Where Seaweed Forests Meet Animal Forests: The Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem

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Abstract

The Mediterranean coralligenous and the intertropical coral reef ecosystems are similar in several aspects, such as their ability to thrive in nutrient-poor waters and the communities associated with them. For example, these ecosystems encompass communities ranging from bioconstructions by calcified blade-forming coralline macroalgae, bioconstructions by calcified hexacorallians, canopy-forming seaweed forests, canopy-forming gorgonian (animal) forests, to turfs of macroalgae. They depend mainly upon available light, temperature, and herbivore pressure. In spatial terms, these communities can constitute a complex mosaic. Over time, they can follow each other throughout ecological successions, i.e., a suite of shifts, or phase-shift events, as a consequence of natural or anthropogenic disturbances. Some of these communities, of which the autogenic ecosystem engineers are esthetically pleasing, large-sized, and long-lived, such as blade-forming corallines, gorgonians, and hexacorallians, are often explicitly or implicitly, but erroneously, regarded as the whole ecosystem, whereas they are in fact only part of it. Both coral reefs and the Mediterranean coralligenous ecosystems dwell in highly oligotrophic waters. Their success hinges upon mutualism with unicellular primary producers (dinobionts), the efficient recycling of nitrogen, and diazotrophy (coral reefs), and upon the input of allochthonous organic matter (coralligenous), rather than on the primary production of macroalgae alone (e.g., *Cystoseira*, *Sargassum*, *Turbinaria*, and turf-forming species). In addition, species diversity is high, which substantially helps to make these ecosystems

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species diversity hotspots. The close intertwining of the different communities (seaweed forests, heterotrophic animal forests, photosynthetic animal forests – via mutualism – and highly productive macroalgal turfs) within these two ecosystems, together with the massive precipitation of calcium carbonate, makes the structure and functioning of these ecosystems highly original, without counterpart in the terrestrial realm.

Keywords
Animal forests • Coralligenous • Coral reefs • *Cystoseira* • Disturbances • Mediterranean Sea • *Sargassum* • Scleractinians • Seaweed forests • *Turbinaria*

Contents

1 Introduction

The term “forest” is traditionally associated with tall, long-lived trees in the terrestrial realm. These trees are autogenic ecosystem engineers (as defined by Jones et al. 1994). They belong to Magnoliophyta (Embryophyta, Viridiplantae, kingdom Archaeplastida; see Fig. 1, Boudouresque 2015; Boudouresque et al. 2015). Subsequently, the term “forest” has been extended to marine habitats. At first, it only referred to large and perennial canopy-forming “seaweeds,” such as *Macrocystis pyrifera* and *Laminaria* spp. (“brown algae,” Phaeophyceae, Chromobionta, kingdom Stramenopiles; Fig. 1), algae reaching ~30–40 m and 5 m in height, respectively (Steneck et al. 2002). Then, it was also used for smaller, long-lived, canopy-forming seaweeds, such as *Cystoseira* spp. and *Sargassum* spp., a few tens of centimeters high in the Mediterranean Sea (e.g., Hereu et al. 2008). Finally, the term “forest” has also been applied to habitats structured by large long-lived sessile metazoans such as gorgonians, scleractinians, and sponges (Rossi 2013) (Metazoa, kingdom Opisthokonta; Fig. 1), which are the focus of the present volume.

The term “algae” has been traditionally applied to “lower plants,” characterized by a so-called primitive and simple pattern of organization. The vegetative apparatus, called “thallus,” was considered by nineteenth- and early twentieth-century authors as devoid of specialized tissues organized into specialized organs, e.g., stems, leaves, and vascular tissues which distribute resources, such as products of

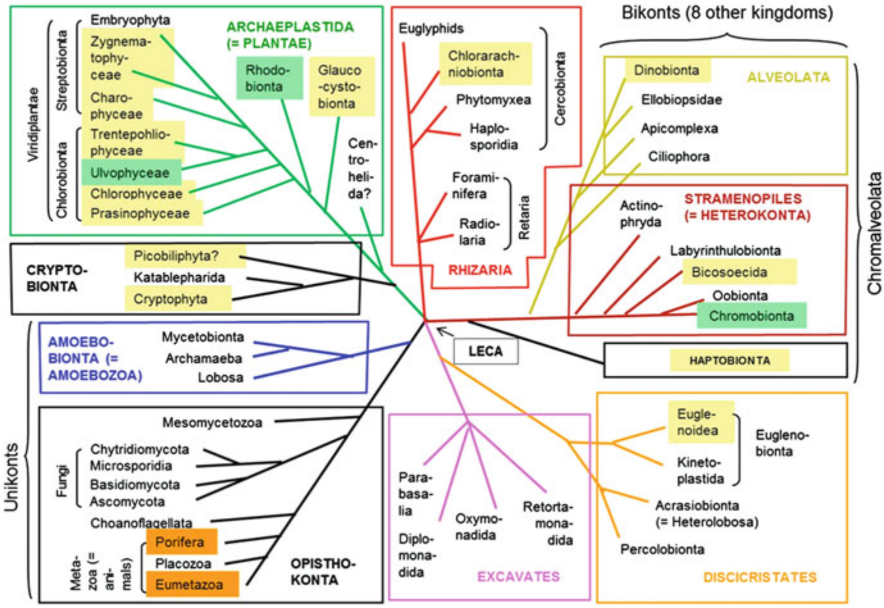

Fig. 1 The simplified phylogenetic tree of eukaryotes: most high-level taxa are not presented, e.g., within Chlorobionta, Dinobionta, Chromobionta, and Metazoa. *Boxes*: kingdoms. To simplify the diagram, certain classes (e.g., within Chromobionta) or most classes (e.g., within Chlorobionta) have not been shown. Highlighted *green* taxa correspond to multicellular “algae” (seaweeds, i.e., macroalgae), prone to constitute seaweed forests. Highlighted *yellow* taxa (in addition to the former) correspond to the customary notion of “algae.” Highlighted *orange* taxa correspond to metazoans prone to constitute animal forests. *LECA* last eukaryotic common ancestor (From Boudouresque (2015), modified)

photosynthesis, through the plant. In contrast, higher plants, such as Magnoliophyta, featured the abovementioned characters. Long before the arrival of molecular phylogenies, this simple approach, which dates from the time of Linnaeus, almost three centuries ago, has been questioned and rejected, on the basis of biochemistry, cytology, and anatomy. By the 1980s, molecular phylogenies had confirmed and clarified the breakdown of animal and plant kingdoms into a dozen kingdoms, each one encompassing former plants and animals. Today, “algae” are just a customary notion. They consist in a highly polyphyletic set of taxa, which belongs to seven kingdoms, namely, Archaeplastida, Rhizaria, Alveolata, Stramenopiles, Haptobionta, Discicristates, and Cryptobionta (Fig. 1). As regards “macroalgae,” i.e., multicellular photosynthetic organisms (MPOs), they encompass Ulvophyceae and Trebouxiophyceae (Chlorobionta, Viridiplantae, kingdom Archaeplastida; “green algae”), Rhodobionta (kingdom Archaeplastida; “red algae”), and Phaeophyceae (Chromobionta, kingdom Stramenopiles, “brown algae”) (Fig. 1; Boudouresque 2015; Boudouresque et al. 2015 and references therein). In the present work, the term “seaweed” is used as a synonym of macroalgae.

