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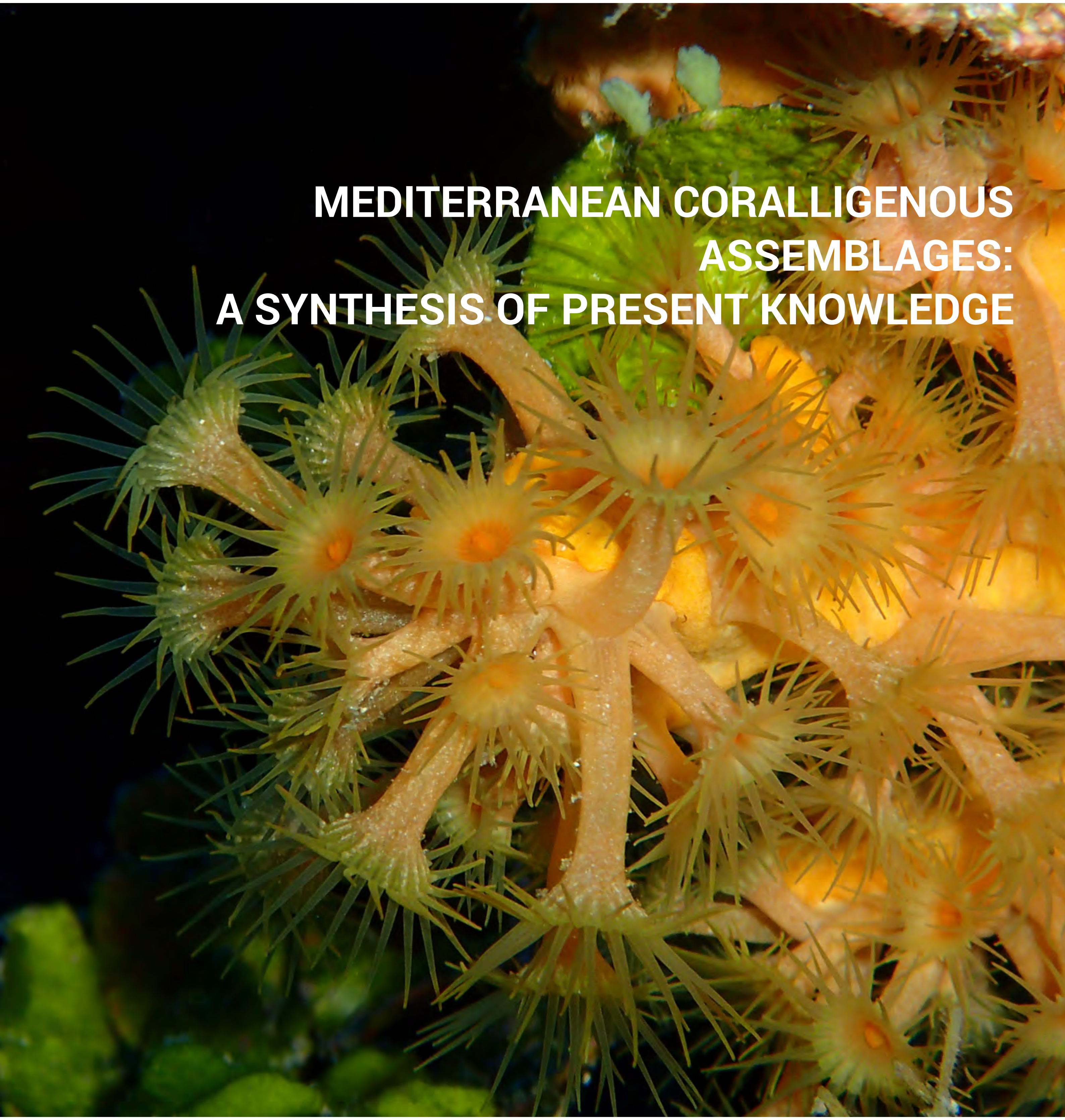

MEDITERRANEAN CORALLIGENOUS ASSEMBLAGES: A SYNTHESIS OF PRESENT KNOWLEDGE

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MEDITERRANEAN CORALLIGENOUS ASSEMBLAGES: A SYNTHESIS OF PRESENT KNOWLEDGE

MedKeyHabitats II project

FOREWORD

The coralligenous assemblages are among the most typical ones in the Mediterranean Sea. They are bioconstructions, which host the highest level of benthic species diversity in the Mediterranean Sea and are important suppliers of highly valuable ecosystem services (ESs) and benefits and have a fundamental role in supporting human wellbeing.

However, coralligenous assemblages are particularly vulnerable to several anthropogenic pressures that are increasingly threatening coastal waters worldwide, including those in the Mediterranean Sea. Indeed, the Mediterranean Sea is currently facing multiple anthropic pressures which affect the ecological, economic, and social spheres.

Coralligenous assemblages are highly threatened by local and global stressors, which often interact with one another. These stressors include intensive coastal development, pollution, invasive alien species, unsustainable fishing practices, poorly planned tourism, and global drivers of climate change.

The strategic action programme for the conservation of biological diversity in the Mediterranean region (SAP BIO) adopted in 2003 identified among its 7 priorities, the conservation of sensitive habitats, species and sites. In this context, the Contracting Parties to Barcelona Convention adopted the Action Plan for the Conservation of Coralligenous and other calcareous bio-concretions of Mediterranean in 2008 and updated it in 2016. This regional strategy is giving high priority to collecting and improving scientific knowledge and circulating data at Mediterranean level.

