeted, comparative analyses among taxa that share ecological functions (Webb et al. 2010). At a community level, octocorals and trees have been linked through the concept of "animal forests" sensu Rossi et al. (2017). Similar to the function of trees in terrestrial forests, octocorals can act as foundation species on coral reefs, creating complex, three-dimensional structures that fundamentally alter the abiotic environment (Fig. 4), directly or indirectly modulate the availability of resources for other organisms, and provide spaces and protection for other organisms to live, feed, and shelter (Paoli et al. 2016) (Fig. 5).

Some ecological functions occur in different ways in tree and coral forests. For example, biogeochemical cycling in corals occurs exclusively through benthic pelagic coupling and symbiont activity, hence primarily above the substrate. In trees, on the other side, carbon and nutrient cycling occurs also belowground, through interactions with root systems. Despite those obvious differences, the consequences of these functions are very similar.

At an individual level, octocorals and trees also share many similarities in form and function due to their sessile, modular nature (Lasker et al. 2003; Goffredo and Lasker 2006; Lartaud et al. 2016). In contrast to unitary organisms, modular organisms are functionally subdivided structural individuals (Vuorisalo and Tuomi 1986; Benedetti et al. 2020). Growth in these modular organisms occurs through an iterative process, where the basic functional units (i.e., modules) are replicated to

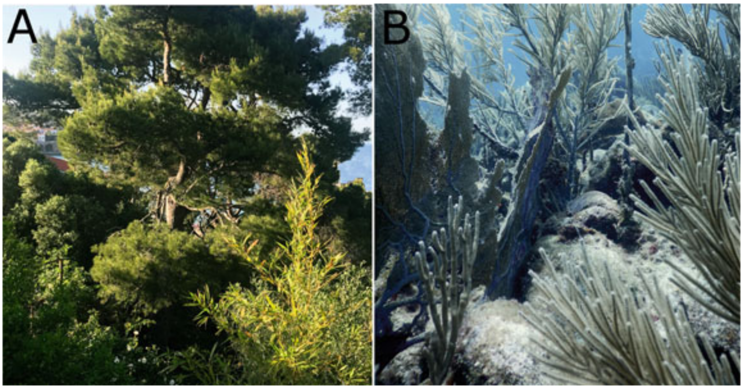

Fig. 4 Terrestrial and underwater forest. (**a**) Tree forest. (**b**) Gorgonian forest. (Photo credits: L. Bramanti)

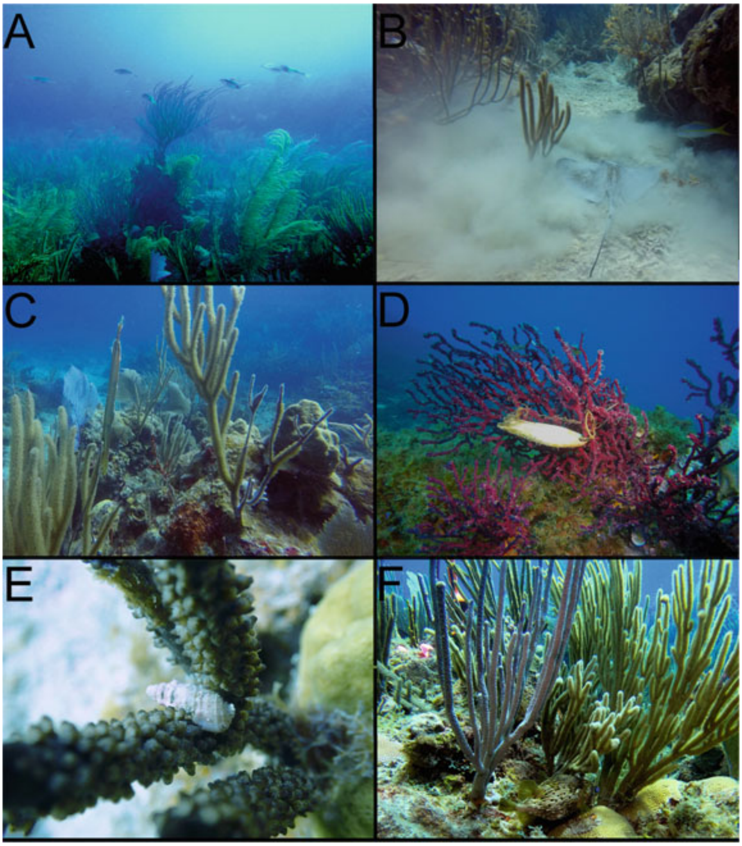

Fig. 5 Gorgonian forest is used as shelter by different organisms: (**a**) Caribbean reef squids (*Sepioteuthis sepioidea*) hunting on a gorgonian forest. (**b**) A southern stingray (*Hypanus americanus*) feeding inside a gorgonian forest. (**c**) Trumpetfish (*Aulostomus maculatus*) in camouflage inside a gorgonian forest. (**d**) Shark egg (*Scyliorhinus canicula*) attached to a Mediterranean gorgonian (*Paramuricea clavata*). (**e**) Hermit crab lying on a gorgonian (*Eunicea sp*). (**f**) Porcupine fish (*Diodon holocanthus*) finding shelter inside a gorgonian forest. (Photo credits: L. Bramanti)

form an individual (Ryland and Warner 1986; Vuorisalo and Tuomi 1986; Tuomi and Vuorisalo 1989; De Kroon et al. 2005; Lartaud et al. 2016).

Modules have been defined by Vuorisalo and Tuomi (1986) as “partially self-maintaining, repetitive, multicellular parts of structural individuals.” Modules refer to polyps in octocorals (Fig. 6b) (Rosen 1986; Lasker et al. 2003) and the products of a single apical meristem in trees (Fig. 6a) (Tuomi and Vuorisalo 1989; Pedersen and Tuomi 1995). In both taxa, these modules are organized into structures (i.e., branches) that are themselves repeated (Lasker et al. 2003; Benedetti et al. 2020). Modular organisms are renowned for their flexibility in size and shape in response to changing environments, allowing these organisms to adapt easily to changes in their

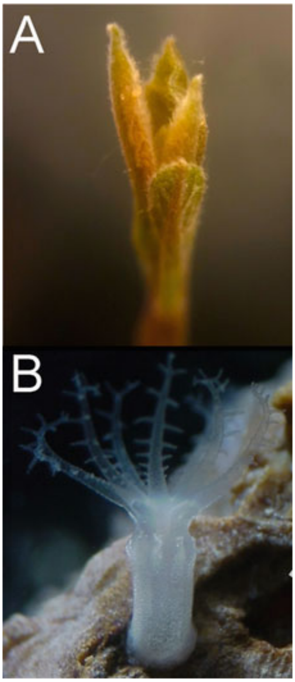

Fig. 6 Unitary modules in plants and corals. (**a**) Apical meristem of the tree *Persea americana*. (**b**) Polyp of the octocoral *Eunicella singularis*. (Photo credits: L. Bramanti)

environment (Marfenin 1997; Hughes 2005; Rossi et al. 2018; Kahramanoğulları et al. 2019). Together, the similarities between octocorals and trees at the scale of communities and organisms suggest that concepts developed in the terrestrial plant literature, such as self-thinning and shading, could be used to further our understanding of octocoral communities.

3 Self-Thinning

Density dependence has been defined as “a dependence of per capita population growth rate on present and/or past population densities” (Murdoch and Walde 1989). One of the most best known forms of density dependence is self-thinning, which refers to a reduction in the abundance of a cohort of growing organisms due to competition for limiting resources, such as food or space (Frechette and Lefaivre 1990). As organisms grow in a community, there is space for fewer and fewer individuals, which often results in a negative power function between the average size (e.g., biomass) of individuals in an assemblage and the density of individuals in that assemblage (Westoby 1981; White et al. 2007). This relationship, known as the “self-thinning law,” was first observed in trees (Yoda 1963; Westoby 1981), but has since been described in a variety of plants (Kenkel et al. 1989; Anfodillo et al. 2013;

Liu et al. 2016) and sessile marine organisms (Hughes and Griffiths 1988; Guiñez and Castilla 2001; Rossi et al. 2012; Cau et al. 2016; Edmunds and Lasker 2019).

Establishing self-thinning relationships in marine or terrestrial forests is useful as a management tool because the presence of populations that fall below the self-thinning line can be used to distinguish between young, disturbed, or low recruiting populations (Linares et al. 2008).

In temperate octocoral populations, self-thinning relationships (i.e., a negative correlation between density and biomass) have been described in two species, *Corallium rubrum* (Cau et al. 2016) and *Paramuricea clavata* (Linares et al. 2008), which form dense, monospecific stands. In contrast, *Eunicella singularis* populations do not exhibit any relationship between density and mean size, suggesting that factors other than competition, such as predation and disturbances, determine their population structure (Linares et al. 2008).

The link between energetic balance and self-thinning rule has been observed by Rossi et al. (2012) in the hydrozoan *Eudendrium racemosum*, for which the increase in colony size is linked to an increase of feeding efficiency. The fast life cycle of this species allowed to detect that the changes in colony size are inversely related to changes in colony density according the self-thinning rule.

There has been little investigation of self-thinning relationships in tropical octocoral communities, aside from one study in the US Virgin Islands (Edmunds and Lasker 2019), which found little evidence for such relationships. It is unclear if the failure to detect self-thinning in these tropical octocoral communities arises from different mechanisms structuring these communities or simply reflects the difficulty of detecting self-thinning in multispecific assemblages. The majority of evidence for self-thinning in plants comes from monospecific stands (Westoby 1984), although there are some empirical studies suggesting that it may also apply to mixed-species assemblages (White and Harper 1970; Enquist and Niklas 2001).

4 Density Dependence and Canopy Effect

Despite the lack of studies on self-thinning in tropical octocoral communities, the presence of other density-dependent mechanisms has been well documented in these communities. Dense, submerged aquatic canopies, such as those created by octocorals, can alter hydrodynamic environments (Ackerman and Okubo 1993; Nepf 1999, 2012; Lowe 2005; Guizien and Ghisalberti 2016), creating regions of diminished flow that promote sedimentation and increase the retention time of water-borne resources, such as zooplankton, dissolved and particulate organic matter, and bicarbonate ions (Nepf et al. 2007).

The density of adult octocorals has been correlated positively with the density of octocoral recruits in the US Virgin Islands, which could be due to entrainment of octocoral larvae from ambient seawater above the canopy, self-recruitment (i.e., larvae retained from adults in canopy), and/or enhanced fertilization and post-settlement success within canopies (Privitera-Johnson et al. 2015).

Density also has been demonstrated to modulate octocoral growth. For example, one study demonstrated that gorgonian colonies on the outside of experimentally created canopies grew faster because the colonies on the periphery had better access to flow, a result consistent with the expectations of exploitative competition for water-borne resources in these colonies (Kim and Lasker 1997).

The strong effects of density on tropical octocoral reefs suggest that self-thinning warrants further investigation in these communities.

5 Shading

In terrestrial forest communities, shading influences the ecology of understory life in a myriad of ways, including determining forest structure and diversity, altering atmospheric and substrate conditions, and mediating facilitation and stress attenuation in ecosystems with extreme climatic conditions (Valladares et al. 2016). While the role of shading in terrestrial forest communities is well established, the role of shading in structuring octocorals colonies has comparatively received little attention.

The importance of shading in octocoral communities cannot be considered without an explicit discussion of the relative importance of autotrophy versus heterotrophy in octocorals. Corals generally are considered "mixotrophs" in the sense that they are able to acquire energy and nutrients through both autotrophy (from their symbiotic dinoflagellate partners) and heterotrophy. In general, octocoral nutrition is understood poorly relative to scleractinian corals (Fabricius and Klumpp 1995). Very few studies have examined the natural diet of tropical octocorals, but a laboratory study by Sorokin (1991) suggests the spectrum of heterotrophic feeding varies among species.

Most stony corals are able to derive all of their respiratory carbon requirements from their endosymbiotic algae in high light environments (Falkowski et al. 1984; Edmunds and Davies 1989), while the few studies on symbiotic octocoral energy budget showed that several species show a high level of mixotrophy being able to rely on particle capture as well as on endosymbiotic algae for their energy needs (Gori et al. 2012b; Viladrich et al. 2017; Rossi et al. 2020).

Tropical octocorals have been observed to have lower nematocyst density and fewer nematocyst types than scleractinian corals, which suggests their predatory abilities should be poor compared to hard corals (Mariscal and Bigger 1977; Lasker 1981). Moreover, octocorals are considered as less efficient in the use of heterotrophic sources of energy compared to symbiotic scleractinians (Sorokin 1991; Ribes et al. 1998). However, octocorals should be more efficient than hard corals at feeding on particulate and dissolved organic matter due to the presence of pinnae on their tentacles (Fig. 7) (Sorokin 1991; Ribes et al. 1998, 2003; Coma et al. 2001; Tsounis et al. 2006; Rossi et al. 2020). The nematocysts they do possess, in fact, are considered simple and may be either ineffective or incapable of paralyzing zooplankton (Mariscal and Bigger 1977), and lab studies have demonstrated that many octocorals are unable to capture large zooplankton (Lasker 1981) (but see Lopez-

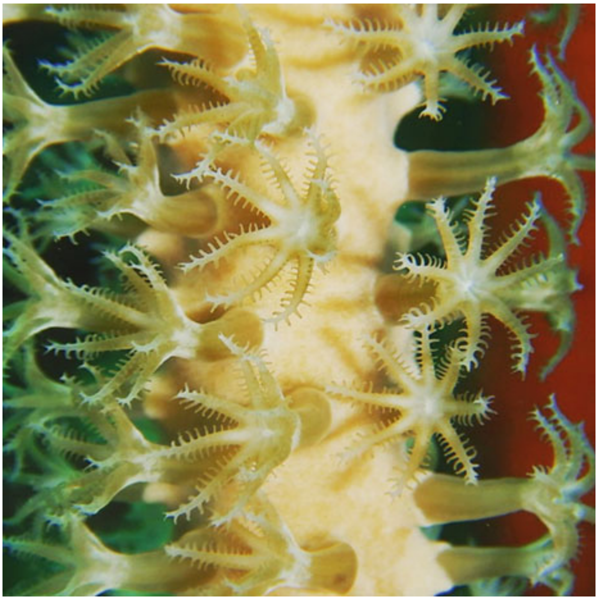

Fig. 7 Octocoral polyps. Feathery pinnae fringe the eight tentacles of each polyp. (Photo credits: L. Bramanti)

Gonzalez et al. 2018; Rossi et al. 2019). Field observations have indicated that zooplankton contacting the tentacles of several species of mixotrophic octocorals often swim away unaffected (Mariscal and Bigger 1977) and many tropical octocorals seem to contract at night, when plankton abundance is highest on reefs (Lasker 1981). The diet of Red Sea soft corals consists mainly of phytoplankton rather than zooplankton (Fabricius et al. 1995; Coma et al. 2001).

All of these observations have led some scientists to conclude that heterotrophy plays a relatively small role in tropical gorgonians, suggesting instead that most of their carbon and nitrogen requirements are derived from symbiotic zooxanthellae.

While some studies have found a lack of evidence for a strong role of heterotrophy in mixotrophic gorgonians, other studies have demonstrated that heterotrophy might actually constitute a large proportion of gorgonian feeding and nutrition (Ribes et al. 1998, 2003; Tsounis et al. 2006; Gori et al. 2012b). A study conducted on octocoral colonies in the Pacific demonstrated that octocorals were able to feed on zooplankton, bacteria, and detrital organic matter (DOM), with heterotrophic feeding at optimum food conditions satisfying 10–100% of their energy requirements (Sorokin 1991).

The Mediterranean zooxanthellate species *Eunicella singularis* can shift between autotrophic and heterotrophic feeding according to the depth (Gori et al. 2012a). In general, there is more evidence for significant heterotrophic feeding in azooxanthellate octocorals (Ribes et al. 2003; Tsounis et al. 2006; Cocito et al. 2013), but in temperate waters, where zooplankton is more abundant than in tropical ones, zooplankton is an important source of food for several octocoral species (Coma et al. 1994), and it have also been found in the gut contents of some symbiotic species (Ribes et al. 1998). The role of heterotrophy in octocorals may also be underestimated because the pulse feeding strategy of several species was not taken into account (Tsounis et al. 2006; Rossi et al. 2019) and also because many studies focus principally on zooplankton, instead of the whole range of heterotrophic food sources, which also includes particulate organic matter (POM), sedimentary organic matter (SOM), phytoplankton, and bacteria. In addition to having reduced cnidocytes, octocorals have a different tentacle structure compared to scleractinian corals. The edges of octocoral tentacles are lined with pinnules (Fig. 7), which may be used to capture fine particulate matter (Sorokin 1991). The surface of disc and tentacles of octocoral are covered with densely packed microvilli, which are hypothesized to have an absorptive function, allowing octocorals to take up dissolved organic matter (DOM) from the surrounding water (Lewis 1982). Laboratory studies using radiocarbon labeling have demonstrated that some species are able to perform sedimentary feeding and feed on dissolved organic matter (DOM) (Sorokin 1991). Suspension feeding may be particularly important among octocorals because plant and animal detritus make up a large fraction of suspended matter on reefs and represent an excellent food source due to the microbial populations inhabiting the particles (Azam et al. 1983). In addition, mucus flocs are common in reef waters and also possess a high nutritional value (Coles and Strathmann 1973).

Indirect evidence for the importance of shading in octocoral communities can be found in work by Brazeau and Lasker (1988), who documented how the morphology of the octocoral species *Plexaurella homomalla* and *Eunicea flexuosa* changes with depth. Deep colonies of both these species have longer branch lengths and fewer accessory branches than shallower colonies, which likely represents a strategy to increase the efficiency of light capture at low-light levels by minimizing self-shading. Shading by tabular *Acropora* corals affects the growth and mortality of neighboring branching scleractinian species (Stimson 1985). A significant reduction of light, due to increased turbidity associated with terrestrial runoff, has led to altered community structure on stony coral reefs (Fabricius 2005). The strong effects of shading in terrestrial forests and stony coral reefs suggest that light may play a similar role in structuring octocoral communities.

6 Future Directions

We have shown how the transfer of theoretical and practical knowledge from terrestrial to marine environment could allow quick advances in octocoral ecology. Some of the ideas developed in forestry ecology, such as self-thinning and shading, could help marine scientists to understand basic mechanisms driving octocoral ecology. It is not uncommon, in science, that advances in some field are not the result of novel discoveries, but rather derive from the application of established concepts to new research fields. Despite the differences between terrestrial and marine forests, it is worth a focus on common mechanisms to fill the gaps in marine ecology and to face future conservation challenges with a better equipped arsenal of knowledge.

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References

Ackerman JD, Okubo A (1993) Reduced mixing in a marine macrophyte canopy. Funct Ecol 7:305. https://doi.org/10.2307/2390209

Anfodillo T, Carrer M, Simini F et al (2013) An allometry-based approach for understanding forest structure, predicting tree-size distribution and assessing the degree of disturbance. Proc R Soc B Biol Sci 280:20122375. https://doi.org/10.1098/rspb.2012.2375

Ateweberhan M, Feary DA, Keshavmurthy S et al (2013) Climate change impacts on coral reefs: synergies with local effects, possibilities for acclimation, and management implications. Mar Pollut Bull 74:526–539. https://doi.org/10.1016/j.marpolbul.2013.06.011

Azam F, Fenchel T, Field J et al (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263. https://doi.org/10.3354/meps010257

Bartlett LA, Brinkhuis VIP, Ruzicka RR, et al (2018) Dynamics of stony coral and octocoral juvenile assemblages following disturbance on patch reefs of the Florida reef tract. In: Beltran CD, Camacho ET (eds) Corals in a changing world. InTech

Bayer FM (1961) The shallow-water Octocorallia of the west Indian region. Stud Fauna Curaçao Caribb Isl 12:1–373

Bell JJ, Davy SK, Jones T et al (2013) Could some coral reefs become sponge reefs as our climate changes? Glob Change Biol 19:2613–2624. https://doi.org/10.1111/gcb.12212

Benedetti MC, Bramanti L, Priori C et al (2020) Polyp longevity in a precious gorgonian coral: hints toward a demographic approach to polyp dynamics. Coral Reefs. https://doi.org/10.1007/s00338-020-01942-6

Brazeau DA, Lasker HR (1988) Inter- and intraspecific variation in gorgonian colony morphology: quantifying branching patterns in arborescent animals. Coral Reefs 7:139–143. https://doi.org/10.1007/BF00300973

Bruno JF, Sweatman H, Precht WF et al (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484. https://doi.org/10.1890/08-1781.1

Carr MH, Neigel JE, Estes JA et al (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecol Appl 13:90–107. https://doi.org/10.1890/1051-0761(2003)013[0090:CMATEI]2.0.CO;2

Cau A, Bramanti L, Cannas R et al (2016) Habitat constraints and self-thinning shape Mediterranean red coral deep population structure: implications for conservation practice. Sci Rep 6:23322. https://doi.org/10.1038/srep23322

Cerrano C, Bavestrello G, Bianchi CN et al (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-Western Mediterranean), summer 1999. Ecol Lett 3:284–293. https://doi.org/10.1046/j.1461-0248.2000.00152.x

Cocito S, Ferrier-Pagès C, Cupido R et al (2013) Nutrient acquisition in four Mediterranean gorgonian species. Mar Ecol Prog Ser 473:179–188. https://doi.org/10.3354/meps10037

Coles SL, Strathmann R (1973) Observations on coral mucus “flocs” and their potential trophic significance 1. Limnol Oceanogr 18:673–678. https://doi.org/10.4319/lo.1973.18.4.0673

Coma R, Gili J-M, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbiontic gorgonian *Paramuricea clavata*. Mar Ecol Prog Ser 115:257–270

Coma R, Ribes M, Gili J, Hughes R (2001) The ultimate opportunists: consumers of seston. Mar Ecol Prog Ser 219:305–308. https://doi.org/10.3354/meps219305

De Kroon H, Huber H, Stuefer JF, Van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants: research review. New Phytol 166:73–82. https://doi.org/10.1111/j.1469-8137.2004.01310.x

Dinesen ZD (1983) Patterns in the distribution of soft corals across the central great barrier reef. Coral Reefs 1:229–236. https://doi.org/10.1007/BF00304420

Edmunds PJ, Davies PS (1989) An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. Coral Reefs 8:37–43. https://doi.org/10.1007/BF00304690

Edmunds P, Lasker H (2016) Cryptic regime shift in benthic community structure on shallow reefs in St. John, US Virgin Islands. Mar Ecol Prog Ser 559:1–12. https://doi.org/10.3354/meps11900

Edmunds P, Lasker H (2019) Regulation of population size of arborescent octocorals on shallow Caribbean reefs. Mar Ecol Prog Ser 615:1–14. https://doi.org/10.3354/meps12907

Edmunds PJ, Zimmermann SA, Bramanti L (2019) A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. Coral Reefs 38:1329–1341. https://doi.org/10.1007/s00338-019-01846-0

Enochs IC, Manzello DP, Wirshing HH et al (2016) Micro-CT analysis of the Caribbean octocoral *Eunicea flexuosa* subjected to elevated pCO_2. ICES J Mar Sci 73:910–919. https://doi.org/10.1093/icesjms/fsv159

Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. Nature 410:655–660. https://doi.org/10.1038/35070500

Enríquez S, Méndez ER, Prieto RI (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol Oceanogr 50:1025–1032. https://doi.org/10.4319/lo.2005.50.4.1025

Enríquez S, Méndez ER, Hoegh-Guldberg O, Iglesias-Prieto R (2017) Key functional role of the optical properties of coral skeletons in coral ecology and evolution. Proc R Soc B Biol Sci 284:20161667. https://doi.org/10.1098/rspb.2016.1667

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Fabricius K, Klumpp D (1995) Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Mar Ecol Prog Ser 125:195–204. https://doi.org/10.3354/meps125195

Fabricius KE, Metzner J (2004) Scleractinian walls of mouths: predation on coral larvae by corals. Coral Reefs 23. https://doi.org/10.1007/s00338-004-0386-x

Fabricius KE, Benayahu Y, Genin A (1995) Herbivory in asymbiotic soft corals. Science 268:90–92. https://doi.org/10.1126/science.268.5207.90

Falkowski PG, Dubinsky Z, Muscatine L, Porter JW (1984) Light and the bioenergetics of a symbiotic coral. Bioscience 34:705–709. https://doi.org/10.2307/1309663

Fox HE, Pet JS, Dahuri R, Caldwell RL (2003) Recovery in rubble fields: long-term impacts of blast fishing. Mar Pollut Bull 46:1024–1031. https://doi.org/10.1016/S0025-326X(03)00246-7

Frechette M, Lefaivre D (1990) Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. Mar Ecol Prog Ser 65:9

Gabay Y, Fine M, Barkay Z, Benayahu Y (2014) Octocoral tissue provides protection from declining oceanic pH. PLoS One 9:e91553. https://doi.org/10.1371/journal.pone.0091553

Goffredo S, Lasker HR (2006) Modular growth of a gorgonian coral can generate predictable patterns of colony growth. J Exp Mar Biol Ecol 336:221–229. https://doi.org/10.1016/j.jembe.2006.05.012

Goldberg WM (1973) The ecology of the coral-octocoral communities off the Southeast Florida coast: geomorphology, species composition, and zonation. Bull Mar Sci 24

Gómez CE, Paul VJ, Ritson-Williams R et al (2015) Responses of the tropical gorgonian coral *Eunicea fusca* to ocean acidification conditions. Coral Reefs 34:451–460. https://doi.org/10.1007/s00338-014-1241-3

Gori A, Bramanti L, López-González P et al (2012a) Characterization of the zooxanthellate and azooxanthellate morphotypes of the Mediterranean gorgonian *Eunicella singularis*. Mar Biol 159:1485–1496. https://doi.org/10.1007/s00227-012-1928-3

Gori A, Viladrich N, Gili J-M et al (2012b) Reproductive cycle and trophic ecology in deep versus shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). Coral Reefs 31:823–837. https://doi.org/10.1007/s00338-012-0904-1

Goulet T, Coffroth M (2003) Stability of an octocoral-algal symbiosis over time and space. Mar Ecol Prog Ser 250:117–124. https://doi.org/10.3354/meps250117

Goulet TL, Shirur KP, Ramsby BD, Iglesias-Prieto R (2017) The effects of elevated seawater temperatures on Caribbean gorgonian corals and their algal symbionts, Symbiodinium spp. PLoS One 12:e0171032. https://doi.org/10.1371/journal.pone.0171032

Graham NA, Cinner JE, Norström AV, Nyström M (2014) Coral reefs as novel ecosystems: embracing new futures. Curr Opin Environ Sustain 7:9–14. https://doi.org/10.1016/j.cosust.2013.11.023

Guiñez R, Castilla JC (2001) An allometric tridimensional model of self-thinning for a gregarious tunicate. Ecology 82:2331–2341. https://doi.org/10.1890/0012-9658(2001)082[2331:AATMOS]2.0.CO;2

Guizien K, Ghisalberti M (2016) Living in the canopy of the animal forest: physical and biogeochemical aspects. In: Rossi S, Bramanti L, Gori A, Orejas Saco del Valle C (eds) Marine animal forests. Springer International, Cham, pp 1–22

Hoegh-Guldberg O (2014) Coral reef sustainability through adaptation: glimmer of hope or persistent mirage? Curr Opin Environ Sustain 7:127–133. https://doi.org/10.1016/j.cosust.2014.01.005

Hoegh-Guldberg O, Mumby PJ, Hooten AJ et al (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742. https://doi.org/10.1126/science.1152509

Hughes RN (2005) Lessons in modularity: the evolutionary ecology of colonial invertebrates. Sci Mar 69:169–179. https://doi.org/10.3989/scimar.2005.69s1169

Hughes RN, Griffiths CL (1988) Self-thinning in barnacles and mussels: the geometry of packing. Am Nat 132:484–491. https://doi.org/10.1086/284866

Hughes TP, Barnes ML, Bellwood DR et al (2017) Coral reefs in the Anthropocene. Nature 546:82–90. https://doi.org/10.1038/nature22901

Kahramanoğulları O, Bramanti L, Benedetti MC (2019) Stochastic mechanisms of growth and branching in Mediterranean coral colonies. In: Martín-Vide C, Pond G, Vega-Rodríguez MA (eds) Theory and practice of natural computing. Springer International, Cham, pp 57–69

Kenkel NC, Hoskins JA, Hoskins WD (1989) Local competition in a naturally established jack pine stand. Can J Bot 67:2630–2635. https://doi.org/10.1139/b89-339

Kim K, Lasker HR (1997) Flow-mediated resource competition in the suspension feeding gorgonian *Plexaura homomalla* (Esper). J Exp Mar Biol Ecol 215:49–64. https://doi.org/10.1016/S0022-0981(97)00015-4

Lartaud F, Galli G, Raza A et al (2016) Growth patterns in long-lived coral species. In: Rossi S, Bramanti L, Gori A, Orejas Saco del Valle C (eds) Marine animal forests. Springer International, Cham, pp 1–32

Lasker HR (1981) A comparison of the particulate feeding abilities of three species of gorgonian soft coral. Mar Ecol Prog Ser 5:61–67

Lasker HR (2005) Gorgonian mortality during a thermal event in the Bahamas. Bull Mar Sci 76:8

Lasker HR, Boller ML, Castanaro J, Sánchez JA (2003) Determinate growth and modularity in a gorgonian octocoral. Biol Bull 205:319–330. https://doi.org/10.2307/1543295

Lasker HR, Martínez-Quintana Á, Bramanti L, Edmunds PJ (2020) Resilience of octocoral forests to catastrophic storms. Sci Rep 10:4286. https://doi.org/10.1038/s41598-020-61238-1

Lenz EA, Bramanti L, Lasker HR, Edmunds PJ (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34:1099–1109. https://doi.org/10.1007/s00338-015-1315-x

Lewis JB (1982) Feeding behaviour and feeding ecology of the Octocorallia (Coelenterata: Anthozoa). J Zool 196:371–384. https://doi.org/10.1111/j.1469-7998.1982.tb03509.x

Linares C, Coma R, Garrabou J et al (2008) Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. J Appl Ecol 45:688–699. https://doi.org/10.1111/j.1365-2664.2007.01419.x

Liu G, Shi P, Xu Q et al (2016) Does the size–density relationship developed for bamboo species conform to the self-thinning rule? For Ecol Manag 361:339–345. https://doi.org/10.1016/j.foreco.2015.11.030

Lopez-Gonzalez PJ, Bramanti L, Escribano-Álvarez P et al (2018) Thread-like tentacles in the Mediterranean corals *Paramuricea clavata* and *Corallium rubrum*. Mediterr Mar Sci. https://doi.org/10.12681/mms.13807

Lowe RJ (2005) Oscillatory flow through submerged canopies: 1 Velocity structure. J Geophys Res 110:C10016. https://doi.org/10.1029/2004JC002788

Maida M, Sammarco P, Coll J (1995) Effects of soft corals on scleractinian coral recruitment. I: Directional allelopathy and inhibition of settlement. Mar Ecol Prog Ser 121:191–202. https://doi.org/10.3354/meps121191

Maida M, Sammarco PW, Coll JC (2001) Effects of soft corals on Scleractinian coral recruitment. II: Allelopathy, spat survivorship and reef community structure. Mar Ecol 22:397–414. https://doi.org/10.1046/j.1439-0485.2001.01709.x

Marfenin NN (1997) No title found. Hydrobiologia 355:153–158. https://doi.org/10.1023/A:1003069831832

Mariscal RN, Bigger CH (1977) Possible ecological significance of octocoral epithelial ultrastructure. In: Proceedings of the third international coral reef symposium. Miami, FL, pp 127–134

McCauley M, Goulet TL (2019) Caribbean gorgonian octocorals cope with nutrient enrichment. Mar Pollut Bull 141:621–628. https://doi.org/10.1016/j.marpolbul.2019.02.067

McClanahan TR, Weil E, Baird AH (2018) Consequences of coral bleaching for sessile reef organisms. In: van Oppen MJH, Lough JM (eds) Coral bleaching. Springer International, Cham, pp 231–263

Menge BA, Chan F, Dudas S et al (2009) Terrestrial ecologists ignore aquatic literature: asymmetry in citation breadth in ecological publications and implications for generality and progress in ecology. J Exp Mar Biol Ecol 377:93–100. https://doi.org/10.1016/j.jembe.2009.06.024

Murdoch WW, Walde SE (1989) Analysis of insect population dynamics. In: Grubb PJ, Whittaker JB (eds) Toward a more exact ecology. Blackwell, Oxford, pp 113–140

Nepf HM (1999) Drag, turbulence, and diffusion in flow through emergent vegetation. Water Resour Res 35:479–489. https://doi.org/10.1029/1998WR900069

Nepf HM (2012) Flow and transport in regions with aquatic vegetation. Annu Rev Fluid Mech 44:123–142. https://doi.org/10.1146/annurev-fluid-120710-101048

Nepf H, Ghisalberti M, White B, Murphy E (2007) Retention time and dispersion associated with submerged aquatic canopies: renewal in submerged canopies. Water Resour Res 43:W04422. https://doi.org/10.1029/2006WR005362

Nishihira M (1974) Human interference with the coral community and Acanthaster infestation of Okinawa. In: Proceedings of 2nd international coral reef symposium, vol 1, pp 577–590

Norström A, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306. https://doi.org/10.3354/meps07815

Osborne K, Thompson AA, Cheal AJ et al (2017) Delayed coral recovery in a warming ocean. Glob Change Biol 23:3869–3881. https://doi.org/10.1111/gcb.13707

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422. https://doi.org/10.1126/science.1204794

Paoli C, Montefalcone M, Morri C et al (2016) Ecosystem functions and services of the marine animal forests. In: Rossi S, Bramanti L, Gori A, Orejas Saco del Valle C (eds) Marine animal forests. Springer International, Cham, pp 1–42

Pedersen B, Tuomi J (1995) Hierarchical selection and fitness in modular and clonal organisms. Oikos 73:167. https://doi.org/10.2307/3545905

Prada C, Weil E, Yoshioka PM (2010) Octocoral bleaching during unusual thermal stress. Coral Reefs 29:41–45. https://doi.org/10.1007/s00338-009-0547-z

Privitera-Johnson K, Lenz EA, Edmunds PJ (2015) Density-associated recruitment in octocoral communities in St. John, US Virgin Islands. J Exp Mar Biol Ecol 473:103–109. https://doi.org/10.1016/j.jembe.2015.08.006

Ribes M, Coma R, Gili J-M (1998) Heterotrophic feeding by gorgonian corals with symbiotic zooxanthella. Limnol Oceanogr 43:1170–1179. https://doi.org/10.4319/lo.1998.43.6.1170

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar Ecol Prog Ser 254:141–150. https://doi.org/10.3354/meps254141

Rosen BR (1986) Modular growth and form of corals: a matter of metamers? Philos Trans R Soc Lond Ser B Biol Sci 313:115–142. https://doi.org/10.1098/rstb.1986.0029

Rossi S, Bramanti L, Broglio E, Gili J (2012) Trophic impact of long-lived species indicated by population dynamics in the short-lived hydrozoan *Eudendrium racemosum*. Mar Ecol Prog Ser 467:97–111. https://doi.org/10.3354/meps09848

Rossi S, Bramanti L, Gori A, Orejas C (2017) An overview of the animal forests of the world. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer International, Cham, pp 1–26

Rossi S, Schubert N, Brown D et al (2018) Linking host morphology and symbiont performance in octocorals. Sci Rep 8:12823. https://doi.org/10.1038/s41598-018-31262-3

Rossi S, Rizzo L, Duchêne J-C (2019) Polyp expansion of passive suspension feeders: a red coral case study. PeerJ 7:e7076. https://doi.org/10.7717/peerj.7076

Rossi S, Schubert N, Brown D et al (2020) Trophic ecology of Caribbean octocorals: autotrophic and heterotrophic seasonal trends. Coral Reefs 39:433–449. https://doi.org/10.1007/s00338-020-01906-w

Ruzicka R, Colella M, Porter J et al (2013) Temporal changes in benthic assemblages on Florida keys reefs 11 years after the 1997/1998 El Niño. Mar Ecol Prog Ser 489:125–141. https://doi.org/10.3354/meps10427

Ryland JS, Warner GF (1986) Growth and form in modular animals: ideas on the size and arrangement of zooids. Philos Trans R Soc Lond Ser B Biol Sci 313:53–76. https://doi.org/10.1098/rstb.1986.0025

Sammarco PW, Strychar KB (2013) Responses to high seawater temperatures in Zooxanthellate octocorals. PLoS One 8:e54989. https://doi.org/10.1371/journal.pone.0054989

Sánchez JA, Gómez-Corrales M, Gutierrez-Cala L et al (2019) Steady decline of corals and other benthic organisms in the sea flower biosphere reserve (Southwestern Caribbean). Front Mar Sci 6:73. https://doi.org/10.3389/fmars.2019.00073

Sorokin Y (1991) Biomass, metabolic rates and feeding of some common reef zoantharians and octocorals. Mar Freshw Res 42:729–741

Steele JH (1991) Can ecological theory cross the land-sea boundary? J Theor Biol 153:425–436. https://doi.org/10.1016/S0022-5193(05)80579-X

Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. Ecology 66:40–53. https://doi.org/10.2307/1941305

Stobart B, Teleki K, Buckley R et al (2005) Coral recovery at Aldabra atoll, Seychelles: five years after the 1998 bleaching event. Philos Trans R Soc Math Phys Eng Sci 363:251–255. https://doi.org/10.1098/rsta.2004.1490

Tsounis G, Edmunds PJ (2017) Three decades of coral reef community dynamics in St. John, USVI: a contrast of scleractinians and octocorals. Ecosphere 8:e01646. https://doi.org/10.1002/ecs2.1646

Tsounis G, Rossi S, Laudien J et al (2006) Diet and seasonal prey capture rates in the Mediterranean red coral (*Corallium rubrum* L.). Mar Biol 149:313–325. https://doi.org/10.1007/s00227-005-0220-1

Tuomi J, Vuorisalo T (1989) Hierarchical selection in modular organisms. Trends Ecol Evol 4:209–213. https://doi.org/10.1016/0169-5347(89)90075-X

Valladares F, Laanisto L, Niinemets Ü, Zavala MA (2016) Shedding light on shade: ecological perspectives of understorey plant life. Plant Ecol Divers 9:237–251. https://doi.org/10.1080/17550874.2016.1210262

van de Leemput IA, Hughes TP, van Nes EH, Scheffer M (2016) Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35:857–865. https://doi.org/10.1007/s00338-016-1439-7

Viladrich N, Bramanti L, Tsounis G et al (2017) Variation of lipid and free fatty acid contents during larval release in two temperate octocorals according to their trophic strategy. Mar Ecol Prog Ser 573:117–128. https://doi.org/10.3354/meps12141

Vuorisalo T, Tuomi J (1986) Unitary and modular organisms: criteria for ecological division. Oikos 47:382. https://doi.org/10.2307/3565452

Webb CT, Hoeting JA, Ames GM et al (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecol Lett 13:267–283. https://doi.org/10.1111/j.1461-0248.2010.01444.x

Westoby M (1981) The place of the self-thinning rule in population dynamics. Am Nat 118:581–587

Westoby M (1984) The self-thinning rule. Advances in ecological research. Elsevier, pp 167–225

White J, Harper JL (1970) Correlated changes in plant size and number in plant populations. J Ecol 58:467–485. https://doi.org/10.2307/2258284

White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends Ecol Evol 22:323–330. https://doi.org/10.1016/j.tree.2007.03.007

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in over-crowded pure stands under cultivated and natural conditions. Intra-specific competition among higher plants. J Biol 14:107–129

Invasive Alien Species and Their Effects on Marine Animal Forests

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Abstract Nonindigenous species are increasingly transported around the world through multiple pathways by a diversity of vectors. Invasive species are a subset of those that are introduced into the receptor community, where they establish and increase their population to a size where they impact the native system. Marine invasive species can therefore interact with and modify native animal forests and/or create novel ones resulting in simple-to-complex changes in material cycling, energy flow, ecosystem structure, and function. Despite the ever increasing number of

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studies dealing with marine invasive species, mostly biological invasions are mentioned generically as one of a number of threats of direct and indirect effects of human activities on animal forests. In order to redress this imbalance, this chapter focuses on invasive species as modifiers and creators of marine animal forests. As well as some theoretical consideration of biological invasion, we consider how pathways and vectors have changed over time and the importance of historical collections. We overview the available information regarding the main taxonomic groups of marine species that are invasive to animal forests, what makes them successful invaders, and how they interact with and effect the receptor community. The establishment of novel animal forests through biological invasion is also reviewed. We identify knowledge gaps and present perspectives and challenges for future research.

Keywords *Carijoa riisei* · Ecosystem engineer · Invasive · *Mytilus galloprovincialis* · Nonindigenous · *Oculina patagonica* · Pathways · Reproduction strategies · *Tubastraea* spp. · Vectors

1 Introduction

Biological invasions, as one of the most detrimental and pervasive impacts of human-induced global change, are one of the biggest conservation concerns. Biological invasions involve unwanted cascade effects altering natural ecosystems, while invasive species have profound impacts in what has become an integrated, globally connected society (Aguin-Pombo 2012; Sánchez 2017). A major consequence of biological invasions is the occurrence of ecological regime shifts, which are dramatic, abrupt changes between states of populations, communities, and/or whole ecosystems that are persistent in time and include key structural species (Conversi et al. 2015). In marine environments, invasive species threaten biodiversity, ecosystem functions and services, the economy (including fisheries and tourism), and human health (Bax et al. 2003; Sorte et al. 2010b). Global maritime traffic is predicted to increase by 240–1209% by 2050 resulting in a 3- to 20-fold increase in global invasion risk (Sardain et al. 2019).

Marine animal forests (MAFs) are megabenthic communities dominated by sessile suspension feeders (such as sponges, corals, and bivalves) which form three-dimensional habitats and provide architectural complexity and shelter for several species (Rossi et al. 2017a). Invasive species may have numerous direct or indirect effects on the structure and ecological functioning of marine animal (and algal) forests. For MAFs these consequences fall into two groups: (1) they form novel marine animal forests where they did not exist before; (2) they change the structure and functioning of existing marine animal forests (Table 1).

In this chapter we focus on the role that invasive species have and will play in creating or modifying the structure and function of MAFs by considering the theory behind the invasion of MAFs, invasion history and evolution, the vectors and

Table 1 Theoretical transformations which nonindigenous species (NIS) may bring about the following invasions

Mechanism	Direction	Example
Invasion by dominant alga	MAF → Algal forest	*Caulerpa racemosa* (Forsskål) J. Agardh replacing gorgonian forests (Mediterranean; Cebrian et al. 2012)
Invasion by dominant animal (structural: ecosystem engineer; competitive exclusion)	MAF1 → MAF2	*Pyura doppelgangera* Rius & Teske, 2013 replacing green-lipped mussel *Perna canaliculus* (Gmelin, 1791) (New Zealand, Davis et al. 2018)
Invasion by keystone animal with indirect or cascading effects (interactive: predator, parasite, trophic cascade)	MAF1 → MAF2 or MAF → Algal forest	Lionfish *Pterois volitans* (Linnaeus, 1758) and *P. miles* (Bennett, 1828) (coral-to-algae trophic cascade, Bahamas; Lesser and Slattery 2011)
Invasion by dominant space occupying animal (structural: ecosystem engineer; competitive exclusion)	Algal forest → MAF	*Oculina patagonica* de Angelis, 1908 [phase shifts from macroalgal-to coral-dominated state, Mediterranean (Serrano et al. 2012) (Fig. 1a)]
Invasion by herbivore or animal causing trophic cascade	Algal forest → MAF	[a], but see prediction regarding potential rabbitfish [*Siganus luridus* (Rüppell, 1829) and *S. rivulatus* Forsskål & Niebuhr, 1775] invasion of the Caribbean Sea (Bellwood and Robert Goatley, 2017)
Substratum modification by invasive species	MAF → Algal forest or Algal forest → MAF	Asian mussel *Arcuatula senhousia* (Benson, 1842) (=*Musculista senhousia*) (hard substrate on soft bottoms, Crooks 1998); *Didemnum vexillum* Kott, 2002 (mat forming on soft bottoms; Mercer et al. 2009) (Algal forest → MAF = [a])
Multiple invasive species act together (coupled invasion or invasional meltdown)	MAF → Algal forest or Algal forest → MAF	*Eucheuma* J. Agardh, 1847, *Kappaphycus* Doty, 1988, *Gracilaria salicornia* (C. Agardh) E. Y. Dawson, and *Acanthophora spicifera* (M. Vahl) Børgesen (coral reefs to algal, Kane'ohe Bay (O'ahu, Hawai'i, USA; Conklin and Smith, 2005) *Tubastraea coccinea* Lesson, 1830 and *T. tagusenis* Wells, 1982 (algal forest to mussel bed to corals, Brazil; Mantelatto and Creed 2015; Paula et al. 2017) (Fig. 1b)

[a] Unknown

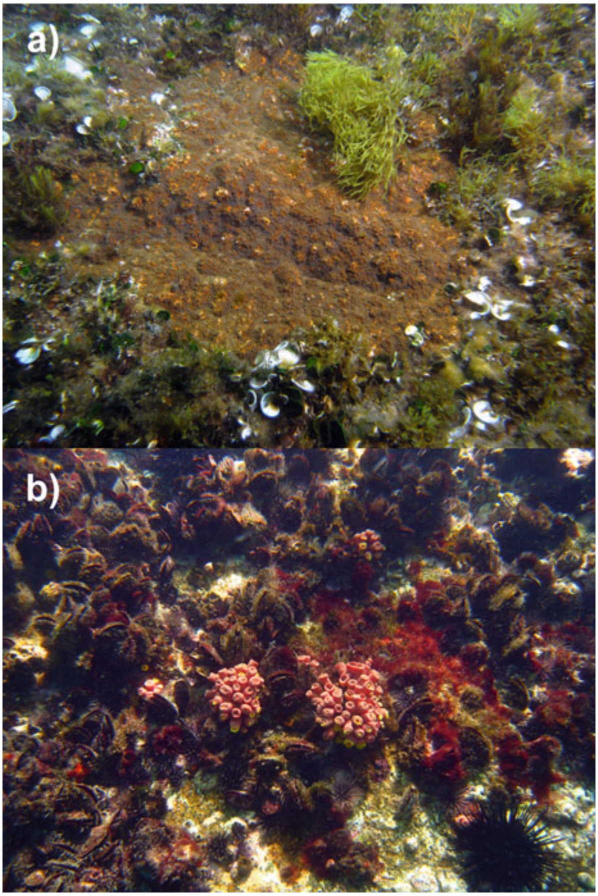

Fig. 1 Photographs of invasive species which create novel or modify existing nonindigenous marine animal forests: (**a**) *Oculina patagonica* replacing algal forests on rocky reefs in the Spanish Mediterranean; (**b**) the sun coral *Tubastraea* spp. invading a nonindigenous mussel (*Perna perna*) beds on a tropical rocky reef wall in southeast Brazil. Photo credits: Eduard Serrano Gras (**a**) and Marcelo Mantelatto (**b**)

pathways, and the main invasive taxa. Furthermore we consider the chemical and microbial ecology of invasion, which nonindigenous species (NIS) form novel MAFs, and present some case studies as well as perspectives and challenges for future research.