Seaweed forests are common worldwide in the infralittoral and circalittoral zones (sensu Pérès and Picard 1964; Pérès 1982) of temperate and cold seas. The autogenic ecosystem engineers generally belong to the Phaeophyceae: Fucales (e.g., genera *Cystophora*, *Cystoseira*, *Durvillaea*, *Phyllospora*, *Sargassum*, *Turbinaria*) and Laminariales (e.g., genera *Agarum*, *Ecklonia*, *Eisenia*, *Laminaria*, *Lessonia*, *Macrocystis*, *Saccharina*) (Boudouresque 1971; Tegner and Dayton 1991; Schiel and Foster 2006; Coleman et al. 2008). Within these forests, sessile and mobile animals (Metazoa) are abundant (species richness, number of individuals) and play a conspicuous role in the functioning of the ecosystems (e.g., herbivores, detritus feeders, suspension feeders, predators). However, in contrast to the canopy-forming seaweeds, they cannot strictly be considered as ecosystem engineers. Canopy-forming species constituting seaweed forests are perennial. Some of them are relatively short-lived, such as *Macrocystis pyrifera* that never exceeds the age of 6 years (Tegner et al. 1997), while others are long-lived, such as *Cystoseira zosteroides* that may exceed 50 years (Ballesteros et al. 2009) and probably much more, perhaps centuries.

Animal forests, i.e., habitats structured by long-lived sessile metazoans, playing the role of autogenic ecosystem engineers (Rossi 2013), are also common worldwide, in the infralittoral and littoral zones, where metazoans can be associated with photosynthetic organisms (mutualistic or not). Animal forests devoid of photosynthetic primary producers are limited to greater depths, beyond the photic zone, e.g., deep-sea corals (Mortensen et al. 2001). The latter habitats are the subject of specific chapters in this book.

Seaweed and animal forests share a number of characters, and can be distinguished by certain other characters, although the differences are far from being clear-cut and there is rather a continuum between them (Table 1).

Here, the juxtaposition, in space or time, of seaweed and animal forests is investigated on the basis of two case studies of emblematic ecosystems: the intertropical coral reefs and the Mediterranean coralligenous. Coral reefs are ecosystems, of which the autogenic ecosystem engineers of the most iconic facies are calcified cnidarians, mainly hexacorallians (Scleractinia) harboring mutualistic photosynthetic dinobionts (Symbiodiniaceae, kingdom Alveolata). The coralligeneous is a Mediterranean ecosystem of which the autogenic ecosystem engineers of the most iconic facies are calcified blade-forming corallines ("red algae"), canopy-forming Fucales ("brown algae"), and/or sea fan gorgonians (Alcyonacea, cnidarians). Both ecosystems, coral reefs and the Mediterranean coralligenous, exhibit a variety of facies (hereafter "communities"), ranging from crustose corallines and sponges, turf macroalgae, low stands of erect macroalgae, high canopy-forming seaweed forests, and high canopy-forming animal forests. These communities depend mainly upon available light, temperature, water movement, nutrients, herbivore pressure, and the overall ecosystem functioning. In space, these communities can constitute a complex mosaic. Over time, these communities can follow each other throughout ecological successions and phase shifts, as a consequence of natural and/or anthropogenic disturbances.

Table 1 Some similarities and differences between seaweed forests and animal forests. These similarities and differences go far beyond those of the ecosystems which are the focus of the present chapter. They concern the proper seaweed and animal forest communities, not the wider ecosystem which these communities are part of (e.g., coral reefs and the Mediterranean coralligenous ecosystem). "Yes" or "No" deals with major and general features, not with marginal processes and/or uncommon exceptions. *POM* particulate organic matter

		Seaweed forests	Animal forests
Structure	Three-dimensional (3D)	Yes	Yes
Habitat	Depth limitation (photic zone)	Yes	No
Life history traits	Long-lived autogenic ecosystem engineers	Yes	Yes
	Climax of a long-lasting succession	Yes	Yes
	Calcium carbonate precipitation	No	Yes
Ecosystem functioning	Importance of diazotrophy	Low	Low
	Importance of chemosynthesis	Low	Low
	Primary production mainly based upon multicellular photosynthetic organisms (MPOs)	Yes	Yes or No
	Primary production mainly based upon unicellular mutualistic organisms	No	Yes or No
	Biomass (primary and secondary producers)	Moderate	High
	Necromass	No	Yes
	Carbon sequestration	No	Yes
	Nutrient sequestration	No	Yes or No
	Conspicuous input of organic carbon	No	Yes
	Major role of filter and suspension feeders	No	Yes
	Herbivory	Low	High
	Food-web length (i.e., the number of trophic levels)	Short or long	Long
	Conspicuous output of organic carbon (POM, detritus)	No	Yes or No

2 The Mediterranean Coralligenous Ecosystem

2.1 Community Structure and Ecosystem Functioning

There is no consensus among scientists studying benthic communities regarding what the Mediterranean coralligenous ecosystem is (Ballesteros 2006 and references therein). According to Ballesteros (2006), a coralligenous reef is a hard substratum of biogenic origin that is mainly produced by the accumulation of calcareous blade-forming and crustose corallines (red algae, Rhodobionta) growing under dim light conditions. It usually develops on almost vertical walls, on gently sloping bottoms near the base of a wall, and on overhangs. The thickness of coralline

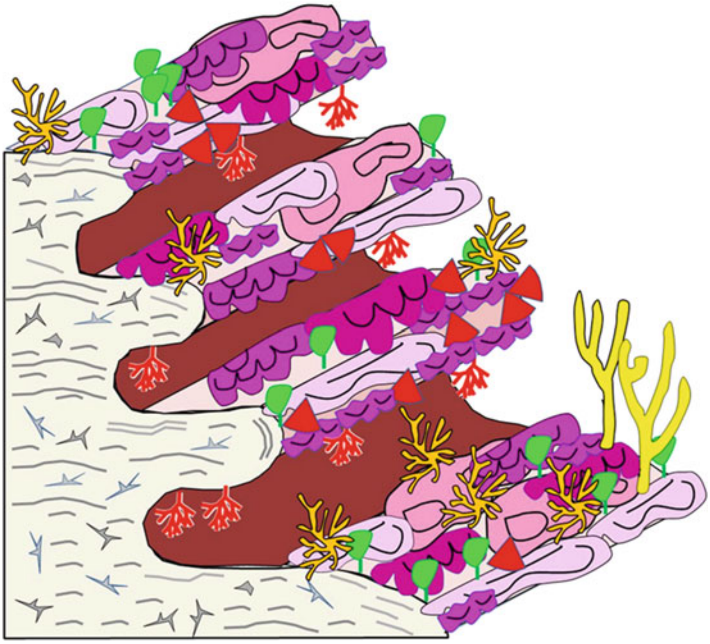

Fig. 2 A 3D sketch of coralligenous biogenic constructions in the form of shelves, near the base of an underwater wall. *Gray* (*left*): dead parts of biogenic constructions, with remains of corallines and metazoans. Dark and light *pink*: blade-forming corallines. *Red* triangles: *Peyssonnelia* spp. (Rhodobionta); *Green*: *Flabellia flabellata* (Chlorobionta). *Light yellow*: *Axinella polypoides* (sponge). *Orange*: bryozoans. *Red* inverted trees: the precious red coral *Corallium rubrum* (cnidarians). *Dark brown*: shady cavities beneath overhanging biogenic constructions (Original drawing (Charles F. Boudouresque))

bioconstructions may reach several dozen centimeters, sometimes several meters (Laubier 1966; Laborel 1987; Sartoretto et al. 1996). Near the base of underwater walls, coralline algae may constitute shelf-like structures, 50–100 cm wide and 20–40 cm thick, with characteristic spatial variations on the vertical and down-facing surfaces (Fig. 2; Virgilio et al. 2006). In addition to these biogenic red algal constructions, where blade-forming corallines are the autogenic ecosystem engineers (Fig. 4), three associated communities are considered here: **(i)** Seaweed forests composed of *Cystoseira zosteroides* and other Fucales (Fig. 3; Ballesteros et al. 2009); **(ii)** Animal forests consisting of gorgonians, e.g., *Eunicella* spp. and *Paramuricea clavata*, large erect sponges such as *Axinella polypoides* (Fig. 4), and bryozoans such as *Turbicellepora* spp. and *Pentapora fascialis*; **(iii)** Stands of crustose but not bio-constructing corallines, with turf and bushy macroalgae and small-sized sessile metazoans belonging mainly to bryozoans, ascidians and sponges (Boudouresque 1973). This last community is often known as "precoralligene" (Fig. 5; Pérès and Picard 1964). Despite the Latin prefix "pre-" (meaning "before"),