Following the acquisition of new information on these habitats through research and monitoring projects in the region (location, composition, ecology, threats, etc.), this updated desktop study is more than necessary to reflect current knowledge since its first publication in 2003[1]. It is a collaborative work to which all the Contracting Parties have contributed through internal consultations.

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[1] http://sapbio.rac-spa.org/b1eng.pdf

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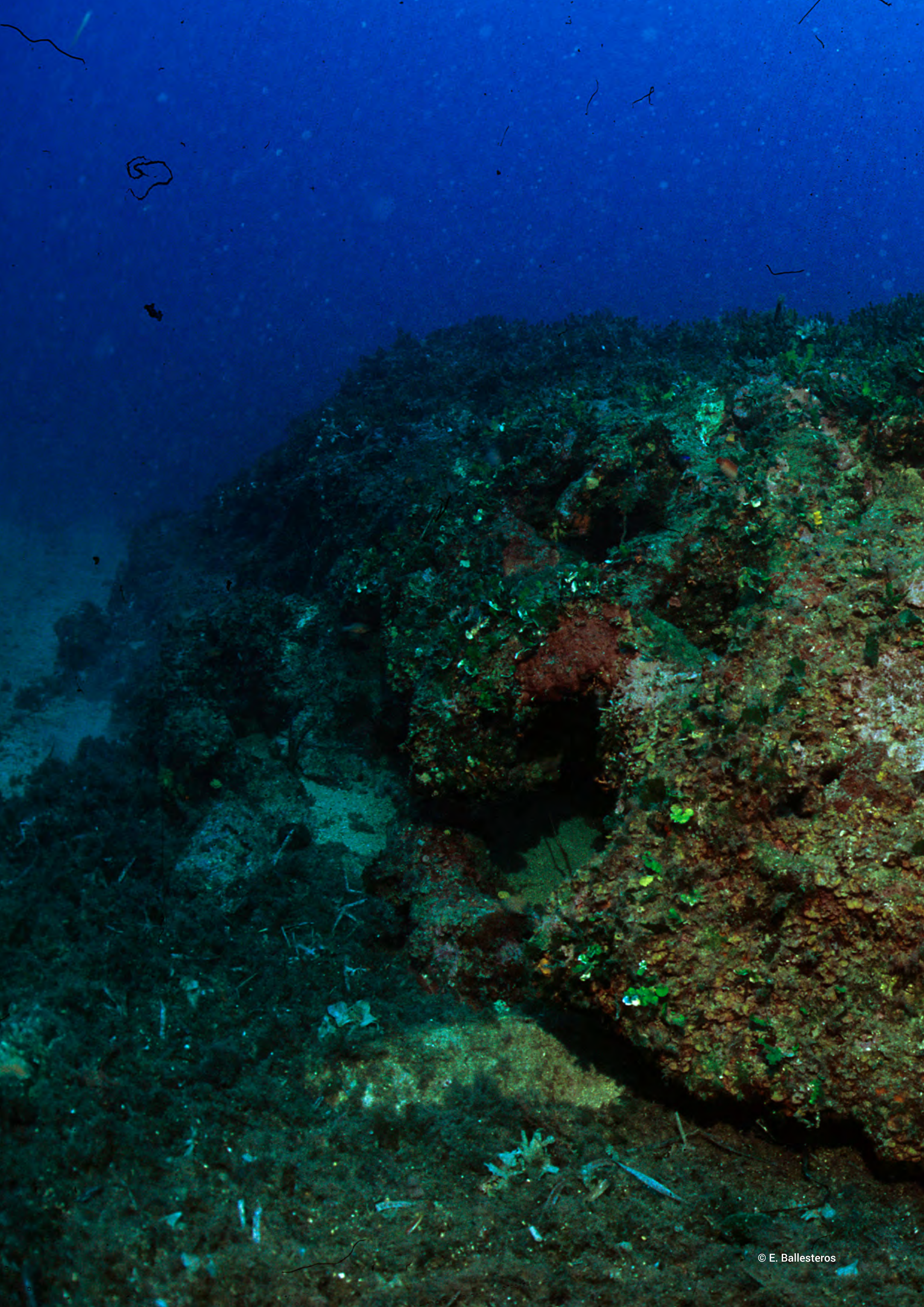
ABSTRACT

Coralligenous buildups, a unique calcareous biogenic concretion from Mediterranean benthic environments, are produced by the accumulation of encrusting algae growing in dim light conditions.

This review provides an overview of the results obtained by the main studies dealing with this formation, including the environmental factors which influence the development of coralligenous communities, their distribution, types, assemblages, builders and eroders, the biotic relationships and processes that create and destroy coralligenous assemblages, their spatial variability and dynamics (from seasonal to millenial scales), the connectivity and the characteristics and functioning of several outstanding and key species.

Special attention is devoted to the biodiversity of coralligenous communities and we provide an estimation of the number of species reported for this habitat. Major stressors affecting coralligenous habitats are reported and commented: warming, diseases, overgrowth by mucilaginous and filamentous algae, pollution, fishing, red coral harvesting, marine litter, anchoring, diver frequentation, catastrophic storms, increased sedimentation and invasive species. We also add acidification that, even if we do not see any effect at all at present, it can be a major driver of changes by the end of the century. We also address conservation and monitoring issues and its importance as provider of ecosystem services.

Finally, we list the main gaps in current scientific knowledge about coralligenous communities and make some recommendations regarding their protection.