2 Theoretical Considerations

Invasion ecology theory has been useful for explaining the success of invasive species such as aspects of invasive species attributes, the characteristics of invaded communities, resource availability in invaded systems, or predator-prey interactions (Davis et al. 2000; Keane and Crawley 2002). This centers on a controversial discussion in ecology: are species distributions and abundances more influenced by deterministic or stochastic processes? (Adler et al. 2007). The Niche (Chesson

2000) and Neutral theories (Hubbell 2001; Rosindell et al. 2011; Volkov et al. 2003) have been broadly used to explain species regulation processes which are relevant to invasion ecology theory.

The Niche theory is commonly invoked in studies of invasive species (Shea and Chesson 2002) and suggests that differences in species' ecological traits influence advantage in resource use, ability to establish in new areas, or how invader performance is influenced by the environment (Caswell 1978). Interpretations of this theory suggest that the success of an invader is based on niche differences between it and native species. According to this theory, each species can persist under a limited set of conditions, and coincidence of limiting factors can control whether a new species establishes in the community (MacDougall et al. 2009).

Niche-based mechanisms underpin the diversity-resistance hypothesis, which suggests that the greater the diversity of competitors in a community, the greater the resistance to the establishment of a NIS (Elton 1958). Communities with lower diversity are considered to be more easily invaded (Stachowicz and Tilman 2005), as they are more likely to offer vacant niches and invaders may have biological traits that do not exist in the receptor communities (MacDougall et al. 2009). These arguments can be supported by the enemy escape hypothesis which states that NIS are more likely to establish and become dominant when free from the negative effects of natural enemies such as competitors, predators, and pathogens (Keane and Crawley 2002).

Neutral theory is a more recent and alternative view which assumes that species of the same functional group are ecologically equivalent and that stochastic forces such as drift, limitation of dispersion, extinction, and speciation influence the abundance of these species in a random fashion over time (Hubbell 2001; Daleo et al. 2009; Rosindell et al. 2011). This view suggests that rules of community structuring are grounded in dispersion rather than in the niche. Interpretations of this theory suggest that both high- and low-diversity communities are equally susceptible to invasion and that all species have the same capacity and likelihood to invade and persist, as well as to impact a given environment in a similar and stochastic way (Daleo et al. 2009).

These arguments have gained strength mainly because Niche theory fails to explain empirical evidence of invasions, such as in the case of NIS with niches similar to those of resident species that succeed in invading, which is contrary to that predicted by the theory (MacDougall et al. 2009). However, the Neutral theory also fails to fully explain why some invasive species with different biological characteristics can impact native communities.

From the point of view of scale, studies that evaluate the relationship between the biodiversity of the receptor community and its susceptibility to invasion have found different answers according to the scale of observation, a phenomenon that has been called the "invasion paradigm" (Fridley et al. 2004). Work carried out from observations at broad scales usually find positive relationships between the success of biological invaders and native biodiversity (Fridley et al. 2007), supporting the neutral view that the biodiversity of the resident community does not change susceptibility to invasion. In contrast, studies at smaller scales have found negative correlations between the diversity of native biota and the invasion by NIS (Fridley et al. 2007), corroborating the view associated with the niche, in which a more biodiverse community would reduce susceptibility to invasion (Daleo et al. 2009).

Despite controversy surrounding the two theories, several more recent studies have proposed their unification (Adler et al. 2007; MacDougall et al. 2009). These studies highlight the importance of the observational scale and the context of the investigated process, which can be explained by niche-based mechanisms and complementary neutrality. MAFs are widespread throughout the world's oceans (Rossi et al. 2017b) but locally dominated by specific sessile suspension feeders (such as sponges, corals, and bivalves) that are capable of generating three-dimensional frameworks, with high structural complexity that give shelter to other species (Rossi et al. 2017a). As such, they are useful and interesting systems where hypotheses and theories regarding invasion processes and mechanisms may be tested over different spatial scales.

Latitudinal patterns of richness in NIS indicate that the number of invasions relative to tropical regions is low when compared to the temperate regions (Wells 2019), maybe because of a greater biotic resistance (Cheng et al. 2019) in the tropics. Evolutionary theory predicts that interactions between species are stronger and more specialized in the tropics, resulting in higher rates of diversification and greater species richness, thus decreasing the success of colonization, establishment, abundance, and dispersion of invasive species (Sax 2001).

On the other hand, there is a second hypothesis that predicts that many tropical areas may be under-sampled, causing an underestimation of the number of non-native species (Freestone et al. 2013). We may have insufficient taxonomic knowledge when it comes to MAFs such as tropical reefs, which may prevent the recognition of invasive species in most groups (Hewitt 2002). The question of the disparity, in taxonomic terms, between tropical and temperate systems was not supported by the results of research on the coast of Australia (Hewitt 2002). In the Pilbara region on the western coast of Australia, both hypotheses have been tested, and the relatively low number of invasive species in the region is not due to lack of knowledge or lack of sampling but because of biological factors (Wells 2019).

3 Historical and Evolutionary Considerations

It is probable that marine species were being carried around in the sea by human activity before the Common Era, maybe as much as 9000 years BP (Bednarik 1997). The introduction of marine species to new areas has occurred over most of the last millennium (Ojaveer et al. 2018). This has led to an appreciation of a number of historical difficulties in recognizing NIS today (reviewed by Carlton 2009) as well as important advances regarding historical overviews of marine biological invasions which have confirmed these "deep invasions" (Carlton 2009). A good example is the brown mussel *Perna perna* (Linnaeus, 1758), native to Africa and likely introduced into the Americas during the slave trade (Hicks and Tunnell 1993) (Fig. 2a).

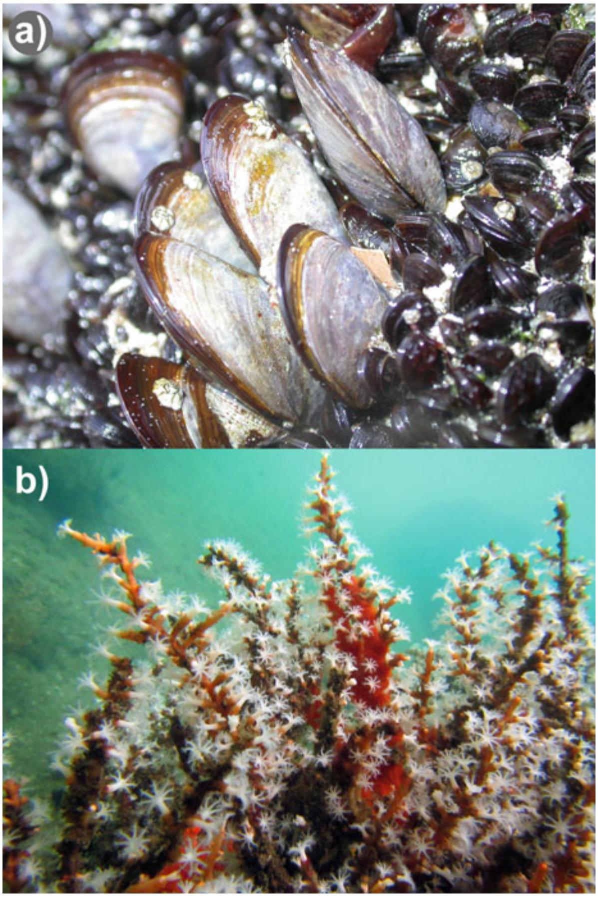

Fig. 2 Photographs of two species which have a deep history of invasion and which create novel nonindigenous marine animal forests. (**a**) the brown mussel *Perna perna* competing for space with native mussels [*Mytilaster solisianus* (d'Orbigny, 1842)] and barnacles; (**b**) the snowflake coral *Carijoa riisei* which has a stoloniferous growth form (note the associated commensal sponge on the central erect portion). Photo credits: Joel C. Creed

However, it has also been recognized that our perception of the history of marine biological invasions is tainted by the "shifting baseline" syndrome, leading to underestimation of change (Ojaveer et al. 2018).

It is clear that the history of biological invasions in the sea is compatible with timescales over which evolution may occur, especially in MAFs mainly composed of sessile invertebrate suspension feeders (Rossi et al. 2017a). For example, there is a systematic increase in body size in receptor communities compared to origin in a number of invasive marine invertebrates (Grosholz and Ruiz 2003) which may be explained by escape from natural enemies allowing NIS to reallocate resources from defense to growth and competitive ability via evolutionary mechanisms (Chan and Briski 2017).

Today, coastal environments comprise the most invaded ecosystems in the world, yet research on the long-term ecological and evolutionary consequences is lagged with respect to continental systems (Grosholz 2002). Invasive species induce two-fold evolutionary changes (Lee 2002). Both NIS and species in invaded communities are subject to new selective pressures. In part, success during an invasion depends on invaders adapting rapidly to new environments, and there are always effects on native species in receptor communities including competitive displacement, predation, or even extinction (Mooney and Cleland 2001). Sometimes the movement of species across biogeographic boundaries provides new opportunities and habitats for NIS. This is the case in the invasive snowflake coral *Carijoa riisei* (Duchassaing & Michelotti, 1860) (Fig. 2b; Sect. 10.5), which occurs at relatively low abundances within its donor range in the western Atlantic, except on shipwrecks (Barbosa et al. 2014), but dominates the landscape and outperforms local octocorals in invaded Eastern Pacific animal forests (Sánchez and Ballesteros 2014; Sánchez 2017).

Ultimately, the success of an invasive species depends on evolution, mainly with regard to abiotic conditions acting on traits responding successfully to clines (Hodgins et al. 2018). In the case of *C. riisei*, one such trait could be the facultative presence of the mutualistic sponge, *Desmapsamma anchorata* (Carter, 1882), conferring the coral cytotoxic activity on contact with other corals (Calcinai et al. 2004) (Sect. 10.5). MAFs offer a natural laboratory for studying the evolutionary effects on invasions in the marine realm.

4 Role of Reproduction Strategies

Owing to their large and dense populations, MAFs need successive, overlapping generations of its member species for construction (Potts 1983, 1984), which is easiest to achieve if recruits are of local origin, coupling high reproductive capacity with rapid growth, as seen in cloning species that employ fragmentation (Hoeksema et al. 2018). The latter may appear to show short generation times, but in fact the ongoing cloning results in long-lasting generations. Hence, the species composition of MAFs largely depends on the reproduction strategies of its component species. The role of asexual reproduction is usually not considered but may be particularly important for sessile benthic invertebrates as a strategy also facilitating biological invasion (Capel et al. 2017). Studies of the life histories of free-living corals (Fig. 3) suggest that mixed species assemblages are likely generated by sexual reproduction, as shown in French Polynesia (Hoeksema and Benzoni 2013), whereas monospecific aggregations appear to be produced by asexual reproduction, either budding or fragmentation, as seen in Indonesia (Hoeksema 2004; Hoeksema and Gittenberger 2010; Hoeksema et al. 2019), and only rarely by a combination of sexual and asexual reproduction, as oberved in New Caledonia (Heintz and Laboute 2020). After autotomy (self-fragmentation), the clones are free-living and, depending on the species, can colonize sandy and/or hard bottoms (Walker and Bull 1983; Hoeksema 2012). Some cnidarians and sponges show reattachment after accidental damage (Wulff 2010; Coppari et al. 2019). Reattachment can also occur in invertebrates that have colonies with a tendency to multiply by fission, such as ascidians and octocorals (McFadden 1997; Muñoz et al. 2015). Some benthic invertebrates use

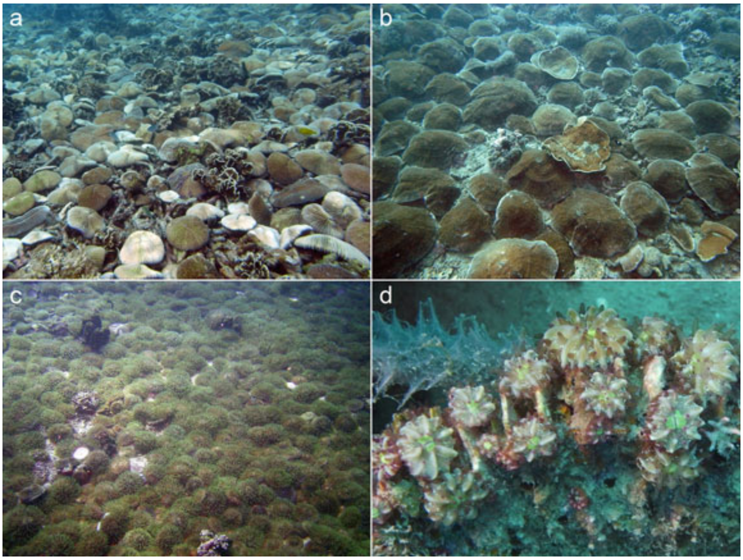

Fig. 3 Photographs of mushroom coral fields: (**a**) Mixed assemblage of free-living species at Koh Tao (Thailand); (**b**) Monospecific aggregation of fragmenting corals (*Zoopilus echinatus*) with multiple mouths at NW Lombok (Indonesia); (**c**) Monospecific aggregation of budding corals with a single mouth (*Heliofungia fralinae*) at East Kalimantan (Indonesia); (**d**) Buds (asexually derived propagules) sprouting from the margin of a dying *H. fralinae* at NW Lombok (Indonesia). Photo credits: Bert Hoeksema/Naturalis

stolons to expand rapidly, such as octocorals, scleractinians, and bryozoans (Kahng and Grigg 2005; Quintanilla et al. 2017; Schack et al. 2019).

Reproduction strategies can play a crucial role in invasion of existing MAFs or by forming a new substrate for a MAF when composed of itself. Well-known examples of negatively impacted MAFs usually concern cultivated animals that live at shallow depths. In these cases, harmful invasive species usually overgrow native ones, such as the common slipper limpet [*Crepidula fornicata* (Linnaeus, 1758)], Japanese oysters [*Magallana gigas* (Thunberg, 1793) (=*Crassostrea gigas*)], and stalked sea squirts (*Styela clava* Herdman, 1881) outcompeting mussels and flat oysters in Western Europe (Lützen 1999) and sun corals (*Tubastraea* spp.) overgrowing mussel beds in Brazil (Mantelatto and Creed 2015) (Fig. 1b). Except for the sun corals (see below), there are no signs of asexual reproduction playing a role here, since the attackers arrive as sexually derived offspring that settle on the shells, which eventually may lead to MAFs becoming overgrown by the intruders. Overgrowth and smothering have also been employed by invasive octocoral species (*Xenia* sp. in Venezula, *C. riisei* in Hawaii) that have been observed to overgrow native coral species (Sects. 10.2 and 10.5).

Invasives can also affect native species by competitive exclusion, such as *Tubastraea* spp. causing damage to native corals and aggregations of zoantharians (Creed 2006; Miranda et al. 2016; Luz and Kitahara 2017; Fig. 4). Sexual

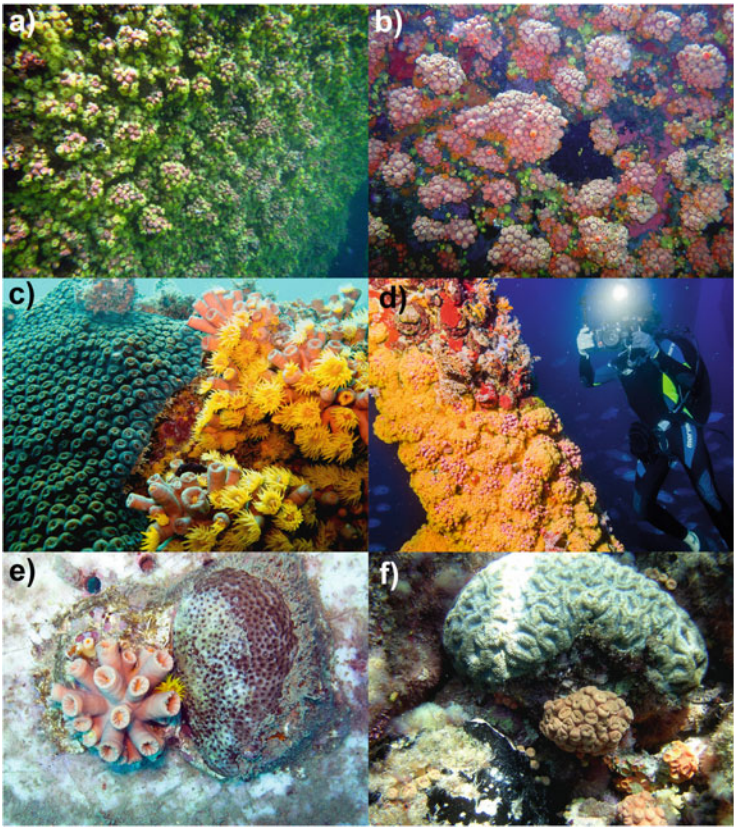

Fig. 4 Photographs of the invasive sun corals *Tubastraea* spp. in Brazil. (**a**) a marine animal forest dominated by *T. tagusensis*; (**b**) a subtidal rock reef dominated by *T. coccinea*; (**c**) a coral reef being invaded by *T. tagusensis*; (**d**) an offshore natural gas platform covered with sun corals; (**e**) experimental transplant of *T. tagusensis* beside the native coral *Siderastarea stellata*, showing lighter necrosing area; (**f**) natural contact between *T. coccinea* and the native coral *Mussismilia hispida*, showing deformed growth. Photo credits: Ricardo J. Miranda (**c**, **e**), Leonardo Schlögel Bueno (**d**) and Joel C. Creed (**a**, **b**, **f**)

reproduction in *Tubastraea* spp. appears to be continuous but of minor importance as Brazilian populations are highly clonal (Capel et al. 2017) and their reproduction success and dispersal are due to both sexually and asexually produced larvae which settle near the parent colonies (Paula et al. 2014). *Tubastraea* spp. are also well able to regenerate damaged polyps (Luz et al. 2018) and "bail out" polyps under stressful environmental conditions (Capel et al. 2014). This is probably the reason why their populations are able to dominate large, rocky surfaces.

5 Vectors and Pathways

Marine traffic is the principal pathway for the introduction of marine NIS (Carlton 1985; Hewitt et al. 2009). For example, ship sub-vectors include the fouling of hull and niche areas, the boring of organisms into the vessel structure and uptake of organisms associated with ballast, heavy material, such as gravel, sand, iron, lead, or water placed low in a vessel to improve its stability (Hewitt et al. 2009). The early ships had wooden hulls and solid ballast, so hull fouling, the boring of shipworms and gribbles, and marine derived solid ballast were important sub-vectors. Solid ballast was replaced by bulk seawater around 1880, and solid ballast was phased out by 1950 (Hewitt et al. 2009), which resulted in a new suite of different, mainly pelagic, species being transported. The use of steel resulted in very little opportunity for boring organisms, and, due to improved antifouling biocide paints (Qian et al. 2013), hull fouling was perceived to be a less important vector. Thus, ballast water became the most important shipping vector for marine NIS (Carlton 1985), and due to environmental concerns about further species introductions, the "International Convention on the Control and Management of Ship's Ballast Water and Sediments" was adopted. Unfortunately the highly efficient tributyltin antifouling paints caused toxicity to organisms in nontarget habitats (Antizar-Ladislao 2008) and with the restricted use/ban of tributyltin in antifouling paint concern focused once again on biofouling (Minchin et al. 2009).

There is no doubt that shipping has transported NIS that have impacted MAFs. For example, the sun corals *Tubastraea* spp. have been transported around the world on oil platforms (Creed et al. 2017; Fig. 4d) on which they are usually the dominant organism (Friedlander et al. 2014). In fact, oil platforms may transport entire virtually intact reef communities (Hopkins and Forrest 2010; Wanless et al. 2010).

Other marine vectors are also important. Sea canals have allowed the transference of a large number of organisms across biogeographical barriers, either by their own means (swimming, crawling, or drifting) or on shipping (Gollasch et al. 2006). For example, more than half of the NIS in the Mediterranean Sea have been introduced through the Suez Canal (Galil et al. 2018). Other invasive species that create or impact MAFs have been introduced intentionally or unintentionally through aquaculture. Non-native oysters have been introduced around the world (Ruesink et al. 2005), and as they are ecosystem engineers, they can have substantial impact because of their influence on habitat quantity and quality. In most cases oyster introductions have created new MAFs as biotic reef structure is enhanced, as was the case for the Pacific oyster *M. gigas* introduced into northern Patagonia, Argentina (Escapa et al. 2004). However, introduced oysters may also modify the structure of MAFs by outcompeting native species, as did the oyster *Magallana ariakensis* (Fujita, 1913) (=*Crassostrea ariakensis*) with the native *Crassostrea virginica* (Gmelin, 1791) in North Carolina, USA (Grabowski et al. 2004).

Ornamental species are imported in the aquaria trade and because keeping animals or algae alive in aquaria is challenging; the industry probably passively filters hardy, fast growing, and widely tolerant species. When released accidentally

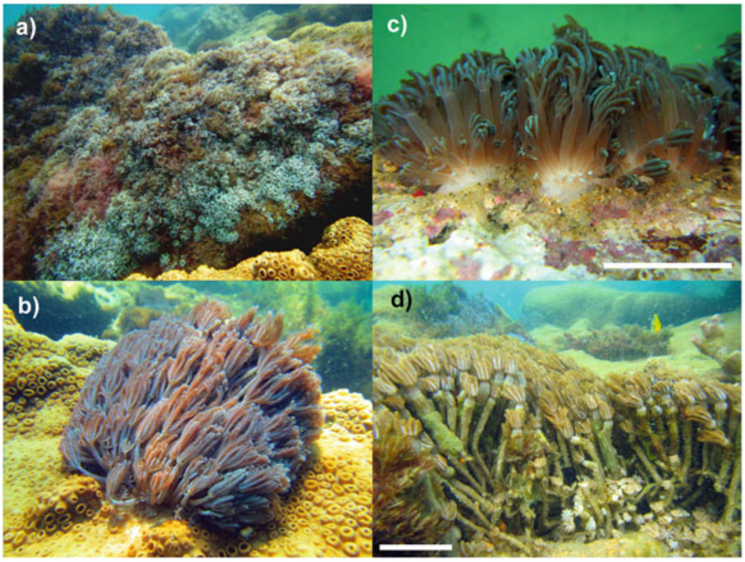

Fig. 5 Photographs of the two nonindigenous soft corals of aquarium origin invading animal forests in the southwestern Atlantic, Brazil. (**a**) tropical shallow subtidal rocky reef covered with *Sansibia* sp.; (**b**) detail of a colony of *Sansibia* sp. surrounded by native zoantharian *Palythoa caribaeorum* forrest; (**c**) *Sansibia* sp.; (**d**) *Clavularia* cf. *viridis*; scale bar = 2 cm. Photo credits: Joel C. Creed

or on purpose into the environment, species with these characteristics may be most likely to survive and/or become highly invasive. The tropical red lionfish (*P. volitans*) and devil firefish (*P. miles*) and the "Xenia blue" and "Green Star Polyp" soft coral (*Sansibia* sp. and *Clavularia viridis* (Quoy & Gaimard, 1833) cf. *viridis*, respectively) are examples of released aquarium species which have impacted MAFs (Lesser and Slattery 2011; Mantelatto et al. 2018; Fig. 5). Furthermore, entire communities can be imported, such as those on "live rock" sold in aquarium stores, which may harbor dozens of species (Padilla and Williams 2004).

An increasing quantity of marine anthropogenic debris spread across the planet via drifting along coastlines and across oceans and which may support, maintain, and transport living organisms (Carlton and Fowler 2018). Because of this phenomenon, rafting on floating debris is becoming an increasingly important vector of invasion (Carlton et al. 2017), particularly for the kinds of invertebrate species which are major invaders for MAFs.

6 Overview of Marine Invasive Groups

6.1 Sponges

Sponges are an important component of benthos in all habitats (Wulff 2012; Pawlik et al. 2018), playing a diversity of roles in the structure and functioning of marine environments (Bell 2008; de Goeij et al. 2013). Sponge invasions are still poorly reported (Carlton 2009), but the number of studies reporting new NIS of sponges has increased over the last decade (van Soest et al. 2007; Longo et al. 2007), despite little information on their effects on the invaded ecosystem. All the cases reported are of fouling species (Ávila and Carballo 2009), given that sponge larvae usually have very short life spans in the water column (Guardiola et al. 2012). Such fouling may be on ships' hulls (Ávila and Carballo 2009) or aquaculture systems (Longo et al. 2007).

A common strategy of sponges to better compete for space with corals on reefs is by overgrowth (Wulff 2012; Mclean et al. 2015), and for invasive sponges, this is a particularly important strategy for the consolidation and expansion in the receptor community. The presence of chemical compounds toxic to corals has been described in several species of sponges, used in order to outcompete surrounding benthic invertebrates (Wulff 2012). In Hawaii, two introduced species of the genus *Mycale* Gray, 1867, *M. grandis* Gray, 1867 and *M. armata* Thiele, 1903, have been reported overgrowing and killing the coral *Porites compressa* Dana, 1846 (Coles and Bolick 2007). Similarly, in the Mexican Pacific, the invasive sponge *Chalinula nematifera* showed a very high specificity for living on live corals of the genus *Pocillopora* Lamarck, 1816 (94% vs. 6% on rocks), overgrowing coral tissue, and killing the polyps underneath (Ávila and Carballo 2009). Additionally, *Terpios hoshinota* Rützler & Muzik, 1993 is commonly described as an invasive sponge on Pacific coral reefs, overgrowing and killing mainly Poritidae, Acroporidae, and Merulinidae (Ashok et al. 2019).

Paraleucilla magna Klautau, Monteiro & Borojevic, 2004, a sponge which has invaded the Mediterranean Sea and has been widely studied (Longo et al. 2007; Guardiola et al. 2012), adopts an *r*-strategy that allows it to successfully establish for long periods (at least 10 years) (Longo et al. 2007). This sponge is able to grow on the native algae *Halopteris* spp. and *Corallina* spp. (Guardiola et al. 2012) and has been reported to negatively impact mollusk farming (Longo et al. 2007).

As feeders on suspended particles, sponges may filter up to 24,000 L of seawater per day per kilogram of sponge, leaving the expelled water pretty sterile (Hentschel et al. 2002). They also capture large quantities of phytoplankton, thus regulating primary and, consequently, secondary production (Kimmerer et al. 1994). Filtering by *Hymeniacidon sinapium* de Laubenfels, 1930, which has invaded California, is thought to influence the composition of the soft bottom habitat community there (Wasson et al. 2001).

6.2 Cnidarians

The phylum Cnidaria Verrill, 1865, contains about 11,000 species which occur in aquatic habitats. The state of knowledge regarding NIS cnidarians has been recently reviewed (González-Duarte et al. 2016), so here we provide an overview emphasizing groups or species which may be particularly important in creating or modifying MAFs.

A number of (stony) hexacorals (Scleractinia) have been introduced around the world. The mushroom coral *Lobactis scutaria* (Lamarck, 1801) (=*Fungia scutaria*) endemic to the Indo-Pacific was purposefully introduced onto coral reefs at Discovery Bay, Jamaica, in the 1960s (LaJeunesse et al. 2005). Three species of the now notoriously invasive azooxanthellate coral genus *Tubastraea* Lesson, 1830 (Scleractinia: Dendrophylliidae): *T. coccinea*, *T. tagusensis*, and *T. micranthus* (Ehrenberg, 1834), have also been introduced from the Pacific to the tropical and subtropical Atlantic (Brazil, Caribbean Sea, Gulf of Mexico, Canary Islands, as well as on oil platforms off Africa, Brazil, and in the Gulf of Mexico; Fig. 4) (Creed et al. 2017; López et al. 2019).

Oulastrea crispata (Lamarck, 1816) is a zooxanthellate scleractinian native to nearshore coral reefs in the central Indo-Pacific which has been found in shallow waters of Corsica and Catalonia (western Mediterranean Sea) since 2012 and is a native of nearshore coral reefs of the central Indo-Pacific. Also in the Mediterranean, a large colony of the zooxanthellate coral *O. patagonica* was found in 1966 near Savona harbour (Gulf of Genoa, Italy) and was found "prosperous and spreading" when surveyed again in 1971 and 1972 (Zibrowius 1974) (Fig. 6). During the last decades, *O. patagonica* has spread throughout the Mediterranean and colonized new

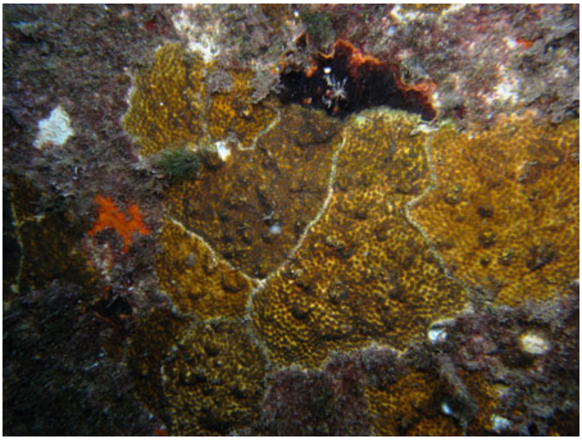

Fig. 6 Photograph of novel marine animal forests formed by invasive incrusting stony coral *Oculina patagonica* in a rocky reef community in the Spanish Mediterranean. Photo credit: Eduard Serrano Gras

areas from the subtropical eastern Atlantic and tropical western Atlantic (Fine et al. 2001; Colín García et al. 2018; Serrano et al. 2018; López et al. 2019; see Sect. 9).

A number of sea anemones (Actiniaria) have also been reported as NIS around the world. For example, four *Diadumene* Stephenson, 1920 species [(*D. cincta* Stephenson, 1925, *D. franciscana* Hand, 1956, *D. leucolena* (Verrill, 1866), and *D. lineata* (Verrill, 1869)] are members of the widespread fouling community, despite being ephemeral in nature (reviewed by González-Duarte et al. 2016). *D. lineata* is particularly widespread, originated from the Asian Pacific, but now found in Western Europe, the Mediterranean Sea, the east coast of North America, the Gulf of Mexico, Brazil, and Argentina, as well as Malaysia, Hawaii, Chile, and additional sites in the Pacific Ocean (Häussermann et al. 2015). *Aiptasiomorpha minima* (Stephenson, 1918) has been reported as a NIS to Japan (Mito and Uesugi 2004). González-Duarte et al. (2016) attribute two NIS of the genus *Aiptasia* [*A. pulchella* Carlgren, 1943 and *A.* cf. *insignis*] to *A. pallida* [now *Exaiptasia diaphana* (Rapp, 1829), a notoriously weedy invasive which overgrows corals and is a pest in aquaria] (Fig. 7). Other NIS of sea anemones are listed and discussed by González-Duarte et al. (2016).

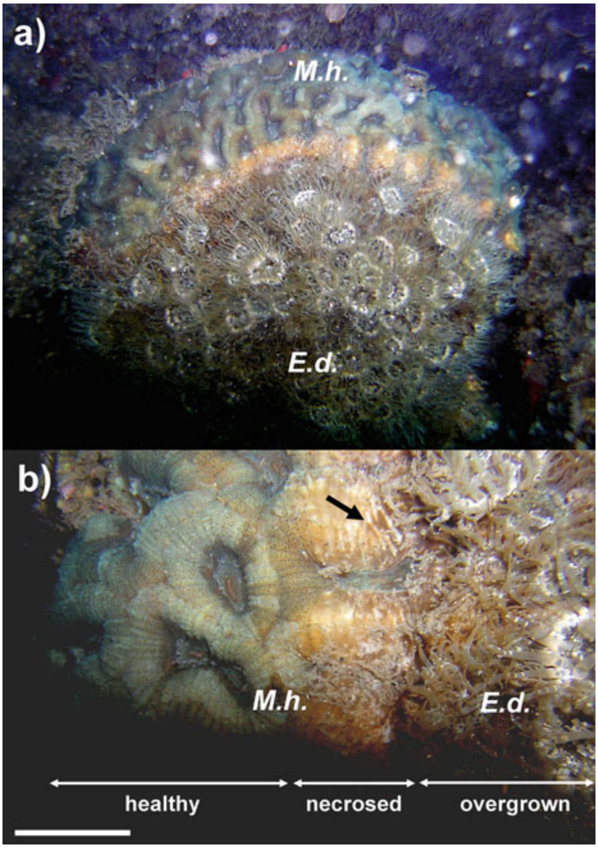

Fig. 7 Photographs of invasive *Exaiptasia diaphana* (*E.p.*) overgrowing a whole colony of the stony coral *Mussismilia hispida* (*M.h.*); (**b**) detail of the healthy, necrosed and overgrown zones. Note the septa becoming visible in the necrosing zones (arrow). Scale bar = 1 cm. Photo credits: Joel C. Creed

Seven NIS of octocorals [Clavulariidae (three species), Xeniidae (two), Melithaeidae (one), and Nephtheidae (one)] are known. All three clavulariids are NIS to the southwest Atlantic (Brazil), but while *Carijoa riisei* is a widespread invasive fouling species (see Sect. 10.5; Fig. 2b), *Clavularia viridis* cf. *viridis* has only been reported from one location as an aquarium release (Mantelatto et al. 2018; Fig. 5c, d). The third species, *Stragulum bicolor* van Ofwegen & Haddad, 2011, has recently spread along the Brazilian coastline, was described for the first time from Brazil, but is not native to the Atlantic and of unknown origin (Van Ofwegen and Haddad 2011).

Similarly, the nephtheid *Chromonephthea braziliensis* van Ofwegen, 2005 was introduced in southeastern Brazil from the Indo-Pacific on oil platforms and was also described for the first time from Brazil, of unknown origin (van Ofwegen 2005; Ferreira et al. 2009; Mantelatto et al. 2018).

The gorgonian *Melithaea erythraea* (Ehrenberg, 1834) (=*Acabaria erythraea*) which is native to the Red Sea has invaded the Mediterranean through Lessepsian migration and was first reported in the harbor of the Hadera power station, Israel in 1999 (Fine et al. 2005). In 2015 specimens were found on a natural substrate about 23 km north, so it is restricted but expanding its distribution (Grossowicz et al. 2020).

A single colony of an invasive xeniid soft coral with close genetic affinities to *Xenia membranacea* Schenk 1896 native from Indonesia was first found in 2007 on a reef in the Venezuelan Caribbean and has increased in abundance, dominated substrates, and extended its range several kilometers away to other sites after a few years, overgrowing native corals (Ruiz Allais et al. 2014). In 2017 another xeniid, *Sansibia* sp., was detected in communities on shallow subtidal tropical rocky reefs in southeast Brazil (Mantelatto et al. 2018; Fig. 5a, b). *Sansibia* sp. has now dominated deeper communities, associated positively with some macroalgae and negatively with the zoantharian *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), which probably provided greater initial biotic resistance to invasion (Mantelatto et al. 2018; Fig. 5a, b). As *Sansibia* Alderslade, 2000, is a newly described genus, its origin is unknown but as this species and *C. viridis* (see above; Fig. 5) were both found at the same site and time and are typical ornamental species, they were probably derived from the same aquarium release.

Regarding the Hydrozoa Owen, 1843 which comprise about 3500 valid species (Daly et al. 2007), those which occur in the benthos (hydroids) can be highly conspicuous and/or dominant and play an important role in shallow coastal assemblages. They may be especially abundant on artificial substrates such as those associated with ports, docks, and floating vectors which may act as primary receptor hubs. Furthermore they may access multiple vectors of invasion such as ballast water and fouling.

González-Duarte et al. (2016) reviewed six NIS of hydrozoans whose negative effects have been studied or that have a high invasive potential: *Blackfordia virginica* Mayer, 1910; *Clytia hummelincki* (Leloup, 1935); *Cordylophora caspia* (Pallas, 1771); *Eudendrium carneum* Clarke, 1882; *Garveia franciscana* (Torrey, 1902); and *Macrorhynchia philippina* Kirchenpauer, 1872. However, while these species are known to impact plankton and potentially fish stocks by predating eggs and larvae, as well as cause economic impacts by fouling boats and other artificial substrates, there is little information available about how they impact native MAFs or contribute to the creation of novel MAFs, as hydroids are a neglected component of MAFs in general (Di Camillo et al. 2017). However, *C. hummelincki* represents one case of an invasive hydroid that forms meadows (Gravili et al. 2008; Di Camillo et al. 2017). This introduced species is particularly abundant in the central Mediterranean at 0.5–2 m depth in sea urchin barrens, mainly in full light, on bare substrates covered by encrusting coralline algae, being absent on sandy and muddy ones (Gravili et al. 2008).

As a response to ocean warming, several cnidarian species are expanding their native distribution range poleward (Vergés et al. 2014; Canning-Clode and Carlton 2017). However it is not yet clear whether novel animal forests will emerge as a result (Vergés et al. 2014). When large-scale change in communities occurs as a result of range expansion, phase shifts can occur (Lonhart 2009). One example is the corallimorpharian *Rhodactis howesii* Saville-Kent, 1893, which was discovered smothering coral reefs at Palmyra in 2007. Its distribution around a shipwreck and mooring buoys fastened by iron chains suggested that substances leaching from metals might have been driving the spread of the infestation on the reef (Work et al. 2008, 2018). Similarly phase shift from corals to the zoantharian *Palythoa* cf. *variabilis* on reefs in the southwest Atlantic is thought to be mediated by human-induced environmental impacts (Cruz et al. 2015).

6.3 Bryozoans

The phylum Bryozoa contains about 6400 species which form encrusting, arborescent, or stolonic colonies. Around 80 species have been reported as introduced (Ahyong et al. 2019). Fouling species have been introduced in many regions, among which *Bugula neritina* (Linnaeus, 1758), *B. stolonifera* (Ryland, 1960), and *Amathia verticillata* (delle Chiaje, 1822) have wide distributions but no evidence of impact on MAFs.

The bryozoan *Tricellaria inopinata* d'Hondt & Occhipinti-Ambrogi, 1985, is among the fouling species typically found in European ports and marinas. Considered to be of Pacific origin, it was first reported in Italy in 1982 and has since then established itself in many regions in the Mediterranean and Atlantic Europe (Occhipinti-Ambrogi and Savini 2003; Streftaris and Zenetos 2006). In 2010 it was reported in the USA, where it outcompeted previously established bryozoans (Johnson et al. 2012). Not only does this species overgrow algae, ascidians, sponges, mussels, and other calcareous organisms, but it also creates a novel MAF because of its erect and complex architecture. A study in Cadiz, Spain (Gavira-O'Neill et al. 2018), revealed three introduced crustaceans associated with this bryozoan: the amphipods *Caprella scaura* Templeton, 1836 and *Monocorophium sextonae* (Crawford, 1937) and the isopod *Paracerceis sculpta* (Holmes, 1904), comprising

52.5% of all individual crustaceans found. The creation of this new MAF thus may facilitate the establishment of other invaders, a process so-called invasion meltdown [by which the negative impacts induced on native ecosystems by one invading NIS are exacerbated by interactions with another exotic species, posing further threat to native biodiversity (Simberloff and Von Holle 1999)].

Bryozoans of the genus *Watersipora* Neviani, 1896, grow as a single encrusting layer or as a complex structure of erected folded sheets that provide abundant settlement substrate for sessile epifauna and potential refuge for mobile epifauna (Sellheim et al. 2010a). The identity of species in this genus has been confused, but a recent taxonomic review indicates that three species have been transported worldwide: *W. subtorquata* (d'Orbigny, 1852), *W. subatra* (Ortmann, 1890), and *W. arcuata* Banta, 1969 (Vieira et al. 2014).

Watersipora (probably *W. subatra*) has invaded California, USA, modifying MAFs composed of a native ascidian that forms aggregations on artificial substrates; in experiments a different community composition was evident after 2 or 6 months (Sellheim et al. 2010b). In a longer-term study, historical data revealed an apparent shift in foundation species from mussels (*Mytilus californianus* Conrad, 1837 and the mussel complex *Mytilus trossulus* Gould, 1850/*Mytilus galloprovincialis* Lamarck, 1819) to *Watersipora*. The mussels were dominating pier pilings and floating docks in ~1976 but were scarce or absent by 2004 (Needles and Wendt 2013). The mechanism of change has not been determined, but an increase in sea otter predation of mussels or climate change may have enhanced *Watersipora*, given that it is very resistant to water warming (Sorte et al. 2010a). Whichever, the dominance of *Watersipora* resulted in the reduction of several native species and the establishment of an alternative stable state. Recently the bryozoan has been documented on natural substrates in Central California (Zabin et al. 2018) which raises concerns about community shifts to this novel type of MAF.

6.4 Polychaetes

A recent review listed 292 polychaete species as introduced in at least 1 site with Families Sabellidae, Serpulidae, and Spionidae being most invasive worldwide (Çinar 2013). Many species of Serpulidae and Sabellidae are notorious foulers that produce large aggregations that modify communities and ecosystem dynamics through competition for space and food, change in water circulation, deplete plankton, and increase deposition of feces. Examples include the serpulid *Hydroides elegans* (Haswell, 1883) that invaded harbor environments worldwide but is absent in natural communities (Schwan et al. 2016). *Sabella spallanzanii* (Gmelin, 1791) is originally from the Mediterranean and invaded Western Australia in the 1960s. It is found in the shallow subtidal, preferring sheltered harbors and embayments where it influences recruitment of other sessile taxa (Holloway and Keough 2002). More recently it has spread its distribution to the southern coast of Australia (Murray and Keable 2013) and New Zealand (Read et al. 2011). *Branchiomma* Kölliker, 1858 is another sabellid genus with at least five species with a history of invasion (Keppel et al. 2015). Three of these species have been reported in the Mediterranean Sea, *B. bairdi* (McIntosh, 1885), *B. luctuosum* Grube, 1870, and *B. boholense* (Grube, 1878), where they have spread to many harbor areas. Their aggregation behavior, high densities, and high filtration capacities suggest they may modify the environment. *B. luctuosum* has reduced the abundance of the native *S. spallanzanii*, and the differences in size, density, and clearance rates of those species suggest that further ecosystem changes will occur (Mastrototaro et al. 2015).

Ficopomatus enigmaticus (Fauvel, 1923) is another iconic example of a NIS able to create novel MAFs. It is distributed in most brackish waters in temperate zones throughout the world, being abundant in low-current, turbid eutrophic waters where it builds reefs as high as 40 cm on vertical stone walls (Le Havre, France; Charles et al. 2018) or forms circular reefs up to 7 m in diameter by 0.5 m in height on soft bottoms (Mar Chiquita coastal lagoon, Argentina; Schwindt et al. 2004) (Fig. 8a). Apart of these ecosystem-level effects, the invasive polychaete reefs also interfere at the local scale by accumulating more diverse infauna than the sediment around them and modifying the native benthic community structure creating refuges for the macrofauna (Schwindt et al. 2001; McQuaid and Griffiths 2014). MAFs formed

Fig. 8 Photographs of aggregations of the Australian tubeworm *Ficopomatus enigmaticus* in Argentina. (**a**) banks on soft bottoms; (**b**) the polychaete profiting from new construction in estuaries. Photo credits: Alejandro Bortolus

by *F. enigmaticus* are increasing in area and biomass, profiting from new construction in estuaries as well as garbage accumulation that provide hard substrate for larval initial attachment (Schwindt et al. 2004; McQuaid and Griffiths 2014; Fig. 8b). For example, in the Zandvlei Estuary, South Africa, over 25 years, mass per unit area has tripled, and 25% of the total area is now covered (McQuaid and Griffiths 2014), while in the Mar Chiquita coastal lagoon, Argentina, the reef covers about 40 km^2, representing 86% of the lagoon (Schwindt et al. 2001).