Fig. 3 A coralligenous ecosystem at Cap Caveaux (Provence, France), 40 m depth. A seaweed forest (*Cystoseira zosteroides*) occupies most of the scene. On the *right*, an individual of the gorgonian *Eunicella singularis* (Photo © Frédéric Zuberer (courtesy of F. Zuberer))

Fig. 4 A coralligenous ecosystem at La Gabinière Island (Port-Cros National Park, Provence, France), 40 m depth. In the foreground, bioconstruction by blade-forming corallines, covered with soft macroalgae. The brown blades are *Phyllariopsis brevipes*. The fish school is constituted of *Anthias anthias*. In the background, an animal forest of gorgonians, *Paramuricea clavata* (Photo © Sandrine Ruitton)

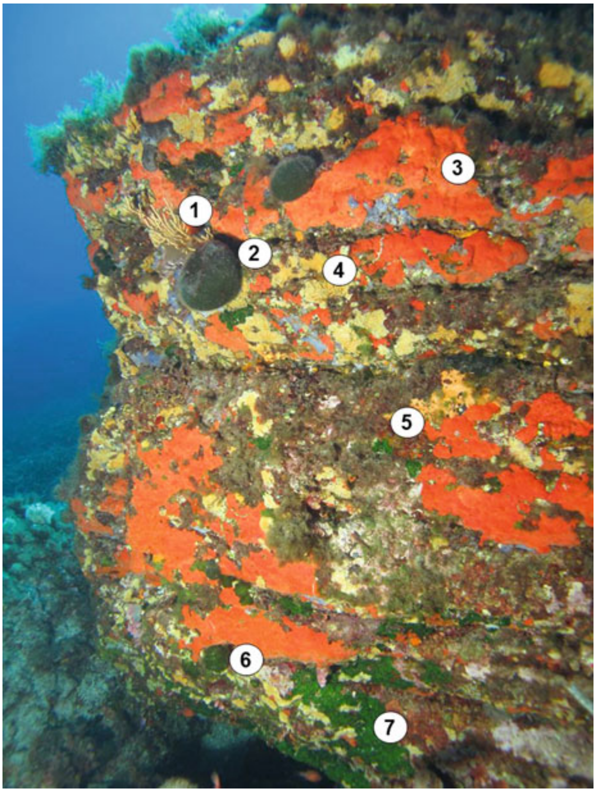

Fig. 5 A coralligenous ecosystem at La Gabinière Island (Port-Cros National Park, Provence, France), 15–18 m depth. The precoralligene community. Numbers indicate the different species and are placed on the right of the shown species. *1 Eunicella cavolini* (Cnidaria). *2 Codium bursa* (Ulvophyceae, Chlorobionta). *3 Crambe crambe* (Porifera). *4* Bryozoa. *5 Peyssonnelia* sp. (Rhodobionta). *6 Codium coralloides* (Ulvophyceae, Chlorobionta). *7 Palmophyllum crassum* (Pyramimonadophyceae, Chlorobionta). (Photo © Sandrine Ruitton)

there is no evidence that the precoralligene community would always represent a stage towards another coralligeneous community.

The reason why these four communities are here considered together is that they are closely intertwined into a mosaic of patches and successional stages, so that on the basis of an ecosystem-based approach, they constitute one ecosystem (Fig. 6; Ruitton et al. 2014). This complexity led Laubier (1966) to consider the coralligenous ecosystem as an ecological crossroad. The mobile fauna (fish, crustaceans, etc.) move from one habitat to the next, while the four communities share most of the features that characterize an ecosystem, namely, the coralligenous ecosystem, such as the importation of organic matter from the water column and adjacent ecosystems, the importance of calcified and long-lived organisms, etc. (see below).

Light, seawater temperature, and sediment deposition are the most important environmental forcing factors with respect to the distribution of the four communities of the coralligenous ecosystem (Morganti et al. 2001; Balata et al. 2005; Ballesteros 2006). Light is very important for the development and growth of coralligenous macroalgae, which need enough light to grow but which cannot withstand high levels of irradiance. They are able to develop at irradiances ranging

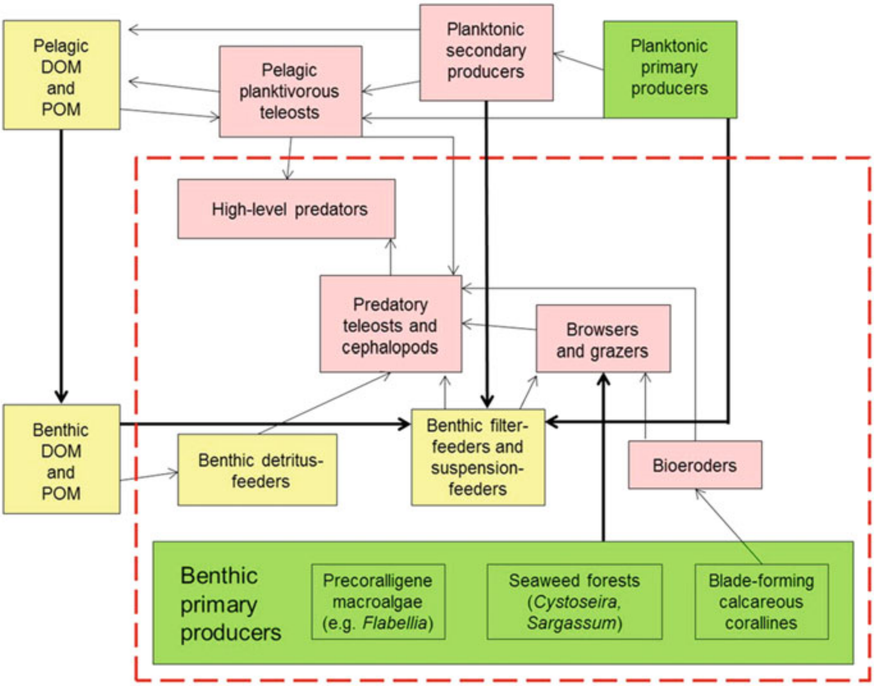

Fig. 6 Conceptual model of the functioning of a coralligenous ecosystem (*red* hatched rectangle). Primary producers are in *green*. Particulate organic matter (POM), dissolved organic matter (DOM), detritus feeders, filter feeders, and suspension feeders are in *yellow*. Bioeroders, browsers, grazers, and predators are in *pink*. *Arrows,* energy flows; *bold arrows*, main energy flows (Modified and redrawn from Ruitton et al. (2014))

from 0.05 to 3% of the sea surface irradiance (Ballesteros 1992). The quality of light should also be taken into account: the light that reaches this habitat belongs only to the blue and green wavelengths (Pérès and Picard 1964; Laubier 1966; Ballesteros 1992, 2006). Most coralligenous organisms withstand a temperature range of 10, 12–20, and 23 °C (minimum, usual range, and maximum) (Laubier 1966; Ballesteros 2006). However, some of them display a relatively high stenothermy, especially those participating in the animal forest community; events of mass mortality affecting gorgonians (e.g., the sea fans *Eunicella cavolini*, *E. singularis*, and *Paramuricea clavata*, and the precious red coral *Corallium rubrum*), other cnidarians (e.g., *Caryophyllia smithii*), and sponges (e.g., *Aplysina cavernicola*, *Cacospongia scalaris*, *Spongia officinalis*) have been attributed to unusually long-lasting periods of high temperature during summer (Cerrano et al. 2000; Perez et al. 2000; Coma et al. 2006; Bensoussan et al. 2010).