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1. Description

There is no real consensus among scientists studying the benthic communities in the Mediterranean Sea about what a coralligenous habitat is. Giaccone (2007, 2009) defines the coralligenous environment as a complex of biodiversity-rich biocoenoses that make a seascape of perennial benthic animals and photosynthetic organisms with a build-up of calcareous algae.

Nevertheless, other authors like Harmelin (2009) also include in the term coralligenous habitats the submerged walls dominated by macroinvertebrates without a significant coverage of calcareous algae. In this review we will use the definition of Ballesteros (2003, 2006), who considers a coralligenous habitat to be a hard bottom of biogenic origin that is mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions (Figure 1), but we will also include those assemblages developing in vertical to subvertical walls with a reduced concretion of calcareous encrusting algae (Figure 2).

Figure 1. Coralligenous build-up dominated by encrusting calcareous algae and *Halimeda tuna* (Tossa de Mar, -24 m) (Photo by E. Ballesteros).

Figure 2. Coralligenous wall dominated by suspension feeders at Jbel Moussa (-30 m) (Photo by E. Ballesteros).

According to Ingrosso *et al.* (2018) the coralligenous is the main Mediterranean biogenic reef or bioconstruction. Although more extended in the circalittoral zone, coralligenous outcrops can also develop in the infralittoral zone, provided that light is dim enough to allow growth of the coralline algae that produce buildup; therefore, infralittoral coralligenous concretions always develop in almost vertical walls, deep channels, or overhangs, and occupy reduced surfaces. The sciaphilic communities developing near sea level, in sites of heavy hydrodynamism and usually below the mediolittoral biogenic rim of the coralline alga *Lithophyllum byssoides* (Boudouresque & Cinelli, 1976), are not considered in this review, even though they may exhibit small buildups of coralline algae. Other algal dominated communities thriving in the circalittoral zone, such as rhodolith beds (Basso & Tomaselli, 1994; Basso *et al.*, 2017) or *Ericaria zosteroides* assemblages (Ballesteros, 1990; Ballesteros *et al.*, 2009), are also excluded, as they grow in horizontal to subhorizontal bottom where the coralline algal concretion is reduced or almost nil. Some facies of coralligenous communities - and which are categorised as "pre-coralligenous" by several authors (e.g. Pérès & Picard, 1964; Gili & Ros, 1985; Ros *et al.*, 1985) - are also excluded from this review, but only if they refer to sciaphilic communities without a basal buildup of coralline algae.

The coralligenous bioherm is always very complex in structure and, in fact, allows the development of several kinds of communities (Laborel, 1961; Laubier, 1966), including those dominated by living algae (upper part of the concretions), suspension feeders (lower part of the concretions, vertical walls, cavities, and overhangs of the buildup), borers (inside the concretions), and even soft-bottom fauna (in the sediment deposited in cavities and holes). Due to its complex structure and dimensions, the coralligenous habitat should be considered to be more like a submarine landscape (= seascape) or community puzzle rather than a single community (Ballesteros, 2003, 2006; Giaccone, 2007; Bavestrello *et al.*, 2016) in close similarity with coral reefs (Boudouresque *et al.* 2016). Coralligenous bottoms are, together with the seagrass meadows of *Posidonia oceanica*, the most complex Mediterranean ecosystems thriving on the continental shelf (Paoli *et al.*, 2016).

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2. History and main studies

2.1. General and faunal studies

The word 'coralligenous' (coralligène in French) was first used by Marion (1883) to describe the hard bottoms, known as *broundo* by fishermen from Marseilles, which are found at depths of 30 to 70 meters, located below seagrass meadows of *Posidonia oceanica* and above coastal muddy bottoms. Coralligène means "producer of coral" and is related to the abundance of red coral (*Corallium rubrum*) found in this type of bottom. Marion includes long lists of fauna collected in these coralligène bottoms.

Pruvot (1894, 1895) used also the word coralligène to describe similar bottoms in the region of the Mediterranean Pyrenees (Banyuls), and this terminology was included in bionomical descriptions of Mediterranean Sea bottoms from the end of the nineteenth century.

Feldmann (1937) described in detail the algal composition of the coralligenous assemblages from Banyuls and identified the main calcareous algae responsible for coralligenous buildup. He also made observations of the animals contributing to buildup and of bioeroders.

Pérès & Picard (1951) continued the work of Marion (1883) on the coralligenous bottoms from the region of Marseilles, defining the components of the coralligenous assemblages; they showed their high microspatial variability and described the environmental factors which allow them to develop.

Bacci (1947), Tortonese (1958), Rossi (1958, 1961), Parenzan (1960) and Molinier (1960) characterized the pre-coralligenous and coralligenous buildups in some areas of the Italian coast and Corsica.

Pérès & Picard (1958) characterized the coralligenous communities from the northeastern Mediterranean, and reported several warm water species, as well as the absence of various species that dominate coralligenous buildups in the western Mediterranean.

Laborel (1960, 1961) also expanded the study of coralligenous communities to other Mediterranean areas, including the eastern Mediterranean. He described five main coralligenous types (cave and overhang concretions, wall concretions, concretions at the base of submarine walls, concretions over flat rocky surfaces and platform coralligenous assemblages) and, in his 1960 paper, also provided the first quantified lists of algal and animal species obtained by scuba diving.