Spionidae includes invasive boring species belonging to the genera *Boccardia* Carazzi, 1893, *Dipolydora* Verrill, 1881, and *Polydora* Bosc, 1802 that can cause severe damage to shells of commercially grown oysters and mussels (Çinar 2013). In the 1880s an invasion of a mudworm (*Polydora* sp.) supposedly from New Zealand to Australia caused a catastrophic disappearance of native MAFs formed by beds of subtidal oysters that have never recovered since (Ogburn et al. 2007). A century later, another group of three spionid species of the genus *Marenzelleria* Mesnil, 1896 have invaded soft bottoms in the Baltic Sea and appear to have established abundances as high as 16,955 individuals m^{-2} in the region in less than 30 years (Kauppi et al. 2015). Despite the high density, taxa richness did not decrease, and turnover and number of traits actually increased at one study site (Hewitt et al. 2016). However, the polychaete significantly enhanced all bioturbation metrics examined, with implications for ecosystem functioning, especially in deeper, hypoxia-affected areas, where *Marenzelleria* spp. are sometimes the only macrofaunal taxon present (Kauppi et al. 2018).

6.5 Barnacles

As conspicuous ship-fouling organisms, it is expected that many barnacle species have their modern distribution explained by human-mediated translocations (Carlton et al. 2011). Out of a total of 185 Balanidae species known, 128 (69%) have been reported as NIS at some location around the world (Torres et al. 2012). The gregarious behavior of these intertidal and shallow subtidal species creates well-known MAFs in horizontal zones dominated by barnacles that, in many cases, ameliorate conditions for associated species. Prior to the invasion of *Amphibalanus improvisus* (Darwin, 1854) in the northern Baltic Sea, there were no other benthic suspension-feeding species. *A. improvisus* altered the habitat through the construction of dense crusts on hard surfaces, and those dense populations facilitated the arrival of associated species, such as chironomid larvae, ostracods, copepods, and juvenile bivalves (Leppäkoski and Olenin 2000).

Besides creating new MAPs, NIS of barnacle can interact with native species and other invasive MAFs. *Balanus glandula* Darwin, 1854 invaded Japan 30–50 years ago and is becoming a dominant species in the upper littoral fringe, especially in embayments, largely at the expense of the tropical endemic barnacle *Fistulobalanus albicostatus* (Pilsbry, 1916) (Kado 2003). In Hawaii, *Chthamalus proteus* Dando & Southward, 1980 arrived ~40 year ago and is now the most abundant and widespread non-native barnacle in the intertidal zone on the island of Oahu, where the abundance of an earlier invader, the larger and faster growing barnacle *Amphibalanus reticulatus* Utinomi, 1967, is reduced via substrate preemption in the zone of overlap between the two barnacle species (Zabin 2009).

6.6 Bivalves

Bivalves are among the most successful MAF invaders in marine systems. Mussel and oyster invasions have been documented throughout the world (e.g., Ruiz et al. 1997). An iconic example is the mussel *M. galloprovincialis*—a widespread species forming dense beds—originally from Europe (mostly in the Mediterranean, the Black Sea, and the eastern Atlantic). This mussel species is among the 100 of the World's Worst Invasive Aliens (Lowe et al. 2000), having being introduced by human activities and aquaculture. It has overgrown and replaced other intertidal benthic taxa both on natural and man-made hard substrata. Similar colonization patterns have been recorded for the brown mussel *P. perna*, native to Africa, likely introduced during the slave trade in the eighteenth century into North and South America and now considered a well-established and commercially exploited species (Hicks and Tunnell 1993; Ferreira et al. 2009) (Figs. 1b and 2a).

A classic example of the impact on resident communities is the Asian mussel *A. senhousia* (=*Musculista senhousia*), which became a pest on mudflats in the Eastern Pacific, by altering sediment properties and the resident native benthic assemblages, forming complex byssal mats (Crooks 1998) (Fig. 9a, b).

The Indo-Pacific mussel *Brachidontes pharaonis* (P. Fischer, 1870) in the Mediterranean Sea (Rilov et al. 2004) and the purse oyster *Isognomon bicolor* (C. B. Adams, 1845) (Fig. 9c, d) in the western Atlantic are two examples of invasive bivalves that form novel MAFs leading to monospecific beds that exclude native species (Domaneschi and Martins 2002). *B. pharaonis* entered into the Mediterranean from the Red Sea just after the opening of the Suez Canal in 1869 but remained rare until the 1990s. During the few last decades, anthropogenic impacts along the Eastern Mediterranean rocky shores likely facilitated the outbreak of *B. pharaonis* populations and the subsequent high pressure of invasive propagules resulted in exclusion of the native mussel beds of *Mytilaster minimus* (Poli, 1795) (Safriel and Sasson-Frosting 1988; Rilov et al. 2004; Didham et al. 2007). Similarly, *I. bicolor*—likely introduced by oil platforms—has caused dramatic changes in the receptor communities, leading to a competitive displacement of native MAFs composed of barnacle populations on rocky shores along the Brazilian coast (Breves-Ramos et al. 2010) (Fig. 9c, d).

The establishment of an invasive MAF may also ameliorate stressful conditions which a native MAF may undergo, thus ultimately leading to coexistence rather than a dominance shift. This kind of facilitation process has been demonstrated between the blue mussel *Mytilus edulis* Linnaeus, 1758 and the Pacific oyster *M. gigas* (=*Crassostrea gigas*) in the Wadden Sea (North Sea) (Reise et al. 2017). About

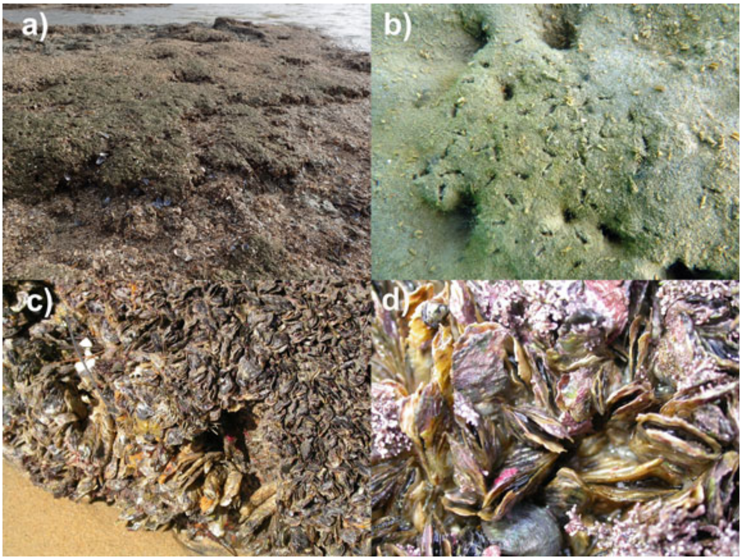

Fig. 9 Photographs of invasive bivalves that form novel marine animal forests. (**a**) bank of, and, (**b**) detail of the Asian date mussel *Arcuatula senhousia* (=*Musculista senhousia*) in Kiapara Harbour, New Zealand; (**c**) bed of the purse oyster *Isognomon bicolor* competing with barnacles on a tropical rocky reef in Brazil, (**d**) creating new habitat. Photo credits: Chris Woods (**a**, **b**); Joel C. Creed (**c**, **d**)

25 years after the introduction of Pacific oysters for aquaculture purposes, the community effect of the invaders shifted from a competitive displacement to a co-dominance, with layers of resident mussel beds receiving shelter from physical and natural disturbances by upper-level invasive oyster reefs (Reise et al. 2017).

6.7 Ascidians

Ascidians are sessile filter-feeding animals considered models in studies of invasion success because of the significant ecological and economic damage to invaded habitats (Zhan et al. 2015). Among the 3000 currently described species, Shenkar and Swalla (2011) recognized 64 species that had been introduced in at least 1 site, with 27 records in tropical regions and 50 in temperate environments. A few species, such as *Botrylloides violaceus* Oka, 1927, *B. schlosseri* (Pallas, 1766), *Ciona intestinalis* (Linnaeus, 1767), *C. robusta* Hoshino & Tokioka, 1967, *D. vexillum* Kott, 2002, *Microcosmus squamiger* Michaelsen, 1927, *S. clava*, and *Styela plicata* (Lesueur, 1823) (Zhan et al. 2015), have received most of the attention because of their negative impact on the bivalve industry, but most of this does not concern natural MAFs.

Fig. 10 Photographs of a bed of the invasive cunjevoi *Pyura praeputialis* in the intertial zone at Antofagasta, Chile. Photo credits: Patricio Manriquez

Solitary ascidians of the *Pyura stolonifera* (Heller, 1878) complex, of which three are invasive species, are engineering species capable of dominating the space in the intertidal and shallow subtidal zones (Rius et al. 2017). *Pyura praeputialis* (Heller, 1878) has been introduced in the Bay of Antofagasta, Central Chile, probably at the beginning of the twentieth century (Castilla et al. 2002) (Fig. 10). This species is originally from Australia where it mainly occurs on horizontal wave exposed, rocky substrates where it forms dense aggregates (Rius and Teske 2011). *P. praeputialis* dominates the mid-to-low intertidal rocky shore fringe replacing the former MAF dominated by the mussel *Perumytilus purpuratus* (Lamarck, 1819) (Caro et al. 2011). A consequence of this new MAF was a dramatic increase in local rocky shore biodiversity: whereas over 110 species of macroinvertebrates and algae coexist on and within the *P. praeputialis* bed, only 28 species live along adjacent coastlines (Cerda and Castilla 2002), suggesting unoccupied niche space is being exploited.

Pyura doppelgangera, originally from the southern shores of Bass Strait, invaded the northern tip of New Zealand in the beginning of this century and has now been recorded at more than 22 locations where it is replacing the MAF formed by the green-lipped mussel *P. canaliculus* (Davis et al. 2018). While gastropod mollusks and crustaceans dominated the assemblage within mussels, tubicolous polychaetes dominate the fauna associated with the ascidian. Furthermore, sessile filter-feeding epifauna, notably barnacles and calcareous tube-dwelling polychaetes which were common on mussels, are never found in the ascidian forest.

Styela is another genus of solitary ascidians which can be invasive. In contrast to *Pyura*, *Styela* is more common in fouling communities associated with artificial, rather than natural, substrates. However, recent reports of *S. clava* in Northern Patagonia, Argentina, show that although the invasion occurred after 2012, the species has already spread onto natural substrates, both in intertidal and subtidal zones down to 20 m, reaching densities of 84 ind. m^{-2} (Pereyra et al. 2015). Specific impacts on local communities are unknown, but *Styela* is one of the main substrates

Fig. 11 Photograph of a marine animal forest invaded by the colonial ascidian *Eudistoma carolinense* (gray, lobed colony in the foreground) at Guaratuba, Brazil. Photo credit: Rosana M. Rocha

for the recruitment of another introduced species, the alga *Undaria pinnatifida* (Harvey), facilitating the introduction of this species. As both ascidia and alga are bioengineers, local communities are expected to be substantially transformed. In northwest Europe, *S. clava* grows on various substrates, including shells of living mussels [*M. edulis*, *Modiolus modiolus* (Linnaeus, 1758)], oysters, and barnacles (Lützen 1999), but the impacts to those MAFs have not been studied.

As well as aggregations of solitary NIS of ascidians, some colonial species can also form three-dimensional habitats, as it is the case of *Eudistoma carolinense* Van Name, 1945 which was first observed forming a horizontal belt along the sublittoral fringe in south Brazilian rocky shores in 1996 (Moreno and Rocha 2006) (Fig. 11). The invader has occupied space originally used by *P. perna* (also nonindigenous, see Sects. 2 and 6.6 and Figs. 1b and 2a) and created a new MAF providing habitat for 128 different taxa, including vagile polychaetes, crustaceans, mollusks, among others, as well as providing substrate for sessile bryozoans, hydrozoans, ascidians, and sponges (Moreno and Rocha 2006).

Colonial invaders can also impact MAFs, usually by competing for space and smothering competitors. Three years after its introduction in Long Island Sound—USA around 2002, the temperate didemnid *D. vexillum* had colonized at least 230 km^2 of the soft bottom, overgrowing sea scallops, mussels, sponges, bryozoa, hydrozoa, calcareous tube worms, and other native colonial ascidians (Valentine et al. 2007). The species also acts as an ecosystem engineer, forming a mat on soft bottoms, altering benthic-pelagic coupling and influencing the biogeochemical cycling of many nutrients and elements. It does so by creating a physical barrier between the underlying seafloor and the water column above, resulting in subtle shifts in community structure and functional group dominance (Mercer et al. 2009).

6.8 Algae

Macroalgae are one of the most successful invasive groups (Chapman et al. 2006). Invasive algae, such as *Womersleyella setacea* (Hollenberg) R. E. Norris, *Kappaphycus alvarezii* (Doty) Doty ex P. C.Silva, and *Dictyosphaeria cavernosa* (Forsskål) Børgesen have altered gorgonian (Cebrian et al. 2012), sponge (de Caralt and Cebrian 2013), and coral populations (Stimson et al. 2001; Chandrasekaran et al. 2008) on Indian and Hawaiian coral reefs. Furthermore, on Mediterranean reefs, the alga *Asparagopsis taxiformis* (Delile) Trevisan de Saint–Léon has induced changes in coral microbial communities (Greff et al. 2017), and on Hawaiian reefs, the alga *Gracilaria salicornia* (C. Agardh) E. Y. Dawson has modified physical habitat quality by reducing irradiance, increasing sedimentation, and brought about greater variation in dissolved oxygen and pH in the water negatively impacting reef corals (Martinez et al. 2012).

Ramsay-Newton et al. (2016) presented rare empirical data showing effects of the invasive red alga *Dasysiphonia japonica* (Yendo) H.-S. Kim on native species, community, and ecosystem-level responses in the western North Atlantic Ocean. The effects included decreases in biodiversity, changes in nutrient uptake of algal assemblages over time, and changes in the functional characteristics of invaded communities, with implications for ecosystem-level processes such as nutrient fluxes.

Species of the genus *Caulerpa* J. V. Lamouroux have also received attention due to their negative impacts on MAFs in reef systems. Invasive traits, such as thallus size and density, levels of asexual reproduction (fragmentation), and total biomass are important to their invasion success in some areas such as in Australia (Wright 2005) (Fig. 12). *Caulerpa taxifolia* (M. Vahl) C. Agardh has strong negative effects on the reproductive traits (timing of reproductive development and spawning; follicle and gamete production) of the native bivalve *Anadara trapezia* (Deshayes, 1839), even though the invader has positive effects on recruitment (Gribben and Wright 2006; Gribben et al. 2009). *C. taxifolia* biomass is positively associated with the composition and abundance of the epifaunal community but negatively correlated with the abundance of infauna (Gribben et al. 2013).

Bulleri et al. (2010) demonstrated that *C. racemosa*, once established, can enhance sediment accumulation, favoring algal turfs persistence over erect algal forms, and enables them to monopolize space. Additionally, this invasive alga impacted survival, necrosis rates, and population biomass of the gorgonian forests of *Paramuricea clavata* (Risso, 1826) on Mediterranean rocky reefs (Cebrian et al. 2012). Some authors comment that *Caulerpa* species that rely on disturbance to

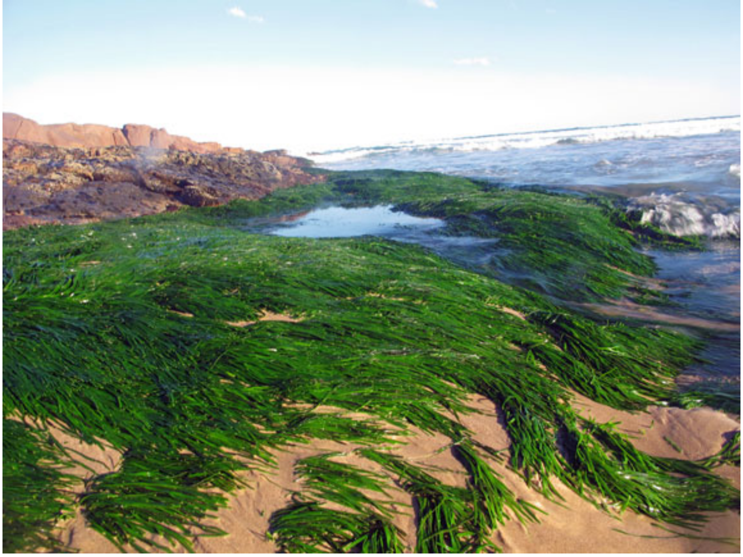

Fig. 12 Photograph of the invasive green alga *Caulerpa filiformis* dominating and transforming the substratum at Anna Bay, Port Stephens, New South Wales, Australia. Photo credit: Ricardo J. Miranda

establish can subsequently become the main drivers of ecological change (Bulleri et al. 2010).

More recently, studies have evaluated combined effects of invasive algae and sea warming on native species and ecological processes (Kersting et al. 2015; Miranda et al. 2019). The results can be complex involving direct negative or indirect positive effects. For example, the invasive algae *Caulerpa cylindracea* Sonder and *Lophocladia lallemandii* (Montagne) F.Schmitz combined with warming increased tissue necrosis and reduced photosynthetic efficiency of native coral *Cladocora caespitosa* (Linnaeus, 1767) (Kersting et al. 2015). *C. filiformis* presence can indirectly influence reduction of gastropod herbivory intensity on native kelp *Ecklonia radiata* (C. Agardh) J. Agardh under future warming scenarios (Miranda et al. 2019) (Fig. 12).

6.9 Fish

The Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are among the most invasive marine predators of recent years (reviewed by Andradi-Brown 2019). They have spread rapidly across the western Atlantic, increasing in abundance dramatically between 2004 and 2010 to a level where they represent nearly 40% of the total predator biomass in the ecosystem. The increase in lionfish abundance has been paralleled with a 65% decline in the biomass of the lionfish's 42 Atlantic prey fish species in just 2 years (Green et al. 2012). These invaders are now also becoming abundant on eastern Mediterranean rocky reefs (Azzurro et al. 2017), with currently unknown impacts on the local communities.

Given that their prey include parrotfishes (Albins and Hixon 2008; Morris and Akins 2009), Albins and Hixon (2013) pointed out that predation by invasive lionfish may have indirect effects on Atlantic and Caribbean reef-building corals, a major MAF group. On mesophotic coral reefs in the Bahamas, the lionfish invasion has caused a phase shift to increased algal cover from 31% to 94% at 46 m and from 8% to 92% at 61 m over 4 years (Lesser and Slattery 2011; Andradi-Brown 2019). Coral cover at 46 m changed from 19% in 2005 to less than 2% over the same period, an indication that phase shift to algal dominance may have been caused by the abovementioned trophic cascade, resulting in algae competitively excluding corals and other benthos (Lesser and Slattery 2011; Andradi-Brown 2019).

Numerous studies of coral reefs have shown that overfishing of herbivores reduces the health of reef corals by reducing herbivory allowing seaweeds from outcompeting corals and/or restricting coral recruitment (Mumby and Steneck 2008). So when lionfish effectively “overfish” juvenile parrotfish and other small herbivores, they can have devastating indirect effects. In areas where trophic cascades already occur [where top predators such as large groupers that prey on mesopredators that feed on herbivores are already overfished—a phenomenon called “mesopredator release” (Prugh et al. 2009)]—lionfish can increase the stress on herbivores even further and lead to a total domination of algae on the reef.

7 Chemical Ecology

The study of chemically mediated interactions among members of biological communities is a recent approach to understanding ecosystems. Chemical signals emitted by marine organisms (natural products or secondary metabolites) act as a language for communication between members of sea life. However, the impact of these signals is still very poorly understood. These substances strongly affect the populations and communities’ structures and the function of ecosystems (Hay 2009). Several theoretical models on resource allocation have been developed to explain the pattern of the secondary metabolites in marine organisms in response to chemical, physical, and biological stresses (Cronin 2001). The ecological and evolutionary consequences of secondary metabolites and their effects on marine biodiversity are increasingly recognized (Hay and Fenical 1996). However, there is little evidence of the adaptive response of marine invasive species under selective pressure from a new environment.

Some marine organisms are prolific in providing unique bioactive chemicals, such as terpenes, steroids, fatty acids, polyketides, and alkaloids, with ecological functions, such as defense against predators, competitors, and fouling organisms. For some invasive species, their chemical defenses may enhance their invasion success. Regarding MAFs the invasive Porifera *T. hoshinota* (Demospongiae)

(Pacific Ocean to Central Pacific Reef) aggressively competes for space by killing and overgrowing living corals (Rützler and Muzik 1993). This coral-killing sponge is known to produce the bioactive compounds terpiodiene, nakitriol, nakiterpiosin, and nakiterpiosinone that are toxic to corals (Teruya et al. 2002; Uemura et al. 2009). Wang et al. (2012) showed that endosymbiotic cyanobacteria are engulfed by *Terpios* cells and may be responsible for the "black disease" that results from outbreaks of this cyanobacteria-sponge holobiont and cause death of stony corals (Yang et al. 2018).

Cup corals *T. coccinea* and *T. tagusensis* (Scleractinia), which have invaded the Caribbean, Gulf of Mexico, and the Brazilian coast from the Indo-Pacific Ocean (Paula and Creed 2004; Creed et al. 2017; Figueroa et al. 2019; Figs. 1 and 4), produce chemical defenses that influence interactions with predators (generalist fish), foulers, and competitors. Their methanolic crude extracts exclude and decrease the settlement and survival of the fouling organisms such as crustose algae *Lithophyllum* sp. and the green alga *Cladophora* sp., respectively (Lages et al. 2010). In a competition interaction experiment, necrosis has been detected on the tissues of the coral *Mussismilia hispida* (Verrill, 1902), and this species induced variation in sterol, alkaloid, and fatty acid production in *Tubastraea* tissues. In this way, they are able to affect community structure and ecosystem dynamics (Lages et al. 2011, 2012; Paula et al. 2017).

Field experimental assays with the NIS (Indo-Pacific Ocean) soft coral *C. braziliensis* (Alcyonacea), also invasive on the Brazilian coast, showed that chemicals from this coral have an allelopathic effect causing large necrotic patches on tissues of the endemic gorgonian *Phyllogorgia dilatata* (Esper, 1806). Bioassay-guided experiments with fractions from the unpalatable hexane extract from this coral revealed a new steroid, 23-ketocladiellin-A, which exhibited potent feeding deterrence against fish, suggesting a reason for the observed success of the invasion by this NIS coral (Lages et al. 2006; Fleury et al. 2008).

Cebrian et al. (2012) reported the strong and consistently negative effects on different components of fitness of the Mediterranean gorgonian *Paramuricea clavata* by the invasive algae *C. racemosa* and *W. setacea*. Although secondary metabolites of *W. setacea* are unknown and the caulerpenyne concentration in *C. racemosa* is low (Jung et al. 2002), they did not rule out possible allelopathic activity (Cebrian et al. 2012). The alkaloids and crude extracts from invasive ascidian *Didemnum* spp. (Ascidiacea) also inhibit predators and foulers (Pisut and Pawlik 2002).

8 Microbial Ecology

As seen above, a holobiont-approach is often needed to assess if the associated microbiota confer invasive species advantages over native species in MAFs. Competitive exclusion by the invader can be enhanced by carrying pathogens that act as biological weapons (Vilcinskas 2015). Disease-mediated invasions include cases as diverse as grasses, salt marshes plants, ladybirds, squirrels, and crawfish carrying parasites such as fungi and viruses that infect native competitors successfully decimating their populations (Li et al. 2014; Young et al. 2017).

In octocoral animal forests on rocky reefs in the Eastern Pacific, fungal diseases and bacterial dysbiosis have been consistently observed in gorgonian coral populations where the invasive snowflake coral *C. riisei* is present (Barrero-Canosa et al. 2012; Sánchez and Ballesteros 2014; Sánchez et al. 2014; Quintanilla et al. 2018). However, further research is needed to study the microbiota and pull out which potential pathogens are carried by the snowflake coral.

Invasive species can also disrupt mutualistic symbiotic interactions. In general, continental case studies have preliminary concluded that symbionts do not comprise as serious threat to natives, given the facultative nature of mutualism (Aslan et al. 2015). Similar cases have been found in MAFs, coral reefs, with zooxanthellae (Symbiodiniaceae) (LaJeunesse et al. 2018). *Durusdinium trenchii* (LaJeunesse) from the Indo-Pacific, previously known as clade D, is considered a recent invader in the western Atlantic, where corals engage in symbiosis with this opportunistic zooxanthella after bleaching, but rarely keep it due to their unfit mutualism (Pettay et al. 2015). A similar case could be zooxanthellae of the genus *Gerakladium* LaJeunesse, which are exclusively found in the sponge genus *Cliona* Grant, 1826 (Granados et al. 2008). They show very little divergence between Indo-Pacific and western Atlantic species, whereas the sponges can also associate with algae of the genera *Zooxanthella* K. Brandt (=*Symbiodinium*) and *Cladocopium* LaJeunesse and H. J. Jeong (Granados et al. 2008; Hill et al. 2011; Ramsby et al. 2017). Although it may not be a recent invasion, it is a case showing that the most recent mutualistic arrival in the region is still facultative among several species. Further research is needed of other mutualistic coral symbionts, such as apicomplexan corallicollids (Kwong et al. 2019), euendolithic algae (Gonzalez-Zapata et al. 2018b), and endosymbiotic prokaryotes (Gonzalez-Zapata et al. 2018a).

9 Formers of Novel MAFs

Invasive ecosystem engineers (IEE) are potentially one of the most influential types of biological invaders, and some can be formers of new MAFs. They are expected to have extensive ecological impacts by altering the physical-chemical structure of ecosystems, thereby changing the rules of existence for a broad range of resident biota. A recent review and meta-analysis have shown that most studied IEE are macrophytes, but some are also animals, most notably bivalves, colonial worms, and corals (Guy-Haim et al. 2018). IEE were shown to cause dramatic shifts in local biodiversity (both increasing or decreasing taxa richness) and have strong impacts on ecosystem functions in the invaded areas, but there are very few studies that examined the interaction between both impacts. One well-known example is the tubeworm *F. enigmaticus*. This polychaete forms massive reefs within invaded lagoons including mudflats without hard substrate, dramatically modifying the physical properties and processes in the area as well as strongly impacting the resident biota (Schwindt et al. 2001, 2004) (Fig. 8). The worm has great potential for transferring pelagic production to the benthos: changes water quality and light penetration by filtering large volumes of water (Davies et al. 1989), reduces phytoplankton biomass (Bruschetti et al. 2008), increases carbonate sediments through the accumulation of calcareous tubes (Schwindt et al. 2001), and produces feces and pseudo-feces with organic matter content 20× normal sediment with a *C*/*N* ratio of biodeposits of 8 (Bruschetti et al. 2011).

Another example extensively studied and discussed by Crooks (2009) is the soft-sediment dwelling invasive mussel *A. senhousia* (=*Musculista senhousia*). *A. senhousia* forms dense byssus bound mats on intertidal and subtidal soft sediments (Crooks 1998) (Fig. 9). At small spatial scales, the mussel appears to benefit many small organisms that occur in higher abundances within the complex mat matrix when compared to nearby, mat-free areas (Crooks 1998) by offering physical structure (Crooks and Khim 1999). However, it has a detrimental effect on larger organisms such as other bivalves and eelgrass (Reusch and Williams 1998; Crooks 2001).

The encrusting zooxanthellate scleractinian *O. patagonica* was first recorded in the Mediterranean Sea in 1966, with an original description based on ~10,000 years old fossils from the western Atlantic (Zibrowius 1974). However, the origin and taxonomic identification of *O. patagonica* in its present range is uncertain because it is cryptogenic (Zenetos et al. 2017). *O. patagonica*'s range has expanded in multiple directions and established abundant populations over a broad geographical scale, including both western and eastern Mediterranean basins, the subtropical eastern Atlantic (Canary Islands harbor area), and tropical Caribbean Sea (on coral reefs nearby the Veracruz Port, Mexico) (Fine et al. 2001; Serrano et al. 2013; Colín García et al. 2018; López et al. 2019). It exhibits an invasive behavior at both geographical distribution range and population outbreak levels, being able to form novel MAFs in shallow waters and drive phase shifts from macroalgal- to coral-dominated states across the Mediterranean (Serrano et al. 2012, 2018; Salomidi et al. 2013) (Figs. 1a and 6).

The successful proliferation of *O. patagonica* resembles that of the azooxanthellate scleractinians *Tubastraea* spp. (Figs. 1b and 4). Native to the tropical Indo-Pacific, *T. coccinea* was first recorded in some Caribbean islands in the 1930s, probably introduced by fouling floating platforms (Creed et al. 2017). They are increasing their range on rocky and coral reefs throughout the tropical-subtropical Atlantic from the Canary Islands to Southern Brazil, Caribbean Sea, and Gulf of Mexico (Creed et al. 2017; Figueroa et al. 2019; López et al. 2019). The capacity of *T. tagusensis* (Fig. 4a) and *T. coccinea* (Fig. 4b) to reproduce both sexually and asexually (Capel et al. 2014; Paula et al. 2017) and exploit man-made substrates (oil and gas platforms, buoys, and ships; Fig. 4d) has assisted their wide geographic dispersal (Creed et al. 2017).

They have life-history traits similar to those documented for *O. patagonica* (Kramarsky-Winter et al. 1997; Fine et al. 2001). Both invasive *Tubastraea* and *Oculina* have broad tolerance to environmental parameters, are opportunistic high fecundity colonizers and generalists in terms of substratum utilization, and benefit from current human-related impacts (e.g., their population growth is enhanced in artificial habitats, which likely act as corridors for successful dispersal (e.g., Fine et al. 2001; Serrano et al. 2013, 2018; Mantelatto and Creed 2015; Creed et al. 2017; López et al. 2019).

10 Case Studies

10.1 Vermetid Reefs

Vermetids are gastropod mollusks, some of which can form reefs as biogenic MAFs with the help of encrusting coralline algae (Safriel 1975; Fine et al. 2017). They are important in intertidal and shallow subtidal habitats in subtropical and temperate waters. They have a key role as habitat engineers, hosting high biodiversity levels and providing ecosystem services such as coastal protection and regulation of sediment transport and deposition (Milazzo et al. 2017). Likely, the most well-studied vermetid reefs are those from the temperate Mediterranean Sea (Ingrosso et al. 2018), the main reef-building genus being *Dendropoma* Mörch, 1861. In the southeastern Mediterranean (Levant Sea), this ecosystem has experienced a massive population explosion of a Red Sea mussel, *B. pharaonis* that formed extensive mussel beds during the 1980–1990s (Rilov et al. 2004). During the 1990s and the 2000s, the endemic reef-building species *Dendropoma anguliferum* (Monterosato, 1878), itself went ecologically extinct on the Israeli coast for unknown reasons, along with many other native species (Rilov 2016). Similarly, along the Lebanese coast, only a single remnant small population of *D. anguliferum* was found (Badreddine et al. 2019). These findings attest to the potential domination of vermetid MAFs by invasive species and other human disturbances, but the link between the invasion and the MAF loss is not clearcut.

10.2 Coral Reefs

Reef corals are MAFs that form calcified skeletons that can act as substrate and form habitats for other kinds of benthic invertebrates on rocky benthic assemblages (Sheppard et al. 2009). Loose coral boulders and free-living reef corals can move downslope and tumble onto soft bottoms underneath, where they can act as solid substrate for attached benthos and thus assist in reef expansion (Sheppard 1981). Most reefs occur in tropical shallow coastal waters, where reef-building corals grow rapidly owing to their symbiosis with light-dependent unicellular algae (zooxanthellae) inside their soft tissue (Muller-Parker et al. 2015). These MAFs have been invaded in Hawaii and India by macroalgae (Stimson et al. 2001; Chandrasekaran et al. 2008), in the western Atlantic by the azooxanthellate coral *Tubastraea*

(Miranda et al. 2016; Fig. 4c), in the tropical Atlantic by lionfish (Andradi-Brown 2019), and in the Venezuelan Caribbean by a xeniid soft coral (Ruiz Allais et al. 2014).

In the last decade, there has been an increase in research attention toward the mesophotic zone (30–150 m depth), where tropical coral communities might be more sheltered from negative human impacts but receive less sunlight than at shallower depths (Laverick et al. 2018). Mesophotic reef MAFs have been transformed by trophic cascades caused by invasive lionfish (Lesser and Slattery 2011; Andradi-Brown 2019). Nothing is known about the biological invasion of the deepest coral reefs, so-called cold-water reefs, where corals live in permanent darkness and without zooxanthellae but still can form extensive frameworks over long periods of time (Roberts and Cairns 2014; Hebbeln et al. 2019).

10.3 Temperate Reefs

Invasive animal species can profoundly transform native ecosystems, particularly when they impact native engineer species. A striking example of marine regime shifts is found on shallow-water temperate reefs where global change has first led to widespread phase shifts from canopy-forming macroalgae- to barren-dominance (Harley et al. 2012). More recently, sea warming-enhanced poleward shifts of subtropical and tropical zooxanthellate corals have lead to tropicalization of temperate ecosystems by coral-dominated assemblages (Vergés et al. 2014).

Tosa Bay, in southern Japan, provides one of the most well-known examples where the healthy temperate macroalgae-dominated ecosystem of the 1980s was first replaced by barrens in the 2000s and now by zooxanthellate scleractinian corals such as reef-building *Acropora* species, resulting in a novel coral-dominated ecosystem (Serisawa et al. 2004; Takao et al. 2015). Marginal habitats for coral reefs are predicted to expand poleward under future climate scenarios (Burrows et al. 2011), and small increases in sea temperature in the past have resulted in the appearance of coral reefs at higher latitudes (Greenstein and Pandolfi 2008), which is consistent with the hypothesis and evidence that algal forests in temperate regions are being transformed into coral-dominated forests in an era of global warming.

10.4 Mediterranean Coralligenous Ecosystem

The Mediterranean coralligenous ecosystems are calcareous formations of biogenic origin that are mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions (Ballesteros 2006). Cavities and crevices within the coralligenous structure sustain a complex community dominated by forests of suspension feeders. The high biodiversity of animal builders contributes to the coralligenous framework, including most taxonomic groups such as bryozoans, serpulid polychaetes, sponges, cnidarians, mollusks, and tunicates (Boudouresque et al. 2017). Sea warming has increased the frequency of heat waves that have been linked to severe mass mortality events in coralligenous benthic invertebrates over broad geographical scales (Garrabou et al. 2009; Crisci et al. 2011). In turn, some invasive species can thrive in the coralligenous habitat, but only introduced algal species are currently threatening the coralligenous ecosystems. Remarkably harmful is the red turf alga *W. setacea*, which forms a dense and thick carpet over encrusting calcareous algae, thus inhibiting photosynthesis and growth of the main framework builders, and the recruitment of animal species inhabiting the coralligenous community (Airoldi et al. 1995; Ballesteros et al. 1998; Piazzi et al. 2002). New mass mortality events depleting animal forests in coralligenous habitats are expected under projected climate warming scenarios, and invasive algal species are increasing through the Mediterranean (Marbà et al. 2015), suggesting the ongoing transformation of coralligenous animal forests into algal-dominated forests. Although the impact of invasive species is increasingly recognized in shallow-water Mediterranean coralligenous ecosystems, little is known of the presence of non-native species beyond the continental shelf (Galil et al. 2019). However invasive fish may spread to depths and impact unique, diverse, and fragile mesophotic animal forests (Gori et al. 2017; Galil et al. 2019).

10.5 Carijoa

The snowflake coral *C. riisei* (Fig. 1b) is a tropical stoloniferous zooxanthellate octocoral (Order Alcyonacea, Family Clavulariidae) that occurs in shallow water. It was considered native to the tropical western Atlantic and throughout the Caribbean (Bayer 1961), but recent molecular studies indicate that it is actually native to the Indo-West Pacific (Concepcion et al. 2010; Quintanilla et al. 2017). It is thus nonindigenous from Florida, USA, to Santa Catarina, Brazil, as well as on some Atlantic islands (Galván-Villa and Ríos-Jara 2018), and on oil platforms off Gabon, Southeast Atlantic (Friedlander et al. 2014). In the Pacific, *C. riisei* has invaded the southern part of India, the Hawaiian Archipelago, and Tropical Eastern Pacific (Panamá, Colombia, and Ecuador—Quintanilla et al. 2017; Mexico—Galván-Villa and Ríos-Jara 2018). According to genetic evidence, the introduction to the Hawaiian Islands occurred from the Indo-Pacific, separately from its arrival to the Caribbean (Concepcion et al. 2010). Furthermore the Colombian Eastern Pacific invasion was probably derived from the Atlantic (Quintanilla et al. 2017).

In Hawaii, *C. riisei* was first reported in 1972 at Pearl Harbor. Since then, it has spread throughout the archipelago and heavily impacted MAFs. According to Grigg (2003), a survey of the Maui Black Coral Bed carried out in 2001 showed that up to 90% of *Antipathes dichotoma* Pallas, 1766, and *A. grandis* Verrill, 1928, colonies had been overgrown by the snowflake coral and died. They are commercially valuable species ($30 million) used to make precious coral jewelry (Grigg 2004). It is believed that epifauna provides a beachhead which *C. riisei* uses to settle on black corals; it then spreads vegetatively, its' stolons smothering the natives (Kahng and Grigg 2005), transforming the MAFs into "virtual graveyard for black coral" (Grigg 2003). Shallower, *C. riisei* was observed to overgrow other scleractinian plate corals (*Leptoseris* sp. and *Pavona* sp.), transforming the seascape into "an underwater "prairie" of white polyps" (Kahng and Grigg 2005). In Pacific Colombia *C. riisei* can overgrow the native octocoral fauna, such as the sea fans *Pacifigorgia* Bayer, 1951 and sea whips *Leptogorgia* Milne Edwards, 1857 on oceanic and coastal rocky reefs. In fact, large-scale mortality of native octocorals, particularly of *Pacifigorgia* spp. and *Muricea* spp., has been reported (Quintanilla et al. 2017), and at one site, >87% of octocorals [*Pacifigorgia* spp. and *Leptogorgia alba* (Duchassaing & Michelotti, 1864)] died as a result of *C. riisei* interaction (Sánchez and Ballesteros 2014).

According to Quintanilla et al. (2017), the invasive success of *C. riisei* is attributable to its fast stoloniferous growth mode, generalist filter-feeding behavior, few natural predators, and a symbiotic interaction with the sponge *D. anchorata* which has cytotoxic compounds (Calcinai et al. 2004). Kahng et al. (2008) further demonstrated that under favorable conditions *C. riisei* exhibits high polyp fecundity and has asynchronous, continuous spawning of gametes which may allow it to dominate ephemeral space through high and continuous production of larvae.

11 Conclusions, Perspectives, and Challenges for Future Research

The expansion of global trade will increase the number of marine biological invasions, and MAFs will be increasingly impacted by those species that create, modify, or exclude them. However we still know very little-to-nothing about invasive species and their impacts on MAFs in many deeper and less accessible systems, such as shallow-water, benthic communities in Antarctica (Aronson et al. 2007; Hughes et al. 2020), mesophotic reefs (Loya et al. 2019; Soares et al. 2019), and deep sea ecosystems in general (e.g., Galil et al. 2019), including hydrothermal vent communities. This may be because we know little about these systems or that they are less susceptible to invasion, or both. Whichever, these systems urgently need to be better addressed (Galil et al. 2019; Hughes et al. 2020).

We have difficulty and must also address how we recognize "deep invasions" in MAFs (Carlton 2009). Furthermore, we need to better distinguish which mechanisms create novel or modify existing MAFs, be they impacts of "traditional" biological invasions (jumps through barriers by vectors along pathways) or range expansions caused by human-induced change.

Global warming, particularly, has been predicted and/or has now resulted in the formation, modification, or exclusion of MAFs through poleward expansion of tropical and subtropical species toward temperate reefs (Greenstein and Pandolfi 2008; Burrows et al. 2011; Vergés et al. 2014; Takao et al. 2015; Canning-Clode and

Carlton 2017) and temperate species toward the poles (Aronson et al. 2007). An additional challenge is distinguishing these human-mediated range expansions from natural processes such as dispersal not mediated by human activities (Lonhart 2009). Further baseline studies of less well-known MAF systems, coupled with predictive modeling, are crucial to detect and forecast future ecosystem changes as a result of human-mediated range expansion and invasion.

Given the usual high diversity of interacting species they harbor, MAFs offer a natural laboratory for the study of the evolutionary effects on invasions in the marine realm. Studies of the invasive holobiont as a whole are currently incipient, but new, cheaper molecular tools should open up this field for future studies which will better understand the complex multiple mechanisms, including the chemical ecology, of the holobiont invasion. Understanding the history, pathways and vectors and the reproduction strategies of invasive MAF-forming species and those of invasive predators on native MAFs are crucial for developing methods for their control.