Coralligenous communities are widespread in the Mediterranean Sea, with the possible exception of the coasts of Lebanon and Israel (Laborel 1987). The animal forest community, characterized by large erect gorgonians, such as *Paramuricea* *clavata*, is usually restricted to the cooler areas of the Mediterranean. However, this is an artifact, since the knowledge of animal forests can be limited by the depth limit of SCUBA diving, while they thrive, in Greek and Turkish waters, at 60–80 m depth (Gili et al. 2014). The minimum depth (i.e., the upper limit) for coralline bioconstructions and animal forests of the coralligenous ecosystem depends upon the water transparency: 12 m in the Gulf of Fos, near the mouth of the Rhône River (Provence), 20 m around Marseille (Provence), and 50 m at Cabrera (Balearic Islands). They can occur down to 120 m in the southern and eastern Mediterranean (Laborel 1987; Ballesteros 2006). *Cystoseira zosteroides* forests are known down to 100 m in the clearest waters (Aurélie Blanfuné and Thierry Thibaut, unpublished data). The precoralligene community displays an even wider depth range.

The coralligenous ecosystem displays a number of features, the combination of which is unique and therefore characteristic (Fig. 6; Boudouresque et al. 2014; Ruitton et al. 2014). Some of these features are not shared by all the communities delineated here. **(i)** The species richness varies according to the scale, from moderate (point diversity) to high (alpha diversity) for macroalgae and from moderate (point diversity) to very high (alpha diversity) for metazoans. Overall, the coralligenous ecosystem constitutes an important species diversity hotspot, harboring around 20% of the Mediterranean species (Garrabou et al. 2002; Ballesteros 2006; Piazzi et al. 2010; Cánovas Molina et al. 2016). **(ii)** The photosynthetic primary production (PP) is low, because of the oligotrophy of the Mediterranean Sea and the depth, despite the presence of photosynthetic pigments that enhance energy harvesting in the light wavelengths still present at depth; the ecosystem belongs to the low nutrient–low chlorophyll (LNLC) category. The chemosynthetic PP is absent. **(iii)** The biomass of photosynthetic primary producers is low (not taking into consideration the mass of calcium carbonate), especially in animal forests. **(iv)** The ratio between PP and biomass is moderate. **(v)** Part of the PP is palatable and follows the herbivore pathway, while another part is poorly consumed because of mechanical defenses (calcification). However, this non-consumed PP does not enter the litter and the detritus pathway; rather, it constitutes a carbon sink. **(vi)** The importation of organic matter from adjacent ecosystems, as dissolved organic matter (DOM) and particulate organic matter (POM), is pivotal in the ecosystem functioning. Adjacent ecosystems are the pelagic ecosystem (the water column), infralittoral ecosystems such as rocky reefs and the *Posidonia oceanica* seagrass meadows, which exports large amounts of dead leaves and other detritus (Boudouresque et al. 2012; Personnic et al. 2014), as well as circalittoral ecosystems, such as the coastal detritic bottoms (maerl and free-living rhodoliths). The imported DOM and POM play a prominent role as food source for most metazoans of the coralligenous communities, which are either filter feeders or suspension feeders, especially those which play a role in the animal forest. Overall, the ecosystem is a heterotrophic one, with low primary production which cannot support the entire secondary production and which depends therefore upon imported organic matter. **(vii)** In contrast with its high dependence upon organic matter importations, the coralligenous ecosystem is a weak exporter. **(viii)** The growth of blade-forming coralline macroalgae results in a rise of the bottom (in the community of bioconstructions by blade-forming

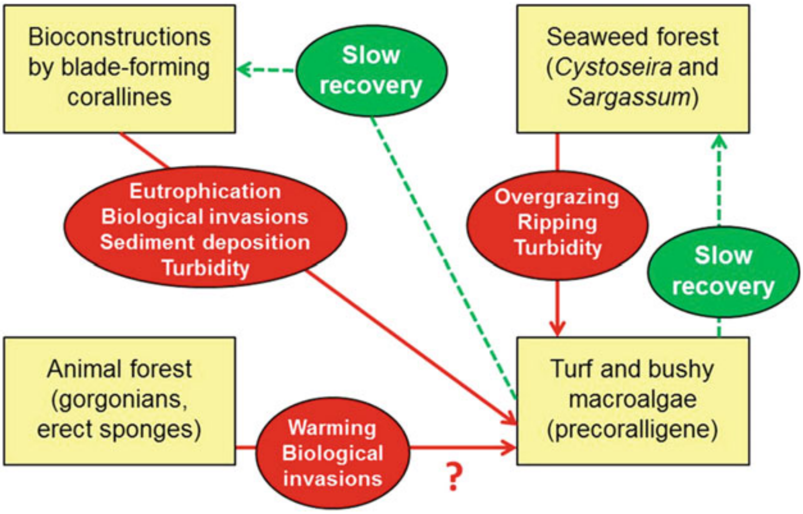

Fig. 7 Temporal dynamics of the four communities that constitute the coralligenous ecosystem, in a context of disturbances (*red* ovals) and recovery (*green* ovals) (Original drawing (Charles F. Boudouresque))

corallines; see Figs. 4 and 7). This trend, however, is offset by organisms that erode or dissolve the bioconstructions. The latter organisms belong to Cyanobacteria (e.g., *Hyella caespitosa*, *Mastigocoleus testarum*, and *Leptolyngbya terebrans*), perforating sponges (e.g., *Cliona celata* and *C. viridis*), boring mollusks (e.g., *Hiatella arctica*, *Lithophaga lithophaga*), sipunculids (e.g., *Aspidosiphon muelleri*), and grazing sea urchins (e.g., *Sphaerechinus granularis*) (Sartoretto and Francour 1997; Sartoretto 1998; Ballesteros 2006). The rise of the bioconstructions depends on a positive balance between building and bioeroding processes (e.g., Garrabou and Ballesteros 2000). **(ix)** The relatively high level of calcium carbonate precipitation is a key character of the ecosystem, more precisely of the community of bioconstructions by blade-forming corallines.

2.2 Macroalgae

At least 315 species of macroalgae have been reported within the four communities of the coralligenous ecosystem, which includes the blade-forming coralline bioconstructions, seaweed forests, animal forests, and the precoralligene community (Boudouresque 1973; Ballesteros 2006).

Blade-forming coralline macroalgae that build the coralligenous bioconstructions belong to a variety of species and genera of Corallinales and Hapalidiales (Rhodobionta). The most important species are *Mesophyllum expansum* (previously misidentified as *M. lichenoides*) and *Titanoderma* sp. (Sartoretto et al. 1996). Other important building species are *Lithophyllum frondosum* (usually reported as

Pseudolithophyllum expansum), *L. stictaeforme*, *L. cabiochae*, *Mesophyllum macroblastum* (previously misidentified as *M. alternans*), *M. macedonis*, *M. sphaericum*, and *Neogoniolithon mamillosum* (Ballesteros 2006). Several species of the genus *Peyssonnelia*, which belongs to the Peyssonneliales (Rhodobionta), mostly *P. polymorpha* and *P. rosa-marina*, also participate in the bioconstruction. These last species precipitate aragonite during calcification (James et al. 1988), in contrast to Corallinales and Hapalidiales, which precipitate calcite (Ballesteros 1992). The presence and the relative abundance of Corallinales, Hapalidiales, and Peyssonneliales vary according to the considered region and depth. A number of calcified non-photosynthetic organisms also contribute to the bioconstruction, e.g., the foraminiferan *Miniacina miniacea* (kingdom Rhizaria), cnidarians, and bryozoans (Metazoa, kingdom Opisthokonta).

Canopy-forming macroalgae that are part of the seaweed forests belong to Fucales (Phaeophyceae, kingdom Stramenopiles). In addition to the most common species, *Cystoseira zosteroides* (Fig. 3), *C. foeniculacea* f. latiramosa, *C. funkii*, *C. jabukae*, *C. spinosa* var. compressa, *C. usneoides*, *Sargassum acinarium*, *S. hornschuchii*, and *S. vulgare* can also be found. A rare species of *Laminaria* (Laminariales, Phaeophyceae), endemic to the Mediterranean Sea, *L. rodriguezii*, can occur, generally at a greater depth (Fredj 1972; Aguilar et al. 2010; Boisset et al. 2016; Žuljević et al. 2016).