Pérès & Picard (1964) summarized knowledge about coralligenous communities, defining the notion of pre-coralligenous and simplifying the categories of Laborel (1961) into two coralligenous types: coralligenous assemblages over littoral rock and bank or platform coralligenous assemblages, according to the original substrate (rock or sediment) where buildup began. They proposed an evolutive series relating the different biocenosis of the circalittoral zone in the Mediterranean and suggested that the coralligenous community was the climax biocenosis of this zone. They also used the word 'precoralligenous' to refer to facies with a great development of erect, non-calcareous, sciaphilic algae and a low cover of invertebrates. A summarized English version of Pérès & Picard's (1964) work can be found in Pérès (1967).

Vaissière (1964), Fredj (1964) and Carpine (1964) made interesting contributions to the distribution and bionomic description of coralligenous concretions in the region of Nice and Monaco, east of Marseilles.

Gamulin Brida (1965) conducted the first bionomical studies of coralligenous communities in the Adriatic Sea and concluded that they are biogeographically very similar to those found in the northwestern Mediterranean, there being a great abundance of large bryozoans, gorgonians and alcyonarians.

Laubier (1966) made a major contribution to knowledge about invertebrates living in coralligenous assemblages, this study being based on buildups from the Mediterranean Pyrenees. He was the first to report the high biodiversity of these bottoms, carefully studied the fauna of the concretions (particularly accurate are the studies on polychaetes, copepods and echinoderms), and defined the physico-chemical conditions allowing the coralligenous communities to develop. He was also the first to make a large number of observations related to the natural history of the species inhabiting coralligenous assemblages and, in particular, referred to the relationships of epibiosis, endobiosis, commensalism and parasitism.

Sarà (1968, 1969) described the coralligenous communities in the Apulia region (Italy).

True (1970) collected quantitative samples from the coralligenous assemblages of Marseilles, providing data on the biomass of the main species of suspension feeders.

Hong (1980, 1982) exhaustively described the coralligenous communities from Marseilles and the effects of sewage on the fauna inhabiting the coralligenous concretions. He also reported the animals that contribute to these coralligenous concretions and defined four different categories of invertebrates, which can be distinguished by attending to their ecological significance in the coralligenous assemblages. Extensive lists of several taxonomic groups (mainly foraminifers, sponges, molluscs, picnogonids, amphipods and bryozoans) greatly increased knowledge about the biodiversity of coralligenous communities.

Gili & Ros (1984) reviewed the coralligenous communities of the Medes Islands, off the northeast coast of Spain, and accurately evaluated the total surface area occupied by coralligenous assemblages in this marine reserve (Gili & Ros, 1985). Detailed species lists of most vegetable and animal groups for coralligenous communities from specific areas of the Spanish Mediterranean can also be found in Ballesteros *et al.* (1993) and Ballesteros & Tomas (1999).

Sartoretto (1996) studied the growth rate of coralligenous buildups by radiocarbon dating and related the growth periods to different environmental conditions, mainly the eustatic water level and the transparency of the water column. He also identified the main calcareous algae that finally produce buildup and emphasized the importance of *Mesophyllum alternans*. The effect of sedimentation and erosion by browsers and borers was also quantified.

In the twenty-first century the number of studies dealing with general knowledge in coralligenous assemblages has rocketed. We found general descriptions in the Northwestern and Central Mediterranean (Parravacini *et al.* 2007; Bianchi *et al.*, 2007, 2009; Cossu *et al.* 2009; Bo *et al.* 2009; Ballesteros *et al.*, 2013; Cánovas-Molina *et al.* 2014, 2016a), with the first detailed descriptions of coralligenous environments found in seamounts using Remote Operated Vehicles (ROVs) like Vercelli seamount (Italy) (Bo *et al.* 2011) or Ausias March, Emile Baudot, Chella Bank or Palos Seamounts (Spain) (Aguilar *et al.* 2009).

Following first descriptions of Sarà (1968), the study of coralligenous concretions in the Adriatic Sea have increased with the contributions of Kipson *et al.* (2009) (Croatia), Ramos Esplà *et al.* (2014) (Lebanon), Lipej *et al.* (2016) (Slovenia) and Torchia *et al.* (2016a) (Montenegro). However, the major increase in knowledge comes from the study of the mesophotic habitats called trezze or tegnùe in the northern Adriatic, which are rocky outcrops scattered in sedimentary bottoms and formed by a base rock overgrown by a concretion of vegetal and animal organisms (Stefanon *et al.* 2000; Casellato & Stefanon, 2008; Casellato *et al.*, 2009). Tegnùe outcrops rise up to 4 m above the sediment (Gordini *et al.*, 2012). Tossi *et al.* (2017) and Franchi *et al.* (2018) give an accurate description of the origins and lithification processes through petrographic analysis of the outcrops nucleus that provides the basis for the development of the biogenic build-up. Gabriele *et al.* (2003) report up to 116 species and Casellato *et al.* (2007) conclude that suspension feeders are the dominant group of organisms, with a diversity that is much higher than those found in nearby soft bottoms and even higher than the observed in normal coralligenous outcrops. Algal turfs and encrusting algae also live in the outcrops (Falace *et al.* 2015; Fava *et al.*, 2016). Fava *et al.* (2009) and Ponti *et al.* (2011) provide information on main encrusting calcareous algae and bioeroders. Spatial heterogeneity prevailed over temporal variation and was related to geomorphological features of the outcrops and environmental variables (Ponti *et al.*, 2011). Algal turfs, encrusting sponges and bioeroders characterize near shore reefs strongly affected by riverine inputs while encrusting calcareous algae and colonial ascidians dominate offshore reefs (Ponti *et al.*, 2014; Tossi *et al.* 2017). Falace *et al.* (2015) describe three different main habitats situated across an inshore-offshore gradient related to the influence of riverine inputs and develop a predictive model that provides information for habitat cartographic purposes. Fava *et al.* (2011, 2016) provide information on the colonization patterns of the rocky outcrops, local larval supply being important in early recruitment and settlement processes and dispersion from nearby assemblages play a major role in structuring mature assemblages.