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References

Adler PB, HilleRislambers J, Levine JM (2007) A niche for neutrality. Ecol Lett 10:95–104. https://doi.org/10.1111/j.1461-0248.2006.00996.x

Aguin-Pombo D (2012) Biological invasions and global trade. In: Mendonca A, Cunha A, Chakrabarti R (eds) Natural resources, sustainability and humanity: a comprehensive view. Springer, Dordrecht, pp 83–99. https://doi.org/10.1007/978-94-007-1321-5_6

Ahyong S, Costello MJ, Galil BS, Gollasch S, Hutchings P, Katsanevakis S, Lejeusne C, Marchini A, Occhipinti A, Pagad S, Poore GCB, Rius M, Robinson TB, Sterrer W, Turon X, Willan RC, Zhan A (2019) World Register of Introduced Marine Species (WRiMS). http://www.marinespecies.org/introduced. Accessed 19 June 2019. https://doi.org/10.14284/347

Airoldi L, Rindi F, Cinelli F (1995) Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment influenced, rocky subtidal shore. Bot Mar 38:227–237

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367:233–238

Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Environ Biol Fish 96:1151–1157. https://doi.org/10.1007/s10641-011-9795-1

Andradi-Brown DA (2019) Invasive lionfish (*Pterois volitans* and *P. miles*): distribution, impact, and management. In: Loya Y, Puglise KA, Bridge TCL (eds) Mesophotic coral ecosystems. Springer International, Cham, pp 931–941. https://doi.org/10.1007/978-3-319-92735-0_48

Antizar-Ladislao B (2008) Environmental levels, toxicity and human exposure to tributyltin (TBT)-contaminated marine environment. A review. Environ Int 34:292–308. https://doi.org/10.1016/j.envint.2007.09.005

Aronson R, Thatje S, Clarke A, Peck LS, Blake DB, Wilga CD, Seible BA (2007) Climate change and invasibility of the Antarctic benthos. Annu Rev Ecol Evol Syst 3:129–154

Ashok AM, Schönberg CHL, Laju RL, Edwards JKM (2019) Coral-killing sponge *Terpios hoshinota* in Southeast India—bested by *Acropora muricata*? Mar Biodivers 49:1069–1070

Aslan CE, Sikes BA, Gedan KB (2015) Research on mutualisms between native and non-native partners can contribute critical ecological insights. NeoBiota 26:39–54. https://doi.org/10.3897/neobiota.26.8837

Ávila E, Carballo JL (2009) A preliminary assessment of the invasiveness of the Indo-Pacific sponge *Chalinula nematifera* on coral communities from the tropical eastern Pacific. Biol Invasions 11:257–264

Azzurro E, Stancanelli B, Di Martino V, Bariche M (2017) Range expansion of the common lionfish *Pterois miles* (Bennett, 1828) in the Mediterranean Sea: an unwanted new guest for Italian waters. BioInvasion Rec 6:95–98

Badreddine A, Milazzo M, Abboud-Abi SM, Bitar G, Mangialajo L (2019) Threatened biogenic formations of the Mediterranean: current status and assessment of the vermetid reefs along the Lebanese coastline (Levant basin). Ocean Coast Manag 169:137–146

Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. In: Gibson R, Atkinson R, Gordon J (eds) Oceanography and marine biology: an annual review. Taylor and Francis, pp 123–195

Ballesteros E, Sala E, Garrabou J, Zabala M (1998) Community structure and frond size distribution of a deep water stand of *Cystoseira spinosa* (Phaeophyta) in the northwestern Mediterranean. Eur J Phycol 33:121–128

Barbosa TM, Gomes PB, Bergeron AS, Santos AM, Chagas C, Freitas EMS, Perez CD (2014) Comparisons of sexual reproduction in *Carijoa riisei* (Cnidaria, Alcyonacea) in South Atlantic, Caribbean, and Pacific areas. Hydrobiologia 734:201–212. https://doi.org/10.1007/s10750-014-1893-6

Barrero-Canosa J, Dueñas LF, Sánchez JA (2012) Isolation of potential fungal pathogens in gorgonian corals at the tropical eastern Pacific. Coral Reefs 32:35–41. https://doi.org/10.1007/s00338-012-0972-2

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Bayer FM (1961) The shallow-water Octocorallia of the west Indian region. Stud Fauna Curaçao Caribbean Islands 12:1–373

Bednarik RG (1997) The earliest evidence of ocean navigation. Int J Naut Archaeol 26:183–191

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353

Bellwood DR, Robert Goatley CH (2017) Can biological invasions save Caribbean coral reefs? Curr Biol 27:R13–R14

Boudouresque CF, Blanfuné A, Harmelin-Vivien M, Personnic S, Ruitton S, Thibaut T, Verlaque M (2017) Where seaweed forests meet animal forests: the examples of macroalgae in coral reefs and the Mediterranean coralligenous ecosystem. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham, pp 369–396

Breves-Ramos A, Junqueira AOR, Lavrado HP, Silva SHG, Ferreira-Silva MAG (2010) Population structure of the invasive bivalve *Isognomon bicolor* on rocky shores of Rio de Janeiro state (Brazil). J Mar Biol Assoc UK 90(3):453–459

Bruschetti M, Luppi T, Fanjul E, Rosenthal A, Iribarne O (2008) Grazing effect of the invasive reef-forming polychaete *Ficopomatus enigmaticus* (Fauvel) on phytoplankton biomass in a SW Atlantic coastal lagoon. J Exp Mar Biol Ecol 354(2):212–219. https://doi.org/10.1016/j.jembe.2007.11.009

Bruschetti CM, Bazterrica C, Fanjul E, Luppi T, Iribarne O (2011) Effect of biodeposition of an invasive polychaete on organic matter content and productivity of the sediment in a coastal lagoon. J Sea Res 66(1):20–28. https://doi.org/10.1016/j.seares.2011.04.007

Bulleri F, Balata D, Bertocci I, Tamburello L, Benedetti-Cecchi L (2010) The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. Ecology 91:2205–2212

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM et al (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science 334:652–655

Calcinai B, Bavestrello G, Cerrano C (2004) Dispersal and association of two alien species in the Indonesian coral reefs: the octocoral *Carijoa riisei* and the demosponge *Desmapsamma anchorata*. J Mar Biol Assoc UK 84:937–941

Canning-Clode J, Carlton JT (2017) Refining and expanding global climate change scenarios in the sea: Poleward creep complexities, range termini, and setbacks and surges. Divers Distrib 23:463–473

Capel KC, Migotto AE, Zilberberg C, Kitahara MV (2014) Another tool towards invasion? Polyp bail-out in *Tubastraea coccinea*. Coral Reefs 33:1165. https://doi.org/10.1007/s00338-014-1200-z

Capel KCC, Toonen RJ, Rachid CTCC, Creed JC, Kitahara MV, Forsman Z, Zilberberg C (2017) Clone wars:asexual reproduction dominates in the invasive range of *Tubastraea* spp. (Anthozoa: Scleractinia) in the South-Atlantic Ocean. PeerJ 5:e3873

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water oceanography. Mar Biol 23:313–371

Carlton JT (2009) Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 13–56

Carlton JT, Fowler AE (2018) Ocean rafting and marine debris: a broader vector menu requires a greater appetite for invasion biology research support. Aquat Invasions 13:11–15

Carlton JT, Newman WA, Pitombo FB (2011) Barnacle invasions: introduced, cryptogenic, and range expanding cirripedia of north and South America. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place – Alien Marine Crustaceans: distribution, biology and impacts. Springer, Dordrecht, pp 159–213. https://doi.org/10.1007/978-94-007-0591-3

Carlton JT, Chapman JW, Geller JB, Miller JA, Carlton DA, McCuller MI, Treneman NC, Steves BP, Ruiz GM (2017) Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. Science 357:1402–1406

Caro AU, Guiñez R, Ortiz V, Castilla JC (2011) Competition between a native mussel and a non-indigenous invader for primary space on intertidal rocky shores in Chile. Mar Ecol Prog Ser 428:177–185. https://doi.org/10.3354/meps09069

Castilla JC, Collins AG, Meyer CP, Guiñez R, Lindberg DR (2002) Recent introduction of the dominant tunicate, Pyura praeputialis (Urochordata, Pyuridae) to Antofagasta, Chile. Mol Ecol 11(8):1579–1584

Caswell H (1978) Predator-mediated coexistence: a nonequilibrium model. Am Nat 112:127–154

Cebrian E, Linares C, Marschal C, Garrabou J (2012) Exploring the effects of invasive algae on the persistence of gorgonian populations. Biol Invasions 14:2647–2656. https://doi.org/10.1007/s10530-012-0261-6

Cerda M, Castilla JC (2002) Diversity and biomass of macro-invertebrates in intertidal matrices of the tunicate *Pyura praeputialis* (Heller, 1878) in the Bay of Antofagasta, Chile. Rev Chilena Hist Nat 74:841–853

Chan FT, Briski E (2017) An overview of recent research in marine biological invasions. Mar Biol 164:121. https://doi.org/10.1007/s00227-017-3155-4

Chandrasekaran S, Nagendran NA, Pandiaraja D, Krishnankutty N (2008) Bioinvasion of *Kappaphycus alvarezii* on corals in the Gulf of Mannar, India. Curr Biol 94:1167–1172

Chapman D, Ranelletti M, Kaushik S (2006) Invasive marine algae: an ecological perspective. Bot Ver 72:153–178

Charles M, Faillettaz R, Desroy N, Fournier J, Costil K (2018) Distribution, associated species and extent of biofouling “reefs” formed by the alien species *Ficopomatus enigmaticus* (Annelida, Polychaeta) in marinas. Estuar Coast Shelf Sci 212:164–175. https://doi.org/10.1016/j.ecss.2018.07.007

Cheng BS, Ruiz GM, Altieri AH, Torchin ME (2019) The biogeography of invasion in tropical and temperate seagrass beds: testing interactive effects of predation and propagule pressure. Divers Distrib 25:285–297

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Çinar ME (2013) Alien polychaete species worldwide: current status and their impacts. J Mar Biol Assoc UK 93(5):1257–1278. https://doi.org/10.1017/S0025315412001646

Coles SL, Bolick H (2007) Invasive introduced sponge *Mycale grandis* overgrows reef corals in Kāne'ohe Bay, O'ahu, Hawai'i. Coral Reefs 26:911–911

Colín García N, Campos J, Tello Musi J, Perez España H, Carrara X (2018) First record of the invasive coral *Oculina patagonica* (Cnidaria, Scleractinian) in the Gulf of Mexico. Check List 14:613–617

Concepcion G, Kahng S, Crepeau M, Franklin E, Coles S, Toonen R (2010) Resolving natural ranges and marine invasions in a globally distributed octocoral (genus *Carijoa*). Mar Ecol Prog Ser 401:113–127

Conversi A, Dakos V, Gårdmark A, Ling S, Folke C, Mumby PJ et al (2015) A holistic view of marine regime shifts. Philos Trans R Soc B: Biol Sci 370:20130279

Coppari M, Mestice F, Betti F, Bavestrello G, Castellano L, Bo M (2019) Fragmentation, re-attachment ability and growth rate of the Mediterranean black coral *Antipathella subpinnata*. Coral Reefs 38:1–14. https://doi.org/10.1007/s00338-018-01764-7

Creed JC (2006) Two invasive alien azooxanthellate corals, Tubastraea coccinea and Tubastraea tagusensis, dominate the native zooxanthellate Mussismilia hispida in Brazil. Coral Reefs 25:350–350. https://doi.org/10.1007/s00338-006-0105-x

Creed JC, Fenner D, Sammarco P, Cairns S, Capel K, Junqueira AOR, Cruz I, Miranda RJ, Carlos-Junior L, Mantelatto MC, Oigman-Pszczol S (2017) The invasion of the azooxanthellate coral *Tubastraea* (Scleractinia: Dendrophylliidae) throughout the world: history, pathways and vectors. Biol Invasions 19:283–305

Crisci C, Bensoussan N, Romano JC, Garrabou J (2011) Temperature anomalies and mortality events in marine communities: insights on factors behind differential mortality impacts in the NW Mediterranean. PLoS One 6(9):e23814

Cronin G (2001) Resource allocation in seaweeds and marine invertebrates: chemical defense patterns in relation to defense theories. In: McClintock, Baker (eds) Marine chemical ecology. CRC, Boca Raton (EUA), pp 325–353

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar Ecol Prog Ser 162:137–152

Crooks JA (2001) Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. Biol Invasions 3:23–36

Crooks JA (2009) The role of exotic marine ecosystem engineers. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 287–304

Crooks JA, Khim HS (1999) Architectural vs. biological effects of habitat-altering, exotic mussel, *Musculista senhousia*. J Exp Mar Biol Ecol 240:53–75

Cruz ICS, Kikuchi RKP, Longo LL, Creed JC (2015) Evidence of a phase shift to *Epizoanthus gabrieli* Carlgreen, 1951 (Order Zoanthidea) and loss of coral cover on reefs in the Southwest Atlantic. Mar Ecol 36:318–325

Daleo P, Alberti J, Iribarne O (2009) Biological invasions and the neutral theory. Divers Distrib 15:547–553. https://doi.org/10.1111/j.1472-4642.2009.00576.x

Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, Fautin DG, France SC, McFadden CS, Opresko DM, Rodriguez E (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa 1668:127–182

Davies BR, Stuart V, de Villiers M (1989) The filtration activity of a serpulid polychaete population (*Ficopomatus enigmaticus* (Fauvel)) and its effects on water quality in a coastal marina. Estuar Coast Shelf Sci 29(6):613–620. https://doi.org/10.1016/0272-7714(89)90014-0

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Davis AR, Walls K, Jeffs A (2018) Biotic consequences of a shift in invertebrate ecosystem engineers: invasion of New Zealand rocky shores by a zone-forming ascidian. Mar Ecol 39 (3):e12502. https://doi.org/10.1111/maec.12502

de Caralt S, Cebrian E (2013) Impact of an invasive alga (*Womersleyella setacea*) on sponge assemblages: compromising the viability of future populations. Biol Invasions 15:1591–1600. https://doi.org/10.1007/s10530-012-0394-7

de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342:108–110

Di Camillo CG, Bavestrello G, Cerrano C, Gravili C, Piraino S, Puce S, Boero F (2017) Hydroids (Cnidaria, Hydrozoa): a neglected component of animal forests. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham, pp 397–427

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496

Domaneschi O, Martins CM (2002) *Isognomon bicolor* (C. B. Adams) (Bivalvia, Isognomonidae): primeiro registro para o Brasil, redescrição da espécie e considerações sobre a ocorrência e distribuição de *Isognomon* na costa brasileira. Rev Bras Zool 19(2):611–627

Elton C (1958) The ecology of invasions by animal and plants. Methuen, London

Escapa CM, Isacch JP, Daleo P, Alberti J, Iribarne OO, Borges ME, Dos Santos EP, Gagliardini DA, Lasta M (2004) The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. J Shellfish Res 23:765–772

Ferreira CEL, Junqueira AOR, Villac MC, Lopes RM (2009) Marine bioinvasions in the Brazilian coast: brief report on history of events, vectors, ecology, impacts and management of non-indigenous species. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 459–478

Figueroa DF, McClure A, Figueroa NJ, Hicks DW (2019) Hiding in plain sight: invasive coral *Tubastraea tagusensis* (Scleractinia:Hexacorallia) in the Gulf of Mexico. Coral Reefs. https://doi.org/10.1007/s00338-019-01807-7

Fine M, Zibrowius H, Loya Y (2001) *Oculina patagonica*: a non-lessepsian scleractinian coral invading the Mediterranean Sea. Mar Biol 138:1195–1203

Fine M, Aluma Y, Meroz-Fine E, Abelson A, Loya Y (2005) *Acabaria erythraea* (Octocorallia: Gorgonacea) a successful invader to the Mediterranean Sea? Coral Reefs 24:161–164

Fine M, Tsadok R, Meron D, Cohen S, Milazzo M (2017) Environmental sensitivity of *Neogoniolithon brassica-florida* associated with vermetid reefs in the Mediterranean Sea. ICES J Mar Sci 74:1074–1082

Fleury BG, Lages BG, Barbosa JP, Kaiser CR, Pinto AC (2008) New hemiketal steroid from introduced soft coral *Chromonephthea braziliensis* is a chemical defense against predatory fishes. J Chem Ecol 34:987–993. https://doi.org/10.1007/s10886-008-9499-y

Freestone AL, Ruiz GM, Torchin ME (2013) Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. Ecology 94:1370–1377

Fridley JD, Brown RL, Bruno JF (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. Ecology 85:3215–3222. https://doi.org/10.1890/03-0676

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Holle ABV (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. https://doi.org/10.1890/0012-9658

Friedlander AM, Ballesteros E, Fay M, Sala E (2014) Marine communities on oil platforms in Gabon, West Africa: high biodiversity oases in a low biodiversity environment. PLoS One 9: e103709

Galil BS, Marchini A, Occhipinti-Ambrogi A (2018) East is east and west is west? Management of marine bioinvasions in the Mediterranean Sea. Estuar Coast Shelf Sci 201:7–16

Galil BS, Danovaro R, Rothman SBS, Gevili R, Goren M (2019) Invasive biota in the deep-sea Mediterranean: an emerging issue in marine conservation and management. Biol Invasions 21:281–288

Galván-Villa CM, Ríos-Jara E (2018) First detection of the alien snowflake coral *Carijoa riisei* (Duchassaing and Michelotti, 1860) (Cnidaria: Alcyonacea) in the port of Manzanillo in the Mexican Pacific. Bioinvasions Rec 7:1–6

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M et al (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Chang Biol 15:1090–1103

Gavira-O'Neill K, Guerra-García JM, Moreira J, Ros M (2018) Mobile epifauna of the invasive bryozoan *Tricellaria inopinata*: is there a potential invasional meltdown? Mar Biodivers 48 (2):1169–1178. https://doi.org/10.1007/s12526-016-0563-5

Gollasch S, Galil BS, Cohen AN (eds) (2006) Bridging divides: maritime canals as invasion corridors, vol 83. Monographiae Biologicae. Springer Science & Business Media, Cham, 316 pp. https://doi.org/10.1007/978-1-4020-5047-3

González-Duarte MM, Megina C, López-González PJ, Galil B (2016) Cnidarian alien species in expansion. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, past, present and future: the world of medusa and her sisters. Springer International, Cham, pp 139–160

Gonzalez-Zapata FL, Bongaerts P, Ramírez-Portilla C et al (2018a) Holobiont diversity in a reef-building coral over its entire depth range in the mesophotic zone. Front Mar Sci 5. https://doi.org/10.3389/fmars.2018.00029

Gonzalez-Zapata FL, Gómez-Osorio S, Sánchez JA (2018b) Conspicuous endolithic algal associations in a mesophotic reef-building coral. Coral Reefs 37:705–709

Gori A, Bavestrello G, Grinyó J, Dominguez-Carrió C, Ambroso S, Bo M (2017) Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham, pp 207–223

Grabowski JH, Peterson CH, Powers SP, Gaskill D, Summerson H (2004) Growth and survivorship of non-native (*Crassostrea gigas* and *Crassostrea ariakensis*) versus native eastern oysters (*Crassostrea virginica*). J Shellfish Res 23:781–793

Granados C, Camargo C, Zea S, Sánchez JA (2008) Phylogenetic relationships among zooxanthellae (*Symbiodinium*) associated to excavating sponges (*Cliona* spp.) reveal an unexpected lineage in the Caribbean. Mol Phylogenet Evol 49:554–560. https://doi.org/10.1016/j.ympev.2008.07.023

Gravili C, D'Ambrosio P, Di Camillo C, Renna G, Bouillon J, Boero F (2008) *Clytia hummelincki* (Hydroidomedusae: Leptomedusae) in the Mediterranean Sea. J Mar Biol Assoc UK 88:1547–1553

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS One 7:e32596

Greenstein BJ, Pandolfi JM (2008) Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. Glob Chang Biol 14:513–528

Greff S, Aires T, Serrão EA, Engelen AH, Thomas OP, Pérez T (2017) The interaction between the proliferating macroalga *Asparagopsis taxiformis* and the coral *Astroides calycularis* induces changes in microbiome and metabolomic fingerprints. Sci Rep 7:42625. https://doi.org/10.1038/srep42625

Gribben PE, Wright JT (2006) Sublethal effects on reproduction in native fauna?: are females more vulnerable to biological invasion? Oecologia 149:352–361. https://doi.org/10.1007/s00442-006-0452-x

Gribben PE, Wright JT, Connor WAO, Doblin MA, Eyre B, Steinberg PD (2009) Reduced performance of native infauna following recruitment to a habitat-forming invasive marine alga. Oecologia 158:733–745. https://doi.org/10.1007/s00442-008-1181-0

Gribben PE, Byers JE, Wright JT, Glasby TM (2013) Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. Oikos 122:816–824. https://doi.org/10.1111/j.1600-0706.2012.20868.x

Grigg R (2003) Invasion of a deep black coral bed by an alien species, *Carijoa riisei*, off Maui, Hawaii. Coral Reefs 22:121–122

Grigg RW (2004) Harvesting impacts and invasion by an alien species decrease estimates of black coral yield off Maui, Hawai'i. Pac Sci 58:1–6

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22–27. https://doi.org/10.1016/S0169-5347(01)02358-8

Grosholz ED, Ruiz GM (2003) Biological invasions drive size increases in marine and estuarine invertebrates. Ecol Lett 6:700–705

Grossowicz M, Shemesh E, Martinez S, Benayahu Y, Tchernov D (2020) New evidence of *Melithaea erythraea* colonization in the Mediterranean. Estuar Coast Shelf Sci 236:106652

Guardiola M, Frotscher J, Uriz MJ (2012) Genetic structure and differentiation at a short-time scale of the introduced calcarean sponge *Paraleucilla magna* to the western Mediterranean. Hydrobiologia 687:71–84

Guy-Haim T, Lyons DA, Kotta J, Ojaveer H, Queirós AM, Chatzinikolaou E, Arvanitidis C, Como S, Magni P, Blight AJ, Orav-Kotta H, Somerfield PJ, Crowe TP, Rilov G (2018) Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. Glob Chang Biol 24:906–924

Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA et al (2012) Effects of climate change on global seaweed communities. J Phycol 48:1064–1078

Häussermann V, Spano C, Thiel M, Lohrmann KB (2015) First record of the sea anemone *Diadumene lineata* (Verrill, 1869) from the Chilean coast. Spixiana 38:39–42

Hay ME (2009) Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. Annu Rev Mar Sci 1:193–212

Hay ME, Fenical W (1996) Chemical ecology and marine biodiversity: insights and products from the sea. Oceanography 9:10–20

Hebbeln D, Portilho-Ramos RC, Wienberg C, Titschack J (2019) The fate of cold-water corals in a changing world: a geological perspective. Front Mar Sci 6:119. https://doi.org/10.3389/fmars.2019.00119

Heintz T, Laboute PA (2020) Monospecific aggregation of free-living mushroom corals derived from asexual and sexual reproduction in New Caledonia. Mar Biodivers 50:13

Hentschel U, Horn M, Friedrich AB, Wagner M, Moore BS, Hopke J, Horn M, Friedrich AB, Wagner M, Hacker J et al (2002) Molecular evidence for a uniform microbial community in sponges from different oceans. Appl Environ Microbiol 68:4431–4440

Hewitt CL (2002) Distribution and biodiversity of Australian tropical marine bioinvasions. Pac Sci 56:213–222

Hewitt CL, Gollasch S, Minchin D (2009) The vessel as a vector – biofouling, ballast water and sediments. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 117–131. https://doi.org/10.1007/978-3-540-79236-9_6

Hewitt JE, Norkko J, Kauppi L, Villnäs A, Norkko A (2016) Species and functional trait turnover in response to broad-scale change and an invasive species. Ecosphere 7(3):e01289. https://doi.org/10.1002/ecs2.1289/full

Hicks DW, Tunnell JW (1993) Invasion of the South Texas coast by the edible brown mussel *Perna perna* (Linnaeus, 1758). Veliger 36:92–94

Hill M, Allenby A, Ramsby B et al (2011) *Symbiodinium* diversity among host clionaid sponges from Caribbean and Pacific reefs: evidence of heteroplasmy and putative host-specific symbiont lineages. Mol Phylogenet Evol 59:81–88. https://doi.org/10.1016/j.ympev.2011.01.006

Hodgins KA, Bock DG, Rieseberg LH (2018) Trait evolution in invasive species. Annu Plant Rev Online 1:1–37

Hoeksema BW (2004) Impact of budding on free-living corals at East Kalimantan, Indonesia. Coral Reefs 23:492. https://doi.org/10.1007/s00338-004-0402-1

Hoeksema BW (2012) Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde shelf, South Sulawesi. Raffles Bull Zool 60:183–212

Hoeksema BW, Benzoni F (2013) Multispecies aggregations of mushroom corals in the Gambier Islands, French Polynesia. Coral Reefs 32:1041

Hoeksema BW, Gittenberger A (2010) High densities of mushroom coral fragments at West Halmahera, Indonesia. Coral Reefs 29:691

Hoeksema BW, Bouwmeester J, Range P, Ben-Hamadou R (2018) A large aggregation of self-fragmenting mushroom corals in the Arabian/Persian Gulf. Ecology 99(5):1236–1238

Hoeksema BW, Giyanto, Suharsono (2019) The role of maximum shelf depth versus distance from shore in explaining a diversity gradient of mushroom corals (Fungiidae) off Jakarta. Diversity 11:46

Holloway MG, Keough MJ (2002) An introduced polychaete affects recruitment and larval abundance of sessile invertebrates. Ecol Appl 12(6):1803–1823

Hopkins GA, Forrest BM (2010) Challenges associated with pre-border management of biofouling on oil rigs. Mar Pollut Bull 60:1924–1929

Hubbell SP (2001) MacArthur and Wilson's radical theory. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ, pp 3–29

Hughes KA, Pescott OL, Peyton J, Adriaens T, Cottier-Cook EJ, Key G, Rabitsch W, Tricarico E, Barnes DKA, Baxter N, Belchier M, Blake D, Convey P, Dawson W, Frohlich D, Gardiner LM, González-Moreno P, James R, Malumphy C, Martin S, Martinou AF, Minchin D, Monaco A, Moore N, Morley SA, Ross K, Shanklin J, Turvey K, Vaughan D, Vaux AGC, Werenkraut V, Winfield IJ, Roy HE (2020) Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. Glob Change Biol. https://doi.org/10.1111/gcb.14938

Ingrosso G, Abbiati M, Badalamenti F, Bavestrello G, Belmonte G, Cannas R, Benedetti-Cecchi L et al (2018) Mediterranean bioconstructions along the Italian coast. Adv Mar Biol 79:61–136

Johnson CH, Winston JE, Woollacott RM (2012) Western Atlantic introduction and persistence of the marine bryozoan *Tricellaria inopinata*. Aquat Invasions 7(3):295–303. https://doi.org/10.3391/ai.2012.7.3.001

Jung V, Thibaut T, Meinesz A, Pohnert G (2002) Comparison of the wound-activated transformation of caulerpenyne by invasive and noninvasive *Caulerpa* species of the Mediterranean. J Chem Ecol 28:2091–2105

Kado R (2003) Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Mar Ecol Prog Ser 249:199–206

Kahng SE, Grigg RW (2005) Impact of an alien octocoral, *Carijoa riisei*, on black corals in Hawaii. Coral Reefs 24:556–562

Kahng SE, Benayahu Y, Wagner D, Rothe N (2008) Sexual reproduction in the invasive octocoral *Carijoa riisei* in Hawaii. Bull Mar Sci 82:1–17

Kauppi L, Bernard G, Bastrop R, Norkko A, Norkko J (2018) Increasing densities of an invasive polychaete enhance bioturbation with variable effects on solute fluxes. Sci Rep 8(7619):1–12. https://doi.org/10.1038/s41598-018-25989-2

Kauppi L, Norkko A, Norkko J (2015) Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes Marenzelleria spp. in the Baltic Sea. Biol Invasions 17(7):2055–2074. https://doi.org/10.1007/s10530-015-0860-0

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Keppel E, Tovar-Hernández MA, Ruiz G (2015) First record and establishment of *Branchiomma coheni* (Polychaeta: Sabellidae) in the Atlantic Ocean and review of non-indigenous species of the genus. Zootaxa 4058(4):499–518. https://doi.org/10.11646/zootaxa.4058.4.3

Kersting DK, Cebrian E, Casado C, Teixidó N, Garrabou J, Linares C (2015) Experimental evidence of the synergistic effects of warming and invasive algae on a temperate reef-builder coral. Sci Rep 5:1–8. https://doi.org/10.1038/srep18635

Kimmerer WJ, Gartside E, Orsi JJ (1994) Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Mar Ecol Prog Ser 113:81–94

Kwong WK, del Campo J, Mathur V et al (2019) A widespread coral-infecting apicomplexan with chlorophyll biosynthesis genes. Nature 568:103

Kramarsky-Winter E, Fine M, Loya Y (1997) Coral polyp expulsion. Nature 387:137

Lages BG, Fleury BG, Ferreira CEL, Pereira RC (2006) Chemical defense of an exotic coral as invasion strategy. J Exp Mar Biol Ecol 328:127–135

Lages BG, Fleury BG, Hovel AMC, Rezende CM, Pinto AC, Creed JC (2012) Proximity to competitors changes secondary metabolites of non-indigenous cup corals, *Tubastraea* spp., in the Southwest Atlantic. Mar Biol 159:1551–1559. https://doi.org/10.1007/s00227-012-1941-6

Lages BG, Fleury BG, Menegola C, Creed JC (2011) Change in tropical rocky shore communities due to an alien coral invasion. Mar Ecol Prog Ser 438:85–96. https://doi.org/10.3354/meps09290

Lages BG, Fleury BG, Pinto AC, Creed JC (2010) Chemical defenses against generalist fish predators and fouling organisms in two invasive ahermatypic corals in the genus *Tubastraea*. Mar Ecol 31:473–482. https://doi.org/10.1111/j.1439-0485.2010.00376.x

LaJeunesse TC, Lee S, Bush S, Bruno JF (2005) Persistence of non-caribbean algal symbionts in Indo-Pacifc mushroom corals released to Jamaica 35 years ago. Coral Reefs 24:157–159

LaJeunesse TC, Parkinson JE, Gabrielson PW et al (2018) Systematic revision of symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol 28:2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008

Laverick JH, Piango S, Andradi-Brown DA, Exton DA, Bongaerts P, Bridge TCL et al (2018) To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. Environ Evid 7:15. https://doi.org/10.1186/s13750-016-0068-5

Lee CE (2002) Evolutionary genetics of invasive species. Trends Ecol Evol 17:386–391. https://doi.org/10.1016/S0169-5347(02)02554-5

Leppäkoski E, Olenin S (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biol Invasions 2:151–163. https://doi.org/10.1023/A:1010052809567

Lesser MP, Slattery M (2011) Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biol Invasions 13:1855–1868. https://doi.org/10.1007/s10530-011-0005-z

Li H, Zhang X, Zheng R et al (2014) Indirect effects of non-native *Spartina alterniflora* and its fungal pathogen (*Fusarium palustre*) on native saltmarsh plants in China. J Ecol 102:1112–1119. https://doi.org/10.1111/1365-2745.12285

Longo C, Mastrototaro F, Corriero G (2007) Occurrence of *Paraleucilla magna* (Porifera: Calcarea) in the Mediterranean Sea. J Mar Biol Assoc UK 87:1749–1755

Lonhart SI (2009) Natural change and climate change mediated invasions. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 57–69

López C, Clemente S, Moreno S, Ocaña O, Herrera R, Moro L, Monterroso O, Rodríguez A, Brito A (2019) Invasive *Tubastraea* spp. and *Oculina patagonica* and other introduced scleractinian corals in the Santa Cruz de Tenerife (Canary Islands) harbor: ecology and potential risks. Reg Stud Mar Sci 29:100713

Lowe SJ, Browne M, Boudjelas S (2000) 100 of the World's worst invasive alien species. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland

Loya Y, Puglise KA, Bridge TCL (eds) (2019) Mesophotic coral ecosystems, vol 12. Coral reefs of the world. Springer International, Cham. https://doi.org/10.1007/978-3-319-92735-0

Lützen J (1999) *Styela clava* Herdman (Urochordata, Ascidiacea), a successful immigrant to North West Europe: ecology, propagation and chronology of spread. Helgoländer Meeresun 52:383–391. https://doi.org/10.1007/BF02908912

Luz BLP, Capel KCC, Zilberberg C, Flores AAV, Migotto AE, Kitahara MV (2018) A polyp from nothing: the extreme regeneration capacity of the Atlantic invasive sun corals *Tubastraea coccinea* and *T. tagusensis* (Anthozoa, Scleractinia). J Exp Mar Biol Ecol 503:60–65. https://doi.org/10.1016/j.jembe.2018.02.002

Luz BLP, Kitahara MV (2017) Could the invasive scleractinians *Tubastraea coccinea* and *T. tagusensis* replace the dominant zoantharian *Palythoa caribaeorum* in the Brazilian subtidal? Coral Reefs 36:875. https://doi.org/10.1007/s00338-017-1578-5

MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. J Ecol 97:609–615. https://doi.org/10.1111/j.1365-2745.2009.01514.x

Mantelatto MC, Silva AG, Louzada TS, McFadden CS, Creed JC (2018) Invasion of aquarium origin soft corals on a tropical rocky reef in the Southwest Atlantic, Brazil. Mar Pollut Bull 130:84–94

Mantelatto MC, Creed JC (2015) Non-indigenous sun corals invade mussel beds in Brazil. Mar Biodivers 45:605–606

Marbà N, Jordà G, Agustí S, Girard C, Duarte CM (2015) Footprints of climate change on Mediterranean Sea biota. Front Mar Sci 2:56

Martinez JA, Smith CM, Richmond RH (2012) Invasive algal mats degrade coral reef physical habitat quality. Estuar Coast Shelf Sci 99:42–49. https://doi.org/10.1016/j.ecss.2011.12.022

Mastrototaro F, Chimienti G, Matarrese A, Gambi MC, Giangrande A (2015) Growth and population dynamics of the non-indigenous species *Branchiomma luctuosum* Grube (Annelida, Sabellidae) in the Ionian Sea (Mediterranean Sea). Mar Ecol 36(3):517–529. https://doi.org/10.1111/maec.12160

McFadden CS (1997) Contributions of sexual and asexual reproduction to population structure in the clonal soft coral, *Alcyonium rudyi*. Evolution 51:112–126. https://doi.org/10.1111/j.1558-5646.1997.tb02393.x

Mclean EL, Rützler K, Pooler PS (2015) Competing for space: factors that lead to sponge overgrowth when interacting with octocoral. Open J Mar Sci 5:64–80

McQuaid KA, Griffiths CL (2014) Alien reef-building polychaete drives long-term changes in invertebrate biomass and diversity in a small, urban estuary. Estuar Coast Shelf Sci 138:101–106. https://doi.org/10.1016/j.ecss.2013.12.016

Mercer JM, Whitlach RB, Osman RW (2009) Potential effects of the invasive colonial ascidian (*Didemnum vexillum* Kott, 2002) on pebble-cobble bottom habitats in Long Island Sound, USA. Aquat Invasions 4(1):133–142. https://doi.org/10.3391/ai.2009.4.1.14

Milazzo M, Fine M, La Marca EC, Alessi C, Chemello R (2017) Drawing the line at neglected marine ecosystems: ecology of vermetid reefs in a changing ocean. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer, Cham, 345–367 pp

Minchin D, Gollasch S, Cohen AN, Hewitt CL, Olenin S (2009) Characterizing vectors of marine invasion. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems ecological, management, and geographic perspectives. Ecological studies, vol 204. Springer, Berlin, pp 109–116. https://doi.org/10.1007/978-3-540-79236-9_5

Miranda RJ, Coleman MA, Tagliafico A, Rangel MS, Mamo LT, Barros F, Kelaher BP (2019) Invasion-mediated effects on marine trophic interactions in a changing climate: positive feedbacks favour kelp persistence. Proc R Soc B 286:1–7

Miranda RJ, Cruz ICS, Barros F (2016) Effects of the alien coral *Tubastraea tagusensis* on native coral assemblages in a southwestern Atlantic coral reef. Mar Biol 163:45. https://doi.org/10.1007/s00227-016-2819-9

Mito T, Uesugi T (2004) Invasive alien species in Japan: the status quo and the new regulation for prevention of their adverse effects. Glob Environ Res 8:171–193

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Natl Acad Sci 98:5446–5451. https://doi.org/10.1073/pnas.091093398

Moreno TR, Rocha RM (2006) Associated fauna with *Eudistoma carolinense* (Tunicata, Ascidiacea) compared with other biological substrates with different architectures. J Coast Res SI 39:1695–1699

Morris JA, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environ Biol Fish 86:389

Muller-Parker G, D'Elia CF, Cook CB (2015) Interactions between coral and their symbiotic algae. In: Birkeland C (ed) Coral reefs in the Anthropocene. Springer, Dordrecht, pp 99–116. https://doi.org/10.1007/978-94-017-7249-5_5

Muñoz J, Page M, McDonald JI, Bridgwood SD (2015) Aspects of the growth and reproductive ecology of the introduced ascidian *Didemnum perlucidum* (Monniot, 1983) in Western Australia. Aquat Invasions 10:265–274. https://doi.org/10.3391/ai.2015.10.3.02

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563

Murray A, Keable SJ (2013) First report of *Sabella spallanzanii* (Gmelin, 1791) (Annelida: Polychaeta) from Botany Bay, New South Wales, a northern range extension for the invasive species within Australia. Zootaxa 3670(3):394–395

Needles LA, Wendt DE (2013) Big changes to a small bay: introduced species and long-term compositional shifts to the fouling community of Morro Bay (CA). Biol Invasions 15:1231–1251. https://doi.org/10.1007/s10530-012-0362-2

Occhipinti-Ambrogi A, Savini D (2003) Biological invasions as a component of global change in stressed marine ecosystems. Mar Pollut Bull 46:542–551

Ogburn D, White I, Mcphee D (2007) The disappearance of oyster reefs from eastern Australian estuaries – impact of colonial settlement or mudworm invasion? Coast Manag 35 (2–3):271–287. https://doi.org/10.1080/08920750601169618

Ojaveer H et al (2018) Historical baselines in marine bioinvasions: implications for policy and management. PLoS One 13:e0202383. https://doi.org/10.1371/journal.pone.0202383

Padilla DK, Williams SL (2004) Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Front Ecol Environ 2:131–138

Pawlik JR, Loh T-L, McMurray SE (2018) A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what's old, what's new, and future directions. PeerJ 6:e4343

Paula AF, Creed JC (2004) Two species of the coral *Tubastraea* (Cnidaria, Scleractinia) in Brazil: a case of accidental introduction. Bull Mar Sci 74:175–183

Paula AF, Fleury BG, Lages BG, Creed JC (2017) Experimental evaluation of the effects of management of invasive corals on native communities. Mar Ecol Prog Ser 572:141–154

Paula AF, Pires DO, Creed JC (2014) Reproductive strategies of two invasive sun corals (*Tubastraea* spp.) in the southwestern Atlantic. J Mar Biol Assoc UK 94:481–492. https://doi.org/10.1017/S0025315413001446

Pereyra PJ, Narvarte M, Tatián M, González R (2015) The simultaneous introduction of the tunicate *Styela clava* (Herdman, 1881) and the macroalga *Undaria pinnatifida* (Harvey) Suringar, 1873, in northern Patagonia. BioInvasions Rec 4:179–184

Pettay DT, Wham DC, Smith RT et al (2015) Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. Proc Natl Acad Sci 112:7513–7518. https://doi.org/10.1073/pnas.1502283112

Piazzi L, Pardi G, Balata D, Cecchi E, Cinelli F (2002) Seasonal dynamics of a subtidal North-Western Mediterranean macroalgal community in relation to depth and substrate inclination. Bot Mar 45:243–252

Pisut DP, Pawlik JR (2002) Anti-predatory chemical defenses of ascidians: secondary metabolites or inorganic acids? J Exp Mar Biol Ecol 270:203–214

Potts DC (1983) Evolutionary disequilibrium among Indo-Pacific corals. Bull Mar Sci 33:619–632

Potts DC (1984) Generation times and the quaternary evolution of reef-building corals. Paleobiology 10:48–58

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59:779–791

Qian P-Y, Chen L, Xu Y (2013) Mini-review: molecular mechanisms of antifouling compounds. Biofouling 29:381–400. https://doi.org/10.1080/08927014.2013.776546

Quintanilla E, Ramírez-Portilla C, Adu-Oppong B et al (2018) Local confinement of disease-related microbiome facilitates recovery of gorgonian sea fans from necrotic-patch disease. Sci Rep 8:14636. https://doi.org/10.1038/s41598-018-33007-8

Quintanilla E, Wilke T, Ramírez-Portilla C, Sarmiento A, Sánchez JA (2017) Taking a detour: invasion of an octocoral into the tropical Eastern Pacific. Biol Invasions 19:2583–2597

Ramsay-Newton C, Drouin A, Hughes AR, Bracken MES (2016) Species, community, and ecosystem-level responses following the invasion of the red alga *Dasysiphonia japonica* to the western North Atlantic Ocean. Biol Invasions 19:537–547. https://doi.org/10.1007/s10530-016-1323-y

Ramsby BD, Hill MS, Thornhill DJ et al (2017) Sibling species of mutualistic *Symbiodinium* clade G from bioeroding sponges in the western Pacific and western Atlantic oceans. J Phycol 53:951–960. https://doi.org/10.1111/jpy.12576

Read GB, Inglis G, Stratford P, Ahyong ST (2011) Arrival of the alien fanworm *Sabella spallanzanii* (Gmelin, 1791) (Polychaeta: Sabellidae) in two New Zealand harbours. Aquat Invasions 6(3):273–279. https://doi.org/10.3391/ai.2011.6.3.04

Reise K, Buschbaum C, Büttger H, Wegner KM (2017) Invading oysters and native mussels: from hostile takeover to compatible bedfellows. Ecosphere. 8(9):e01949

Reusch TBH, Williams SL (1998) Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia 113:428–441

Rilov G (2016) Multi-species collapses at the warm edge of a warming sea. Sci Rep 6:36897

Rilov G, Benayahu Y, Gasith A (2004) Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. Biol Invasions 6:347–364

Rius M, Teske PR (2011) A revision of the *Pyura stolonifera* species complex (Tunicata, Ascidiacea), with a description of a new species from Australia. Zootaxa 2754:27–40

Rius M, Teske PR, Manríquez PH, Suárez-Jiménez R, Mcquaid CD, Castilla JC (2017) Ecological dominance along rocky shores, with a focus on intertidal ascidians. Oceanogr Mar Biol Annu Rev 55:55–84

Roberts JM, Cairns SD (2014) Cold-water corals in a changing ocean. Curr Opin Environ Sustain 7:118–126

Rosindell J, Hubbell SP, Etienne RS (2011) The unified neutral theory of biodiversity and biogeography at age ten. Trends Ecol Evol 26:340–348. https://doi.org/10.1016/j.tree.2011.03.024

Rossi S, Bramanti L, Gori A, Orejas C (2017a) Animal forests of the world: an overview. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham, pp 1–28. https://doi.org/10.1007/978-3-319-21012-4_1

Rossi S, Bramanti L, Gori A, Orejas C (eds) (2017b) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham. https://doi.org/10.1007/978-3-319-21012-4

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. Annu Rev Ecol Evol Syst 36:643–689

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Integr Comp Biol 37(6):621–632

Ruiz Allais JP, Amaro ME, McFadden CS, Halász A, Benayahu Y (2014) The first incidence of an alien soft coral of the family Xeniidae in the Caribbean, an invasion in eastern Venezuelan coral communities. Coral Reefs 33:287–287

Rützler K, Muzik H (1993) *Terpios hoshinota*, a new cyanobacteriosponge threatening Pacific reefs. Sci Mar 57:395–403

Safriel UN (1975) The role of vermetid gastropods in the formation of Mediterranean and Atlantic reefs. Oecologia (Berlin) 20:85–101

Safriel UN, Sasson-Frosting Z (1988) Can colonizing mussel outcompete indigenous mussel? J Exp Mar Biol Ecol 117:211–226

Salomidi M, Katsanevakis S, Issaris Y, Tsiamis K, Katsiaras N (2013) Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. Biol Invasions 15:1961–1971

Sánchez JA (2017) Diversity and evolution of octocoral animal forests at both sides of tropical America. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International, Cham, pp 111–143. https://doi.org/10.1007/978-3-319-21012-4_39

Sánchez JA, Ardila NE, Andrade J et al (2014) Octocoral densities and mortalities in Gorgona Island, Colombia, Tropical Eastern Pacific. Rev Biol Trop 62:209–219

Sánchez JA, Ballesteros D (2014) The invasive snowflake coral (*Carijoa riisei*) in the tropical eastern Pacific, Colombia. Rev Biol Trop 62:197–207

Sardain A, Sardain E, Leung B (2019) Global forecasts of shipping traffic and biological invasions to 2050. Nat Sustain 2:274–282. https://doi.org/10.1038/s41893-019-0245-y

Sax FD (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. J Biogeogr 28:139–150

Schack CR, Gordon DP, Ryan KR (2019) Modularity is the mother of invention: a review of polymorphism in bryozoans. Biol Rev 94:773–809. https://doi.org/10.1111/brv.12478

Schwan IDS, Brasil ACDS, Neves D, Dias GM (2016) The invasive worm *Hydroides elegans* (Polychaeta – Serpulidae) in southeastern Brazil and its potential to dominate hard substrata. Mar Biol Res 12(1):96–103. https://doi.org/10.1080/17451000.2015.1080370

Schwindt E, Bortolus A, Iribarne OO (2001) Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biol Invasions 3(2):137–149. https://doi.org/10.1023/A:1014571916818

Schwindt E, Iribarne OO, Isla FI (2004) Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. Estuar Coast Shelf Sci 59(1):109–120. https://doi.org/10.1016/j.ecss.2003.06.004

Sellheim K, Stachowicz JJ, Coates RC (2010a) Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities. Mar Ecol 398:69–80

Sellheim K, Stachowicz JJ, Coates RC (2010b) Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities. Mar Ecol Prog Ser 398:69–80. https://doi.org/10.3354/meps08341

Serisawa Y, Imoto Z, Ishikawa T, Ohno M (2004) Decline of the *Ecklonia cava* population associated with increased seawater temperatures in Tosa Bay, southern Japan. Fish Sci 70:189–191

Serrano E, Coma R, Ribes M (2012) A phase shift from macroalgal to coral dominance in the Mediterranean. Coral Reefs 31:1199

Serrano E, Coma R, Ribes M, Weitzmann B, García M, Ballesteros E (2013) Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. PLoS One 8(1):e52739

Serrano E, Ribes M, Coma R (2018) Demographics of the zooxanthellate coral *Oculina patagonica* along the Mediterranean Iberian coast in relation to environmental parameters. Sci Total Environ 634:1580–1592

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176. https://doi.org/10.1016/s0169-5347(02)02495-3

Shenkar N, Swalla BJ (2011) Global diversity of Ascidiacea. PLoS One 6(6):e20657. https://doi.org/10.1371/journal.pone.0020657

Sheppard CRC (1981) The reef and soft-substrate coral fauna of Chagos, Indian Ocean. J Nat Hist 15:607–621

Sheppard CRC, Davy SK, Pilling GM (2009) The biology of coral reefs. Oxford University Press, Oxford

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32. https://doi.org/10.1023/a:1010086329619

Soares MO, Tavares TCL, Carneiro PBM (2019) Mesophotic ecosystems: distribution, impacts and conservation in the South Atlantic. Divers Distrib 25:255–268

Sorte CJB, Fuller A, Bracken MES (2010a) Impacts of a simulated heat wave on composition of a marine community. Oikos 119(12):1909–1918. https://doi.org/10.1111/j.1600-0706.2010.18663.x

Sorte CJB, Williams SL, Carlton JT (2010b) Marine range shifts and species introductions: comparative spread rates and community impacts. Glob Ecol Biogeogr 19:303–316. https://doi.org/10.1111/j.1466-8238.2009.00519.x

Stachowicz JJ, Tilman D (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Sax DV, Stachowicz JJ, Gaines SD (eds) Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates, Sunderland, MA, pp 41–64. https://doi.org/10.1038/2191188b0

Stimson J, Larned ST, Conklin E (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. Coral Reefs. 19:343–357. https://doi.org/10.1007/s003380000123

Streftaris N, Zenetos A (2006) Alien marine species in the Mediterranean – the 100 “worst invasives” and their impact. Mediterr Mar Sci 7(1):87–118

Takao S, Yamano H, Sugihara K, Kumagai NH, Fujii M, Yamanaka Y (2015) An improved estimation of the poleward expansion of coral habitats based on the inter-annual variation of sea surface temperatures. Coral Reefs 34:1125–1137

Teruya T, Nakagawa S, Koyama T, Suenaga K, Uemura D (2002) Terpiodiene: a novel tricyclic alcohol from the Okinawan sponge *Terpios hoshinota*. Chem Lett 31:38–39. https://doi.org/10.1246/cl.2002.38

Torres P, Costa AC, Dionisio M (2012) New alien barnacles in the Azores and some remarks on the invasive potential of Balanidae. Helgol Mar Res 66:513–522. https://doi.org/10.1007/s10152-011-0287-7

Uemura D, Kita M, Arimoto H, Kitamura M (2009) Recent aspects of chemical ecology: natural toxins, coral communities, and symbiotic relationships. Pure Appl Chem 81:1093–1111

Valentine PC, Collie JS, Reid RN, Asch RG, Guida VG, Blackwood DS (2007) The occurrence of the colonial ascidian *Didemnum* sp. on Georges Bank gravel habitat—ecological observations and potential effects on groundfish and scallop fisheries. J Exp Mar Biol Ecol 342(1):179–181. https://doi.org/10.1016/j.jembe.2006.10.038

Van Ofwegen L, Haddad M (2011) A probably invasive new genus and new species of soft coral (Octocorallia: Alcyonacea: Clavulariidae) from Brazil. Zootaxa 3107:38–46

van Soest RWM, de Kluijver MJ, van Bragt PH, Faasse M, Nijland R, Beglinger EJ, de Weerdt WH, de Voogd NJ (2007) Sponge invaders in Dutch coastal waters. J Mar Biol Assoc UK 87:1733–1748

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E et al (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B, Biol Sci 281:20140846

Vieira LM, Jones MS, Taylor PD (2014) The identity of the invasive fouling bryozoan *Watersipora subtorquata* (d’Orbigny) and some other congeneric species. Zootaxa 3857(2):151–182

Vilcinskas A (2015) Pathogens as biological weapons of invasive species. PLoS Pathog 11: e1004714. https://doi.org/10.1371/journal.ppat.1004714

Volkov I, Banavar JR, Hubbell SP, Maritan A (2003) Neutral theory and relative species abundance in ecology. Nature 424:1035–1037. https://doi.org/10.1038/nature01883

Walker TA, Bull GD (1983) A newly discovered method of reproduction in gorgonian coral. Mar Ecol Prog Ser 12:137–143. https://doi.org/10.3354/meps012137

Wang J-T, Hirose E, Hsu C-M, Chen Y-Y, Meng P-J, Chen CA (2012) A coral-killing sponge, *Terpios hoshinota*, releases larvae harboring cyanobacterial symbionts: an implication of dispersal. Zool Stud 51:314–320

Wanless RM, Scott S, Sauer WHH, Andrew TG, Glass JP, Godfrey B, Griffiths C, Yeld E (2010) Semi-submersible rigs: a vector transporting entire marine communities around the world. Biol Invasions 12:2573–2583

Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol Conserv 102 (2):143–153

Wells F (2019) A low number of introduced marine species in the tropics: a case study from Singapore. Manag Biol Invasions 10:23–45

Work TM, Aeby GS, Maragos JE (2008) Phase shift from a coral to a corallimorph-dominated reef associated with a shipwreck on Palmyra Atoll. PLoS One 3:e2989

Work TM, Aeby GS, Neal BP, Price NN, Conklin E, Pollock A (2018) Managing an invasive corallimorph at Palmyra Atoll National Wildlife Refuge, Line Islands, Central Pacific. Biol Invasions 20:2197–2208

Wright JT (2005) Differences between native and invasive *Caulerpa taxifolia*: a link between asexual fragmentation and abundance in invasive populations. Mar Biol 147:559–569. https://doi.org/10.1007/s00227-005-1561-5

Wulff JL (2010) Regeneration of sponges in ecological context: is regeneration an integral part of life history and morphological strategies? Integr Comp Biol 50:494–505. https://doi.org/10.1093/icb/icq100

Wulff J (2012) Ecological interactions and the distribution, abundance, and diversity of sponges. Adv Mar Biol 61:273–344

Yang S-Y, Chen H-J, Ho M-J, Chen Y-J, Hyang Y-Y, Chow WS, Tang S-L, Jeng M-S, Chen CA (2018) Outbreak of coral-killing cyanobacteriasponge, *Terpios hoshinota*, in Taiping Island (Itu Aba), Spratlys, South China, Sea. Bull Mar Sci 94:1543–1544. https://doi.org/10.5343/bms.2018.0023

Young HS, Parker IM, Gilbert GS et al (2017) Introduced species, disease ecology, and biodiversity–disease relationships. Trends Ecol Evol 32:41–54. https://doi.org/10.1016/j.tree.2016.09.008

Zabin CJ (2009) Battle of the barnacle newcomers: niche compression in invading species in Kaneohe Bay, Oahu, Hawaii. Mar Ecol Prog Ser 381:175–182. https://doi.org/10.3354/meps07968

Zabin CJ, Marraffini M, Lonhart SI, McCann L, Ceballos L, King C et al (2018) Non-native species colonization of highly diverse, wave swept outer coast habitats in Central California. Mar Biol 165:31. https://doi.org/10.1007/s00227-018-3284-4

Zenetos A, Çinar ME, Crocetta F, Golani D, Rosso A, Servello G et al (2017) Uncertainties and validation of alien species catalogues: the Mediterranean as an example. Estuar Coast Shelf Sci 191:171–187. https://doi.org/10.1016/j.ecss.2017.03.031

Zhan A, Briski E, Bock DG, Ghabooli S, MacIsaac HJ (2015) Ascidians as models for studying invasion success. Mar Biol 162(12):2449–2470. https://doi.org/10.1007/s00227-015-2734-5

Zibrowius H (1974) *Oculina patagonica*, Scléractiniaire hermatypique introduit en Méditerranée. Helgoländer Meeresun 26:153–173. https://doi.org/10.1007/bf01611381

Plastics: An Additional Threat for Coral Ecosystems

F. Lartaud, A. L. Meistertzheim, J. Reichert, M. Ziegler, E. Peru, and J. F. Ghiglione

Abstract It is now recognized that plastics represent a new challenge for the preservation of biodiversity and the associated resources. Plastic debris mainly disseminates from land and accumulate in the oceans where they represent the major part of marine litter. Global oceanic circulation allows a widespread distribution in surface waters, with the formation of garbage patches such as in the oceanic gyres. Plastics have also been found on the seabed of all seas and oceans across the planet, with higher concentration in areas of low circulation and high sediment accumulation.