The many other species of macroalgae belong to the Rhodobionta (red algae), Ulvophyceae (green algae), and Phaeophyceae (brown algae) and to several functional form groups (sheet, filamentous, coarsely branched, thick leathery, jointed calcareous, crustose). They are long- or short-lived, and most of them are small- or medium-sized, with the exception of e.g., *Phyllariopsis brevipes* (Fig. 4), a non-perennial Tilopteridales (Phaeophyceae). In fact, their only common characteristic is that they are neither builders of calcareous bioconstructions nor canopy-forming fleshy species.

2.3 Seaweed Forests Versus Animal Forests

Within the coralligenous ecosystem, seaweed forests and animal forests coexist, sometimes in close proximity. However, they rarely constitute mixed settlements, i.e., gorgonian forests with some *Cystoseira* and/or *Sargassum* individuals, or *Cystoseira* forests harboring gorgonians (but see Fig. 3). Usually, one of these communities dominates and there is little evidence of competition between them. They occupy slightly differing habitats, in terms of, e.g., depth, slope, light, exposure to currents, and therefore POM/DOM input. Seaweed forests, where *Cystoseira zosteroides* are loosely attached to the substrate, mainly thrive at depth (circalittoral zone), on gently sloping substrates, under dim light, calm conditions, and unidirectional bottom current. On steeper substrates, and with increasing depth and/or decreasing light, the precoralligene community, the bioconstructions with blade-forming corallines, and the animal forests occur successively.

Over time, disturbances can affect seaweed and animal forests. Deep seaweed forests are severely declining throughout the Mediterranean. In many areas, such as the French Riviera and French Catalonia, most *Cystoseira* and *Sargassum* species are locally or functionally extinct (Thibaut et al. 2005, 2015; but see Thibaut et al. 2016). In French Catalonia, *C. zosteroides*, once frequent, is now rare, *C. spinosa* var. compressa, formerly abundant, is currently extinct, together with *C. foeniculacea* f. latiramosa, *C. funkii*, *Sargassum acinarium*, *S. hornschuchii*, and *S. vulgare* (Thibaut et al. 2005). Several factors may be responsible for these regressions: overgrazing by sea urchins, due to the overfishing of their teleost predators (Labridae, Sparidae), ripping by fishing nets, increase in turbidity and biological invasions (Thibaut et al. 2005, 2015, 2016). Extreme storms, such as the 50-year storm (i.e., the most violent storm for 50 years) that occurred on December 26, 2008, in Spanish Catalonia, can also be responsible for massive pulling up of *C. zosteroides* (Navarro et al. 2012; Teixidó et al. 2013). The seaweed forest is then replaced by stands of encrusting, but not bio-constructing corallines, with turf and bushy macroalgae (precoralligene community) (Fig. 7). In the case of *Cystoseira* spp., when the disturbance ceases, the dissemination of the eggs at very short distance (probably a few meters) from the surviving individuals and very low recruitment make any recolonization very difficult and slow.

Blade-forming coralline bioconstructions are threatened by eutrophication (Piazzi et al. 2011, 2012). Nutrient enrichment can cause an increase in turf-forming native macroalgae (Piazzi et al. 2012) and an increased growth of turf-forming invasive macroalgae (Gennaro and Piazzi 2011) that hinder the photosynthesis of blade-forming corallines. Eutrophication also enhances the activity of bioeroder organisms, making negative the balance between bioconstruction and bioerosion (Hong 1980). As a result, blade-forming coralline bioconstructions can be replaced by turf and bushy macroalgae (“precoralligene” community) (Fig. 7). In a context of global change, coralline macroalgae may also be impacted, in the future, by the acidification of marine water (Martin and Gattuso 2009; Martin et al. 2013). Blade-forming coralline bioconstructions are also threatened by turbidity, sediment deposition, and biological invasions, such as *Caulerpa taxifolia*, *C. cylindracea* (Ulvophyceae, Chlorobionta), and *Womersleyella setacea* (Rhodobionta), especially if they occur in concert with other stress factors (Piazzi et al. 2012; Gatti et al. 2015; Cánovas Molina et al. 2016). In the same way as eutrophication, these disturbances putatively hinder the photosynthesis of blade-forming corallines.

Finally, animal forests of gorgonians and erect sponges are threatened by warm episodes (extreme high temperature events), which cause mass mortality episodes, as observed since the late 1990s in the northwestern Mediterranean (Cerrano et al. 2000; Perez et al. 2000; Coma et al. 2006; Lejeusne et al. 2010). The precious red coral *Corallium rubrum* can also be affected (Garrabou et al. 2001). In the context of the global warming, the reduction of the time-interval between extreme warm events (Diffenbaugh et al. 2007), or the persistence of a near-lethal high temperature, might hinder the recovery of the canopy-forming metazoans. Invasive macroalgae, such as *Caulerpa cylindracea* and *Womersleyella setacea*, might also hinder the recovery of gorgonians, by affecting the growth and survivorship of recruits (Cebrian et al. 2012). The animal forest could then be replaced by turf and bushy macroalgae, i.e., the "precoralligene" community (Ponti et al. 2014; Fig. 7).

Professional and recreational fishing activities, with the harvesting of fish and crustacean compartments, of major importance in the ecosystem functioning, and the damage by fishing lines and nets, which uproot gorgonians and large seaweeds, must be taken into account with regards to all the coralligenous communities (e.g., Cánovas Molina et al. 2016).

Overall, the three most emblematic communities of the coralligenous ecosystem (bioconstructions by blade-forming corallines, animal forests of gorgonians and erect sponges, and seaweed forests of *Cystoseira* and *Sargassum* species) can be changed, under the pressure of various disturbances, into the precoralligene community, far less structurally complex, with only turf and bushy macroalgae (in addition to low sessile metazoans) (Fig. 7).

3 The Coral Reef Ecosystem Complex

3.1 Community Structure and Ecosystem Functioning

Coral reefs are intertropical formations. The autogenic ecosystem engineers are calcified cnidarians, mainly hexacorallians (Scleractinia, Metazoa), harboring mutualistic photosynthetic dinobionts (kingdom Alveolata; see Fig. 1). They are found within the north and south isotherms 20–22 °C (minimum temperature) throughout the world's oceans. The calcareous skeletal material of the hexacorallians is made of aragonite and supplies much of the structural bulk of the coral reef, while the cement consisting of calcite is produced by coralline crustose macroalgae (CCMA; Rhodobionta) (Littler and Littler 1988 and references therein). The latter organisms account for ~25–50% of the total precipitation of calcium carbonate (e.g., Eakin 1996; Hart and Kench 2007). As regards the dinobionts, they were for a long time considered as belonging to *Symbiodinium microadriaticum*. In fact, *S. microadriaticum* encompasses a complex of highly diverging clades; each clade probably encompassing a number of described and undescribed species (e.g., Savage et al. 2002; LaJeunesse and Thornhill 2011; Lee et al. 2015). These dinobionts are often called, incorrectly, "zooxanthellae," a misused term coined at a time when their actual nature was unknown (Boudouresque 2015). The symbiosis between calcified hexacorallians (hereafter hexacorallians) and dinobionts is called mutualism, because both partners are thought to derive benefit from the relationship (Fig. 8; Cowen 1988; Grottoli et al. 2006).

In the coral reef ecosystem, nutrients (including N and P) are tenaciously recycled within the system (Fig. 8), so that there is an immense accumulation of biomass (i.e., energy) in a highly oligotrophic environment. The symbiosis between dinobionts and hexacorallians is advantageous to both partners (i.e., a mutualistic symbiosis) only in an oligotrophic high-light environment (see below) (Cowen 1988).