The Aegean Sea has benefited from general contributions by Gerovasileiou *et al.* (2009) or by other contributions focused on gorgonians (Salomidi *et al.*, 2009), crustaceans (Bakir & Katagan) and coralline algae (Aktan, 2012). Topçu & Öztürk (2014) make an important contribution to the study of octocoral diversity in the Marmara Sea, a gateway between the eastern Mediterranean and the Black Sea.

Knowledge on North African coralligenous assemblages has recently increased thanks to the financial support of the MedKey Habitats project of RAC-SPA. Significant general contributions have been made by Benhissoune *et al.* (2009) (Al-Hoceima, Morocco), Bazairi *et al.* (2013) and Navarro-Branco *et al.* (2014) (Cape Trois Fourches, Morocco), Bazairi *et al.* (2016) (Jbel Moussa, Morocco), Belbacha *et al.* (2009) (Algeria), Ramos Esplà *et al.* (2016) (Rachgoun island, Algeria) and Torchia *et al.* (2016b) (Cap Negro-Cap Serrat, Tunisia).

2.2. Algal studies

Feldmann (1937) was the first to describe unequivocally the algal composition of coralligenous assemblages; he differentiated these bottoms from the deep-water algal beds of *Gongolaria montagnei* and *Ericaria zosteroides* and identified the main calcareous algae responsible for coralligenous buildup. The algal community growing on coralligenous assemblages received the name *Pseudolithophyllum expansum-Lithophyllum hauckii* association.

Scuba diving was first used in the study of algal flora of coralligenous assemblages by Giaccone (1965), who made some rélevés of coralligenous communities and described a particular plant association, the *Pseudolithophyllo-Halimedetum platydiscae* in the area of Palermo (Sicily). Giaccone & de Leo (1966) also used scuba diving to study the coralligenous and precoralligenous communities of the Gulf of Palermo by using the phytosociological method of Braun Blanquet. They distinguished between two types of communities, referring to them as the association of *Lithophyllum expansum* and *Lithothamnion philippi* (coralligenous) and the association of *Halimeda platydisca* and *Udotea desfontainii* (precoralligenous). The population of *Laminaria rodriguezii* growing over a coralligenous community at the island of Ustica was also studied by Giaccone (1967), although this endemic Mediterranean kelp is usually more abundant in deep-water rhodolith beds *(fonds à pralinés)* (Molinier, 1956; Barberá *et al.*, 2012; Joher *et al.*, 2015).

Boudouresque (1970) studied the macroalgal communities of coralligenous concretions as part of a detailed and exhaustive study of the sciaphilic benthic communities in the western Mediterranean. The accurate methodology (Boudouresque, 1971) included scuba sampling and further sorting and identification in the laboratory. Augier *et al.* (1971) used the same method to study the algal sciaphilic communities around the island of Port-Cros (France).

Boudouresque (1973) proposed that the terms coralligenous and precoralligenous be avoided, as they have a physiognomical value but do not refer to any bionomical or phytosociological entity; instead, he joined all the sciaphilic algal settlements under relatively sheltered conditions into one association *(Peyssonnelietum rubrae)*, and created two sub-associations, corresponding to the assemblages developing in the infralittoral zone *(Peyssonnelietum aglaothamnietosum)* and the circalittoral zone *(Peyssonnelietum rodriguezelletosum)*. He reported the high biodiversity of these assemblages and defined the ecological group of algae characteristics of coralligenous concretions (CC or *Rodriguezellikon*).

Augier & Boudouresque (1975) argued that the algal composition of coralligenous communities thriving in deep water differs from that of sciaphilic assemblages from the infralittoral zone and named it *Rodriguezelletum strafforellii* according to the phytosociological nomenclature.

Boudouresque (1980) and Coppejans & Hermy (1985) made significant contributions to the study of algal assemblages of coralligenous communities in Corsica.

Ballesteros (1991a, 1991b, 1991c, 1992) reported the first data on the dynamics and small-scale structure of algal assemblages from coralligenous communities.

Giaccone *et al.* (1994) conducted a phytosociological review of sciaphilic assemblages described for the Mediterranean. According to this review, most phytobenthic coralligenous assemblages should be included in the order *Lithophylletalia*, where two associations are distinguished: the *Lithophyllo-Halimedetum tunae* described by Giaccone (1965) (Figure 3) and the *Rodriguezelletum strafforellii* described by Augier & Boudouresque (1975) (Figure 4). Phytobenthic assemblages growing in coralligenous concretions from vertical walls and overhangs in the infralittoral zone should be included in the order *Rhodymenietalia*, and mainly belong to the association *Udoteo-Peyssonnelietum squamariae* described by Molinier (1960) in Corsica, and which seems to be identical to the association of *Peyssonnelia squamaria* described by Feldmann (1937) for the Mediterranean Pyrenees (Figure 5). Descriptions in algal species composition and spatial variability of tegnùe reefs in the northern Adriatic are reported in Curiel *et al.* (2012), which found 173 taxa distributed in four main groups of algal assemblages. The morphology of the outcrops, the depth and the distance from the coast accounted for most of the spatial variability (Curiel *et al.*, 2012).