Corals, which are key engineers of shallow and deep marine ecosystems, have been shown to be particularly sensitive to plastic litter. Macrodebris easily gets caught in the three-dimensional structure of the reefs and can cover large portions of coral colonies. Microplastics are directly (when captured by tentacles) or indirectly (ingested by zooplankton that is eaten by corals) transferred to polyp tissues and potentially disturb their physiological functions.

Recent studies that have focused on the effect of plastics on shallow and deep-sea corals report various physiological alterations (growth, necrosis, bleaching) and outbreaks of disease. Evidence was found that plastic contaminants possibly limit the growth of reef-building corals or impair their survival and consequently reduce the complex ecosystems formed by these animal forest organisms. For future research, integrative approaches should take into account the interactions between

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the different biological compartments of the coral holobiont in order to investigate the resilience of corals to the plastic threat.

Keywords Macro- and microplastics · Coral reefs · Ecotoxicological effects · Ecological risk

1 Introduction

Each year, an estimated 8–15 million tons of plastics arrive at sea, mainly from continental sources that include rivers, water treatment effluents and their overflows, recreational coastal activities, illegal coastal or nearshore dumps, and runoffs (Jambeck et al. 2015; Gesamp 2016). Effects of UV light, swell, and currents contribute to the breakdown of plastics into secondary microplastics (i.e., size <5 mm) that, together with the supply of manufactured primary microplastics (e.g., industrial granules, synthetic fibers, or abrasives of cosmetics), generate a large variety of plastic debris that differs in shape, size, and polymer composition. Microplastics represent 90% of floating plastic debris, while it accounts for only about 10% in weight (Gesamp 2019).

Global oceanic circulation facilitates the dispersion of plastics on a large scale, and the physical properties of these plastics and their biological colonization actively promote a vertical transport to the seafloor (Kooi et al. 2017). This results in the contamination of all marine ecosystems, both in tropical and polar waters, on the coast of the most isolated islands, or at great depths, such as in the Mariana Trench down to 11,000 m (Bergmann et al. 2017; Jamieson et al. 2019; Lavers et al. 2019).

Plastic pollution is thus recognized as a major threat by both the scientific community and stakeholders. To address this threat, several environmental programs have been launched, for example, within the Marine Strategy Framework Directive in Europe (Galgani et al. 2010). The major focus of these projects is to study the impact of plastics on marine organisms and the associated risks for human health. Studies of the effect of plastics on organisms mostly focused on commercially important species such as bivalves and fishes, which represent a direct risk for humans (Van Cauwenberghe and Janssen 2014; Mazurais et al. 2015; Paul-Pont et al. 2016; Sussarellu et al. 2016). Recent observations show that up to eight microplastic particles per individual are found in mussel and cockle tissues from various places all over the world (Li et al. 2016; Hermabessiere et al. 2019) and that 100% of mussels from UK supermarkets contain microplastics (Li et al. 2018). Microplastics that accumulate in animal guts and tissues are transferred to humans by consuming seafood, with yet unknown long-term effects on human health (e.g., see review by Barboza et al. 2018).

Coral reefs are among the most biodiverse ecosystems in the ocean, containing 25–33% of known marine life (Plaisance et al. 2011), making them productivity hotspots of ecological and economic importance (Reaka-Kudla 1997). Despite their fundamental societal value, investigations on the impact of plastics on shallow and deep-sea corals only started very recently. This chapter presents the state of the art of the impact of plastics on coral ecosystems, including their distribution in reef habitats, the known effects on coral health, and the ecological risks for associated species. Finally, we propose directions for future research.

2 To What Extent Are Coral Reefs Exposed to Plastic Litter?

Most plastics enter the marine environment through rivers and coastlines, suggesting that coastal ecosystems, such as coral reefs, are particularly exposed to this pollution (Gesamp 2016). The oceanic conveyor further disseminates plastics at a global scale, contaminating coral reefs as well as all other marine ecosystems. Fishing and tourism activities can be a significant additional source of marine litter in coral ecosystems, such as demonstrated in the Southern Great Barrier Reef (Wilson and Verlis 2017). Evidence of plastics in coral reefs has dramatically increased for several years, highlighted by oppressive pictures of plastic debris such as bags, food and drink packages, or fishing-related items entangled in the three-dimensional reef framework and on coral colonies (Fig. 1).

At a large geographic scale, Lamb et al. (2018) estimated 11 billion items of macroplastic on coral reefs in the Asia-Pacific region, which contains more than half (>55%) of global shallow-water coral reefs. This study excluded areas of China and Singapore, which are among the main contributors of plastic at sea, suggesting an underestimation of the number of plastic items in the reefs. A comprehensive quantification of the amount of plastics associated with coral reef environments is lacking and likely variable between geographic regions and oceanic conditions. For instance, published surveys showed a large variation from 0.04×10^{-3} items per m^2 found on Hawaiian beaches; over 0.04–0.90 items per m^3 in trawl surveys of coral ecosystems in Indonesia; 6 items per m^2 in shallow reefs of the Gulf of Aqaba, Red Sea; and up to 530–610 items per kg sediment of coral reef ecosystems in the South China Sea (Abu-Hilal and Al-Nijjar 2009; Donohue et al. 2001; Germanov et al. 2019; Zhang et al. 2019). A recent estimate for the next decade indicated a significant increase in plastic pollution of coral reefs from Brazil and Egypt, and a severe increase in the Asia-Pacific region, including India (Sweet et al. 2019).

Polyethylene, polypropylene, and polystyrene were generally the most commonly found microplastic polymers in surface waters (Hidalgo-Ruz et al. 2012). A few studies dedicated to coral reefs confirm this type of distribution (Cordova et al. 2018; Jensen et al. 2019), although local variation can occur (e.g., polyethylene terephthalate dominates in coral reefs from Xisha Islands of South China Sea) (Ding et al. 2019). Other work indicates that marine microdebris occurs predominantly in the form of fibers (Browne et al. 2011). In addition to plastic bags, other macroplastic debris includes ghost fishing gear and lost or abandoned lobster pots that are particularly harmful for benthic reef communities, as they cause severe physical damage (Lewis et al. 2009). However, tracking the sources of plastic contamination in tropical coral reefs is arduous. For example, Jensen et al. (2019) showed riverine

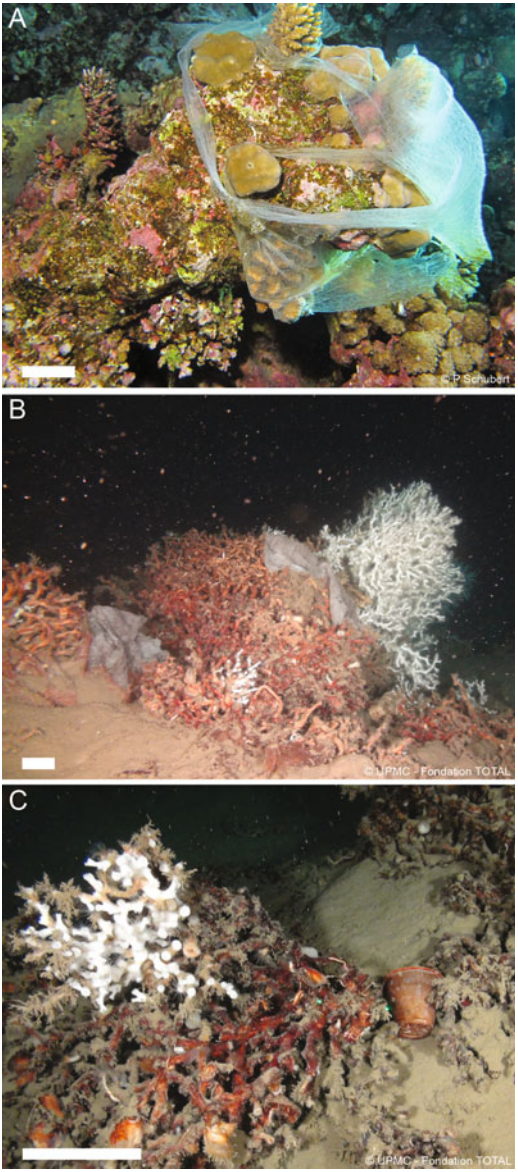

Fig. 1 (**a**) Plastic bag entangled in *Acropora* spp. and *Porites* spp. corals (Dahab, Egypt). (**b**) Plastic bags in *Lophelia pertusa* reefs (530 m depth, Lacaze-Duthiers canyon, NW Mediterranean Sea). (**c**) Coffee cup trapped in a *L. pertusa* colony (same location). Scale bar is 10 cm

discharge as the most likely source of microdebris in nearshore reefs of the Great Barrier Reef (GBR) while debris further offshore originates from other sources. Better characterization of the sources and sinks of plastic debris is thus required, as prioritizing management actions requires spatial information on the dispersal and settlement of plastics from both local and external sources. The use of a fine-resolution hydrodynamic model may help in predicting plastic exposure of coral habitats. Based on this type of model, Critchell et al. (2019) pointed out the importance of considering temporal scale, with higher expected exposure of coral reefs in east Australia during the windy monsoon season.

Plastic pollution in tropical coral reefs is, however, only part of the problem, as the deep sea is recognized as a major sink for plastic debris (Woodall et al. 2014). Colonization of plastic fragments by microbial biofilms influences hydrophobicity and buoyancy, enabling vertical transport. Larger microplastics have a greater probability to reach the deep-sea floor, while smaller particles have been predicted to oscillate at intermediate depths (Kooi et al. 2017). Yet recent observations of microplastic fibers in deep-sea amphipods from the Mariana and other deep ocean trenches contradict this model (Jamieson et al. 2019). Accordingly, 80% of microplastics observed in deep-sea sediments (2340–5570 m) in the Arctic region (west of Svalbard, Norway) are smaller than 25 μm (Bergmann et al. 2017). Both large and small microplastics are thus able to reach the deep-sea floor, likely facilitated by vertical currents or biotic transport. Submarine canyons are among the deep-sea ecosystems most affected by plastic pollution (Pham et al. 2014). These habitats host deep-sea coral reefs (also called cold-water corals), which are particularly exposed to plastic contamination, as highlighted by the number of pictures showing plastic debris in deep-sea Mediterranean and Atlantic reefs (Fiala-Medioni et al. 2012; Fabri et al. 2014; D'Onghia et al. 2017; van den Beld et al. 2017; Cau et al. 2018; Fig. 1b, c). In deep-sea coral reefs from the Bay of Biscay, van den Beld et al. (2017) report a mean density of 4813 macrolitter items km^{-2}, where plastics correspond to >40% of debris, with large variations between canyons (litter density increases up to 59,412 items km^{-2} in the Arcachon canyon).

3 What Are the Effects of Plastics on Coral Physiology?

As for other marine organisms, the expected effects of plastic pollution include (1) direct physical and mechanical damage, (2) entanglement and entrapment, (3) reduction of light exposure for phototrophic animals and creation of low oxygen levels, (4) ingestion and gut blockage, (5) introduction of pathogenic agents colonizing plastics, and (6) exposure to chemical contaminants (Sweet et al. 2019). However, precise quantification of these processes is still lacking for corals, since experimental studies on the effects of plastics on shallow and deep-sea corals have only started a few years ago.

Hall et al. (2015) were the first to show that shallow tropical corals ingest microplastics. Approximately 20% of the studied colonies of the tropical massive coral species *Dipsastraea pallida*, formerly known as *Favia pallida*, sampled at the GBR, ingested microplastics of sizes ranging from 100 μm to 2 mm in a 48-h laboratory exposure treatment. Further experimental studies showed that microplastic ingestion occurs in a wide range of cnidarians, including temperate anthozoans (*Astrangia poculata*), sea anemones (*Exaiptasia diaphana*), and freshwater hydrozoans (*Hydra attenuata*) (Allen et al. 2017; Murphy and Quinn 2018;

Romanó de Orte et al. 2019). Field evidence of plastic particles and/or microfibers found on or in wild-collected organisms underlines that microplastic pollution affects cnidarians in reef ecosystems, for example, deep-sea octocorals and zoanthids, temperate corals, or tropical reef-building corals (Taylor et al. 2016; Ding et al. 2019; Martin et al. 2019; Rotjan et al. 2019), but also other sessile reef-dwelling species (Arossa et al. 2019; La Beur et al. 2019). In certain locations (e.g., New England coast, Atlantic Ocean), microplastic bioaccumulation reached >100 particles per coral polyp, composed mainly of fibers rather than beads and irregularly shaped plastics (Rotjan et al. 2019).

For catching prey and ingestion, coral organisms mainly use their tentacles and mesenterial filaments, which belong to the digestive system of cnidarians (Fig. 2). Further, the process can be facilitated by mucus production (Fig. 2a). A possible explanation for the ingestion of microplastics is that corals may mistake particles for food as they ingest them at similar rates as zooplankton prey (Hall et al. 2015). This could be due to the stimulation by chemosensory elements released by plastics such as polybutylene terephthalate (PBT) (Allen et al. 2017). Some studies argue that the development of a bacterial biofilm on particles may give plastic a smell and taste like food (Romera-Castillo et al. 2018), in particular for animals that rely on chemoreception for food selection, such as birds, fishes (Savoca et al. 2016, 2017), and

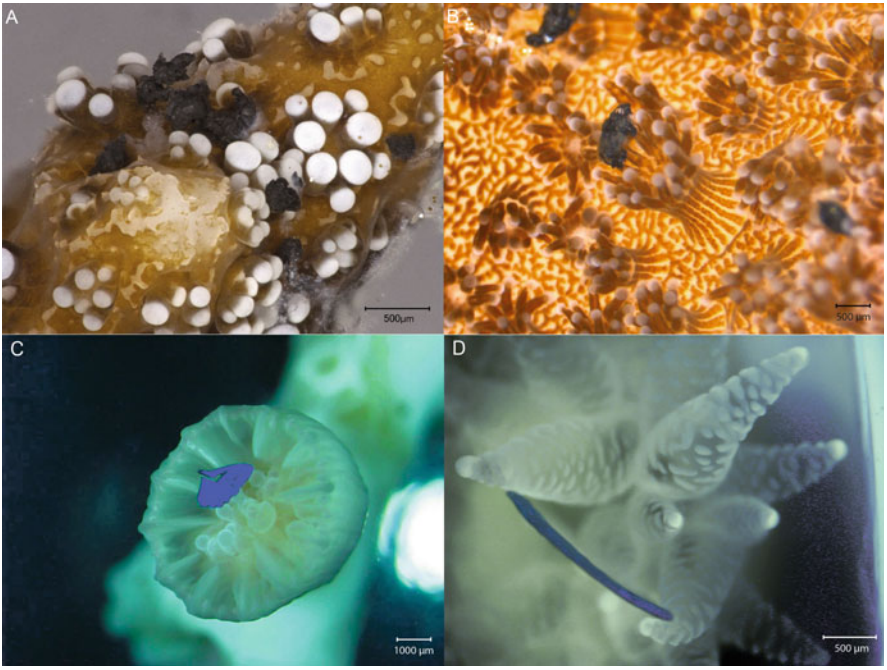

Fig. 2 (**a**) *Stylophora pistillata*, (**b**) *Pocillopora verrucosa*, (**c**) *Desmophyllum dianthus*, and (**d**) *Lophelia pertusa* capturing polyethylene (PE) microfragments by their tentacles and/or trapping with mucus

probably corals. Other studies suggest that biofilms on plastics prevent predation or uptake, likely because the microbial biofilm may obscure phagostimulants on plastic or produce feeding deterrents (Allen et al. 2017). Experimental studies suggest that the uptake of microplastic particles by corals is, in part, a selective process. Interestingly, some species such as the Caribbean tropical corals, *Montastraea cavernosa* and *Orbicella faveolata*, are size-selective and do not feed on plastic particles <250 μm, whereas they actively feed on microbeads of sizes ranging from 425 μm to 2.8 mm (Hankins et al. 2018). Selection for polymer types was observed in the sea anemone *E. diaphana*, which ingested a higher percentage of nylon than polyester and polypropylene microfibers (Romanó de Orte et al. 2019). Apparently, the presence of chemical-feeding stimulants can alter this behavior, and the selection disappears when plastics are offered in the presence of shrimp prey. The presence of prey can also increase plastic ingestion rate, as observed for the Mediterranean coral *Astroides calycularis* (Savinelli et al. 2020). Once ingested, the majority of microplastics were egested within 24–48 h (Allen et al. 2017; Hankins et al. 2018). Interestingly, the retention time increases for organisms that present poor health, as observed for bleached anemones (Romanó de Orte et al. 2019).

At the organismal level, although documentation is still fragmented, macro- and microplastics have been reported to alter energy balance and to reduce growth and fecundity of various marine organisms (Wright et al. 2013; Watts et al. 2015; Sussarellu et al. 2016; Lo and Chan 2018). To date, experimental studies on corals are still scarce, but plastics have been demonstrated to affect different physiological processes. First, ingested plastics may completely fill the gastric cavity, causing a reduction in feeding rates (Murphy and Quinn 2018), likely due to a false sense of satiation and/or an inhibition of food intake (Watts et al. 2015; Rotjan et al. 2019). Changes in feeding behavior were also reported, leading polyps to be more active and allocate more energy to food acquisition (Chapron et al. 2018). Second, when macroplastics act as a barrier to prey capture, some corals species such as the deep-sea reef builder *Lophelia pertusa* seem to accommodate after several months using a bypass strategy based on the change of colony growth orientation, while long-term exposure to microplastics caused a strong decrease in zooplankton capture rates (Mouchi et al. 2019). Lower feeding rates, changes in feeding behavior, and time passed for egestion of microparticles may therefore result in reduced energy storage in tissues. Because (tropical) coral energy reserves, in part, influence the susceptibility to other stressors such as global warming (Grottoli et al. 2006), an indirect negative effect of plastic pollution on coral energy stores may render them more prone to other stressors.

Tropical shallow-water corals harbor photosynthetic algae that provide a large proportion of the coral host's energy demand (Muscatine 1990). Microplastic exposure has been described to disrupt the coral-microalgae symbiotic relationships in the sea anemone *Exaiptasia* sp. and the coral *Favites chinensis* (Okubo et al. 2018). But the response was species-specific, since other tropical coral species did not exhibit significant changes in the density of symbiotic microalgae or chlorophyll content in the presence of microplastics (Tang et al. 2018; Reichert et al. 2019). The photosynthetic performance of the coral-associated photosymbionts, however, seems to be affected under microplastic exposure, as observed for the tropical coral species *Acropora muricata*, *Pocillopora verrucosa*, and *Heliopora coerulea* (Reichert et al. 2019), but it remains to be explored whether this affects coral energy storage.

An important function of corals is their ability to produce large three-dimensional reef structures that provide a habitat for a large diversity of organisms. Exposure to plastics, however, has been demonstrated to limit skeletal growth for both branching growth forms of shallow and deep-sea coral species. The decrease in growth was strong for deepwater corals, as *L. pertusa* exposed to either macro- or microplastics over 2 months exhibited reduced linear extension of 30% compared to control or in situ specimens (Chapron et al. 2018). Over longer time of exposure, the impact on growth was persistent for microplastics but not for macroplastics. Polyp skeleton overgrowth allowed a change in growth orientation likely corresponding to an obstacle avoidance strategy (Mouchi et al. 2019). But the newly produced skeleton was thinner compared to normal biomineralization, making the colony more fragile (Mouchi et al. 2019). Similarly, a tropical reef-building coral and an octocoral species (*A. muricata* and *H. coerulea*) responded with decreased growth after 6 months of exposure to 200 microplastic particles per liter (Reichert et al. 2019). However, the response appeared to be species-specific, and the growth of two other tropical species, *P. verrucosa* and *Porites lutea*, was not affected by microplastics, as also seen for *Montastraea cavernosa* and *Orbicella faveolata* after 48 h of exposure to $>$240 particles per liter (Hankins et al. 2018). Additionally, overgrowth of plastic particles in contact with corals has been documented for various species in areas where cleaning mechanisms (i.e., by mucus production) were ineffective and there was no passive removal by currents (Reichert et al. 2018).

Exposure to microplastic particles further influenced coral health in general (Reichert et al. 2018). Tissue necrosis and bleaching were observed to occur under microplastic exposure, but also seem to be species-specific. For instance, bleaching was found for *Acropora humilis*, *A. millepora*, *Pocillopora damicornis*, *P. verrucosa*, and *Porites cylindrica*, but not for *P. lutea* (Reichert et al. 2018). These negative impacts on coral health may occur quite rapidly (within 4 weeks) and affect large tissue areas (up to 40% of the original surface area affected). Reasons for tissue necrosis and bleaching might be the direct physical damage or indirect effects related to microbiome changes due to a transfer of microbial communities that colonize plastics or to the release of chemicals contained in the plastics or adsorbed on it (Fig. 3).

Plastics harbor a specific microbial community, called “plastisphere,” which differs from that of seawater (Zettler et al. 2013) and particulate organic matter (Dussud et al. 2018). Studies pointed out the role of plastics as a source of disease for marine organisms. *Rhodobacterales*, a group of bacteria involved in outbreaks of coral disease, have been described colonizing polyvinyl chloride (PVC) (Dang et al. 2008). Similarly, potential pathogenic *Vibrio* spp. have been observed on various types of microplastics (Kirstein et al. 2016; Harrison et al. 2018). As demonstrated in a recent study using short-term high exposure conditions (17,000 particles per liter), direct ingestion and subsequent transfer of *Escherichia coli* colonizing the microbeads to *Astrangia poculata* corals support the hypothesis of plastics as vector

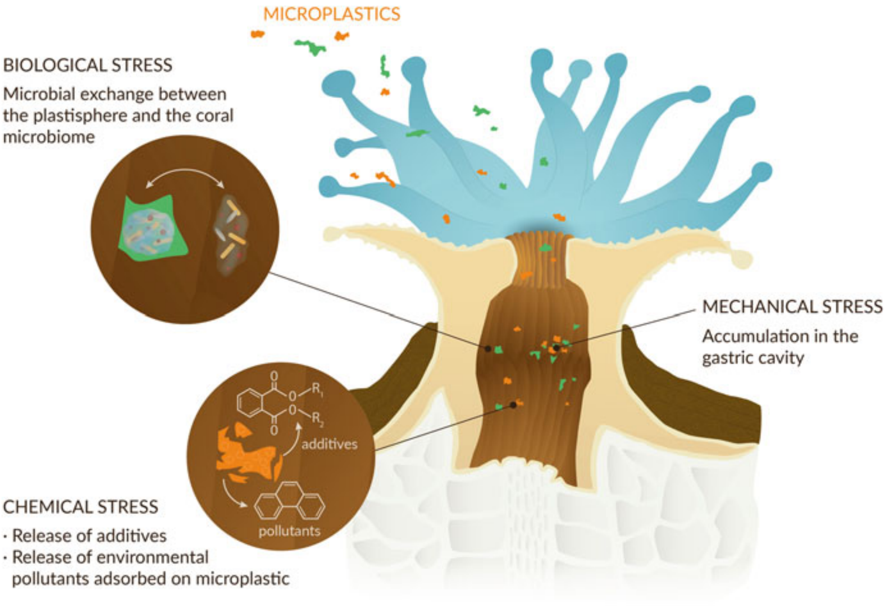

Fig. 3 Synthesis of the main stress pathways to coral exposed to microplastics

of pathogens (Rotjan et al. 2019). Exposure to plastic debris stresses corals by giving pathogens a niche for invasion, yet the virulence and disease dynamics of these pathogens hitching a ride on marine plastic debris are unknown (Quero and Luna 2017; Jacquin et al. 2019). Pathogen infections might also be favored by an increase in stress response and a lower immune function of corals, as experienced by *P. damicornis* to acute microplastic exposure of 9×10^{10} particles per liter (Tang et al. 2018). However, whether such responses occur under realistic plastic concentrations remains to be determined. Based on a large-scale investigation in the Asia-Pacific region, Lamb et al. (2018) have shown that the likelihood of disease increases up to 90% when corals are in contact with large plastic litter, meaning that coral reefs could be dramatically affected.

It has already been shown that plastic pollution has an impact on coral reef-associated organisms, such as marine mammals, seabirds, and fishes (Kühn et al. 2015; Santos et al. 2015; Nunes et al. 2018). For instance, ~20% of the sampled coral reef fish from four genera at Mo'orea, French Polynesia, had ingested microplastics, albeit at comparatively low quantities (1–3 pieces in their gut) (Garnier et al. 2019). 100% of tows and 95% of damselfish from the Great Barrier Reef had ingested plastic microfibers (Jensen et al. 2019). Because some fish species change their diet during ontogeny, juvenile life stages might be more sensitive to the plastic threat (Critchell and Hoogenboom 2018; Ghiglione and Laudet 2020). Although a first study by Berry et al. (2019) indicates that exposure to microplastics has only limited effects on fertilization, early life stages, and settlement of corals, more comprehensive investigations of these susceptible life stages are warranted.

Finally, plastics can act as a cocktail of contaminants for marine species. They are composed of both plastic additives (e.g., plastifiers, antioxidants, stabilizers, hardeners, flame retardants, pigments, solvents) and pollutants adsorbed from the environment (e.g., hydrocarbons, PCBs, pesticides, and heavy metals) (Bakir et al. 2014). The desorption rates of chemicals are faster in the presence of gut surfactant than in natural seawater. Fast exchanges (within hours) are measured between PCBs from low-density polyethylene (LDPE) and polyvinyl chloride (PVC) microplastics and the gut fluid of different organisms, including lugworms and cod, although the transfer is reversible conducing to clean contaminated gut systems (Mohamed Nor and Koelmans 2019). Further, plastic leachates were shown to impair photosynthesis of phytoplankton (Tetu et al. 2019), but their effects on photosynthesis in shallow reef-building corals remain to be explored. Recently, phthalic acid esters (PAE), a class of microplastic-associated contaminants, were observed in *A. muricata* samples from the Maldives (Indian Ocean), in concentrations that were positively correlated with that of microplastics in the surrounding seawater (Saliu et al. 2019), suggesting that chemical leachates from plastics represent an additional facet of this threat to corals.

4 What Is the Ecological Risk for Coral Ecosystems?

Plastics are now part of the environment of marine waters, which reef organisms are constantly exposed to and incorporate them as part of their ecosystem (Fig. 4). However not all coral species are similarly affected by plastic pollution, which may lead to long-term shifts in coral community composition. A long-term experimental study on the exposure of the cold-water corals *L. pertusa* and *Madrepora oculata*, the two main reef-building species in deep waters, revealed that while *L. pertusa* was highly impacted by macro- and microplastics, no effects were reported on *M. oculata*, likely due to differences in prey/plastic size selection (Mouchi et al. 2019). Similar results have been observed for tropical corals, varying from severe to no impacts between species. Several authors suggested that structurally complex corals are more likely to be affected by plastics (Lamb et al. 2018; Reichert et al. 2019). These effects could contribute to modifying the dominant coral species in reef assemblages, as previously described for global warming (Hughes et al. 2018). Based on experimental data, one could expect replacement of branching, sensitive (*Acropora* spp. and *Pocillopora* spp.) by massive, robust (*Porites* spp.) species at shallower depths in tropical waters and replacement of robust reef builders (i.e., *L. pertusa*) by species with limited framework building capacity (i.e., *M. oculata*) at deeper and/or colder sites. These potential changes in coral reef landscapes with subsequent modifications of microhabitats will then impact the associated species occupying these niches.

Another potential risk suggested by some authors is the introduction of invasive species on plastic debris. Among the colonization of 300 non-native species (mainly invertebrates) that reached the shores of the US Pacific Northwest after the 2011 East

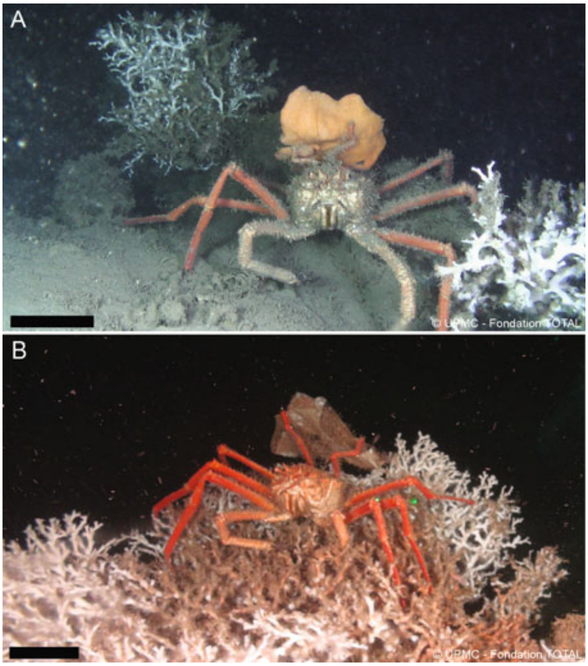

Fig. 4 (**a**) The deep-sea crab *Paromola cuvieri* carrying a sponge for passive covering and active discouraging behavior from competitors or predators (Lacaze-Duthiers canyon, NW Mediterranean Sea). (**b**) In areas where plastic wastes are common, crabs use plastics instead. Scale bar is 10 cm

Japanese earthquake and tsunami, many of these invaders were attached to plastics (Carlton et al. 2017). Yet we still lack a precise characterization of their effects on corals and coral reef ecosystems. Additionally, the expected increase in microplastic concentrations in the near future may enhance the impacts of all aspects of this novel stressor.

5 Further Directions

Following recent recommendations of the United Nations Environment Programme, the various effects of plastics on coral reef ecosystems invite to reconsider the management practices and conservation strategies in reef habitats (Sweet et al. 2019). Although studies on the impact of plastics on corals have started only recently, their numbers increase rapidly. However, as in other plastic research fields (Lenz et al. 2016), the comparability between studies is limited due to a lack of standardized methods in terms of plastic types, applied concentration, and exposure times, hampering the possibility to identify general tendencies. In order to overcome this issue, several points must be addressed to generate baseline knowledge on the novel stressor plastic, in order to define and prioritize appropriate protection measures for coral reef ecosystems.

First, we propose that more effort should be made in characterizing plastic pollution in the field, both at spatial and temporal scales. Although the quantification of plastics at sea is a subject of great attention from scientists and stakeholders, data on fluxes and types of plastic debris in coral ecosystems are still scarce. This also includes data on plastic-associated and released chemicals. Future approaches should consider a greater range of size classes (from nano- to macroplastics), as only little is known about smaller plastic particles, which are difficult to sample and analyze. Further, not only the polymer types but also their origins need to be considered in order to implement more effective protection measures. Additionally, plastic bioaccumulation through trophic chains in coral ecosystems should be studied, in order to better understand high variations in plastic detection patterns. Potentially corals themselves might be used to better characterize plastic loads and exposure levels in the environment. Various emerging programs aim to define appropriate bioindicators of plastic pollution (e.g., based on filtering species such as bivalves). Considering the large geographical distribution of some coral species, from tropical (*Acropora* spp., *Pocillopora* spp., *Porites* spp.), temperate (*A. poculata*), and deep waters (*L. pertusa*), high rates of heterotrophic feeding, and resilience to microplastic pollution, corals could potentially also serve as an indicator of microplastic pollution in their habitat.

Second, we emphasize that experimental studies must be representative of or close to environmental conditions for results to become ecologically relevant. Similar to other toxicological studies, the effect of plastics on coral health was mostly assessed in laboratory aquaria experiments. Given the lack of precise data on concentrations and types of plastics (polymer composition, additives, and sources) in coral ecosystems, the representativeness of laboratory studies is questionable when compared to in situ conditions (e.g., shape, size, and quantity of microplastics used). Thus, caution must be taken when interpreting data generated in high exposure studies that often exceed environmental conditions by several orders of magnitude (Lenz et al. 2016). High concentration in ecotoxicological studies can, however, be used as a proof of concept to assess the potential risks of emerging pollutants and develop biomarkers or an in-depth characterization of phenotypic changes (Huvet et al. 2016). In addition, most studies focus on short exposure times, which makes it difficult to conclude on realistic scenarios. As observed for studies addressing the effects of climate change on corals (Form and Riebesell 2012), and now for their exposure to plastics (Mouchi et al. 2019; Reichert et al. 2019), the use of long-term experiments should be encouraged. Therefore, more long-term studies applying environmentally realistic conditions are needed in order to avoid overreaction to or misinterpretation of results, both in the scientific community and in the public.

Third, considering the impacts of plastics on coral health, studies must address different biological levels of the coral holobiont. Until today, studies have mainly focused on the coral host. However, little is known about the effects of plastics on the microbial communities (prokaryotes and microeukaryotes) of the coral holobiont. Therefore, another key research question would be to investigate the effect of the plastisphere on coral microbiome composition via the holobiont approach, which involves assessing the health of a host organism in the context of its associated microbiome (Rosenberg and Zilber-Rosenberg 2014; Thompson et al. 2015). Moreover, the microbiome contributes to the physiology, development, immunity, and behavior of their coral host, and may respond very rapidly to changing environmental conditions, providing a powerful mechanism for acclimatization and also possibly rapid adaptation of coral reef holobionts (Webster and Reusch 2017; Voolstra and Ziegler 2020). Microorganisms living on plastics have been shown to be different from the surrounding seawater or organic particles (Zettler et al. 2013; Dussud et al. 2018), but the extent to which the plastisphere influences the coral microbiome and consequently its health status needs to be investigated.

Last, as plastics do not occur alone but act in combination with other environmental stressors, such as the impacts of climate change or other pollutants, multi-stressor studies are needed to better determine the resilience of corals. Although a first study found no effects of thermal stress on microplastic ingestion (Axworthy and Padilla-Gamiño 2019), until today, little is known about the interaction of plastic pollution with other stressors.

Taken together, more realistic experimental studies mimicking environmental conditions and addressing all organismal levels of corals, from molecules to population and from the host to its associated microbiome, are needed to better evaluate the threat that plastic pollution poses to coral reef organisms. This will help to develop and prioritize protection measures against plastic pollution in coral reef environments.