The hexacorallians, i.e., the ecosystem engineers of the "animal forest," derive most of their nutritional resources from the primary production of their mutualistic

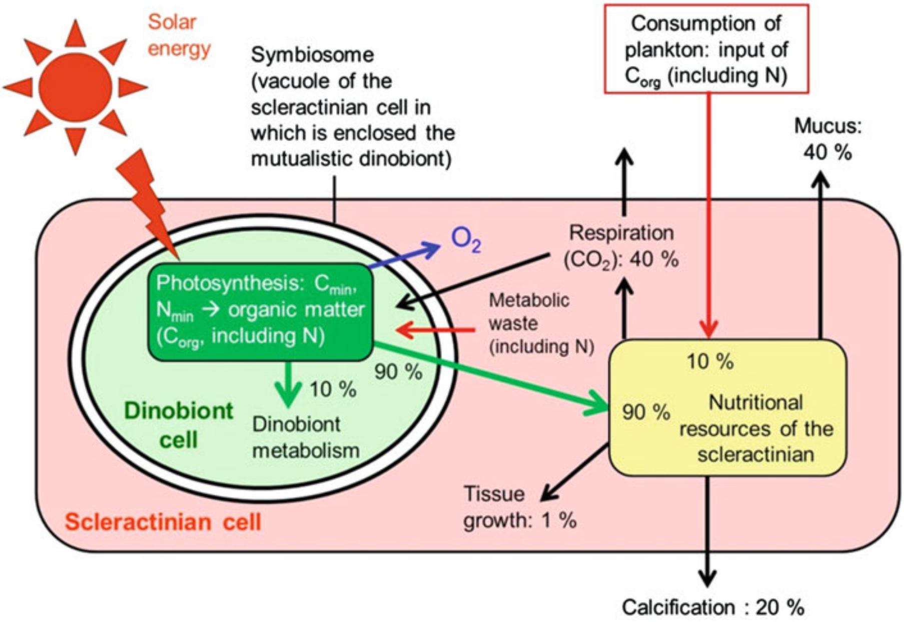

Fig. 8 Model of energy budget of a hexacorallian (scleractinian) and its mutualistic dinobiont. Most of the primary production of the dinobiont is exported toward the hexacorallian, which draws most of its nutritional resources from the mutualistic dinobiont. C_{org}, organic carbon. Data from Cowen (1988) (Redrawn and modified from Paola Furla (Charles F. Boudouresque))

dinobionts (Fig. 8). The proportion of energy transferred from dinobionts to the host, and that used for the host's metabolism and calcification, varies between coral species (Muscatine et al. 1981; Leletkin 2000) and *Symbiodinium* clades and species (e.g., Pettay et al. 2015). As a result, scleractinians could also be regarded as primary producers, and hexacorallian animal forests that characterize coral reefs may be functionally close to seaweed forests.

The coral reef ecosystem is made up of a mosaic of communities (e.g., Pérès and Picard 1969; Bellwood et al. 2004). In addition to the abovementioned hexacorallian forest, the emblematic flagship of coral reefs (Fig. 9), at least four more communities, constitute the coral reef ecosystem. **(i)** Seaweed forests, made up of canopy-forming Fucales (Phaeophyceae, Stramenopiles) such as *Turbinaria* spp. and *Sargassum* spp. (Fig. 10). **(ii)** Non-articulated coralline macroalgae (rhodobionts) of the so-called intertidal algal ridge (Fig. 11). **(iii)** Soft bottom habitats with calcified (in the aragonite form of calcium carbonate) and fleshy chlorobionts belonging to the Bryopsidales and Dasycladales (Ulvophyceae). **(iv)** Turf or mat of filamentous macroalgae and cyanobacteria (Fig. 12). Macroalgae may outcompete corals, through allelopathic compounds (Vieira et al. 2016). A number of other communities, such as animal forests related to gorgonians and sponges and sea urchin barren-grounds, are also important in reef ecosystems (e.g., Bellwood et al. 2004).

Fig. 9 A coral reef ecosystem at Ko Phi Phi Island, Thailand, Adaman Sea, at 8 m depth. An animal forest of hexacorallians. *Left*, branched *Acropora. Right*, tabular *Acropora*. Fish in the foreground: *Chaetodon trifascialis*, a consumer of coral polyps (Photo © Sandrine Ruitton)

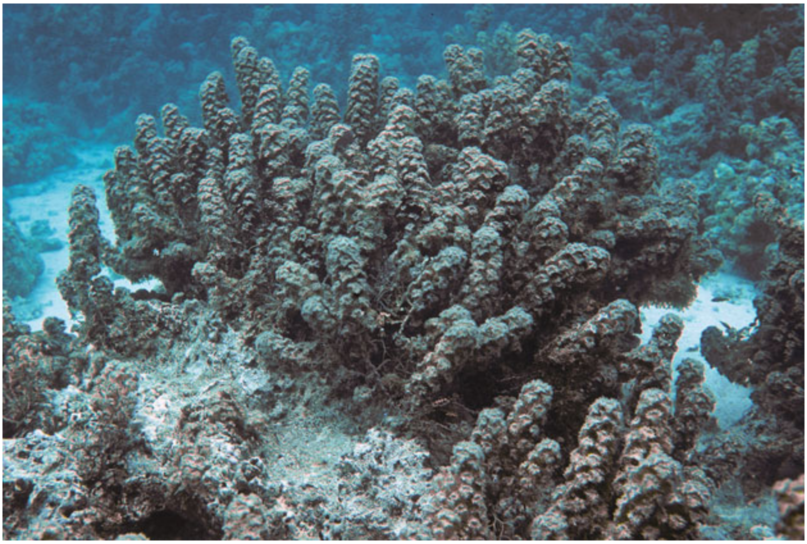

Fig. 10 A coral reef ecosystem at Tiahura, Moorea (French Polynesia). A seaweed forest (*Turbinaria* sp., Phaeophyceae, Chromobionta, Stramenopiles) (Photo © Mireille Harmelin-Vivien)

Fig. 11 A coral reef ecosystem at Tikehau, Tuamotu Islands (French Polynesia). The algal ridge community (Photo © Mireille Harmelin-Vivien)

Fig. 12 A coral reef ecosystem at Bora Bora (French Polynesia). A "garden" of macroalgal turf (center and foreground) on dead hexacorallians, and the farmer damselfish teleost *Stegastes nigricans* (Photo © Sébastien Personnic)

The coral reef ecosystem displays a number of features, the combination of which is unique and therefore characteristic (e.g., Pérès and Picard 1969; Littler et al. 1987; Littler and Littler 1988; Moberg and Folke 1999; Tribollet et al. 2002, 2006; Boudouresque et al. 2014: Glynn and Manzello 2015; Leprieur et al. 2016). Some of these features are not shared by all of the communities delineated here. **(i)** The species richness of macroalgae is between moderate (point diversity) and high (alpha diversity), and that of metazoans is very high (point diversity and alpha diversity). **(ii)** The photosynthetic PP is very high, 50–100 times higher than the PP of the adjacent open ocean. It is enhanced by the efficient retention of nutrients by recycling (Fig. 8) and by nitrogen-fixing (diazotrophic) bacteria (including Cyanobacteria). Endolithic primary producers also significantly contribute to the PP, in dead carbonate substrates. The ecosystem belongs to the low nutrient–high chlorophyll (LNHC) category. The chemosynthetic PP is absent. **(iii)** The biomass of photosynthetic primary producers, not taking into consideration the mass of calcium carbonate, is often regarded as low. In fact, adding the hidden mutualistic dinobiont biomass and the macroalgal biomass, the total biomass of primary producers can be equal to that of the metazoans. **(iv)** The ratio between PP and biomass is low. **(v)** Besides the PP of mutualistic dinobionts (~90% can be transferred to the host; see Fig. 8), part of the macroalgal PP is palatable and follows the herbivore pathway, while calcareous macroalgae, because of mechanical defenses, and fleshy macroalgae, because of chemical defenses, are poorly consumed. Overall, the herbivore pressure is very high and represents a key parameter in the functioning of the ecosystem. **(vi)** The importation of organic matter from adjacent ecosystems, as DOM and POM, plays a role in the ecosystem functioning. Adjacent ecosystems are the pelagic ecosystem (the water column of the lagoon and/or of the open ocean) and infralittoral ecosystems such as seagrass meadows (e.g., *Thalassia hemprichii* in the Indo-Pacific Ocean and *T. testudinum* in the eastern tropical Atlantic Ocean) and mangroves. **(vii)** The coral reef ecosystem is a relatively weak exporter, if compared with seagrass ecosystems (Boudouresque et al. 2014; Personnic et al. 2014). However, a significant part of the secondary production is exported to the open-ocean and deep-sea ecosystems via top predators. **(viii)** The hexacorallian growth results in a rise of the bottom. This trend, however, is offset by organisms that erode or dissolve the bioconstructions. The latter organisms belong to endobiontic Cyanobacteria and chlorobionts, sponges, boring mollusks, and grazing sea urchins and fishes. The rise of the bioconstructions results from a positive balance between calcification as constructive process and bioerosion as destructive process. **(ix)** The very high level of calcium carbonate precipitation constitutes a key character of the ecosystem, and provides ecosystem services of paramount importance (see below) (Jones et al. 2015). **(x)** Coral reefs are typical of an overall top-down control of the food web, especially within the animal forest community; although mats of turf algae could result from the release from this top-down control. Some pristine coral reefs, never impacted by human activities, reveal the possible primeval state of the coral reefs, with a "nasty" top-down control; the brutality of which has perhaps no equivalent in other of the earth's ecosystems (e.g., Pala 2007; Sandin et al. 2008).