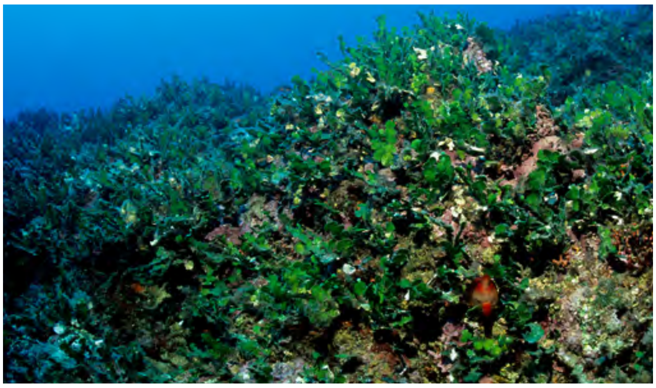

Figure 3. Aspect of the *Lithophyllo-Halimedetum tunae* (Tossa de Mar, -22 m) (Photo by E. Ballesteros).

Figure 4. Aspect of the *Rodriguezelletum strafforellii* (Scandola, Corsica, -40 m) (Photo by E. Ballesteros).

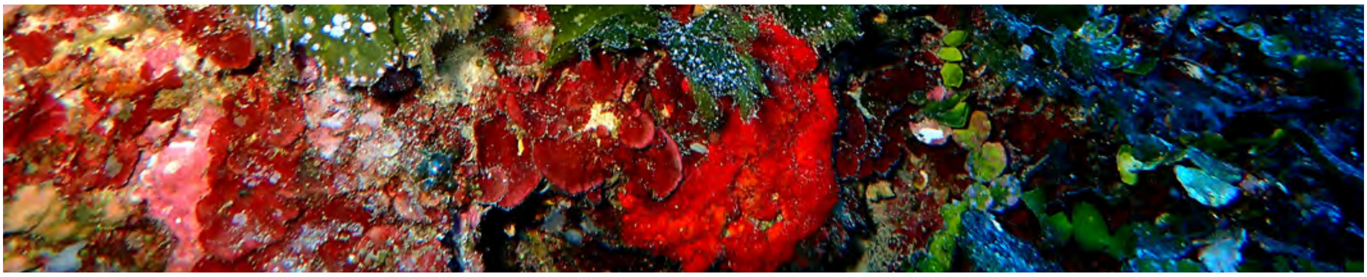

Figure 5. Aspect of the *Udoteo-Peyssonnelietum squamariae* (Columbretes Islands, -20 m) (Photo by E. Ballesteros).

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3. Environmental factors and distribution

3.1. Light

Light is probably the most important environmental factor with respect to the distribution of benthic organisms along the rocky bottoms of the continental shelf (Ballesteros, 1992; Martí, 2002). It is also very important for the development and growth of coralligenous concretions, as its main builders are macroalgae which need enough light to grow but cannot withstand high levels of irradiance (Pérès & Picard, 1964; Laubier, 1966).

According to Ballesteros (1992), coralligenous communities are able to develop at irradiances ranging from 1.3 MJ m^{-2} year-1 to 50-100 MJ m^{-2} year^{-1}, that is, between 0.05% and 3% of the surface irradiance. Similar ranges are reported by Ballesteros & Zabala (1993), who situate the lower light limit for the growth of Mediterranean corallines at around 0.05% of the surface irradiance. These values agree with those obtained by Laubier (1966) in the coralligenous communities of Banyuls, where he reported, at a depth of 32 m, light levels of 1.8-2.6% of surface irradiance at noon in September.

However, light levels reaching different microenvironments of coralligenous communities can differ by at least two orders of magnitude. For example, Laubier (1966) reported light levels in an overhang dominated by red coral to be 17-fold lower than those recorded in an exposed, horizontal surface. Light levels reaching small holes and cavities of coralligenous banks must be almost nil, and similar to light levels reaching the bathyal zone or the innermost part of caves.

The quality of light reaching coralligenous bottoms should also be taken into account. Most of the light belongs to the blue and green wavelengths, with green light dominating in relatively murky waters in wintertime and in coastal continental waters, and blue light dominating in summertime and in offshore banks and islands (Ballesteros, 1992) (Figure 6). Although most authors consider that light quantity is much more important than light quality in determining algal growth and primary production (e.g. Lüning, 1981; Dring, 1981), the absolute dominance of red algae in coralligenous assemblages close to their deepest distribution limit points to the ability of phycobilines to capture light in the "green window" (Ballesteros, 1992).