References

Abu-Hilal A, Al-Nijjar T (2009) Marine litter in coral areas along the Jordan Gulf of Aqaba, Red Sea. J Environ Manag 90:1043–1049

Allen AS, Seymour AC, Rittschof D (2017) Chemoreception drive plastic consumption in a hard coral. Mar Pollut Bull 124:198–205

Arossa S, Martin C, Rossbach S et al (2019) Microplastic removal by Red Sea giant clam (*Tridacna maxima*). Environ Pollut 252:1257–1266

Axworthy JB, Padilla-Gamiño JL (2019) Microplastics ingestion and heterotrophy in thermally stressed corals. Sci Rep 9:18193

Bakir A, Rowland SJ, Thompson RC (2014) Enhanced desorption of persistent organic pollutants from microplastics under simulated physiological conditions. Environ Pollut 185:16–23

Barboza LGA, Dick Vethaak A, Lavorante BRBO et al (2018) Marine microplastic debris: an emerging issue for food security, food safety and human health. Mar Pollut Bull 133:336–348

Bergmann M, Wirzberger V, Krumpen T et al (2017) High quantities of microplastic in Arctic deep-sea sediments from the Hausgarten observatory. Environ Sci Technol 51:11000–11010

Berry KLE, Epstein HE, Lewis PJ et al (2019) Microplastic contamination has limited effects on coral fertilization and larvae. Diversity 11:228

Browne MA, Crump P, Niven SJ et al (2011) Accumulation of microplastic on shorelines woldwide: sources and sinks. Environ Sci Technol 45(21):9175–9179

Carlton JT, Chapman JW, Geller JB et al (2017) Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. Science 357:1402–1406

Cau A, Bellodi A, Moccia D et al (2018) Dumping to the abyss: single-use marine litter invading bathyal plains of the Sardinian margin (Tyrrhenian Sea). Mar Pollut Bull 135:845–851

Chapron L, Peru E, Engler A et al (2018) Macro- and microplastics affect cold-water corals growth, feeding and behaviour. Sci Rep 8:15299

Cordova MR, Hadi TA, Prayudha B (2018) Occurrence and abundance of microplastics in coral reef sediment: a case study in Sekotong, Lombok-Indonesia. AES Bioflux 10:23–29

Critchell K, Hoogenboom MO (2018) Effects of microplastic exposure on the body condition and behaviour of planktivorous reef fish (*Acanthochromis polyacanthus*). PLoS One 13:e0193308

Critchell K, Harmann M, Wildermann et al (2019) Predicting the exposure of coastal species to plastic pollution in a complex island archipelago. Environ Pollut 252:982–991

D'Onghia G, Calculli C, Capezzuto F et al (2017) Anthropogenic impact in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea): observations and conservation straits. Deep Sea Res Part II Top Stud Oceanogr 145:87–101

Dang H, Li T, Chen M et al (2008) Cross-ocean distribution of *Rhodobacterales* bacteria as primary surface colonizers in temperate coastal marine waters. Appl Environ Microbiol 74:52–60

Ding J, Jiang F, Li J et al (2019) Microplastics in the coral reef systems from Xisha Islands of South China Sea. Environ Sci Technol 53:8036–8046

Donohue MJ, Boland RC, Sramek CM, Antonelis GA (2001) Derelict fishing gear in the northwestern Hawaiian islands: diving surveys and debris removal in 1999 confirm threat to coral reef ecosystems. Mar Pollut Bull 42:1301–1312

Dussud C, Meistertzheim AL, Conan P et al (2018) Evidence of niche partitioning among bacteria living on plastics, organic particles and surrounding seawaters. Environ Poll 236:807–816

Fabri MC, Pedel L, Beuck L et al (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep Sea Res II 104:184–207

Fiala-Medioni A, Madurell T, Romans P et al (2012) Rov and submersible surveys on faunal assemblages in a deep-sea canyon (rech Lacaze-Duthiers, western Mediterranean Sea). Vie Milieu 62:173–190

Form AU, Riebesell U (2012) Acclimation to ocean acidification during long-term CO_2 exposure in the cold-water coral *Lophelia pertusa*. Glob Chang Biol 18:843–853

Galgani F, Fleet D, Vazn Franeker J et al (2010) Marine strategy framework directive: task group 10 report: marine litter. Publications Office. In: Zampoukas N (ed) JCR scientific and technical reports, 58 p

Garnier Y, Jacob H, Guerra AS et al (2019) Evaluation of microplastic ingestion by tropical fish from Moorea Island, French Polynesia. Mar Pollut Bull 140:165–170

Germanov ES, Marshall AD, Hendrawan IG et al (2019) Microplastics on the menu: plastics pollute Indonesian manta ray and whale shark feeding feeding grounds. Front Mar Sci 6:679

Gesamp (2016) Sources, fate and effects of microplastics in the marine environment. In: Kershaw PJ, Rochman CM (eds) Rep Stud GESAMP No. 93, 220 p

Gesamp (2019) Guidelines or the monitoring and assessment of plastic litter and microplastics in the ocean. In: Kershaw PJ, Turra A, Galgani F (eds) Rep Stud GESAMP No. 99, 130 p

Ghiglione JF, Laudet V (2020) Marine life cycle: a polluted *Terra Incognita* is unveiled. Curr Biol 30:112–133

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440(7088):1186–1189

Hall NM, Berry KLE, Rintoul L, Hoogenboom MO (2015) Microplastic ingestion by scleractinian corals. Mar Biol 162:725–732

Hankins C, Duffy A, Drisco K (2018) Scleractinian coral microplastic ingestion: potential calcification effects, size limits, and retention. Mar Pollut Bull 135:587–593

Harrison JP, Hoellein TJ, Sapp M et al (2018) Microplastic-associated biofilms: a comparison of freshwater and marine environments. In: Wagner M, Lambert S (eds) Freshwater microplastics – emerging environmental contaminants? The handbook of environmental chemistry, vol 58. Springer, Cham, pp 181–201

Hermabessiere L, Paul-Pont I, Cassone A-L et al (2019) Microplastic contamination and pollutant levels in mussels and cockles collected along the channel coasts. Environ Pollut 250:807–819

Hidalgo-Ruz V, Gotow L, Thompson RC et al (2012) Microplastics in the marine environment: a review of the methods used for identification and quantification. Environ Sci Technol 46:3060–3075

Hughes TP, Kerry JT, Baird AH et al (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

Huvet A, Paul-Pont I, Fabioux C et al (2016) Quantifying the smallest microplastics is the challenge for a comprehensive view of their environmental impacts. Proc Natl Acad Sci USA 113:201607221

Jacquin J, Cheng J, Odobel C et al (2019) Microbial ecotoxicology of marine plastic debris: a review on colonization and biodegradation by the 'plastisphere'. Front Microbiol 10:865

Jambeck JR, Geyer R, Wilcox C et al (2015) Plastic waste inputs from land into the ocean. Science 347:768–771

Jamieson AJ, Brooks LSR, Reid WDK et al (2019) Microplastics and synthetic particles ingested by deep-sea amphipods in six of the deepest marine ecosystems on Earth. R Soc Open Sci 6:180667

Jensen LH, Motti CA, Garm AL et al (2019) Sources, distribution and fate of microfibres on the great barrier reef, Australia. Sci Rep 9:9021

Kirstein IV, Kirmizi S, Wichels A et al (2016) Dangerous hitchhikers? Evidence for potentially pathogenic *Vibrio* spp. on microplastic particles. Mar Environ Res 120:1–8

Kooi M, Nes EH, van Scheffer M et al (2017) Ups and downs in the ocean: effects of biofouling on vertical transport of microplastics. Environ Sci Technol 51:7963–7971

Kühn S, Bravo Rebolledo EL, Van Franeker JA (2015) Deleterious effects of litter on marine life. In: Bergmann M, Gutow L, Klages M (eds) Marine anthropogenic litter. Springer International, Cham, pp 75–116

La Beur L, Henry L-A, Kazanidis G et al (2019) Baseline assessment of marine litter and microplastic ingestion by cold-water coral reef benthos at the east Mingulay marine protected area (sea of the Hebrides, Western Scotland). Front Mar Sci 6:80

Lamb JB, Willis BL, Fiorenza EA et al (2018) Plastic waste associated with disease on coral reefs. Science 359:460–462

Lavers JL, Dicks L, Dicks MR et al (2019) Significant plastic accumulation on the Cocos (Keeling) Islands, Australia. Sci Rep 9:7102

Lenz R, Enders K, Nielsen TG (2016) Microplastic exposure studies should be environmentally realistic. Proc Natl Acad Sci USA 113:E4121–E4122

Lewis CF, Slade SL, Maxwell KE et al (2009) Lobster trap impact on coral reefs: effects of wind-driven trap movement. N Z J Mar Fresh 43-1:271–282

Li J, Qu X, Su L et al (2016) Microplastics in mussels along the coastal waters of China. Environ Pollut 214:177–184

Li J, Green C, Reynolds A et al (2018) Microplastics in mussels sampled from coastal waters supermarket in the United Kingdom. Environ Pollut 241:35–44

Lo HKA, Chan KYK (2018) Negative effects of microplastic exposure on growth and development of *Crepidula onyx*. Environ Pollut 233:588–595

Martin C, Corona A, Mahadik GA et al (2019) Adhesion to coral surface as a potential sink for marine microplastics. Environ Pollut 255:113281

Mazurais D, Ernande B, Quazuguel P et al (2015) Evaluation of the impact of polyethylene microbeads ingestion in European sea bass (*Dicentrarchus labrax*) larvae. Mar Environ Res 112:78–85

Mohamed Nor NH, Koelmans AA (2019) Transfer of PCBs from microplastics under simulated gut fluid conditions is biphasic and reversible. Environ Sci Technol 53:1874–1883

Mouchi V, Chapron L, Peru E et al (2019) Long-term aquaria study suggests species-specific responses of two cold-water corals to macro- and microplastics exposure. Environ Pollut 253:322–329

Murphy F, Quinn B (2018) The effects of microplastic on freshwater *Hydra attenuata* feeding, morphology and reproduction. Environ Pollut 234:487–494

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z (ed) Ecosystems of the world. Coral reefs. Elsevier, Amsterdam, pp 75–87

Nunes JAC, Sampaio CL, Barros F et al (2018) Plastic debris collars: an underreported stressor in tropical reef fishes. Mar Pollut Bull 129:802–805

Okubo N, Takahashi S, Nakano Y (2018) Microplastics disturb the anthozoan-algae symbiotic relationship. Mar Pollut Bull 135:83–89

Paul-Pont I, Lacroix C, Gonzalez-Fernandez C et al (2016) Exposure of marine mussels *Mytilus* spp. to polystyrene microplastics: toxicity and influence on fluoranthene bioaccumulation. Environ Pollut 216:724–737

Pham CK, Diogo H, Menezes G et al (2014) Deep-water longline fishing has reduced impact on vulnerable marine ecosystems. Sci Rep 4:4837

Plaisance L, Caley MJ, Brainard RE et al (2011) The diversity of coral reefs: what are we missing? PLoS One 6:e25026

Quero GM, Luna GM (2017) Surfing and dining on the “plastisphere”: microbial life on plastic marine debris. Adv Oceanogr Limnol 8:199–207

Reaka-Kudla ML (1997) The global diversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II. Understanding and protecting our biological resources. Joseph Henry Press, Washington, pp 83–108

Reichert J, Schellenberg J, Schubert P, Wilke T (2018) Responses of reef building corals to microplastic exposure. Environ Pollut 237:955–960

Reichert J, Arnold AL, Hoogenboom MO et al (2019) Impacts of microplastics on growth and health of hermatypic corals are species-specific. Environ Pollut 254:113074

Romanó de Orte M, Clowez S, Caldeira K (2019) Response of bleached and symbiotic sea anemones to plastic microfiber exposure. Environ Pollut 249:512–517

Romera-Castillo C, Pinto M, Langer TM, Álvarez-Salgado XA, Herndl GJ (2018) Dissolved organic carbon leaching from plastics stimulates microbial activity in the ocean. Nat Commun 9:1430

Rosenberg E, Zilber-Rosenberg I (2014) The hologenome concept: human, animal and plant microbiota. Springer, Heidelberg, pp 109–128

Rotjan RD, Sharp KH, Gauthier AE et al (2019) Patterns, dynamics and consequences of microplastic ingestion by the temperate coral, *Astrangia poculata*. Proc R Soc B Biol Sci 286:20190726

Saliu F, Montano S, Leoni B et al (2019) Microplastics as a threat to coral reef environments: detection of phthalate esters in neuston and scleractinian corals from the Faafu Atoll, Maldives. Mar Pollut Bull 142:234–241

Santos RG, Andrades R, Boldrini MA et al (2015) Debris ingestion by juvenile marine turtles: an underestimated problem. Mar Pollut Bull 93:37–43

Savinelli B, Vega Fernandez T, Maria Galasso N et al (2020) Microplastics impair the feeding performance of a Mediterranean habitat-forming coral. Mar Environ Res 155:104887

Savoca MS, Wohlfeil ME, Ebeler SE et al (2016) Marine plastic debris emits a keystone infochemical for olfactory foraging seabirds. Sci Adv 2:e1600395

Savoca MS, Tyson CW, McGill M et al (2017) Odours from marine plastic debris induce food search behaviours in a forage fish. Proc Royal Soc B: Bio Sci 284:20171000

Sussarellu R, Suquet M, Thomas Y et al (2016) Oyster reproduction is affected by exposure to polystyrene microplastics. Proc Natl Acad Sci USA 113:2430–2435

Sweet M, Stelfox M, Lamb J (2019) Plastics and shallow water coral reefs. Synthesis of the science for policy-makers. United Nations Environment Program, 54 p

Tang J, Ni X, Zhou Z et al (2018) Acute microplastic exposure raises stress response and suppresses detoxification and immune capacities in the scleractinian coral *Pocillopora damicornis*. Environ Pollut 243:66–74

Taylor ML, Gwinnett C, Robinson LF, Woodall LC (2016) Plastic microfibre ingestion by deep-sea organisms. Sci Rep 6:33997

Tetu SG, Sarker I, Schrameyer V et al (2019) Plastic leachates impair growth and oxygen production in *Prochlorococcus*, the ocean's most abundant photosynthetic bacteria. Commun Biol 2(1):184

Thompson JR, Rivera HE, Closek CJ et al (2015) Microbes in the coral holobiont: partners through evolution, development, and ecological interactions. Front Cell Infect Microbiol 4:176

Van Cauwenberghe L, Janssen CR (2014) Microplastics in bivalves cultured for human consumption. Environ Pollut 193:65–70

van den Beld IMJ, Guillaumont B, Menot L et al (2017) Marine litter in submarine canyons of the Bay of Biscay. Deep Sea Res Part II Top Stud Oceanogr 145:142–152

Voolstra CR, Ziegler M (2020) Adapting with microbial help: microbiome flexibility facilitates rapid responses to environmental change. Bioessays 42:e2000004

Watts AJR, Urbina MA, Corr S et al (2015) Ingestion of plastic microfibers by the crab *Carcinus maenas* and its effect on food consumption and energy balance. Environ Sci Technol 49:14597–14604

Webster NS, Reusch TBH (2017) Microbial contributions to the persistence of coral reefs. ISME J 11:2167–2174

Wilson SP, Verlis KM (2017) The ugly face of tourism: marine debris pollution linked to visitation in the southern great barrier reef, Australia. Mar Pollut Bull 117:239–246

Woodall LC, Sanchez-Vidal A, Canals M et al (2014) The deep sea is a major sink for microplastic debris. R Soc Open Sci 1:140317

Wright SL, Rowe D, Thompson RC, Galloway TS (2013) Microplastic ingestion decreases energy reserves in marine worms. Curr Biol 23:1031–1033

Zettler ER, Mincer TJ, Amaral-Zettler LA (2013) Life in the "plastisphere": microbial communities on plastic marine debris. Environ Sci Technol 47:7137–7146

Zhang L, Zhang S, Wang Y et al (2019) The spatial distribution of microplastic in the sands of a coral reef island in the South China Sea: comparisons of the fringing reef and atoll. Sci Total Env 688:780–786

Visual Methods for Monitoring Mesophotic-to-Deep Reefs and Animal Forests: Finding a Compromise Between Analytical Effort and Result Quality

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Abstract Visual methods based on remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) are increasingly used to study and monitor mesophotic-to-deep benthic marine ecosystems. To date, these techniques are frequently used to meet the requirements for benthic habitat mapping of most national and international directives and marine ecosystem management programs (e.g., Marine Strategy Framework Directive (MSFD) and OSPAR Convention), by supporting the exploration of taxonomical composition of biological communities, the identification of ecologically relevant habitat, and the identification of areas of priority for conservation. However, the processing of visual data is challenging in terms of analytical time, with automatic and semi-automatic methods that require ad hoc sampling strategies and/or instrumentation. Therefore, video survey analysis of benthic marine habitat is largely restricted to a limited subset of photograms, often extracted manually. By comparing video frame extractions performed at regular time and distance intervals, this chapter explores how ROV video subset methods may affect the estimation of the substrate cover extent and the taxonomical composition of the biological communities, with the aim to identify an efficient compromise between analytical effort and quality of results.

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1 Introduction

As the human footprint extends deeper into our oceans, information on the seafloor and associated biological communities is required for devising appropriate conservation actions to achieve national and international sustainability goals (e.g., Lundquist and Granek 2005; Davies et al. 2007; Micheli et al. 2013; Zampoukas et al. 2014; Henry and Roberts 2017; Danovaro et al. 2020; Manea et al. 2020). There is growing awareness that the mitigation of anthropic pressure on marine ecosystems (e.g., biodiversity loss, transformed food webs, and marine pollution) relies on a more efficient transfer of scientific knowledge to decision-makers (Cvitanovic et al. 2015).

The rapid development of underwater technologies and the concurrent acceleration in computing permit the gathering and handling of a huge quantity of data. For instance, remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) played a pivotal role for discovery, mapping, and detailed examination of ecosystems at depths that were unimaginable just decades ago (e.g., Cordes et al. 2007; Freiwald et al. 2009; Lundsten et al. 2010; Huvenne et al. 2011; Angeletti et al. 2014; Wynn et al. 2014; Correa et al. 2016; Vanreusel et al. 2016; Danovaro et al. 2017). Habitat mapping techniques are a powerful tool to collect raw information on marine benthic environments that is convertible to quantitative data and to date play a primary role in fulfilling the requirements of national and international directives and marine ecosystem management programs (e.g., Marine Strategy Framework Directive (MSFD) and OSPAR Convention). Typical applications include identifying habitats for priority of conservation (e.g., Fosså et al. 2002; Grasmueck et al. 2006; Bongaerts et al. 2010; Howell et al. 2010; Fabri et al. 2014; Rengstorf et al. 2014; Taviani et al. 2017, 2019; IUCN 2019; Angeletti et al. 2020a; Chaniotis et al. 2020; Prampolini et al. 2020), tracking biological community status providing species abundances and biodiversity indices (e.g., Norcross and Mueter 1999; Buhl-Mortensen et al. 2012; Ayma et al. 2016; Consoli et al. 2016; Trotter et al. 2019; Beccari et al. 2020), monitoring the efficacy of management interventions (fishery restricted areas (FRAs), marine protected areas (MPAs): Huvenne et al. 2016; Rowden et al. 2017; Innangi et al. 2019; Angeletti et al. 2020b among others), and reporting the overall environmental status of benthic ecosystems (e.g., Cánovas-Molina et al. 2016; Enrichetti et al. 2019; Fabri et al. 2019). Visual methods for monitoring benthic marine ecosystems based on ROV (or AUV) video surveys provide a relatively high precision in estimating biodiversity and habitat percentage cover (Savini et al. 2014, 2017; Grinyó et al. 2016; Conti et al. 2019) and represent permanent records allowing the comparison of surveys through time and from different areas (e.g., Lundsten et al. 2010; Langenkämper et al. 2019).

2 Processing Techniques of Benthic Visual Surveys

Most common methods for quantitative benthic cover estimation involve manual point-based approaches (Foster et al. 1991; Meese and Tomich 1992; Leonard and Clark 1993; Carleton and Done 1995) and region-based percentage estimations (Meese and Tomich 1992; Garrabou et al. 2002; Teixidó et al. 2011; Pech et al. 2004; Guinda et al. 2014). Automatic and semi-automatic methods have been tested for faster the analysis of benthic video recordings (Stokes and Deane 2009; Aguzzi et al. 2011), but their application is still labor-intensive or requires ad hoc instrumentation (Foglini et al. 2019; Robert et al. 2020). Some visual method applications need a certain degree of overlap among frames to ensure a complete seafloor representation (e.g., 3D reconstructions, Robert et al. 2020), while others avoid frame overlap to reduce analysis replications (Bo et al. 2014).

In the study of benthic habitats and biological communities, ROV video transects should be carried out along linear paths, navigating at constant speed and altitude from the seafloor (Huvenne et al. 2019). This is particularly important for monitoring purposes (e.g., MSFD program: Zampoukas et al. 2014), in order to guarantee a homogeneous representation of the investigated portion of the seafloor and allow the correct estimation of both habitat extents and community compositions (Eleftheriou and McIntyre 2005). However, ROV transect paths and navigation speeds may be altered by the need for higher detail, by the morphology of the investigated habitat, or by external factors (e.g., weather conditions, technical issues).

3 Frame-Based Video Subsamplings: A Methods Comparison

The plasticity of visual methods to study benthic habitats leaves the doors open to a great variety of analytical techniques. However, the analysis of visual data remains challenging in terms of analytical time, often forcing the analysis to only a limited subset of frames, extracted (often manually) at regular time intervals (e.g., Bo et al. 2014; Fabri et al. 2014; Cau et al. 2015).

Some major questions arise: does the video subsampling strategy influence the quality of results? What is an efficient compromise between analytical effort and results quality?

To explore the accuracy of frame-based methods, we compared the substrate cover estimates and the biological community taxonomical compositions obtained by the analyses of a subset of frames with those resulting from the analysis of the entire videos. We performed video subsamplings by extracting photograms at regular time (4, 10, and 30 s) or distance intervals (0.5, 1, and 3 m).

Three ROV dives were selected for this study from the MS16_II, MS17_II, and MS17_I oceanographic cruises carried out on *R/V Minerva Uno* (Table 1), in the framework of the Italian MSFD monitoring program. The video surveys explored

Table 1 ROV dive metadata

Location	ROV	Date	Start Lat. Long.	End Lat. Long.	Depth range (m)	Length (m)	Velocity (m/s)	DS (m/s)	Target
Amendolara Seamount	MS16_II_83	10/09/16	39°50′36.6″ 16°43′43.9″	39°50′50.4″ 16°43′43.9″	65–80	647.7	0.127	0.140	Coralligenous habitat
Santa Maria di Leuca	MS17_II_115	31/07/17	43°01′21″ 09°41′54.3″	43°01′31.5″ 09°41′47″	95–115	896.7	0.217	0.161	Mesophotic oyster reef
Corsica Channel	MS17_I_135	17/07/17	39°44′01.1″ 18°22′14.9″	39°44′15.5″ 18°22′06.8″	400–430	1041.5	0.212	0.158	Cold-water coral ecosystem

Location, date, target habitat, and water depth of the ROV dives discussed in the text

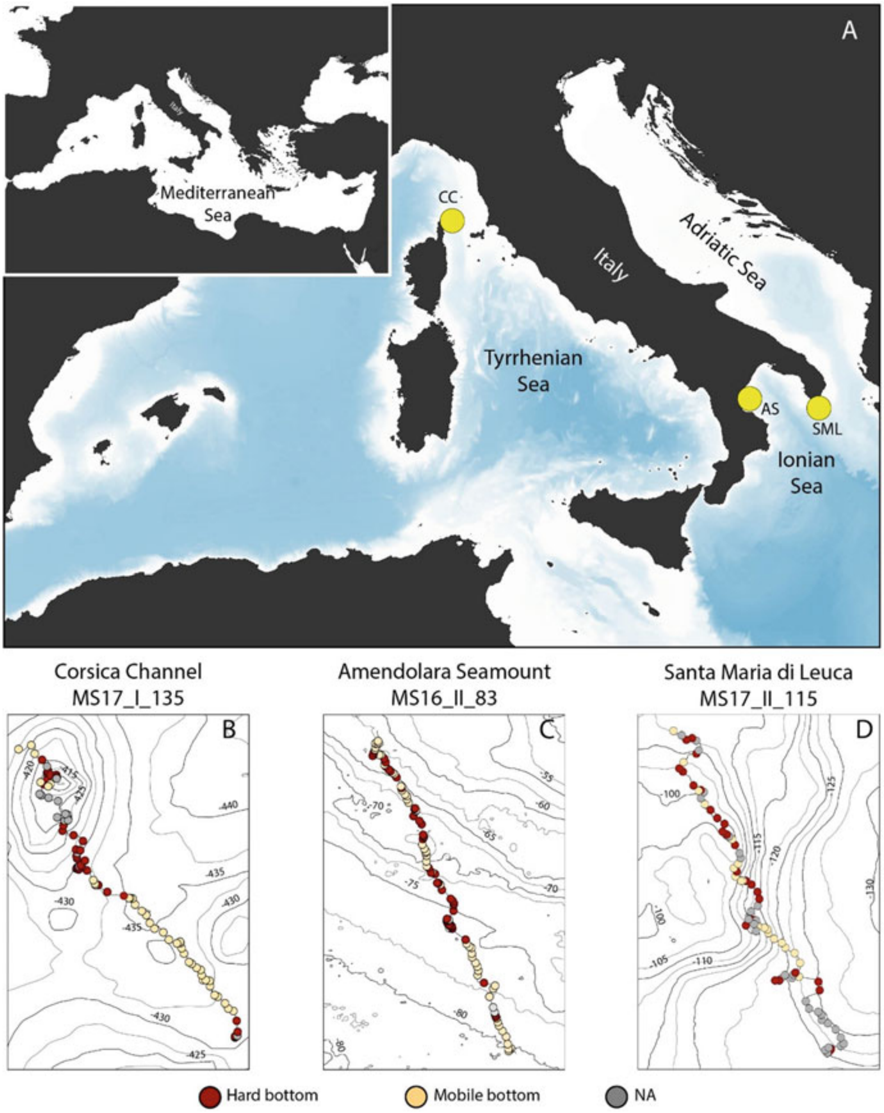


Fig. 1 (**a**) Map illustrating the locations of the ROV surveys used in the study; *CC* Corsica Channel, *AS* Amendolara Seamount, *SML* Santa Maria di Leuca. (**b**, **c**, and **d**) Detailed maps showing the ROV tracks and the substrate mapped by analyzing the entire videos. Bold contour lines stand for 5 m depth intervals; thin lines refer to 2.5 m

three gentle-slope habitats along the Italian margin (Fig. 1): a coralligenous formation between 65 and 80 m on the Amendolara Seamount in the Ionian Sea (Figs. 1a, b and 2A, B; Angeletti et al. 2017), a mesophotic oyster reef off Santa Maria di Leuca in the Ionian Sea between 95 and 115 m (Figs. 1a, c and 2C, D; Castellan et al. 2019;

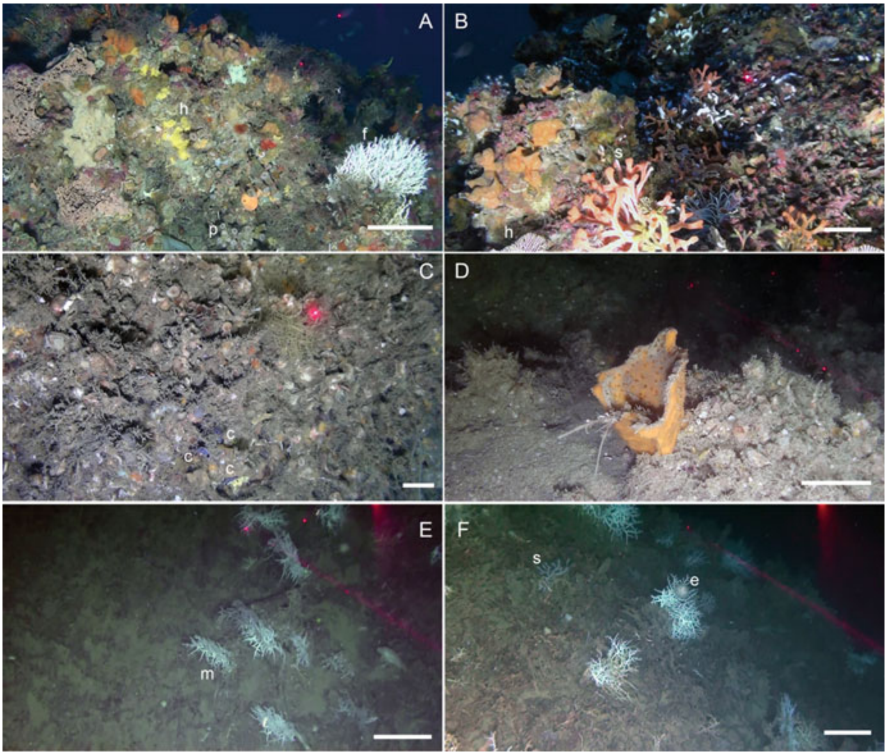


Fig. 2 Examples of the different habitats surveyed. (**A**–**B**) Coralligenous formation at the Amendolara Seamount showing intense faunal cover dominated by several sponges among which *Hexadella detritifera* (h) is easily recognizable and scleractinian corals such as *Phyllangia americana* (p) and *Filograna-Salmacina* complex (f) are also common findings; bar = 20 cm. Close-up (**B**) of coralligenous formation dominated by the bryozoans *Smittina cervicornis* (s) and *Hornera frondiculata* (h); bar = 5 cm. (**C**–**D**) Mesophotic reef dominated by *Neopycnodonte cochlear* at Monopoli. Note the tiny nudibranch *Hypselodoris tricolor* (c) grazing on *Neopycnodonte* shells; bar = 3 cm. The large undetermined orange sponge represents the mega-epifauna at this site; bar = 10 cm. (**E**–**F**) Cold-water coral mound at Corsica Channel site showing the colonial scleractinian *Madrepora oculata* (m) characterizing this site; bar = 20 cm. (**F**) The octocoral *Swiftia pallida* (s) co-occurs at this site, while the echinoid *Echinus melo* (e) is grazing on *M. oculata* framework; bar = 20 cm

Angeletti and Taviani 2020), and cold-water coral (CWC) mounds in the Corsica Channel located in the Tyrrhenian Sea at 400–430 m depth (Figs. 1a, d and 2E, F; Angeletti et al. 2020c).

ROV dives were conducted using a Pollux III (Global Electric Italiana) equipped with a low-resolution CCD video camera for navigation and a high-resolution (2304 × 1296 pixels) video camera. The ROV was equipped with an underwater acoustic tracking system that provided position and depth at 1 s intervals. The ROV velocity along the tracks was calculated as the ratio between the distance of the tracked positions and the relative time gap. Three parallel laser beams (with 20 cm separation) were mounted on the ROV providing a scale on the videos. Dives trackpoints were smoothed utilizing Adelie Video (© Ifremer) and ArcGIS (© ESRI) software. The Adelie Video tool "points to line" was used to produce a line-format track of ROV dives.

Video recordings were done maintaining ca. 2 m of altitude from the seafloor. In Station MS16_II_83, the mean survey speed was equal to 0.13 m/s, and in Station MS17_II_115, the average speed was 0.22 m/s, while in Station MS17_I_135, the ROV sailed at 0.21 m/s (Table 3).

The full-video analysis (hereafter "reference analysis") was performed by extracting one frame every second. The substrate cover was obtained by recording the changes in dominant substrate type, i.e., when a component was >50% in the video frame (Fig. 1b–d). The seafloor was classified as "Hard" (geological or biological hard structures), "Mobile" (soft bottoms), or "NA" (bottom not visible). The substrate covering extension was calculated using ArcGIS software.

Macro- and mega-benthic organisms were identified to the lowest possible taxonomic rank, counted and georeferenced by using Adelie Video software. Taxonomic classification followed the World Register of Marine Species database (WoRMS Editorial Board 2020). Finally, taxa unidentifiable at species level were categorized only as morpho-species or morphological categories (e.g., Angeletti et al. 2019; Santín et al. 2019 with references therein).

To test the efficiency of time-based (TB) subsampling methods, a frame every 4, 10, and 30 s was extracted using Adelie Video software. Frames were analyzed for taxonomical composition and substrate type following the methodology described above.

The intervals used for video subsampling the videos with distance-based (DB) methods were selected to obtain a number of extracted frames similar to those based on time intervals, allowing the comparison among tested methods. A point every 0.5 m, 1 m, and 3 m was generated along the plan view of the ROV tracks using the "Generate points along line" tool in ArcGIS software. The generated points were paired with the ROV tracks by means of the "Spatial Join" tool (Match option: Intersect; Search Radius: 0.05 m) in order to obtain the UTM time for each generated point. Frames were then extracted from video recordings matching the UTM times and analyzed for taxonomical composition and substrate coverings following the methods described above.

For each ROV video, the substrate extents and the number of taxa obtained by each methodology were compared to those resulting from the reference analysis. The percentage errors were calculated. The Kruskal-Wallis test and the post hoc Dunn's test were used to assess the differences in the percentage errors among the sampling intervals (4, 10, and 30 s and 0.5, 1, and 3 m) and subsampling methods (TB and DB). Statistical analyses were performed by using R software (R core team 2013).

With the aim of quantifying the number of overlapped frames, a unique serial ID number was assigned to frames extracted with the same technique showing a new section of seafloor. When adjacent frames duplicated portions of the seafloor (>70% of the frame), the same ID was allotted to those photograms. The ratio between the total number of frames and those presenting a unique ID allowed us to estimate the percentage of overlapping images.

3.1 Method Accuracy

3.1.1 Substrate Cover Extent

The reference analysis performed in Station MS16_II_83 revealed that “Hard” and “Mobile” substrate types almost equally composed the 647.7 m of explored seafloor, covering 44.9% (corresponding to 291.1 m) and 41.4% (286.3 m), respectively. The remaining 13.6% (88.3 m) of the transect was classified as “NA” (Fig. 3a; Table 2).

In Station MS17_II_115, the reference analysis detected “Hard” substrate for 53.7% (481.5 m) and “Mobile” for 30.9% (276.7 m), while 15.4% (138.4 m) was assigned to “NA” (Fig. 3b and Table 2).

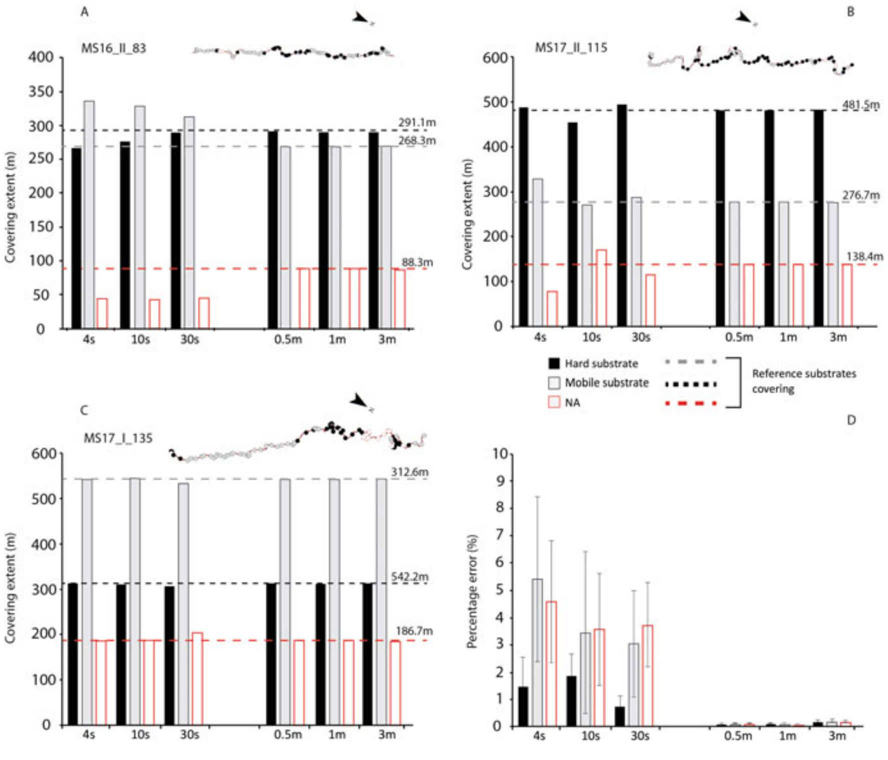


Fig. 3 (**a**–**c**) Bar plot showing the spatial cover extent of different substrate types calculated with the tested techniques. Dashed lines refer to extents calculated by analyzing the entire video footages and used as reference values. (**d**) Average percentage error in the estimation of substrate covering for each method. Error bars represent standard errors

Table 2 Comparative ability of time-based and distance-based video frame extraction methods to estimate substrate coverage and detect the taxonomic composition of biological communities in surveyed stations

	Method	Frames	Hard (m)	Err (%)	Mobile (m)	Err (%)	Uncl. (m)	Err (%)	Overlap (%)	Taxa	Ident. taxa (%)	Err (%)
MS16_II_83	Tot.	6840	291.1		268.3		88.3			50		
	4 s	1712	267.9	3.57	336.1	10.47	43.6	6.90	85.8	50	100	0
	10 s	684	276.5	2.26	328.9	9.35	42.3	7.10	67.3	48	96	4.00
	30 s	228	290.1	0.15	313.1	6.92	44.6	6.74	34.0	43	86	14.00
	0.5 m	1360	291.6	0.08	268.6	0.04	88.0	0.04	85.8	46	92	8.00
	1 m	680	291.1	0	269.1	0.12	88.0	0.04	67.3	45	90	10.00
	3 m	251	291.1	0	270.1	0.28	87.0	0.20	33.3	40	80	20.00
MS17_II_115	Tot.	5060	481.5		276.7		138.4			82		
	4 s	1264	487.6	0.68	329.2	5.85	78.1	6.73	28.1	71	86.59	13.41
	10 s	506	455.0	2.96	270.8	0.65	170.8	3.61	12.3	65	79.27	20.73
	30 s	169	494.6	1.45	287.5	1.21	114.6	2.66	1.5	49	59.76	40.24
	0.5 m	1486	481.6	0.01	276.6	0.01	138.5	0.01	36.7	74	90.24	9.76
	1 m	767	481.8	0.03	276.9	0.02	137.9	0.06	19.2	64	78.05	21.95
	3 m	257	482.8	0.14	275.9	0.09	137.9	0.06	4.1	55	67.07	32.93
MS17_I_135	Tot.	5418	312.6	30.01	542.2		186.7			26		
	4 s	1355	313.7	0.10	542.2	0.00	185.6	0.10	58.7	25	96.15	3.85
	10 s	541	310.0	0.25	544.8	0.24	186.7	0.01	41.7	21	80.77	19.23
	30 s	180	306.5	0.58	532.4	0.94	204.1	1.68	16.9	21	80.77	19.23
	0.5 m	1543	312.8	0.02	542.1	0.01	186.5	0.02	51.1	23	88.46	11.54
	1 m	834	312.3	0.02	542.1	0.01	187.0	0.03	35.6	22	84.62	15.38
	3 m	284	313.3	0.07	543.1	0.09	185.0	0.16	13.6	21	80.77	19.23

The number of frames extracted with each technique and the percentage of overlapped frames are also reported

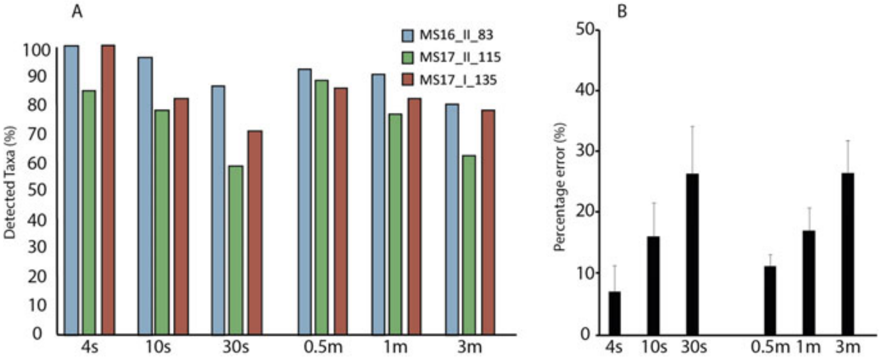


Fig. 4 (**a**) Bar plot reporting the percentage of taxa identified with the tested techniques in each video recording. (**b**) Average percentage error in detecting taxa composition of surveyed biological communities. Error bars represent standard errors

The longest ROV survey was Station MS17_I_135, with 1041.5 m of seafloor explored. The reference analysis classified 30% (312.6 m) of the transect as "Hard," the 52.1% (542.2 m) as "Mobile," and the 17.9% (186.7 m) as "NA" (Fig. 3c and Table 2).

The estimation of substrate cover performed by using TB methods reported strongly higher average percentage errors when compared to DB techniques. The "Hard" class reported percentage errors up to 1.82% ± 0.81 (SE), and the "Mobile" was incorrectly estimated with a maximum average error of 5.44% ± 3.03, while the "NA" was mainly underestimated with errors reaching 4.58% ± 2.24 with TB methods (Fig. 4d and Table 3).

On the contrary, DB methods showed average errors always below the 0.15%. The Kruskal-Wallis test proved the observed differences between TB and DB method accuracy, reporting a p-value <0.01.

3.1.2 Taxonomic Composition

The reference analysis of Station, exploring the coralligenous community of the Amendolara Seamount, led to the identification of $n = 50$ taxa (Table 4). All TB methods efficiently detected the taxonomical composition at this site, showing a performance decrease with wider subsampling time intervals (Fig. 4a and Table 2). The 4 s interval method extracted 1712 frames for taxonomical analysis (Table 2), which resulted in the identification of 100% of taxa ($n = 50$), with respect to the reference analysis. The lower number of photograms extracted by using 10 s and 30 s intervals (684 and 228, respectively) slightly reduced the taxa detection accuracy, with 10 s method reporting 96% ($n = 48$) of total taxa and 86% ($n = 43$) identified by 30 s interval selection. Although the DB methods selected about the same number of frames (Table 2), the percentages of detected taxa were lower when compared to time interval methods: 92% ($n = 46$) were identified with 0.5 m intervals and 90%

Table 3 The average percentage and standard errors in the estimation of substrate coverage and community composition detection for each tested technique

	Hard		Mobile		Uncl.		Frames		Overlap		Taxa identified	
Method	Err (%)	ES	Err (%)	ES	Err (%)	ES	Qnt.	ES	(%)	ES	Err (%)	ES
4 s	1.45	1.07	5.44	3.03	4.58	2.24	1443.67	136.71	57.56	16.67	7.29	4.17
10 s	1.82	0.81	3.41	2.97	3.57	2.05	577.00	54.45	40.45	15.90	15.97	5.99
30 s	0.73	0.38	3.02	1.95	3.69	1.55	192.33	18.11	17.46	9.40	25.73	7.98
0.5 m	0.04	0.02	0.02	0.01	0.02	0.01	1463.00	54.06	57.88	14.55	11.22	1.98
1 m	0.02	0.01	0.05	0.04	0.04	0.01	760.33	44.58	40.71	14.09	17.14	3.79
3 m	0.07	0.04	0.15	0.06	0.14	0.04	264.00	10.15	17.03	8.60	25.32	4.26

The average number of frames extracted and percentage of overlapped frames are also reported

Table 4 List of taxa identified by analyzing the ROV videos

Phylum	Taxa	AS	4 s	10 s	30 s	0.5 m	1 m	3 m
Chlorophyta	sp. 1	10	v	v	v	v	v	v
	Palmophyllum crassum	5	v	v	v	v	v	v
Foraminifera	*Miniacina miniacea*	21	v	v	v	v	v	v
Porifera	*Agelas oroides*	6	v	v	v	v	v	v
	Alypsina sp.	11	v	v	v			
	Demospongiae sp. 1	18	v	v	v	v	v	v
	Demospongiae sp. 2	8	v	v	v	v	v	v
	Demospongiae sp. 3	5	v	v		v	v	
	Demospongiae sp. 4	18	v	v	v	v	v	v
	Demospongiae sp. 5	5	v	v	v			
	Demospongiae sp. 6	61	v	v	v	v	v	v
	Haliclona sp. 1	63	v	v	v			
	Hexadella cf. *dedritifera*	48	v	v	v	v	v	v
	Hexadella racovitzai	29	v	v	v	v	v	v
	Pleraplysilla spinifera	3	v	v	v	v	v	v
	Spongia officinalis	10	v	v	v	v	v	v
Cnidaria	Actinaria sp.	1	v	v	v	v	v	v
	Alcyonium sp.	3	v	v	v	v	v	v
	Balanophyllia sp.	1	v	v	v	v	v	v
	Hydrozoa sp. 1	6	v	v		v	v	
	Hydrozoa sp. 2	41	v	v	v	v	v	v
	Hydrozoa sp. 3	134	v	v	v	v	v	v
	Phyllangia americana mouchezii	281	v	v	v	v	v	v
	Polycyathus pulchellus	44	v	v		v		
Annelida	*Bonellia viridis*	2	v	v		v	v	
	Filograna-Salmacina complex	9	v	v	v	v	v	v
	Polychaeta sp.	55	v	v	v	v	v	v
	Sabellaria sp.	26	v	v	v	v	v	v
	Vermiliopsis sp.	1	v	v	v	v	v	v
Mollusca	*Bolma rugosa*	1	v	v	v	v	v	v
	Gastropoda sp.	2	v	v	v	v	v	v
	Nudibranchia sp.	2	v	v	v	v	v	v
	Pteria hirundo	1	v	v	v	v	v	v
Arthropoda	Paguroidea sp.	1	v			v	v	v
	Palinurus elephas	2	v	v		v	v	
Bryozoa	sp. 1	169	v	v	v	v	v	v
	Cellaria sp.	85	v	v	v	v	v	v
	Hornera frondiculata	55	v	v	v	v	v	v
	Pentapora fascialis	62	v	v	v	v	v	v
	Reteporella sp.	19	v	v	v	v	v	v
	Schizomavella mamillata	582	v	v	v	v	v	v
	Smittina cervicornis	55	v	v	v	v	v	v

(continued)

Table 4 (continued)

Phylum	Taxa	AS	4 s	10 s	30 s	0.5 m	1 m	3 m
Echinodermata	*Centrostephanus longispinus*	5	v	v	v	v	v	v
	Echinaster sepositus	7	v	v	v	v	v	v
	Ophiuroidea sp.	1	v	v	v			
	Peltaster placenta	4	v	v	v	v	v	v
Brachiopoda	*Megerlia truncata*	8	v	v	v	v	v	v
Chordata	Ascidiacea sp.	1	v			v	v	
	Didemnidae sp.	4	v	v	v	v	v	v
	Halocynthia papillosa	4	v	v	v	v	v	v
Phylum	**Taxa**	**SML**	**4 s**	**10s**	**30s**	**0.5 m**	**1 m**	**3 m**
Porifera	*Agelas oroides*	2	v			v	v	
	Aplysina sp.	1	v			v		
	Axinella sp.	11	v	v	v	v	v	
	Chondrosia sp.	2	v			v	v	
	Chondrosia reniformis	1	v					
	Demospongiae sp. 1	4	v	v		v	v	v
	Demospongiae sp. 2	10	v	v	v	v	v	v
	Demospongiae sp. 4	22	v	v		v	v	v
	Demospongiae sp. 5	58	v	v	v	v	v	v
	Demospongiae sp. 7	2		v	v			
	Demospongiae sp. 8	60	v	v	v	v	v	v
	Demospongiae sp. 9	59	v	v	v	v	v	v
	Demospongiae sp. 10	13	v	v	v	v	v	v
	Geodia sp.	1	v	v		v	v	v
	Haliclona sp. 1	309	v	v	v	v	v	v
	Haliclona sp. 2	10	v	v		v	v	v
	Haliclona sp. 3	1		v	v	v	v	v
	Haliclona sp. 4	2	v	v	v	v	v	v
	Haliclona cf. *magna*	2	v			v		
	Hamacantha falcula	10				v		
	Hexadella cf. *dedritifera*	97	v	v	v	v	v	v
	Hexadella racovitzai	181	v	v	v	v	v	v
	Hymedesmiidae sp.	1	v	v	v	v	v	
	Pachastrella monilifera	28	v	v	v	v	v	v
	Petrosia sp.	11	v	v	v	v	v	v
	Poecillastra compressa	91	v	v	v	v	v	v
	Spongia agaricina	1	v	v	v	v	v	v
Cnidaria	*Balanophyllia* sp.	2		v	v			
	Caryophylliidae sp.	1042	v	v	v	v	v	v
	Caryophyllia sp.	2	v			v	v	
	Dendrophyllia cornigera	7	v	v	v	v	v	v
	Eudendrium sp.	1	v	v	v	v	v	v

(continued)

Table 4 (continued)

Phylum	Taxa	AS	4 s	10 s	30 s	0.5 m	1 m	3 m
	Halecium cf. *halecium*	9	v	v		v	v	v
	Nemertesia antennina	2						
	Paramuricea clavata	8	v	v	v	v	v	v
	Sertularella sp.	105	v	v	v	v	v	v
	Sertulariidae sp.	7						
Annelida	*Bonellia viridis*	24	v	v	v	v	v	v
	Filograna-Salmacina complex	161	v	v	v	v	v	v
	Polychaeta sp.	26	v	v	v	v	v	v
	Serpulidae sp.	2				v		
Mollusca	Chromodorididae sp.	2				v		
	Gastropoda sp.	1						
	Hypselodoris tricolor	3	v	v	v	v		
	Neopycnodonte cochlear	1	v			v	v	v
	cf. *Ostrea* sp.	1	v	v	v	v	v	v
Arthropoda	Crustacea sp.	4	v	v	v	v	v	v
	Munida sp.	2	v	v		v	v	
	Paguroidea sp.	2	v	v	v	v	v	v
	Palinurus elephas	1	v	v		v	v	v
Bryozoa	sp. 2	74	v	v	v	v	v	v
	sp. 3	6	v	v	v	v	v	
	sp. 4	5	v	v		v	v	v
	sp. 5	9	v	v		v	v	v
	sp. 6	25	v	v		v	v	v
	sp. 7	12	v	v	v	v	v	
	sp. 8	1				v	v	v
	sp. 9	5	v	v	v	v	v	v
	Cellaria sp.	5	v	v		v	v	v
	Hacelia attenuata	2	v			v		
	Hornera frondiculata	4	v	v	v	v	v	v
	Reteporella sp.	13	v	v	v	v	v	v
	Schizomavella mamillata	1250	v	v	v	v	v	v
	Smittina cervicornis	34	v	v	v	v	v	v
Echinodermata	*Antedon* sp.	1	v			v		
	Antedon mediterranea	17	v	v	v	v	v	v
	Asteroidea sp.	1	v					
	Centrostephanus longispinus	1	v	v				
	Cidaris cidaris	8	v	v	v	v	v	v
	Crinoidea sp.	4	v	v	v	v	v	v

(continued)

Table 4 (continued)

Phylum	Taxa	AS	4 s	10 s	30 s	0.5 m	1 m	3 m
	Coscinasterias tenuispina	1	v	v	v	v	v	
	Echinaster sepositus	21	v	v	v	v	v	v
	Ophiuroidea sp.	3	v	v	v	v	v	v
	Peltaster placenta	20	v	v	v	v	v	v
Brachiopoda	*Megerlia truncata*	3	v	v		v	v	v
Chordata	Didemnidae sp.	11	v	v	v	v	v	v
	Halocynthia papillosa	22	v	v	v	v	v	v
	Lappanella fasciata	3	v	v		v		
	Muraena helena	1		v	v	v	v	v
	Phycis phycis	2	v	v	v	v	v	v
	Scorpaena sp.	3	v	v		v	v	v
	Scorpaena scrofa	1	v	v		v	v	
Phylum	**Taxa**	**CC**	**4 s**	**10 s**	**30 s**	**0.5 m**	**1 m**	**3 m**
Porifera	*Haliclona* sp. 2	86	v	v	v	v	v	v
	Pachastrella monilifera	119	v	v	v	v	v	v
	Phorbas tenacior	17	v	v	v	v	v	v
	Sympagella delauzei	2	v	v	v	v	v	v
Cnidaria	Actinaria sp.	1						
	Acanthogorgia hirsuta	34	v	v	v	v	v	v
	Antipathes dichotoma	2	v	v	v	v	v	v
	Caryophylliidae sp.	679	v	v	v	v	v	v
	Desmophyllum dianthus	67	v	v	v	v	v	v
	Desmophyllum pertusum	39	v	v	v	v	v	v
	Madrepora oculata	395	v	v	v	v	v	v
	Muriceides lepida	2	v	v	v	v	v	v
	Parantipathes larix	2	v	v	v	v	v	v
	Protoptilum carpenteri	1	v			v	v	
	Swiftia dubia	127	v	v	v	v	v	v
Annelida	*Bonellia viridis*	7	v	v	v	v	v	v
Arthropoda	*Anamathia rissoana*	1	v	v	v	v	v	v
	Munida sp.	24	v	v	v	v	v	v
	Paguridae sp.	1	v					
	Plesionika martia	1	v	v	v	v	v	v
Echinodermata	*Cidaris cidaris*	71	v	v	v	v	v	v
	Echinus melo	1	v			v		
Chordata	*Gadiculus argenteus*	1	v					
	Helicolenus dactylopterus	3	v	v	v	v	v	v
	Lepidorhombus boscii	1	v	v	v	v	v	v
	Polyprion americanus	1	v	v	v	v	v	v

For each ROV station, the total quantity of each taxon is indicated. Detected taxa for TB and DB methodology are indicated in columns; note that there are a few taxa documented by the video analysis that were not recorded by the frame analysis methodologies

($n = 45$) by using 1 m intervals, and 80% ($n = 40$) were detected with intervals of 3 m (Fig. 4a).