3.2 Macroalgae

The hexacorallian animal forest can seem, at a diver's first glance, to be devoid of macroalgae. In fact, some macroalgae, e.g., corallines, are located beneath or within the hexacorallian canopy. In addition, turf fast-growing macroalgae may seem inconspicuous, because of their steady grazing by herbivores and therefore their very low biomass; although they are responsible for most (70–80%) of the PP of the community (Littler and Littler 1988). Endobiontic boring chlorobionts, cyanobacteria, and fungi, within the hexacorallian skeletal structure, also play a conspicuous role within the animal forest and crustose coralline communities (Tribollet and Payri 2001; Glynn and Manzello 2015).

The canopy-forming seaweed forest (Fig. 10) is restricted to areas where there is more turbulence and little topographic relief, which hinders herbivore activity (sea urchins and fish). Seaweeds belong mainly to the genera *Turbinaria*, *Sargassum* (Phaeophyceae, Chromobionta, Stramenopiles), and *Acanthophora* (Rhodobionta, Archaeplastida).

The intertidal algal ridge community (also called algal crest), which dwells in turbulent areas, is generally dominated by crustose coralline macroalgae (CCMA; Fig. 11) belonging to the genera *Hydrolithon*, *Lithophyllum*, and *Porolithon* (Rhodobionta): *Hydrolithon craspedium*, *H. gardineri*, *Lithophyllum congestum*, *L. kotschyanum*, *L. pygmaeum*, and *Porolithon onkodes*. These species can withstand considerable desiccation and exposure to high sunlight irradiance (Littler and Littler 1988).

Calcified and soft Ulvophyceae (Chlorobionta) predominate mainly in protected shallow areas on soft bottoms, habitats that are unsuitable for most other macroalgae (community: chlorobiont stands on soft bottoms). The former belongs to the genera *Halimeda*, *Penicillus*, *Rhizocephalus*, and *Udotea*, defended from consumption by herbivores and omnivores by calcification, and which strongly contribute to peripheral reef and lagoon sediments. The latter belongs to the genera *Avrainvillea* and *Caulerpa*, protected against herbivores and omnivores by deterrent chemical compounds (terpenes). The animal forest community exports great amounts of coral debris and coral sand toward the chlorobiont stands on the soft bottom community (Fig. 13).

Finally, hard substrates, either rocks or dead coral bioconstructions, can be densely covered by filamentous macroalgae and cyanobacteria, the thickness of the turf or mat being negatively correlated with the herbivore pressure. It is worth emphasizing that the productivity of these mats, either within the present habitat or beneath the hexacorallian forest (see above), is considerably higher than that of the coarser species of the canopy-forming seaweed forest. In addition to the filamentous macroalgae, the mat harbors diazotrophic (i.e., N_2-fixing) Cyanobacteria, such as *Scytonematopsis crustacea*, an important feature that enhances reef productivity (Littler and Littler 1988). The presence of territorial teleost grazers, such as the damselfish *Stegastes nigricans*, which behave as true farmers, reduces herbivory pressure on turf macroalgae and thus might prevent recolonization by hexacorallians or by canopy-forming seaweeds (Fig. 12) (Hata and Kato 2002; Arnold et al. 2010).

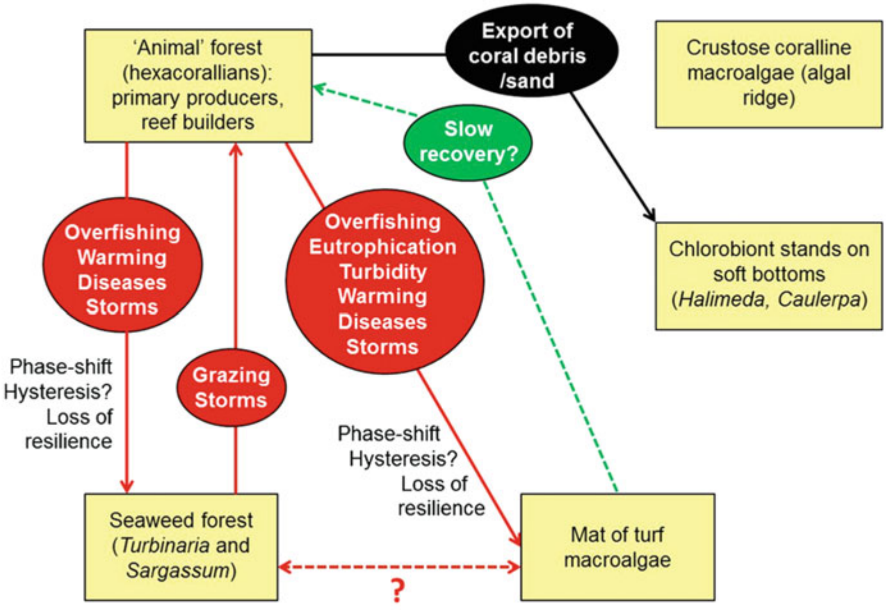

Fig. 13 Temporal dynamics of the five main communities that constitute the coral reef ecosystem, in a context of natural and human-induced disturbances (*red* ovals) and recovery (*green* ovals). Black oval: other processes (Original drawing (Charles F. Boudouresque))

3.3 Seaweed Forests Versus Animal Forests

Within the coral reef ecosystem complex, hexacorallian forests, canopy-forming seaweed forests, and other macroalgal stands compete for space, nutrients, and light. Light is a key factor for all of these communities, as hexacorallians constitute de facto primary producers through their mutualistic dinobionts. Any one of these communities can predominate under specific environmental conditions (Littler and Littler 1988).

Hexacorallian forests are threatened by a variety of natural and/or human impacts, e.g., storm damage, outbreaks of crown-of-thorns starfish (*Acanthaster planci*), diseases, warming resulting in bleaching events, eutrophication, coastal development, overfishing, anchoring, and mining (Smith et al. 2016 and references therein). A phase shift, with possible hysteresis, toward macroalgal turfs or canopy-forming seaweed forests (e.g., *Sargassum* and *Turbinaria*), has been widely reported (Fig. 13) (e.g., Hughes 1994; Bellwood et al. 2004; McManus and Polsenberg 2004; Bruno et al. 2009; Vermeij et al. 2010). Some disturbances (e.g., eutrophication and overfishing) result in a loss of resilience and increased vulnerability to phase shifts (Bellwood et al. 2004). Smith et al. (2016) actually observed that the cover of macroalgal turfs was higher in Pacific inhabited islands than in uninhabited ones, while it was exactly the opposite for the cover of hexacorallian forests (bioconstructions). However, the relationship between macroalgal cover and human impact is unclear, and the apparent link could be due to latitude and then the frequency and intensity of warm events. According to the dataset of Smith et al. (2016), there is no evidence of coral to macroalgal phase shifts, and whether a given community represents a transient state following a disturbance event or is actually an alternate stable state remains unclear (Fig. 13). Besides phase shifts from calcified hexacorallian forests to macroalgal turf or canopy-forming seaweed forests, there are also other phase shifts reported and/or suggested, e.g., from calcified hexacorallians to soft hexacorallians (corallimorpharians)-dominated or to sponge-dominated communities (Norström et al. 2009), which are beyond the scope of the present chapter.