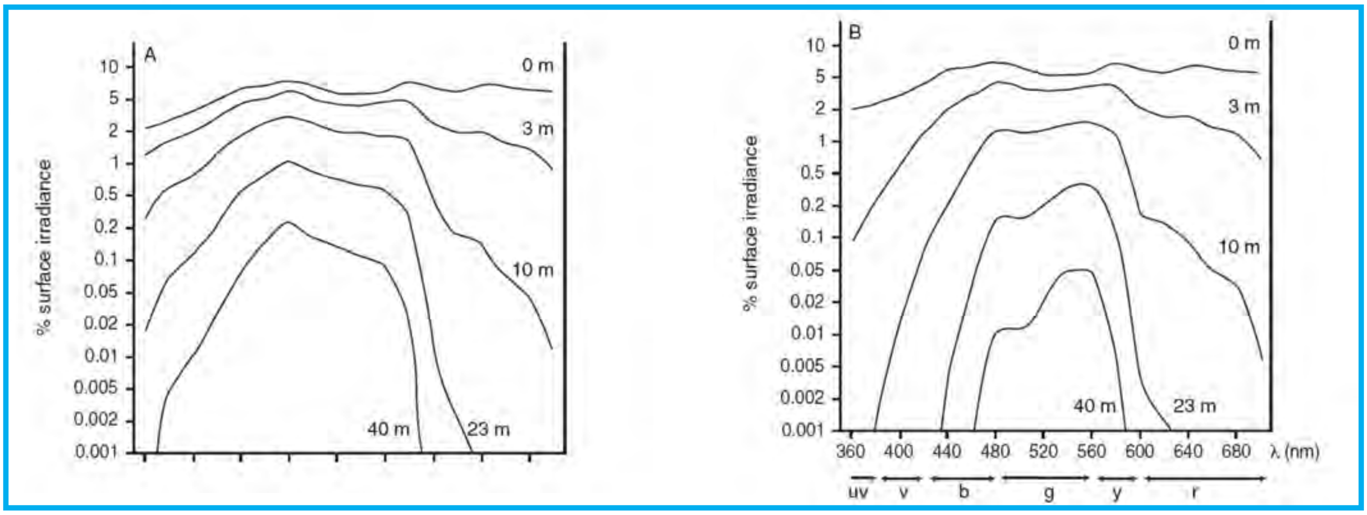

Figure 6. Distribution by wavelength (uv: ultraviolet, v: violet, b: blue, g: green, y: yellow, r: red) of submarine irradiances relative to surface irradiance for several depths in August (A) and November (B) in waters off Tossa de Mar (northwestern Mediterranean). (Redrawn after Ballesteros, 1992).

3.2. Nutrients, POC, DOC

Dissolved nutrients in seawater at coralligenous depths follow the annual pattern described for coastal Mediterranean waters, with the highest values in winter and the lowest in summer. The mean annual water nitrate concentration near the coralligenous concretions at depths of 18 and 40 m at Tossa (northwestern Mediterranean) is around 0.6 µmol l-1, with peaks of 1.5 µmol l-1 in winter and undetectable levels in summer (Ballesteros, 1992) (Figure 7). Similar values are reported for a station in Cabrera, at a depth of 50 m (Ballesteros & Zabala, 1993). However, these values are much lower than those reported from stations situated close to river mouths, such as the coralligenous communities around the Medes Islands, where mean annual values are close to 1 µmol l^{-1} (Garrabou, 1997). Phosphate concentrations are much lower and are always below 0.1 µmol l^{-1} at Tossa and Cabrera (mean concentrations around 0.04 µmol l^{-1} or lower) (Ballesteros, 1992; Ballesteros & Zabala, 1993), and always below 0.2 µmol l^{-1} around the Medes Islands (mean concentrations around 0.13 µmol l^{-1}) (Garrabou, 1997) (Figure 7). Coralligenous communities seem to be adapted to these low nutrient concentrations in seawater, as increased nutrient availability greatly affects the specific composition, inhibits coralligenous construction, and increases destruction rates (Hong, 1980).

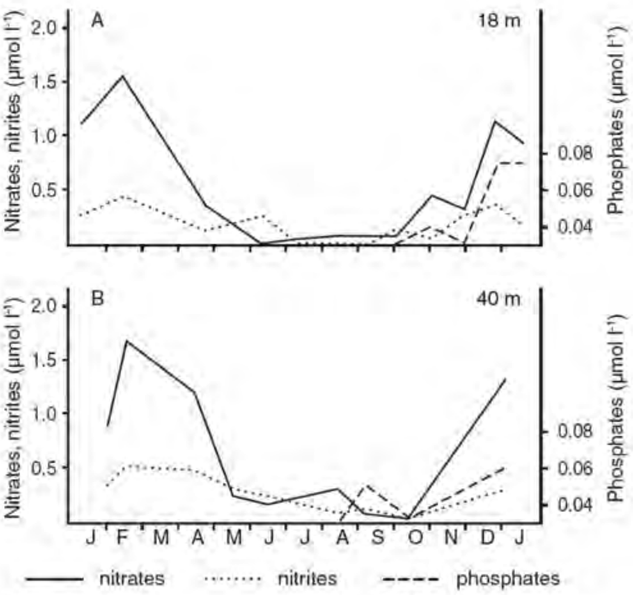

Figure 7. Monthly levels of dissolved nutrient concentrations at depths of 18 and 40 m in seawater close to coralligenous concretions in Tossa de Mar (January 1983-January 1984). (Redrawn after Ballesteros, 1992).

Mean annual particulate organic carbon (POC) rates of 387 µg C l^{-1} are reported for the near-bottom planktonic community at a depth of 15 m around the Medes Islands (Ribes *et al.*, 1999a), although winter and spring values were much higher (500 to 800 µg C l^{-1}). Dissolved organic carbon (DOC) rates, also reported by Ribes *et al.* (1999a) for the same site, amount to 2560 µg C l^{-1}, peaking in spring and summer (Figure 4). Ribes *et al.* (1999a) concluded that the detrital fraction was the dominant component of total organic carbon in the near-bottom planktonic community throughout the year, which could be explained by the importance of run-off particles in the Medes Islands, but may also be due to the input of organic matter by macroalgal (and seagrass) production and the activity of benthic suspension feeders in removing microbial organisms from the plankton. However, further studies are necessary in this regard because the Medes Islands are strongly affected by continental inputs of DOC and POC, which is not usually the case for most Mediterranean coastal areas (mainly in islands or in the southern part).