Station MS17_II_115 explored a mesophotic oyster reef habitat hosting highly diverse biological community where reference analysis identified $n = 82$ taxa. The 0.5 m method showed the highest accuracy, detecting $n = 74$ taxa (90%). The 10 s and 1 m methods reported similar results, identifying $n = 65$ (79%) and $n = 64$ taxa (78%), respectively, while the 3 m interval frame selections showed a higher accuracy ($n = 55$, 67%) when compared to those based on 30 s extractions ($n = 49$, 60%) (Fig. 4a).

Reference analysis of Station MS17_I_135 recorded $n = 26$ taxa surveying the CWC mounds. TB and DB methods showed similar performances (Fig. 4a and Table 2). The 0.5 m method recognized 88% ($n = 23$) of total taxa, while the 4 s method detected 96% ($n = 25$). The selection of frames every 1 m or 10 s gave similar results, reporting 22 (85%) and 21 (81%) taxa, and the efficiencies of 30 s and 3 m interval methods were equal (21 taxa each, 81%).

On average, the 4 s interval missed 7.29% ± 4.82 of total taxa, 15.97% ± 5.99 were not detected extracting frames at the 10 s interval, and the 30 s interval showed an error of 25.73% ± 7.98. DB methods reported lower accuracies: the 0.5 m method reported an error of 11.22% ± 1.98, while 17.14% ± 3.79 of total taxa were not identified using 1 m intervals, and the 3 m technique missed 25.31% ± 4.26 of the taxa (Fig. 4b).

Although no significant differences among sampling intervals and between TB and DB methods were detected by the Kruskal-Wallis test, the results showed that small extraction intervals and, thus, a larger amount of frames extracted were more efficient in the detection of taxa composition.

3.1.3 The Influence of Survey Velocity

Maintenance of a regular velocity during visual surveys is among the major factors to guarantee a homogenous recording of the seafloor (Huvenne et al. 2019) and ensure the detection and identification of features of interest by operators. The ROV navigation velocity, however, may largely vary along the tracks in relation to technical issues (i.e., navigation against current) and the need for higher-detailed recordings. When using video subsampling techniques based on time interval, the variation in ROV velocity may influence frames distribution along the transects, over-sampling in correspondence of ROV slowdown, and under-sampling when the vehicle velocity increases (Fig. 5). Frame density extracted with TB methods was different when compared to DB methods (Fig. 6). An irregular survey velocity along the transect could have positive unintended advantages: the higher number of frames displaying portions of seafloor characterized by highly dense communities populating hard bottoms or hosting specimens that are more difficult to detect (such as infauna inhabiting mobile substrates) can allow a more precise description of the community composition. During visual surveys, specimens may be not clearly recorded or visible but not easily identifiable in a few frames. Extracting more

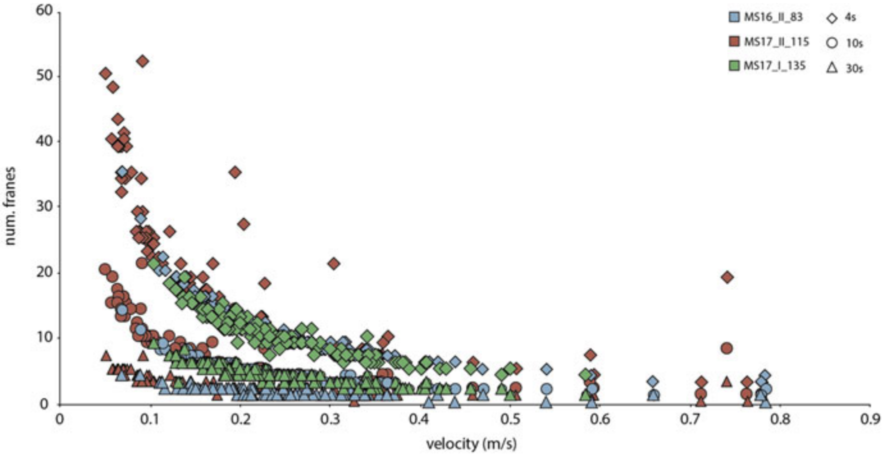


Fig. 5 Scatter plot showing the relationship between survey velocity and number of frames extracted with each method

frames displaying the same specimens could increase the probability of having clearer images, facilitating the taxonomical identification. The comparison between the accuracy of TB methods in the detection of the taxonomical community composition and the coefficient of variation of velocity (CV, used as a proxy of ROV slowdown in correspondence of features of interest, Fig. 7a) suggests that the effect of speed variation on the taxonomical description may be related to the morphology of the habitat explored (e.g., Robert et al. 2020). The highest errors were registered in survey MS17_II_115, which presented the lowest number of ROV slowdowns along the transect (lowest CV value) and the highest velocity. The accuracy showed by TB methods in Station MS16_I_83, thus, suggests that a lower speed and a higher amount of slowdown along the transects may facilitate the detection of the taxonomical composition of biological communities in situations of patchily distributed habitats such as coralligenous outcrops. On the contrary, a regular velocity along the survey transect may instead be sufficient to correctly identify the community composition when exploring large habitat extensions, as the case of MS17_I_135.

Moreover, survey velocity plays an important role in the taxonomical identification accuracy of specimens by influencing the number of overlapped photograms. A larger amount of the latter was, indeed, documented in the slower surveys (Fig. 7b) that reported the higher community composition detection accuracies (Pearson correlation index: $p = 0.86$, Fig. 7c). Percentage overlap decreased with wider sampling intervals in both TM and DB method correlating with a decrease also in the accuracy of community composition detection. Although having fixed spatial intervals between frames along the track, DB selections showed similar or even higher degrees of overlap when compared to TB methods (Table 2). In some segments of the survey, the ROV moved for a few meters, turning around features of interest to collect more detailed images. Therefore, even frames extracted with an

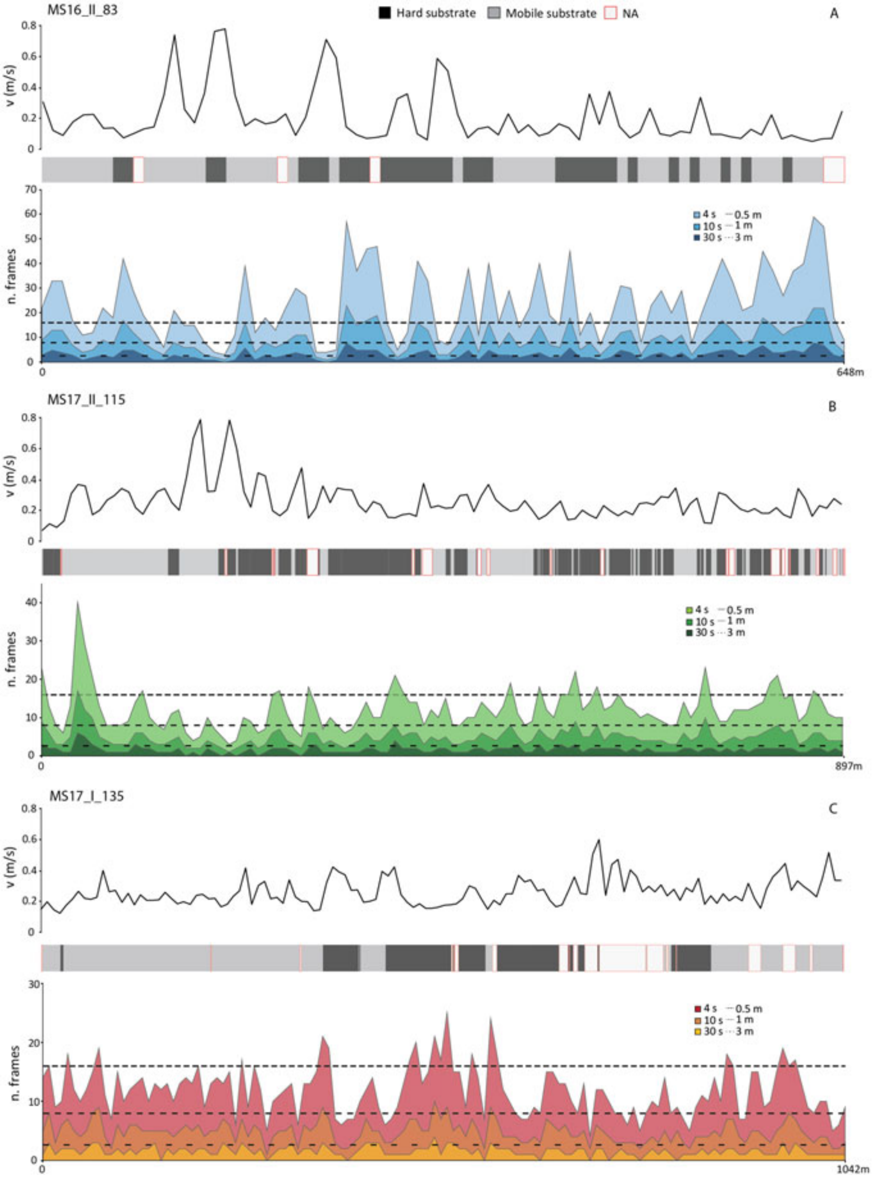
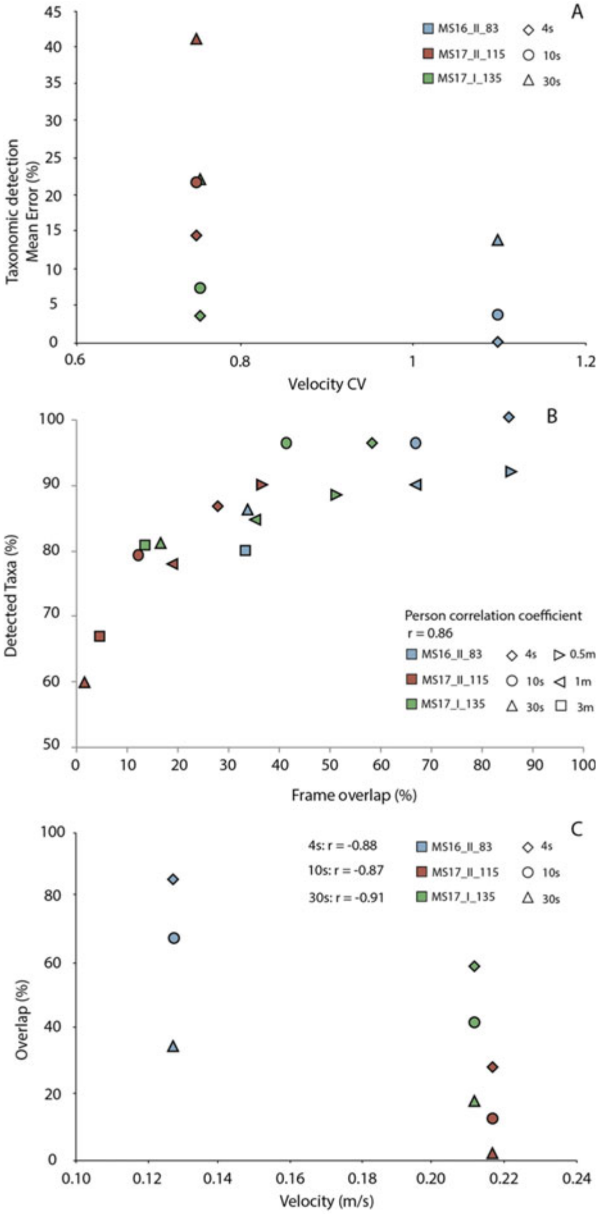


Fig. 6 (**a**, **b**, **c**) The figure shows the ROV velocity variation and the spatial distribution of frames extracted with tested techniques along the analyzed ROV transects. Colored bars represent the different substrate types characterizing the survey transect. Hard substrate, dark gray bars; mobile substrate, light gray bars; NA, white bars with red borders. Color distributions refer to frame densities obtained with the TB methods, while dashed lines represent frame distributions from the DB methods

Fig. 7 (**a**) Scatter plot of the mean percentage error in detecting the taxonomical composition of biological communities resulting from the TB methods vs. the coefficient of variation of survey velocity. The latter was used as proxy of the variation of ROV velocity along the transect. (**b**) Scatter plot showing the significant positive correlation between the percentage of overlapped frames and percentage of taxa detected with each method. (**c**) Plot displaying the significant negative relationship between survey velocity and percentage of overlapped frames extracted with TB methods



interval of 3 m displayed the same portion of the seafloor, producing the higher number of overlapped frames observed. This may potentially have concurred to obtain only slightly lower values of accuracies in community composition detection shown by DB methods when compared to TB values.

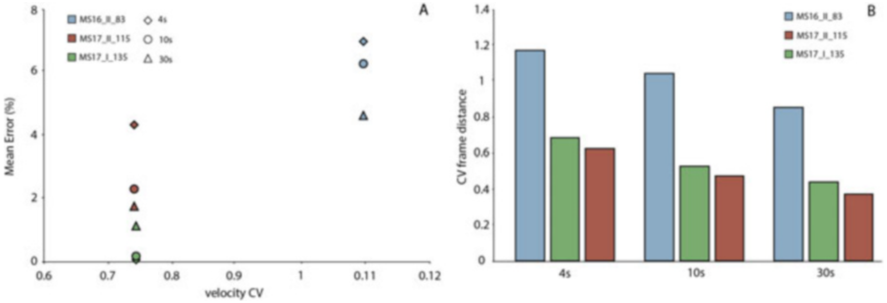


Fig. 8 (**a**) Scatter plot displaying the significant positive correlation between the mean percentage error in estimating the substrate covering extent reported in TB methods and the coefficient of variation of survey speed. (**b**) Bar plot showing the decrease of the variability of distance between adjacent frames with wider sampling TB intervals

However, the survey speed and its variation along the transect may not have only positive or neutral consequences. TB methods show low accuracies in the estimation of substrate covering, with respect to DB methods. The coefficient of variation (CV) of speed was, indeed, positively correlated ($p = 0.83$) with the average percentage error in the substrate cover estimation reported by each tested interval (Fig. 8a). In patchily distributed habitats, performing the survey at high speed (i.e., Station MS17_II_115) or frequently varying the velocity along the transect (i.e., Station MS16_II_83) may influence the correct recording of seafloor sections in correspondence of habitat changes, potentially preventing the accurate mapping of their boundaries. On the contrary, in situations of large habitat extensions (Station MS17_I_135), maintaining a regular velocity along the transect may ensure an accurate estimation of substrate cover, with a corresponding decrease in the accuracy when using wider sampling intervals. In MS16_II_83 and MS17_II_115 stations, however, the error in substrates extension detection shows a counter-intuitive trend, reporting a decrease of error with wider sampling intervals (Table 3). The analysis of the coefficient of variation (CV) of the distances among frames, representing the variability of the distance between adjacent photograms, provides a potential explanation, showing a decrease with higher time intervals (Fig. 8b). In TB methods, the increase of sampling interval reduced the variation in the distance among the extracted frames, leading to a more homogenous distribution of photograms along the transect. The use of wider sampling intervals in stations MS16_II_83 and MS17_II_115 may potentially have concurred in reducing the negative influence of the survey speed on the substrates extents estimation.

3.2 *Method Strengths and Weaknesses*

The choice of the video frame extraction technique for the study of benthic marine ecosystems plays a pivotal role in governing the required analytic effort and, contemporarily, in ensuring the high quality of results. Nevertheless, the selection of the most appropriate frame extraction technique is strongly linked with data collection modalities. Our results showed that variations in ROV speed during the survey influence subsampling methodologies based on time intervals. Alternation of ROV slowdowns and speedups can potentially influence the precise mapping of the spatial limits of the different categories. The variation of survey velocity was, indeed, positively correlated with the error percentages in the estimations of substrate coverings, leading to an increased uncertainty of TB methods when dealing with habitats' extent estimates. Maintaining a regular survey speed is of a paramount importance in ensuring a high efficiency in the substrate cover mapping. However, in situations with large survey velocity fluctuations, the use of wider sampling intervals may potentially reduce the negative influence of survey speed variations on the estimation of the habitat's extents.

On the contrary, DB techniques showed higher accuracy in the estimation of substrate cover extent compared to TB, suggesting that frame extractions based on distance intervals are not affected by ROV navigation speed. The maximum percentage error of 0.3% for DB methods (Table 2) ensures higher confidence in the estimation of substrate cover extents, promoting these techniques as the most appropriate for this purpose.

However, habitat coverage is just one of the applications of visual survey methods. The analysis of community taxonomical compositions is fundamental in the framework of monitoring plans and directives, serving as the foundation for the evaluation of ecosystem status and functioning (e.g., Di Camillo et al. 2013; Grinyó et al. 2016; Chaniotis et al. 2020). TB methods showed higher efficiencies in detecting community's taxonomical composition when compared to DB techniques extracting a similar number of frames.

An irregular survey speed along the track may lead to both a larger number of photograms and a higher amount of overlapped frames extracted with TB methods in correspondence of areas hosting highly dense communities, increasing the accuracy of these methods in the detection of the taxonomic composition. Consequently, the evidence provided suggest that TB methods represent the best approaches for the description of communities' taxonomical composition, especially by using 4 s or 10 s intervals, which showed the lower estimation errors.

However, a larger dimension of frames subsets corresponded to higher taxa detection efficacies in both tested methodologies. But how much does it cost in terms of time?

On average, the 10 s and 1 m techniques missed 15.97% ± 5.99 and 17.14% ± 3.79 of total taxa from the analysis of 577 ± 54.45 and 760.33 ± 44.58 frames (Table 3), respectively, and with overlapping degrees close to 40%. Methodologies with the lower extraction intervals, 4 s and 0.5 m, showed higher accuracies in detecting the taxonomical composition of the communities (percentage errors: 7.29% ± 4.82 and 11.22% ± 1.98, respectively, Table 3), with an overlapping degrees of ca. 57%, and 1443.67 ± 136.71 and 1463 ± 54.06 extracted frames. Summing up, doubling of the frame number and, thus, of the analytical effort ensured a taxa identification error decrease of ca. 9% with the 4 s technique and ca. 6% with 0.5 m intervals. These accuracies' increases are crucial for monitoring and experimental purposes, providing precise information on species abundances and the detection of rare taxa. Therefore, when a complete reporting of community composition is not required, intermediate-width frame extraction intervals (i.e., 10 s and 1 m) strongly reduce the analytical efforts in analyzing video surveys guaranteeing a relatively small error in the taxa detection.

Nevertheless, the technique for the analysis of benthic visual recordings collected with unmanned vehicles is related to the aims and the characteristics of the survey. Distance-based (DB) frame extraction methods provided a much higher efficiency in the estimation of the cover extent of the different substrate types, not being affected by vehicle speed variations during the sampling. On the contrary, the increase of frame density and overlapping degree in correspondence of features of interest partially explains the higher performances in documenting the biological community composition showed by time-based (TB) methods.

The recommendations provided are not meant to be a "one-size-fits-all" solution.

For instance, mesophotic-to-deep habitats may occur in vertical or steeply sloping bottoms where the GPS tracking position may not change substantially along the transects. In these situations, a homogenous representation of the explored seafloor in the final frame subset produced by using DB intervals based on plan view of the ROV track may result challenging. The application of DB methods on habitat of steeply sloping bottoms requires ad hoc techniques, such as the transect visualization and point generation along the track in 3D environments.

The comparable number of frames extracted by both TB and DB low, intermediate, and wide intervals, coupled with the percentage uncertainties in estimating the substrate cover and the taxonomical composition of biological communities provided by the results reported in this chapter, provides the context from which to choose the most efficient techniques for the purposes of analysis (e.g., TB methods for taxonomical composition detection and DB for substrate covering estimation), ensuring the comparison of surveys performed in different areas or time windows.

3.3 Future Directions

The wide range of advantages offered by remotely operated and autonomous vehicles, such as the possibility of high-definition mapping of biological communities and habitats at previously inaccessible depths, together with the rapid technological developments in the field and their increasing availability has enabled an increased use of these methods in the study and monitoring of benthic marine ecosystems. Visual recordings can provide information on substrate types, habitat architecture and biological community composition, allowing also to explore the relationships among organisms (Mueller et al. 2013). Despite the ease of collecting georeferenced image and videos by using underwater visual techniques, the analysis of images still typically requires manual processing by an expert in taxonomic identification. Therefore, new methods to process visual surveys faster are becoming protagonists. In the last decade, the use of automatic and semi-automatic methods to analyze benthic video recordings has become more frequent: machine learning and deep learning techniques for automated feature detection (e.g., Stokes and Deane 2009; Aguzzi et al. 2011; Teixidó et al. 2011), photogrammetric habitat reconstructions for the study of spatial patterns of assemblages on vertical walls (e.g., Robert et al. 2020 among others), and hyperspectral imaging for the taxonomic identification of benthic megafauna (Johnsen et al. 2016; Dumke et al. 2018; Foglini et al. 2019) are just a few of the recently implemented techniques. Thanks to these new intelligent and adaptive methods, it can be expected that the volume of high-resolution seabed mapping data will increase rapidly in the near future, opening exciting opportunities for new insights in mesophotic-to-deep ecology and consolidating the integration between automatic methods and scientific knowledge.

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References

Aguzzi J, Costa C, Robert K, Matabos M, Antonucci F, Juniper SK, Menesatti P (2011) Automated image analysis for the detection of benthic crustaceans and bacterial mat coverage using the VENUS undersea cabled network. Sensors 11:10534–10556. https://doi.org/10.3390/s111110534

Angeletti L, Taviani M (2020) Offshore *Neopycnodonte* oyster reefs in the Mediterranean Sea. Diversity 12:92. https://doi.org/10.3390/d12030092

Angeletti L, Taviani M, Canese S, Foglini F, Mastrototaro F, Argnani A, Trincardi F, Bakran-Petricioli T, Ceregato A, Chimienti G (2014) New deep-water cnidarian sites in the southern Adriatic Sea. Mediterr Mar Sci 263–273

Angeletti L, Basso D, Bavestrello G, Bo M, Bracchi V, D'Ambrosio P, D'Onghia G, Fraschetti S, Grande V, Guarnieri G, Maiorano P, Savini A, Rizzo L, Taviani M (2017) Sottoprogramma 2.2 Monitoraggio dell'estensione dell'habitat a coralligeno. Giugno 2017:1–64. Unpublished Project Report.

Angeletti L, Bargain A, Campiani E, Foglini F, Grande V, Leidi E, Mercorella A, Prampolini M, Taviani M (2019) Cold-water coral habitat mapping in the Mediterranean Sea: methodologies and perspectives. In: Orejas C, Jiménez C (eds) Mediterranean cold-water corals: past, present and future: understanding the deep-sea realms of coral. Springer, Cham, pp 173–189

Angeletti L, Canese S, Cardone F, Castellan G, Foglini F, Taviani M (2020a) A brachiopod biotope associated with rocky bottoms at the shelf break in the Central Mediterranean Sea: geobiological traits and conservation aspects. Aquat Conserv: Mar Freshw Ecosyst 30:402–411. https://doi.org/10.1002/aqc.3255

Angeletti L, Prampolini M, Foglini F, Grande V, Taviani M (2020b) Cold-water coral habitat in the Bari Canyon system, Southern Adriatic Sea (Mediterranean Sea). In: Harris PT, Baker E (eds) Seafloor geomorphology as benthic habitat, 2nd edn. Elsevier, pp 811–824

Angeletti L, Castellan G, Montagna P, Remia A, Taviani M (2020c) The Corsica channel cold water Coral Province (Mediterranean Sea). Front Mar Sci. https://doi.org/10.3389/fmars.2020.00661

Ayma A, Aguzzi J, Canals M, Lastras G, Bahamon N, Mecho A, Company JB (2016) Comparison between ROV video and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the northwestern Mediterranean Sea with observations on behavioural reactions of target species. Deep-Sea Res Pt I 114:149–159. https://doi.org/10.1016/j.dsr.2016.05.013

Beccari V, Basso D, Spazzaferri S, Rüggeberg A, Neuman A, Makovsky Y (2020) Preliminary video-spatial analysis of cold seep bivalve beds at the base of the continental slope of Israel (Palmahim disturbance). Deep-Sea Res Pt II 171:104664. https://doi.org/10.1016/j.dsr2.2019.104664

Bo M, Bava S, Canese S, Angiolillo M, Cattaneo-Vietti R, Bavestrello G (2014) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327. https://doi.org/10.1007/s00338-009-0581-x

Buhl-Mortensen L, Buhl-Mortensen P, Dolan MFJ, Dannheim J, Bellec V, Holte B (2012) Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685:191–219. https://doi.org/10.1007/s10750-011-0988-6

Cánovas-Molina A, Montefalcone M, Bavestrello G, Cau A, Bianchi CN, Morri C, Canese S, Bo M (2016) A new ecological index for the status of mesophotic megabenthic assemblages in the Mediterranean based on ROV photography and video footage. Cont Shelf Res 121:13–20. https://doi.org/10.1016/j.csr.2016.01.008

Carleton JH, Done TJ (1995) Quantitative video sampling of coral reef benthos: large-scale application. Coral Reef 14:35–46. https://doi.org/10.1007/BF00304070

Castellan G, Angeletti L, Taviani M, Montagna P (2019) The yellow coral *Dendrophyllia cornigera* in a warming ocean. Front Mar Sci 6:692. https://doi.org/10.3389/fmars.2019.00692

Cau A, Follesa MC, Moccia D, Alvito A, Bo M, Angiolillo M, Canese S, Paliaga EM, Orrù PE, Sacco F, Cannas R (2015) Deepwater corals biodiversity along roche du large ecosystems with different habitat complexity along the South Sardinia continental margin (CW Mediterranean Sea). Mar Biol 162:1865–1878. https://doi.org/10.1007/s00227-015-2718-5

Chaniotis PD, Robson LM, Lemasson AJ, Cornthwaite AL, Howell KL (2020) UK deep-sea conservation: progress, lessons learned, and actions for the future. Aquat Conserv: Mar Freshw Ecosyst 30:375–393. https://doi.org/10.1002/aqc.3243

Consoli P, Esposito V, Battaglia P, Altobelli C, Perzia P, Romeo T, Canese S, Andaloro F (2016) Fish distribution and habitat complexity on banks of the Strait of Sicily (Central Mediterranean Sea) from remotely-operated vehicle (ROV) explorations. PLoS One 11:e0167809. https://doi.org/10.1371/journal.pone.0167809

Conti LA, Lim A, Wheeler AJ (2019) High resolution mapping of a cold water coral mound. Sci Rep 9:1016. https://doi.org/10.1038/s41598-018-37725-x

Cordes EE, Carney SL, Hourdez S, Carney RS, Brooks JM, Fisher CR (2007) Cold seeps of the deep Gulf of Mexico: community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. Deep-Sea Res Pt I 54:637–653. https://doi.org/10.1016/j.dsr.2007.01.001

Correa TBS, Grasmueck M, Eberli GP, Reed JK, Verwer K, Purkis SAM (2016) Variability of cold-water coral mounds in a high sediment input and tidal current regime, Straits of Florida. Sedimentology 59:1278–1304. https://doi.org/10.1111/j.1365-3091.2011.01306.x

Cvitanovic C, Hobday AJ, van Kerkhoff L, Wilson SK, Dobbs K, Marshall NA (2015) Improving knowledge exchange among scientists and decision-makers to facilitate the adaptive governance of marine resources: a review of knowledge and research needs. Ocean Coast Manage 112:25–35. https://doi.org/10.1016/j.ocecoaman.2015.05.002

Danovaro R, Canals M, Tangherlini M, Dell'Anno A, Gambi C, Lastras G, Amblas D, Sanchez-Vidal A, Frigola J, Calafat AM, Pedrosa-Pàmies R, Rivera J, Rayo X, Corinaldesi C (2017) A submarine volcanic eruption leads to a novel microbial habitat. Nat Ecol Evol 1:1–9. https://doi.org/10.1038/s41559-017-0144

Danovaro R, Fanelli E, Canals M, Ciuffardi T, Fabri M-C, Taviani M, Argyrou M, Azzurro E, Bianchelli S, Cantafaro A, Carugati L, Corinaldesi C, de Haan P, Dell'Anno A, Evans J, Foglini F, Galil B, Gianni M, Goren M, Greco S, Grimalt J, Güell-Bujons Q, Jadaud A, Knittweis L, Lopez JL, Sanchez-Vidal A, Schembri PJ, Snelgrove P, Vaz S, the IDEM Consortium (2020) Towards a marine strategy for the deep Mediterranean Sea: analysis of current ecological status. Mar Policy 112:103781. https://doi.org/10.1016/j.marpol.2019.103781

Davies AJ, Roberts JM, Hall-Spencer J (2007) Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. Biol Conserv 138:299–312

Di Camillo CG, Boero F, Gravili C, Previati M, Torsani F, Cerrano C (2013) Distribution, ecology and morphology of *Lytocarpia myriophyllum* (Cnidaria: Hydrozoa), a Mediterranean Sea habitat former to protect. Biodivers Conserv 22:773–787. https://doi.org/10.1007/s10531-013-0449-9

Dumke I, Purser A, Marcon Y, Nornes SM, Johnsen G, Ludvigsen M, Søreide F (2018) Underwater hyperspectral imaging as an in situ taxonomic tool for deep-sea megafauna. Sci Rep 8:12860. https://doi.org/10.1038/s41598-018-31261-4

Eleftheriou A, McIntyre A (2005) Methods for the study of marine benthos. Blackwell, Oxford

Enrichetti F, Dominguez-Carrió C, Bavestrello G, Betti F, Canese S, Bo M, Patterson HM (2019) Megabenthic communities of the Ligurian deep continental shelf and shelf break (NW Mediterranean Sea). PLoS One 14:e0223949. https://doi.org/10.1371/journal.pone.0223949

Fabri M-C, Pedel L, Beuck L, Galgani F, Hebbeln D, Freiwald A (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep-Sea Res Pt II 104:184–207

Fabri M-C, Vinha B, Allais A-G, Bouhier M-E, Dugornay O, Gaillot A, Arnaubec A (2019) Evaluating the ecological status of cold-water coral habitats using non-invasive methods: an example from Cassidaigne canyon, northwestern Mediterranean Sea. Prog Oceanogr 178:102172. https://doi.org/10.1016/j.pocean.2019.102172

Foglini F, Grande V, Marchese F, Bracchi VA, Prampolini M, Angeletti L, Castellan G, Chimienti G, Hansen IM, Gudmundsen M, Meroni AN, Mercorella A, Vertino A, Badalamenti F, Corselli C, Erdal I, Martorelli E, Savini A, Taviani M (2019) Application of hyperspectral imaging to underwater habitat mapping, Southern Adriatic Sea. Sensors 19:2261. https://doi.org/10.3390/s19102261

Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471:1–12. https://doi.org/10.1023/A:1016504430684

Foster MS, Harrold C, Hardin DD (1991) Point vs. photo quadrat estimates of the cover of sessile marine organisms. J Exp Mar Biol Ecol 146:193–203. https://doi.org/10.1016/0022-0981(91)90025-R

Freiwald A, Beuck L, Rüggeberg A, Taviani M, Hebbeln D, R/V Meteor M70-1 Participants (2009) The white coral community in the Central Mediterranean Sea revealed by ROV surveys. Oceanography 22:58–57

Garrabou J, Ballesteros E, Zabala M (2002) Structure and dynamics of North-Western Mediterranean rocky benthic communities along a depth gradient. Estuar Coast Shelf Sci 55:493–508. https://doi.org/10.1006/ecss.2001.0920

Grasmueck M, Eberli GP, Viggiano DA, Correa T, Rathwell G, Luo J (2006) Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the straits of Florida. Geophys Res Lett 33:L23616. https://doi.org/10.1029/2006GL027734

Grinyó J, Gori A, Ambroso S, Purroy A, Calatayud C, Dominguez-Carrió C, Coppari M, Lo Iacono C, López-González PJ, Gili J-M (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Prog Oceanogr 145:42–56. https://doi.org/10.1016/j.pocean.2016.05.001

Guinda X, Gracia A, Puente A, Juanes JA, Rzhanov Y, Mayer L (2014) Application of landscape mosaics for the assessment of subtidal macroalgae communities using the CFR index. Deep-Sea Res Pt II 106:207–215. https://doi.org/10.1016/j.dsr2.2013.09.037

Henry L-A, Roberts JM (2017) Global biodiversity in cold-water coral reef ecosystems. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests: the ecology of benthic biodiversity hotspots. Springer, Cham, pp 235–256

Howell KL, Davies JS, Narayanaswamy BE (2010) Identifying deep-sea megafaunal epibenthic assemblages for use in habitat mapping and marine protected area network design. J Mar Biol Assoc UK 90:33–68. https://doi.org/10.1017/S0025315409991299

Huvenne VAI, Tyler PA, Masson DG, Fisher EH, Hauton C, Hühnerbach V, Le Bas TP, Wolff GA (2011) A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. PLoS One 6:e28755. https://doi.org/10.1371/journal.pone.0028755

Huvenne VAI, Bett BJ, Masson DG, Le Bas TP, Wheeler AJ (2016) Effectiveness of a deep-sea cold-water coral marine protected area, following eight years of fisheries closure. Biol Conserv 200:60–69. https://doi.org/10.1016/j.biocon.2016.05.030

Huvenne VAI, Robert K, Marsh L, Lo Iacono C, Le Bas T, Wynn RB (2019) ROVs and AUVs. In: Micallef A, Krastel S, Savini A (eds) Submarine geomorphology. Springer, Cham, pp 93–108

Innangi S, Tonielli R, Romagnoli C, Budillon F, Di Martino G, Innangi M, Laterza R, Le Bas T, Lo Iacono C (2019) Seabed mapping in the Pelagie Islands marine protected area (Sicily Channel, southern Mediterranean) using remote sensing object based image analysis (RSOBIA). Mar Geophys Res 40:333–355. https://doi.org/10.1007/s11001-018-9371-6

IUCN (2019) Thematic report – conservation overview of Mediterranean deep-sea biodiversity: a strategic assessment, 122 p. IUCN, Gland

Johnsen G, Ludvigsen M, Sørensen A, Aas LMS (2016) The use of underwater hyperspectral imaging deployed on remotely operated vehicles-methods and applications. IFAC-Papers Online 49(23):476–481. https://doi.org/10.1016/j.ifacol.2016.10.451

Langenkämper D, Simon-Lledó E, Hosking B, Jones DOB, Nattkemper TW (2019) On the impact of citizen science-derived data quality on deep learning based classification in marine images. PLoS One 14(6):e0218086. https://doi.org/10.1371/journal.pone.0218086

Leonard G, Clark R (1993) Point quadrat versus video transect estimates of the cover of benthic red algae. Mar Ecol Progr Ser 101:203–208. https://doi.org/10.3354/meps101203

Lundquist CJ, Granek EF (2005) Strategies for successful marine conservation: integrating socio-economic, political, and scientific factors. Conserv Biol 19:1771–1778. https://doi.org/10.1111/j.1523-1739.2005.00279.x

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, Harvey JBJ, Clague G, Vrijenhoek RC (2010) Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. Deep-Sea Res Pt I 57:1573–1584. https://doi.org/10.1016/j.dsr.2010.09.003

Manea E, Bianchelli S, Fanelli E, Danovaro R, Gissi E (2020) Towards an ecosystem-based marine spatial planning in the deep Mediterranean Sea. Sci Tot Environ 715:136884. https://doi.org/10.1016/j.scitotenv.2020.136884

Meese RJ, Tomich PA (1992) Dots on the rocks: a comparison of percent cover estimation methods. J Exp Mar Biol Ecol 165:59–73. https://doi.org/10.1016/0022-0981(92)90289-M

Micheli F, Levin N, Giakoumi S, Katsanevakis S, Abdulla A, Coll M, Fraschetti S, Kark S, Koutsoubas D, Mackelworth P, Maiorano L, Possingham HP (2013) Setting priorities for regional conservation planning in the Mediterranean Sea. PLoS One 8:e59038. https://doi.org/10.1371/journal.pone.0059038

Mueller CE, Lundälv T, Middelburg JJ, van Oevelen D (2013) The Symbiosis between *Lophelia pertusa* and *Eunice norvegica* stimulates coral calcification and worm assimilation. PLoS One 8:e58660. https://doi.org/10.1371/journal.pone.0058660

Norcross BL, Mueter F-J (1999) The use of an ROV in the study of juvenile flatfish. Fish Res 39:241–251. https://doi.org/10.1016/S0165-7836(98)00200-8

Pech D, Condal AR, Bourget E, Ardisson P-L (2004) Abundance estimation of rocky shore invertebrates at small spatial scale by high-resolution digital photography and digital image analysis. J Exp Mar Biol Ecol 299:185–199. https://doi.org/10.1016/j.jembe.2003.08.017

Prampolini M, Angeletti L, Grande V, Taviani M, Foglini F (2020) Tricase Submarine Canyon: cold-water coral habitats in the southwesternmost Adriatic Sea (Mediterranean Sea). In: Harris PT, Baker E (eds) Seafloor geomorphology as benthic habitat, 2nd edn. Elsevier, pp 793–810

R Core Team (2013) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. http://www.R-project.org/

Rengstorf AM, Mohn C, Brown C, Wisz MS, Grehan AJ (2014) Predicting the distribution of deep-sea vulnerable marine ecosystems using high-resolution data: considerations and novel approaches. Deep-Sea Res Pt I 93:72–82. https://doi.org/10.1016/j.dsr.2014.07.007

Robert K, Jones DOB, Georgiopoulou A, Huvenne VAI (2020) Cold-water coral assemblages on vertical walls from the Northeast Atlantic. Divers Distrib 26:284–298. https://doi.org/10.1111/ddi.13011

Rowden AA, Anderson OF, Georgian SE, Bowden DA, Clark MR, Pallentin A, Miller A (2017) High-resolution habitat suitability models for the conservation and management of vulnerable marine ecosystems on the Louisville seamount chain, South Pacific Ocean. Front Mar Sci 4:335. https://doi.org/10.3389/fmars.2017.00335

Santín A, Grinyó J, Ambroso S, Uriz MJ, Dominguez-Carrió C, Gili JM (2019) Distribution patterns and demographic trends of demosponges at the Menorca Channel (Northwestern Mediterranean Sea). Progr Oceanogr 173:9–25 . https://doi.org/10.1016/j.pocean.2019.02.002

Savini A, Vertino A, Marchese F, Beuck L, Freiwald A (2014) Mapping cold-water coral habitats at different scales within the northern Ionian Sea (Central Mediterranean): an assessment of coral coverage and associated vulnerability. PLoS One 9:e87108. https://doi.org/10.1371/journal.pone.0087108

Savini A, Taviani M, Marchese F, Vertino A, Corselli C, Fabri M-C, Freiwald A, Sarrazin J (2017) Measuring growth structure of reef frameworks in Mediterranean deep-water coral-topped mounds. IMEKO TC19 Workshop on Metrology for the Sea (MetroSea 2017). Naples, Italy, 11–13 October 2017, pp 101–104

Stokes MD, Deane GB (2009) Automated processing of coral reef benthic images. Limnol Oceanogr-Meth 7:157–168. https://doi.org/10.4319/lom.2009.7.157

Taviani M, Angeletti L, Canese S, Cannas R, Cardone F, Cau A, Cau AB, Follesa MC, Marchese F, Montagna P, Tessarolo C (2017) The “Sardinian cold-water coral province” in the context of the Mediterranean coral ecosystems. Deep Sea Res Pt II 145:61–78

Taviani M, Angeletti L, Cardone F, Montagna P, Danovaro R (2019) A unique and threatened deep water coral-bivalve biotope new to the Mediterranean Sea offshore the Naples megalopolis. Sci Rep 9:3411. https://doi.org/10.1038/s41598-019-39655-8

Teixidó N, Albajes-Eizagirre A, Bolbo D, Hir EL, Demestre M, Garrabou J, Guigues L, Gili J-M, Piera J, Prelot T, Soria-Frisch A (2011) Hierarchical segmentation-based software for cover classification analyses of seabed images (Seascape). Mar Ecol Prog Ser 431:45–53. https://doi.org/10.3354/meps09127

Trotter J, Pattiaratchi C, Montagna P, Taviani M, Falter J, Threser R, Hosie A, Haig D, Foglini F, Hua Q, McCulloch M (2019) First ROV exploration of the Perth canyon: canyon setting, faunal observations, and anthropogenic impacts. Front Mar Sci 6:193. https://doi.org/10.3389/fmars.2019.00173

Vanreusel A, Hilario A, Ribeiro PA, Menot L, Arbizu PM (2016) Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. Sci Rep 6:1–6. https://doi.org/10.1038/srep26808

WoRMS Editorial Board (2020) Available online: http://www.marinespecies.org. Accessed 21 Apr 2020

Wynn RB, Huvenne VAI, Le Bas TP, Murton BJ, Connelly DP, Bett BJ, Ruhl HA, Morris KJ, Peakall J, Parsons DR, Summer EJ, Darby SE, Dorrel RM, Hunt JE (2014) Autonomous underwater vehicles (AUVs): their past, present and future contributions to the advancement of marine geoscience. Mar Geol 352:451–468. https://doi.org/10.1016/j.margeo.2014.03.012

Zampoukas N, Palialexis, A Duffek J, Graveland G, Giorgi C, Hagebro G, Hanke S, Korpinen M, Tasker V. Tornero, V, Abaza P, Battaglia M, Caparis R, Dekeling M, Frias Vega, M. Haarich S, Katsanevakis H, Klein W, Krzyminski M, Laamanen JC, Le Gac JM, Leppanen U, Lips T, Maes E, Magaletti S, Malcolm JM, Marques O, Mihail R, Moxon C, O'Brien P, Panagiotidis M, Penna C, Piroddi WN, Probst S, Raicevich B, Trabucco L, Tunesi S, van der Graaf A, Weiss, AS, Wernersson W, Zevenboom, Technical guidance on monitoring for the Marine Strategy Framework Directive (2014) European Commission EUR 26499 – Joint Research Centre – Institute for Environment and Sustainability. Publications Office of the European Union, Luxembourg, pp 1–166. https://doi.org/10.2788/70344

Advances in the Marine Animal Forests Scientific Outreach and Citizen Science

J. Zorrilla-Pujana

Abstract Marine ecosystems, in particular marine animal forests, are facing huge losses, being drastically transformed by different threats that just keep increasing its negative effects. Actual and future research strategies underpin programs with more collaborative and transdisciplinary perspectives, able to create and develop solutions to complex environmental issues that must be inclusive with society in order to be sustainable, not only at economic level but also in space and time. In this chapter, citizen science is presented as a complementary strategy to strengthen research on marine animal forests that show multiple benefits including bridging the gap between science and society. Citizen science is a growing field, becoming also a new paradigm for doing research in conservation. Now is time to realize that the world challenges must be solved through multidisciplinary approaches that include cooperation and engagement with society, in which citizen science can be a powerful tool to achieve conservation goals. In addition, practitioners and developers must not forget that training, capacity building and continuous assessment and support is also needed to reach objectives and maintain stakeholder's engagement and impact results.