Macroalgal turfs (generally less than 2 cm tall) consist of a mat of filamentous species, in association with Cyanobacteria, that quickly colonize dead hexacorallian skeletons. In contrast to CCMAs, which enhance hexacorallian recruitment, they negatively affect the survival capacity of hexacorallian recruits (Smith et al. 2016). Some macroalgae are even capable of bleaching some hexacorallians, via allelopathic compounds (Vieira et al. 2016). The turf macroalgae, both those that characterize a community and those that constitute an understory beneath the hexacorallian forest, play a prominent role within the coral reef ecosystem. They are ubiquitous in coral reefs, and their cover is probably more significant than usually claimed; however, this group of algae is inconspicuous and less iconic than the hexacorallians, so that it is often ignored or lumped together within categories of "dead coral" or "rubble." Similarly, CCMA (with the exception of the algal ridge) are often lumped together with "bare space" or ignored entirely (Smith et al. 2016). For these reasons, some studies, showing the "worrying" presence, the progression, or the supposed progression, of macroalgal turfs should be treated with caution, in the absence of a relevant baseline.

Finally, the CCMA of the algal ridge and the stands of chlorobionts on soft bottoms are confined to very specific habitats. As a result, these two communities weakly interact with the three former communities (Fig. 13).

4 Discussion, Conclusions, and Future Directions

In the terrestrial realm, forests are made up of perennial, more or less tall and long-lived "plants" (in the popular sense of the term) called "trees." These trees are primary producers and autogenic ecosystem engineers: they directly or indirectly modulate the availability of resources (other than themselves) to other species. The environment change is performed via their own physical structures, i.e., their living and dead tissues (Jones et al. 1994). They therefore structure the space, both above- and below ground. Terrestrial metazoans ("animals" sensu stricto; kingdom Opisthokonta; see Fig. 1) can be allogenic (not autogenic) ecosystem engineers: they change the environment by transforming living or nonliving materials from one physical state to another, via mechanical or other means (Jones et al. 1994). The paradigmatic example of a terrestrial allogenic ecosystem engineer is the beaver, which changes the environment via its activity, e.g., constructing a dam holding a reservoir. In the absence of large terrestrial sessile metazoans, animal forests, built by autogenic ecosystem engineers, cannot occur in the terrestrial realm. Terrestrial termite mounds, which locally are dense enough to constitute a kind of forest, could seem an exception; however, termites are allogenic, not autogenic, ecosystem engineers.

Just the opposite occurs in the marine realm. Large sessile metazoans can play the role of trees as autogenic ecosystem engineers. These “animal trees” can coexist, and/or compete, with more classical primary producer “trees,” namely, seaweeds. The theme “animal forests versus seaweed forests” constitutes the central subject of the present chapter.

It focuses on two ecosystems in which animal and seaweed forests are juxtaposed, the intertropical coral reefs and the temperate Mediterranean coralligenous ecosystem, with the aim of disentangling the complexity of their relationships, in space and time.

Most ecosystems consist in a mosaic of patches (here “communities”) that functionally are closely interconnected. The delineation of these communities, which actually constitute a continuum, is somewhat arbitrary. Here, four communities were delineated within the coralligenous ecosystem and five within the coral reef ecosystem. Some of these communities are restricted to a particular habitat and therefore are relatively stable over time, e.g., the crustose coralline macroalgae (CCMA) of the algal ridge, within the coral reefs. Other communities can be stages of ecological successions, possible alternate stable states, with transition from one state to another depending upon time and/or disturbances.

Within the two studied ecosystems (coralligenous and coral reefs), animal forests are intertwined with seaweed forests, more broadly with communities that are dominated by canopy-forming macroalgae (seaweed forests sensu stricto), by blade-forming corallines, by CCMA, by chlorobionts on soft bottoms, and/or by turf macroalgae. Surprisingly, few studies have examined the entire ecosystem, i.e., the different communities, which dictate how a given coralligenous or coral reef ecosystem functions, responds to, and recovers from disturbance events. In fact, most studies have focused on the most iconic communities, namely, bioconstructions by blade-forming corallines and animal forests of gorgonians and erect sponges (Fig. 7; coralligenous ecosystem) and animal forests of hexacorallians (Fig. 13; coral reefs), while neglecting more or less completely the other communities dominated by macroalgae. What is worse, when mentioned, these macroalgal communities are only considered as second-rate communities or degraded stages of the iconic ones. Yet all these communities are involved in the functioning and the natural dynamics of the ecosystems; although the baseline of the whole ecosystem (including macroalgal communities), and their overall functioning, are often poorly known, as stressed by some authors (e.g., Pala 2007; Sandin et al. 2008; Smith et al. 2016).

However, it is worth noting that all the communities that constitute the coralligenous and the coral reef ecosystems are not equally vulnerable to natural and human-induced disturbances, and that the ecological goods and ecosystem services they provide do not have the same weight (Moberg and Folke 1999; Salomidi et al. 2012). Bioconstructions of blade-forming corallines (coralligenous) constitute a 3D habitat that strongly structures the space; they contain a labyrinth of cavities and crevices that hosts extraordinary metazoan species diversity, making the coralligenous a hot spot for species diversity in the Mediterranean Sea (Laubier 1966; Ballesteros 2006). The 3D animal forest of hexacorallians (coral reefs) also harbors extraordinary species diversity, accounting for a large part of the world's ocean species diversity. The loss of the 3D coralligenous and coral reef bioconstructions results in a shift to less structured habitats and in a decline in the hosted species diversity. The capacity of animal forests of hexacorallians to precipitate huge amounts of calcium carbonate, and then to build bioconstructions, is one of the most significant services that coral reefs are known for. In addition, the loss of these bioconstructions would lower the flow of coral debris that "feeds" the coral islands located in the background of the reefs, which would threaten the long-term persistence of these coral islands. The animal forests of hexacorallians (coral reefs) and of gorgonians (coralligenous) provide stunning scenery, among the most highly appreciated in the world by divers, and is thus of paramount importance for diving tourism. The recovery of some communities, after their natural or human-induced shift to another community, can be very slow, if it occurs at all (see phase shifts): e.g., bioconstructions of blade-forming corallines, seaweed forests of *Cystoseira* and *Sargassum* (coralligenous), and animal forests of hexacorallians (coral reefs) (Fig. 7 and 13).

A further, and amusing, illustration of the intertwining of animal and plant forests is presented by the two genera *Turbinaria*. Because of the independence of the botanical and zoological codes of nomenclature, *Turbinaria* J.V. Lamouroux is the accepted name for a genus of Phaeophyceae (Chromobionta, Stramenopiles), therefore of macroalgae (Fig. 10), while *Turbinaria* Oken, 1815, is the accepted name for a genus of Hexacorallia (Cnidaria, Metazoa, Opisthokonta), therefore an animal (Boudouresque 2015). Both genera can coexist in the same geographic areas and even within the same ecosystem, the coral reefs, the first constituting part of the seaweed forests, and the second of the animal forests.

The complex relationship between macroalgae-dominated communities (e.g., seaweed forests, precoralligene, algal turfs) and cnidarian-dominated communities (animal forests) autogenic ecosystem engineers, within intertropical coral reefs and Mediterranean coralligenous ecosystems, makes the structure and functioning of these ecosystems highly original, without counterpart in the terrestrial realm.

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