Keywords Citizen science · Conservation action · Public engagement · Volunteer monitoring · Science and society

1 Introduction

We are living now on the Anthropocene, a proposed new geological epoch in which the *Homo sapiens* as a species has become a major geological force, marked by significant human impacts to the biosphere over a relatively short period of time (Palomo et al. 2014; Steffen et al. 2011). Although the term hasn't still been approved or recognized officially, it is of great consensus that we live in a time in

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which the biodiversity in our planet is driven to a mass extinction caused mainly by anthropogenic activities, in which oceans are being the main character of the actual biodiversity cataclysm. An average of around 25% of species in assessed animal and plant groups are threatened, suggesting that around one million species already face extinction, many within decades, unless action is taken to reduce the intensity of drivers of biodiversity loss (Díaz et al. 2019).

Throughout the middle of the twentieth century, the Apollo 8 revealed to the world that we were living on a blue planet, but it wasn't until 1972, thanks to the Apollo 17 mission, that a composite image of the Earth known as "the blue marble" (NASA) showed the immensity of our oceans and became one of the most-used images in history. During this ambitious space age that captured the attention of the whole world, it was impossible to think about the fragility of this blue Earth and the responsibility we have to conserve it. Despite the big efforts of science to call out for the attention to safeguard the oceans, this huge part of our planet is still very poorly protected given the high level of threats and increase pressure for life and fossil resources that are causing cascade reactions at so many levels (physical, chemical, and biological), that will change life on Earth as we know it.

The equilibrium of our planet has been modified into a point of almost no return. As stated in the last IPBES Global Assessment on Biodiversity and Ecosystem Services report (E. S. Brondizio et al. 2019), sensitive ecosystems such as coral reefs, mangroves, and saltmarshes are already well below natural baseline levels and continue in a fast decline, in which approximately half the live coral cover on coral reefs has been lost since the 1870s, with accelerating losses in recent decades due to climate change and other permanent threats. The rate of global change in nature during the past 50 years is unprecedented in human history. The direct drivers of change in nature with the largest global impact have been (starting with those with most impact) changes in land and sea use; direct exploitation of organisms; climate change; pollution; and invasion of alien species (Díaz et al. 2019). Extensive bleaching effects on coral reefs triggered by the rise on atmospheric and ocean temperatures, destructive fishing practices as cyanide and dynamite fishing, bottom trawling specially on cold-water reef corals, eutrophication episodes, pollution, sedimentation, and so on are threats that just keep increasing its negative effects and may trigger negative feedback that causes further ecosystem decline (Cerrano et al. 2017; Clements and Hay 2019; Rossi 2013).

In the past, the threats and ecological issues were often seen and treated as isolated parts of the same problem, regardless the interactions that occur between threats. Now, we have realized that the world's environmental challenges must be understood and addressed through multidisciplinary approaches with cooperative perspectives to give more assertive responses. Studies on collective intelligence also demonstrates that performance of groups are better than individually, in which communication capacities and social sensitivity and gender distribution play an important role (Woolley et al. 2010).

Currently, huge efforts are being made to create and strengthen MAFs research, with an increasing interest through transdisciplinary working groups on this topic, facilitating bottom-up inclusiveness, and the assemblage of multidisciplinary teams to help tackle current and emerging issues and challenges in the marine domain.

Some programs that have included MAFs are EUROMARINE (European Marine Research Network) and the European Research Programs H2020 on blue growth, that have also included citizen science (CS) as one of the five strategic orientations in "Science with and for Society" (SwafS) program. These programs, besides the promotion of transdisciplinary work, are a stepping stone in the opening of the ivory tower, promoting exchange of practices, encouraging ecosystem services and conservation research strategies programs, with new governance models (Morrison et al. 2020) and, most importantly, with more collaborative perspectives, with the aim to create and construct solutions focused on real challenges involving society and other essential stakeholders as an integral part of the research process and the solution itself.

2 Citizen Science: A Change in the Conservation Paradigm

2.1 Amateur Science and Environmental Education

This is the time that we, as a species, must be part in taking action to solve the enormous marine environmental challenges humankind will have to face if no actions are agreed to be established and delivered with global commitment.

Centuries ago, the contributions of amateurs to science, through observations, nature collections, and recording was the usual way to make science. At the present time, given the relatively recent growth of ecological research as a professional field of study (Miller-Rushing et al. 2012), a change in the way communication of science and ecology is made has generated a big gap in the communication flux from science to society, being in most cases unidirectional, in which scientist are seen as the owners of knowledge and the only ones capable of translate message to society.

Linked with this issue, during the past decades, environmental education and outreach activities have been an important piece to bridge the gap of public awareness and sensitization to foster a more ocean-literate citizens, pro-environmental attitudes, and ecological intention to act for the protection of coral reefs (Branchini et al. 2015; Leisher et al. 2012; Rossi and Orejas 2019; Stepath 2006), making aware of the environmental problem at local level and globally as well in order to contribute to the long-term compliance of reefs management. Almost all environmental focused NGOs and research institutions have dedicated part of their structure and efforts to educational resources for students and teachers and disseminate their research to society, as the National Oceanic and Atmospheric Administration (NOAA), World Wildlife Fund (WWF), Greenpeace, Oceana, and National Geographic Society, among others are examples of big efforts to translate message from research studies and explorations into society.

This is the case of NOAA, a national agency that developed one of the most renowned programs focused specifically in ocean literacy, providing a practical and useful guide to incorporate the ten principles of ocean literacy into the formal education curriculum, integrating coral reefs, sea grass beds, deep sea corals, climate change, and ocean acidification, among others, to foster ocean literacy in schools. As a global initiative, following NOAA steps, the United Nations launched the Ocean Literacy for All (Santoro et al. 2017) to promote a literate society about the ocean, but the concept of Marine Animal Forests (MAFs) is still missing as an integrative model of the 3D living structures that are essential for the ocean life and marine biodiversity.

These demonstrations are shown as the result of research and field campaigns, promoting the contact of scientists with scholars and the general public, to promote knowledge, interest in marine life sciences, and, at the end, promote an ocean-literate society (Uyarra and Borja 2016; Schoedinger et al. 2010; Steel et al. 2005).

The environmental education field has worked during many decades to put together science and society and has been a key piece to make aware and work for an ocean-literate society, engaging individuals in problem-solving, to take action to improve the state of nature and as a complementary area for marine ecosystem management to foster positive changes in knowledge and attitudes, that strengthen compliance with MPA regulations and conservation (Leisher et al. 2012; Zorrilla-Pujana and Rossi 2014).

However, nowadays, we are still far to produce the needed change and achieve deep understanding of environmental issues to make informed and responsible decisions. According to evidence, achieving environmental education objectives is not enough with just proving materials and developing programs encouraging participation in responsible environmental behaviors, pointing out that this is one of the big challenges of the field (Blumstein and Saylan 2007; Marcinkowski 1991).

2.2 *Understanding the Concept*

Having these challenges on the radar, some environmental education programs about marine ecosystems are being transformed to put together science and society, working and collaborating together in solving local, regional, and global environmental issues. This approach, about mutual collaboration, has been demonstrated to be a successful channel, putting together scientist with students (Krasny and Bonney 2005), in order to improve educational, conservation, and research impacts. This transformation from previous environmental and science awareness models, into more participative and engaging ways for doing research nowadays recognized as CS (Jordan et al. 2016; Lee and Roth 2003; Miller-Rushing et al. 2012), that, in terms of impact, results dissemination and commitment, can be considered as a step forward from an awareness design of actions into a more dynamic and engaging model of participation of society in projects involving MAFs but also many other ecosystems on Earth.

In a so rapid-moving field, it is hard to define and establish the state of the art of CS and the role of its practitioners, mainly because of the fast expansion, dynamic of the field, and high diversity of projects and participants, that no single term is appropriate for all contexts (Bela et al. 2016; Eitzel et al. 2017). However there is an agreement that CS is a process where citizens can become an integral part of the research, the data gathering, and results sharing within the wider community, in which the interaction is very much a two-way process. Trying to get a wide perspective of the actual situation regarding CS in marine ecosystems, the European Marine Board has defined a good description that could be summarized in the following statement: "At present, CS is predominantly associated with terrestrial projects. However, CS also has the potential to make significant contributions to marine sciences. Considering the vastness of the ocean, the extensiveness of the coastlines, and the diversity of habitats, communities, and species, a proper understanding of this realm requires intensive research activities over time and space which should lead to an increased consideration of CS as a powerful tool for the generation of scientific knowledge. Additionally, CS initiatives should be promoted because of their benefits in creating awareness of the challenges facing the world's ocean and increasing Ocean Literacy" (http://www.marineboard.eu/citizen-science).

In addition to this general definition, Miller-Rushing et al. (2012) proposed a classification of the different typology of CS projects, according to the different levels of public participation in the scientific process, which are contributory, collaborative, and co-created. With this classification in hand, there is no doubt that people are an active piece on the development of any research that integrates CS, regardless the level of participation. CS as a new paradigm in conservation research suggests that we are not working anymore on a linear basis, but on a multidimensional scale, that starts almost where the previous model of outreach, awareness, and dissemination ends. In this way, the new approach of CS fosters the implication of non-scientific members of the society according to the research objectives but developing new competences and capacity building, beyond an awareness model, that has been hard to show evidence of its effectiveness (Blumstein and Saylan 2007) (Fig. 1).

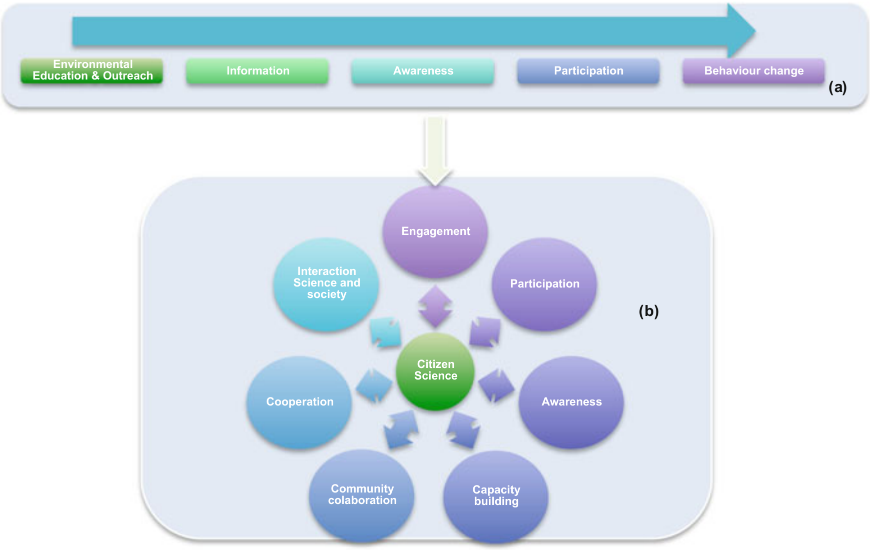


Fig. 1 Change from a linear (**a**) to a multidimensional (**b**) model for engaging society in research and environmental sciences

3 Citizen Science in Marine Animal Forests

It is well known that research on land has been always easier than on the ocean, not only because of economic limitations but also because of the logistics and equipment requirements to do research on aquatic environment and hard to reach ecosystems such as cold-water corals and deep-water marine structures. Another element influencing this fact is the lack of knowledge and interest of a wide spectrum of the society for an unseen part of the nature as oceans are and the failure from the scientist to transfer in a proper way the knowledge to the society about the relationship of a healthy ocean with our own health and welfare (noaa.gov/about/media/bottom-gulf-mexico-corals-and-diversity-sufferedafter-deepwater-horizon-oil-spill.html).

For CS, the case is not different. The water barrier is one of the main constraints to do CS projects beyond the coastline, but once this barrier is removed, opportunities to work with people and engage them in the process of stewardship and conservation keep growing. Despite the difficulties that marine ecosystem represents for doing research, is worth to highlight the great number of CS projects that we can find nowadays. From a recent review of CS projects about marine research, it was found that nearly 10% was dedicated exclusively to coral reefs, apparently by the possibility of involving scuba diving visitors as potential CS contributors (Earp and Liconti 2020). Recreational scuba divers represent an important target group, showing a great relevance for reef monitoring actions, when following common protocols, obtaining comparable data necessary for management plans and promoting sustainable tourism at the same time (Bramanti et al. 2011; Branchini et al. 2015; Lucrezi et al. 2018), improving scientific literacy and increased encouragement for civic engagement (Lloyd et al. 2020).

The term CS can be considered a recent idea, but naturalists and amateur scientists have observed and recorded nature since ancient times (Irwin 2018). The idea of CS appeared independently in the mid-1990s by Rick Bonney in the USA and in the UK by Alan Irwin referring to public participation engagement and science communication projects and the necessity of opening up science and science policy processes to the public, respectively. Since then, the field of CS has evolved rapidly and with the arrival of new technologies, especially smartphones with friendly apps and easy to use accessories, has allowed a new way of sharing, communicating, and collaborating, facilitating a different approach to connect science to society. Technology and fast Internet with almost global access have made possible a great expansion and engagement in a wide variety of CS projects, fostering excellent observation results with low knowledge and equipment for collecting data. In the context of MAFs, some of the most renowned projects are Reef Check, REEF, Coastwatch, Project AWARE, and marine forests alongside many other initiatives like restoration activities. However, the full potential of CS on research projects focusing on coastal and marine ecosystems remains largely untapped (Cigliano et al. 2015).

Many of these projects have started before the concept of CS, as we know it today, even appeared. Some of these are Reef Check (https://reefcheck.org/), one of the most well-known projects that have been on trail more than 20 years, empowering people through research and education to conserve reefs and oceans, by collecting and analyzing data of the state of coral reefs around the world. Their results are used mainly to improve the management of the reefs and also foster partnerships among community volunteers, government agencies, businesses, universities, and other nonprofit organizations to achieve this aim. Coral Watch is another of this kind coming from Australia to measure the health of coral reefs in more than 78 countries. (https://coralwatch.org/).

Following the same trend, there is also the REEF initiative (Reef Environmental Education Foundation) promoting CS and implementing hands-on programs to involve local communities in conservation-focused activities. All data collected are used with the aim to achieve a healthier ocean, networking and partnering with the scientific community and national agencies. One of the programs related with MAFs is the REEF's Invertebrate and Algae Monitoring Program, as valuable indicators of the health and status of local environments and also useful for management and conservation applications (https://www.reef.org/reefs-invertebrate-and-algae-monitoring-program).

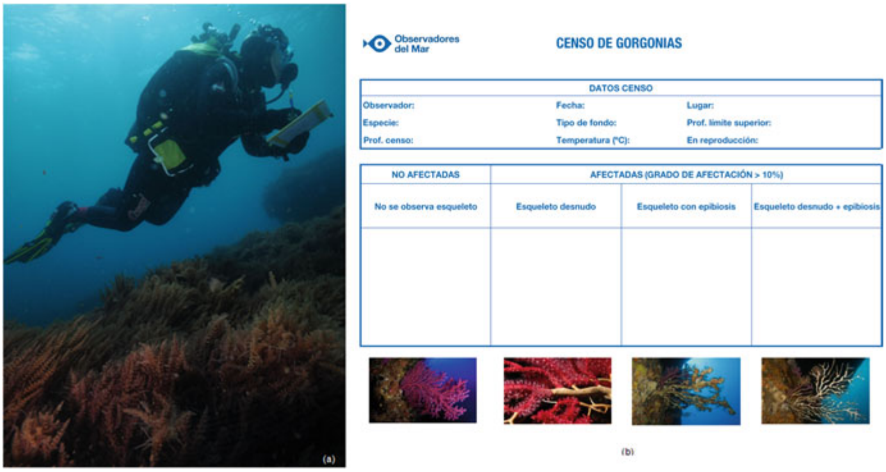
BleachWatch is another example of successful CS project that combined with the Information from NOAA's Coral Reef Watch (CRW) remote sensing and Integrated Coral Observing Network (ICON) provides a comprehensive overview of the state of corals from a global perspective and local view through the volunteer's observations in the Florida Keys National Marine Sanctuary (FKNMS). In this way, it is noteworthy to see how a project can be combined with other databases in projects and improve the detection and monitoring at a local-scale coral bleaching events in southeast Florida, improving the scientific understanding of this episodes by tracking weather conditions and sea surface temperatures for conditions favorable for coral bleaching.

Marine Forests (www.marineforests.com) is an initiative more focused on benthic organisms and not just focused on animals. It integrates also macroalgae and plants as seagrass meadows in which citizen scientist contribute with their observations to register forest-forming species to reach worldwide maps with distribution records.

Beyond data gathering, restoration activities including citizens as is the case of the program Rescue a Reef (RAR) are also becoming featured players, with important relevance from educational perspective but also with significant economic and ecological impacts that improve the task of restoration (Hesley et al. 2017).

Furthermore, there are other CS proposals that focus or keep track of global biodiversity and/or specific taxonomic groups. One of the platforms that have occupied with excellence in this niche is iNaturalist, Natusfera, and Zooniverse which provide a place to record and organize nature findings, meet other nature enthusiasts, and learn about the natural world. These platforms encourage participation of a wide variety of people interested in nature, with the aim of creating extensive community awareness of local biodiversity and promote further exploration of local environments, allowing at the same time people to participate and/or create and manage their own project with a number of users and observations that increase day by day. These initiatives are enhanced with mobile applications that facilitate data recording, with a more complete interphase on their websites. Despite the great expansion of these projects, the MAF concept is not widely spread in use, being an interesting opportunity to fill the gap, by looking for new ways of funding resources, data gathering and findings that can help or feed in some way on going researches of MAFs of the world. These living data reservoirs could also serve as an opportunity to establish contact and setup networks with citizens and researchers that are interested in this subject, proving potential opportunities for expansion of the MAFs as a global concept.

Another immense opportunity of CS is the association and use of results for the management of natural protected areas with the collaboration of researchers, users, and managers. A good example is the case of the Natura 2000 Marine Network within the LIFE IP INTEMARES in Spain (www.intemares.es), one of the biggest projects at a European level for Marine Conservation. In this project, in association with an already created CS platform "*Observadores del Mar*" (Fig. 2), the project looks to achieve an efficient, innovative, and integrated management of marine protected areas, with the active participation of all the sectors involved in this process and research as a basic tool for decision-making and creation of new knowledge. This networking case is a synergetic relation in which experts from different national and international research centers provide and validate data on the impacts, habitats, and species found within the Marine Natura 2000 Network areas while providing also new ways for users and managers to learn and get data from all the protected areas, that in other way would almost be impossible to cover (Dickinson et al. 2010). It is a great occasion to use already existent platforms and adapt them to a specific project, without generating more noise on multiple



CENSO DE GORGONIAS

DATOS CENSO

Observador: Fecha: Lugar:
Especie: Tipo de fondo: Prof. límite superior:
Prof. censo: Temperatura (°C): En reproducción:

NO AFECTADAS	AFECTADAS (GRADO DE AFECTACIÓN > 10%)		
No se observa esqueleto	Esqueleto desnudo	Esqueleto con epibiosis	Esqueleto desnudo + epibiosis

Fig. 2 (**a**) Diver with notebook on red algae bottom—*Observadores del mar*. (**b**) Protocol for gorgonian census

initiatives, and integrate knowledge and findings in just one place. This is also an opportunity to participate and disseminate the concept of MAFs, by scientists, and promote the observation of these amazing organisms and advance in the spreading of the concept.

3.1 Benefits for the Inclusion of Citizen Science in MAFs Research

Although some experts can think that CS is still in its infancy, the data show us that CS has arrive to stay, a trend based on the exponentially increase in number and diversity of CS projects focused on conservation of ecosystem and species, that have demonstrated that in addition of the social benefits of involving the public in scientific research, CS projects also contribute to conservation outcomes (Vaughan 2007; Bonney et al. 2009a, b; Cigliano et al. 2015; Cerrano et al. 2017; Ballard et al. 2018). CS is increasingly gaining ground and reputation, when it has been included as a strategy to complement the monitoring of the Sustainable Development Goals (SDG) by the United Nations (Fritz et al. 2019) and considered for many granting institutions as the European Commission in the "Science with and for Society" (SwafS) Work Programme Horizon 2020 and other funding agencies as the National Science Foundation (NSF)[1] as a effective strategy to foster involvement, engagement, and communication from existing research to society.

Within the MAFs context, CS has become an innovative key piece that together with other strategies as communication, awareness, and education has made possible to increase society engagement in the study and conservation of these 3D-living structures that lie under the sea. Despite the increasing number of initiatives that each day are being developed within this field, it is important to underpin some of the major advantages that CS may contribute, in order to understand better why this strategy has gain so much support among citizens, public administration, research institutions, and governmental agencies.

Some of the main benefits that have been recognized for the inclusion of CS are:

(a) *Increase the area of study*: many research projects that have included CS as a part of their study have been seduced by the great possibilities of obtaining data in large areas and more representative samples that wouldn't be possible for a research team or institute to cover or perform on the required temporal or spatial scales that some projects require (Lucrezi et al. 2018). CS is becoming a powerful monitoring tool for species distribution like the Mediterranean red coral (*Corallium rubrum*) (Bramanti et al. 2011) and seahorses (Goffredo et al. 2004), and now its inclusion has a strong presence for Tier I and Tier II

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[1] The National Science Foundation (NSF) do use PPSR to describe the projects in their portfolio (Eitzel et al. 2017).

indicators of the United Nations Sustainable Development Goals that include the Red List Index as indicator that capture the risk of extinction over time for four taxonomic groups: birds, mammals, amphibians, and corals (Fritz et al. 2019). As Dickinson et al. (2010) underpin on their paper, CS is probably the most feasible way to achieve the geographic reach required to document ecological patterns and address ecological questions at scales, that no other methods or research project can achieve.

(b) *Lowering sampling costs*: promoting and encouraging the participation of people in CS projects linked to research objectives can be a sustainable option to reduce economic costs of long-term and wide distribution research. Recent data from NOAA underpin that only in 2019, 10,970 of their volunteers supported national marine sanctuary CS efforts with a total of 72,219 hours, that when translated to budget, the savings are equivalent to $1.8 million (NOAA n.d.). According to a research from Theobald et al. (2015), “the range of in-kind contribution of the volunteerism in our 388 citizen science projects as between $667 million to $2.5 billion annually. Note that this represents a minimum estimate for biodiversity citizen science worldwide, as our project sampling was restricted to only projects reporting in English and found in major online citizen science clearinghouses”. These are some data examples that reinforce the economic benefits from using CS into monitoring and research projects.

(c) *Citizen engagement in conservation*: This bottom-up movement is possible thanks to the participation of a high volume of enthusiastic volunteers transforming the way conservation research is done, generating high levels of citizen engagement (Irwin 2018), providing an increased workforce over extensive spatial and intensive temporal scales, helping in reducing research costs that implies any conservation process (NOAA n.d.; Thiel et al. 2014), and also an important piece for adaptive management (Aceves-Bueno et al. 2015). Many of the projects that are running within the MAFs scope, and ocean conservation, have included CS as a key puzzle piece to establish connection between people and conservation action.

(d) *Contribution to science*: although most of the efforts done by volunteers from CS initiatives and projects probably don’t end up in a peer-reviewed publication, some data from the Global Biodiversity Information Facility (GBIF) estimate that the group has supplied data for more than 2500 peer-reviewed papers in the past 10 years, which gives a clear image of the high potential of CS as high contributor for the advancement of science (Irwin 2018). In the case of MAFs, publications with contribution from citizens are still a pendent task, but there are already good initiatives to follow as an example in this field (Bramanti et al. 2011; Chimienti 2020).

(e) *Conservation into action*: community capacity building and conservation outcomes can also occur when CS serves as platforms that collectively mobilize for an action. In these cases projects move from data collection to action, from organizing around a clean-up beach or eradicating invasive species such as lionfish that harm native coral reef ecosystems in the Atlantic, Gulf of Mexico, and Caribbean. The case of the lionfish is considered one of the most known cases of negative effects on reef ecosystems, being hard to eliminate, and causing a significant reduction in the recruitment of native reef fishes almost by 79% (Albins and Hixon 2008) and eliminating herbivores that control algal growth, which can be detrimental to the health of coral reefs (NOAA—https://www.fisheries.noaa.gov/feature-story/impacts-invasive-lionfish). Coral restoration is another example in which CS can take place together with research teams beyond data collection and make a substantial contribution to reef restoration, showing no significant difference with the ones out planted by experts, reducing the cost of this tasks (Hesley et al. 2017).

Without doubt, we are currently experiencing a paradigm shift in terms of doing research in ecology and conservation of marine ecosystems (Theobald et al. 2015), including MAFs.

4 Challenges

CS, with an exponential growth of projects all over the world, has showed no signs of flattening the curve of projects generated, making this field a key piece to include in research projects and policies as a necessary element to merge science with society, among other benefits.

In the case of MAFs and the conservation field, there are a lot of opportunities to advance within this new paradigm in which CS can act as a catalyzer for the evolution of a different kind of research, involving citizens and scientists as co-creators of common objectives to foster awareness and knowledge and solve global conservation challenges that MAFs face nowadays. It has been demonstrated that CS projects have an important role in improving knowledge of coral reef biology and ecology and the awareness on tourists and diving stakeholders (Branchini et al. 2015); however as recommended by Lucrezi et al. (2018), there is a need for more investment in professional intermediaries and experts of CS working together with the scientific community and the scuba diving industry, to strengthen this association for a sustainable and fruitful long-term relationship. In an ideal world, tourism, managers, and researchers should work hand in hand, in a win-win relationship, fostering sustainability of resources, knowledge, ocean literacy, and science, through responsible actions as CS, in data gathering for research and management of marine-protected areas and non-protected as well.

All terrestrial plant forests are classified under common terms, basis, CO_2 sequestering capacities, three-dimensional pattern formations, landscape configuration, canopy and undergrowth structures, and other general attributes, but this doesn't occur undersea. It is necessary to apply a similar series of integrative concepts to MAFs and develop common novel language to further facilitate cooperation, collaboration, and synergies for integrative transdisciplinary studies. Indeed, this is a great opportunity for MAFs to develop and continue to reinforce the concept in this cluster of CS platforms, which will help to advance sharing protocols, involvement in the distributing of innovative ideas, methods, and developing and synchronizing a collective language that could be the most appropriate tool for a significant progression in this emerging topic. Generally, when we dive into CS projects, it is usual to perceive that those are focused on observation to record species or taxon but rarely on the concept of a whole ecosystem and the interrelations that occur inside and outside, with some exceptions. Strengthening and consolidating the MAFs model from an ecosystem perspective within CS is also an important challenge, to understand and disseminate the importance of MAFs beyond coral reefs concept, in order to recognize and realize the complexity and the interconnection of all the biodiversity that these ecosystems host for accurate management and policy development at a global level.

One of the greatest challenges that CS faces nowadays is to find new systems capable of sharing data among similar projects and/or platforms in order to group or make data accessible from different information sources. Currently, data gathering and storage is highly atomized, making very it difficult and time-consuming to effectively be able to use information for research and policy decision-making purposes.

Recently, the European Union has launched the Cos4Cloud Project, with the aim of improving CS platforms, through the integration of observations from different CS platforms, using artificial intelligence tools with the objective of improving the interoperability, networking, data quality, and security within the CS observatories. It will also facilitate the networking and knowledge management processes across organizations, people, and initiatives working on citizen observatories that at the end will improve the functionality of different CS projects and at the same time contribute to ensure their sustainability (https://www.cos4cloud-eosc.eu/).

Being able to integrate MAFs and CS within research projects, tourism, schools, diving training, etc. will contribute in setting a baseline of a new era for governance, management, and conservation, that actively includes society in the different stages of the conservation planning, providing at the same time solid basis for policy development and actions that can be sustainable in time, supported by a strong base of an ocean-literate society, according to the degree of implication.

5 Conclusions

Cooperation, socioenvironmental resilience, a leadership organization that integrates the MAFs concept and initiatives related with MAFs and CS worldwide, and training are some of the key issues that have to come in order to advance in this field of CS and MAFs conservation.

As Lynn Margulis stated in the endosymbiotic theory of evolution, life in our planet evolved thanks to cooperation and symbiotic relationships. Now a R-evolution that follows this trend is necessary to act in a rapid changing world that claims for global responses that need to be sustained in time to conserve oceans and all life that depends on it. In this sense and terms, CS can be a catalyzer and a key piece for this new conservation paradigm, in which engagement of society with science and research can become a sustainable win–win relationship.

Resilience on MAFs ecosystem is a very complex and slow process. Because of their composition and growing rates, in addition to the high complexity of 3D structures and heterogeneity display, disturbances of any kind produce great damage making any recovery process a hard task for nature. However, we have now the chance to innovate the resilience concept from a social perspective that can be renamed as socioenvironmental resilience, thinking in CS as a powerful tool, in which the more people are involved, aware, and engaged working together and networking with science, tourism, fishing, and environmental fields, the greater will be the level of knowledge and protection achieved for the benefits and health of these ecosystems, together with a reduction of the disturbing effects. This symbiotic relation can probably endorse policies to protect them, creating collective knowledge (Woolley et al. 2010) and fostering public participation in science and Earth stewardship, to protect biological diversity (Dickinson et al. 2012).

There are many initiatives about MAFs around the world, that vary in size of participants, years of experience, target species, and objectives, but in a global perspective, the knowledge and impact of results seem atomized and with lack of integration among proposals from local, regional, national, and global level. In order to strengthen the CS on MAFs (e.g., as it is on birds), a ground-breaking initiative must be settled, recognized, and supported by different institutions and research groups worldwide, capable of leading and integrating all issues related with CS and MAFs. This entity/institution should be able to facilitate networking, joint initiatives for research, publications, and global projects about MAFs conservation (historical ecology, biogeography, distribution, threats, ecosystem services, restoration, etc.) that can integrate CS as an added value instrument to advance in research and conservation impacts and act as a reference for any new initiative within this field.

In addition to all recommendations from the last IPBES report (E. S. Brondizio et al. 2019), inclusion of society in the tasks of conservation is essential for the sustainability of all ecosystems on Earth, and CS can contribute in many ways to achieve this objective for MAFs conservation. However it is important to realize that research and enthusiastic citizens is not enough and investing in training and support during all the stages of CS initiatives will increase engagement, knowledge, and impact of the actions promoted (Kirkpatrick and Kirkpatrick 2016; Lucrezi et al. 2018), so efforts and actions can last longer than just a firework spectacle, with sustained engagement during the lifespan of the project. There are probably many ongoing projects with high expectations about CS, but there is still a gap in the feedback and recognition that citizens receive from their contributions, and this issue has to be improved in order to keep engagement and strengthen the field in the near future.

With the celebration of the United Nations Decade of Ocean Science for Sustainable Development (2021–2030), there is an outstanding opportunity to foster initiatives in this sense, to help increase knowledge and take action to conserve MAFs within a framework of sustainability and development, where CS will be a key piece demonstrating that *Homo sapiens* can do things much better to change the effects of our presence on Earth.

References

Aceves-Bueno E, Adeleye A, Bradley D, Brandt W, Callery P, Feraud M, Garner K, Gentry R, Huang Y, McCullough I, Pearlman I, Sutherland S, Wilkinson W, Yang Y, Zink T, Anderson S, Tague C (2015) Citizen science as an approach for overcoming insufficient monitoring and inadequate stakeholder buy-in in adaptive management: criteria and evidence. Ecosystems 18:493–506. https://doi.org/10.1007/s10021-015-9842-4

Albins M, Hixon M (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Mar Ecol-Progr Ser 367:233–238. https://doi.org/10.3354/meps07620

Ballard H, Phillips T, Robinson L (2018) Conservation outcomes of citizen science. In: Hecker S, Haklay M, Bowser A, Makuch Z, Vogel J, Bonn A (eds) Citizen science. Innovation in open science, society and policy, 1st edn. UCL Press, London, pp 254–268. https://doi.org/10.14324/111.9781787352339

Bela G, Peltola T, Young JC, Balázs B, Arpin I, Pataki G, Hauck J, Kelemen E, Kopperoinen L, Van Herzele A, Keune H, Hecker S, Suskevics M, Roy HE, Itkonen P, Kulvik M, Laszlo M, Basnou C, Pino J, Bonn A (2016) Learning and the transformative potential of citizen science. Conserv Biol 30(5):990–999. https://doi.org/10.1111/cobi.12762

Blumstein DT, Saylan C (2007) The failure of environmental education (and how we can fix it). PLoS Biol 5(5):e120. https://doi.org/10.1371/journal.pbio.0050120

Bonney R, Ballard H, Jordan R, McCallie E, Phillips T, Shirk J, Wilderman CC (2009a) Participation in scientific research: defining the field and assessing its potential for informal science education. Washington, DC

Bonney R, Ballard H, Jordan R, McCallie E, Phillips, T., Shirk, J., & Wilderman, C. C. (2009b). Public participation in scientific research: defining the field and assessing its potential for informal science education, vol A CAISE In. Center for Advancement of Informal Science Education (CAISE), Washington, DC

Bramanti L, Vielmini I, Rossi S, Stolfa S, Santangelo G (2011) Involvement of recreational scuba divers in emblematic species monitoring: the case of Mediterranean red coral (*Corallium rubrum*). J Nat Conserv 19(5):312–318. https://doi.org/10.1016/j.jnc.2011.05.004

Branchini S, Meschini M, Covi C, Piccinetti C, Zaccanti F, Goffredo S (2015) Participating in a citizen science monitoring program: implications for environmental education. PLoS One 10(7): e0131812. https://doi.org/10.1371/journal.pone.0131812

Brondizio ES, Settele J, Díaz S, Ngo HT (2019) Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services IPBES. Bonn. Retrieved from https://ipbes.net/global-assessment

Cerrano C, Milanese M, Ponti M (2017) Diving for science – science for diving: volunteer scuba divers support science and conservation in the Mediterranean Sea. Aquat Conserv Mar Freshwat Ecosyst 27(2):303–323. https://doi.org/10.1002/aqc.2663

Chimienti G (2020) Vulnerable forests of the pink sea fan *Eunicella verrucosa* in the Mediterranean Sea. Diversity 12(5):176. https://doi.org/10.3390/d12050176

Cigliano JA, Meyer R, Ballard HL, Freitag A, Phillips TB, Wasser A (2015) Making marine and coastal citizen science matter. Ocean Coast Manag 115:77–87. https://doi.org/10.1016/j.ocecoaman.2015.06.012

Clements CS, Hay ME (2019) Biodiversity enhances coral growth, tissue survivorship and suppression of macroalgae. Nat Ecol Evol 3(2):178–182. https://doi.org/10.1038/s41559-018-0752-7

Díaz S, Settele J, Brondízio ES, Ngo HT, Guèze M, Agard J, Arneth A, Balvanera P, Brauman KA, Butchart SHM, Chan KMA, Garibaldi LA, Ichii K, Liu J, Subramanian SM, Midgley GF, Miloslavich P, Molnár Z, Obura D, Pfaff A, Polasky S, Purvis A, Razzaque J, Reyers B, Roy Chowdhury R, Shin YJ, Visseren-Hamakers IJ, Willis KJ, Zayas CN (2019) IPBES – summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn.

Retrieved from https://ipbes.net/sites/default/files/2020-02/ipbes_global_assessment_report_summary_for_policymakers_es.pdf

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annu Rev Ecol Evol Syst 41(1):149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Dickinson JL, Shirk J, Bonter D, Bonney R, Crain RL, Martin J, Phillips T, Purcell K (2012) The current state of citizen science as a tool for ecological research and public engagement. Front Ecol Environ 10(6):291–297. https://doi.org/10.1890/110236

Earp HS, Liconti A (2020) Science for the future: the use of citizen science in marine research and conservation. In: Jungblut S, Liebich V, Bode-Dalby M (eds) YOUMARES 9 – the oceans: our research, our future: proceedings of the 2018 conference for YOUng MArine RESearcher in Oldenburg, Germany. Springer International, Cham, pp 1–19. https://doi.org/10.1007/978-3-030-20389-4_1

Eitzel MV, Cappadonna JL, Santos-Lang C, Duerr RE, Virapongse A, West SE, Kyba CCM, Bowser A, Cooper CB, Sforzi A, Metcalfe AN, Harris ES, Thiel M, Haklay M, Ponciano L, Roche J, Ceccaroni L, Shilling FM, Dörler D, Heigl F, Kiessling T, Davis BY, Jiang Q (2017) Citizen science terminology matters: exploring key terms. Citizen Sci 2(1):1. https://doi.org/10.5334/cstp.96

Fritz S, See L, Carlson T, Haklay M, Oliver JL, Fraisl D, Mondardini R, Brocklehurst M, Shanley LA, Schade S, Wehn U, Abrate T, Anstee J, Arnold S, Billot M, Campbell J, Espey J, Gold M, Hager G, He S, Hepburn L, Hsu A, Long D, Masó J, McCallum I, Muniafu M, Moorthy I, Obersteiner M, Parker AJ, Weisspflug M, West S (2019) Citizen science and the United Nations sustainable development goals. Nat Sustain 2(10):922–930. https://doi.org/10.1038/s41893-019-0390-3

Goffredo S, Piccinetti C, ZACCANTI F (2004) Volunteers in marine conservation monitoring: a study of the distribution of seahorses carried out in collaboration with recreational scuba divers. Conserv Biol 18:1492–1503. https://doi.org/10.1111/j.1523-1739.2004.00015.x

Hesley D, Burdeno D, Drury C, Schopmeyer S, Lirman D (2017) Citizen science benefits coral reef restoration activities. J Nat Conserv 40:94–99. https://doi.org/10.1016/J.JNC.2017.09.001

Irwin A (2018) No PhDs needed: how citizen science is transforming research. Nature 562:7728

Jordan R, Gray S, Sorensen A, Newman G, Mellor D, Newman G, Hmelo-Silver C, LaDeau S, Biehler D, Crall A (2016) Studying citizen science through adaptive management and learning feedbacks as mechanisms for improving conservation. Conserv Biol 30(3):487–495. https://doi.org/10.1111/cobi.12659

Kirkpatrick JD, Kirkpatrick WK (2016) Kirkpatrick's four levels of training evaluation. ATD Press, Alexandria

Krasny M, Bonney R (2005) Environmental education through citizen science and participatory action research. In: Johnson EA, Mappin MJ (eds) Environmental education and advocacy: changing perspectives of ecology and education. Cambridge University Press, Cambridge

Lee S, Roth WM (2003) Science and the "good citizen": community-based scientific literacy. Sci Technol Hum Values 28(3):403–424

Leisher C, Mangubhai S, Hess S, Widodo H, Soekirman T, Tjoe S, Wawiyai S, Neil Larsen S, Rumetna L, Halim A, Sanjayan M (2012) Measuring the benefits and costs of community education and outreach in marine protected areas. Mar Policy 36(5):1005–1011. https://doi.org/10.1016/j.marpol.2012.02.022

Lloyd TJ, Fuller RA, Oliver JL, Tulloch AI, Barnes M, Steven R (2020) Estimating the spatial coverage of citizen science for monitoring threatened species. Glob Ecol Conserv 23:e01048. https://doi.org/10.1016/J.GECCO.2020.E01048

Lucrezi S, Milanese M, Palma M, Cerrano C (2018) Stirring the strategic direction of scuba diving marine citizen science: a survey of active and potential participants. PLoS One 13(8):e0202484. https://doi.org/10.1371/journal.pone.0202484

Marcinkowski T (1991) The relationship between environmental literacy and responsible environmental behavior in environmental education. UNESCO an environmental education approach to the training of middle level teachers: a prototype programme, pp 1–7

Miller-Rushing A, Primack R, Bonney R (2012) The history of public participation in ecological research. Front Ecol Environ 10(6):285–290. https://doi.org/10.1890/110278

Morrison TH, Adger N, Barnett J, Brown K, Possingham H, Hughes T (2020) Advancing coral reef governance into the Anthropocene. One Earth 2(1):64–74. https://doi.org/10.1016/j.oneear.2019.12.014

NOAA (n.d.) Citizen science – partner with scientists to answer real-world questions. National Marine Sanctuaries. Retrieved February 18, 2020, from https://sanctuaries.noaa.gov/involved/citizen-science.html

Palomo I, Montes C, Martín-López B, González JA, García-Llorente M, Alcorlo P, Mora MRG (2014) Incorporating the social-ecological approach in protected areas in the Anthropocene. Bioscience 64(3):181. Retrieved from http://search.proquest.com/docview/1629384359?accountid=15292

Rossi S (2013) The destruction of the ‘animal forests’ in the oceans: towards an over-simplification of the benthic ecosystems. Ocean Coast Manag 84:77–85. https://doi.org/10.1016/j.ocecoaman.2013.07.004

Rossi S, Orejas C (2019) 39 approaching cold-water corals to the society: novel ways to transfer knowledge. Springer, Cham, pp 473–480. https://doi.org/10.1007/978-3-319-91608-8_39

Santoro F, Santin S, Scowcroft G, Fauville G, Tuddenham P (2017) Ocean literacy for all: a toolkit. UNESCO. Retrieved from https://unesdoc.unesco.org/ark:/48223/pf0000260721

Schoedinger S, Tran LU, Whitley L (2010) From the principles to the scope and sequence: a brief history of the ocean literacy campaign. Current (Special Re) 3–7

Steel BS, Smith C, Opsommer L, Curiel S, Warner-Steel R (2005) Public ocean literacy in the United States. Ocean Coast Manag 48(2):97–114. https://doi.org/10.1016/j.ocecoaman.2005.01.002

Steffen W, Persson Å, Deutsch L, Zalasiewicz J, Williams M, Richardson K, Crumley C, Crutzen P, Folke C, Gordon L, Molina M, Ramanathan V, Rockstrom J, Scheffer M, Schellnhuber HJ, Svedin U (2011) The Anthropocene: from global change to planetary stewardship. Ambio 40(7):739–761. https://doi.org/10.1007/s13280-011-0185-x

Stepath C (2006) Coral reefs as sites for experiential environmental education: learning with Australian students – a foundational study

Theobald EJ, Ettinger AK, Burgess HK, DeBey LB, Schmidt NR, Froehlich HE, Wagner C, Hille Ris Lambers J, Tewksbury J, Harsch MA, Parrish JK (2015) Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. Biol Conserv 181:236–244. https://doi.org/10.1016/J.BIOCON.2014.10.021

Thiel M, Penna-Diaz MA, Luna-Jorquera G, SAlas S, Sellanes J, Stotz W (2014) Citizen scientists and marine research: volunteer participants, their contributions, and projection for the future. Oceanogr Mar Biol Annu Rev 52:257–314. https://pdfs.semanticscholar.org/59c2/c9d0bc62ad23f3ef99f58e3a95ec69225e39.pdf

Uyarra MC, Borja Á (2016) Ocean literacy: a ‘new’ socio-ecological concept for a sustainable use of the seas. Mar Pollut Bull 104:1–2. https://doi.org/10.1016/j.marpolbul.2016.02.060

Vaughan H (2007) Citizen science as a catalyst in bridging the gap between science and decision-makers. In McEver C, Bonney R, Dickinson J, Kelling S, Rosenberg K, Shirk J (eds) Citizen science toolkit conference. Cornell Laboratory of Ornithology, Cornell Laboratory of Ornithology, Ithaca, NY. Retrieved from www.citizenscience.org

Woolley AW, Chabris CF, Pentland A, Hashmi N, Malone TW (2010) Evidence for a collective intelligence factor in the performance of human groups. Science 330(6004):686–688. https://doi.org/10.1126/SCIENCE.1193147

Zorrilla-Pujana J, Rossi S (2014) Integrating environmental education in marine protected areas management in Colombia. Ocean Coast Manag 93:67–75. https://doi.org/10.1016/j.ocecoaman.2014.03.006