3.3. Hydrodynamism

Although flowing currents predominate at depths where coralligenous communities develop (Riedl, 1966), hydrodynamism generated by waves is very significant even at depths of 50 m (Ballesteros & Zabala, 1993; Garrabou, 1997) for wave heights greater than 1 m. The year-round average of water motion for a coralligenous community in the Medes Islands at a depth of 25-35 m is 40 mg $CaSO_4$ h^{-1}, that is, one order of magnitude lower than water motion at a depth of 2 m (Garrabou, 1997) (Figure 8). However, due to the intricate morphology of coralligenous concretions, hydrodynamism can differ greatly between various microenvironments, in a similar way to that reported for light levels (Laubier, 1966).

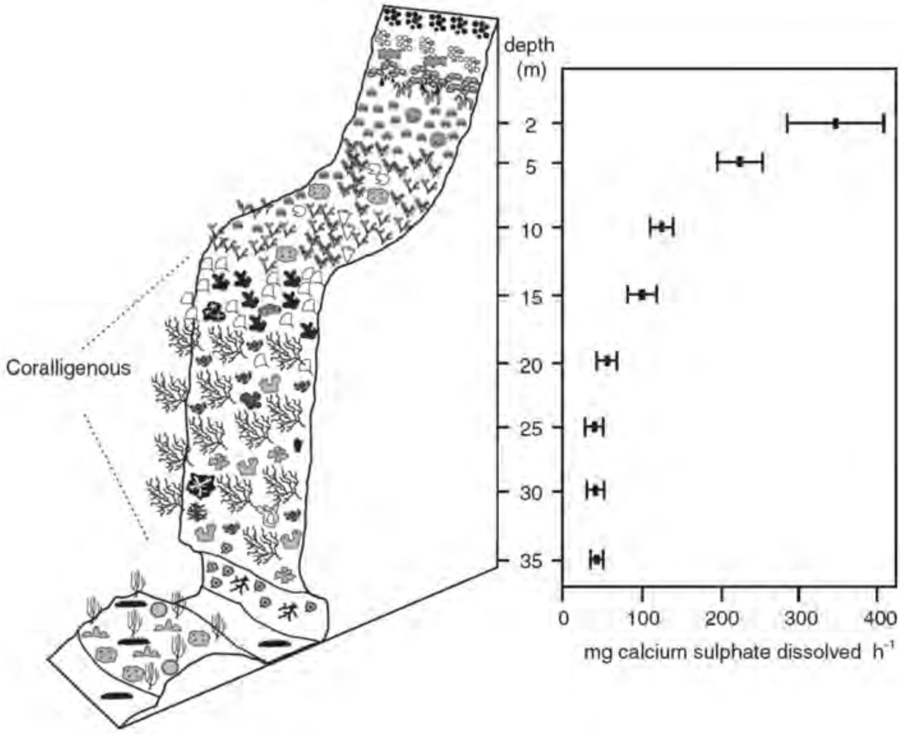

Figure 8. Year-round average in water motion attenuation (mean ± SD) for a depth of between 0 and 35 m in a submarine wall at the Medes Islands. (Redrawn after Garrabou, 1997).

3.4. Temperature

Most of the organisms living in coralligenous communities are able to support the normal seasonal temperature range characteristic of Mediterranean waters. Although Pérès & Picard (1951) stated that coralligenous communities display a relative stenothermy, Laubier (1966) described an annual temperature range of 10 to 23°C in the coralligenous assemblages of Banyuls. Pascual & Flos (1984) found temperatures ranging between 12 and 20°C at the shallowest limit of the coralligenous communities of the Medes Islands (20 m depth), although temperatures ranged from 12 to 16°C close to their deepest limit (60 m depth) (Figure 9). Ballesteros (1992) reported more or less the same temperatures for the coralligenous assemblages developing at depths of 20 and 40 m at Tossa de Mar between the end of November and the end of June (13 to 16°C), but differences of up to 9°C in summer, when the thermocline is situated at a depth of around 35 m; however, peak temperatures of 22°C were detected at the end of August at a depth of 40 m. In the Balearic Islands, where coralligenous communities are restricted to waters below 40 m in depth, water temperature ranges from 14.5 to 17°C for most of the year, although occasional peaks of 22°C are detected at the end of October, when the thermocline is at its deepest (Ballesteros & Zabala, 1993). However, some organisms living in coralligenous assemblages from deep waters seem to be highly stenotherm, as they are never found in shallow waters. This is the case, for example, of the kelp *Laminaria rodriguezii*, which seems to be mainly restricted to depths below 70 m (Joher *et al.*, 2012) and is seldom found between 50 and 70 m, except in areas such as seamounts, upwelling systems or CO_2 vents (Bo *et al.*, 2011; Linares *et al.*, 2015) (Figure 10). Moreover, recent large scale mortality events of benthic suspension feeders thriving in coralligenous communities have been attributed to unusually long-lasting periods of high temperatures during summer (Bavestrello *et al.*, 1994; Cerrano *et al.*, 2000; Perez *et al.*, 2000; Romano *et al.*, 2001; Coma *et al.* 2006; Garrabou *et al.* 2009a; Bensoussan *et al.*, 2010; Kruzic and Rodic, 2014; Kruzic *et al.* 2016; Linares *et al.*, 2018) (Figure 11), although the ultimate cause of these mortalities will be reviewed further on this report.

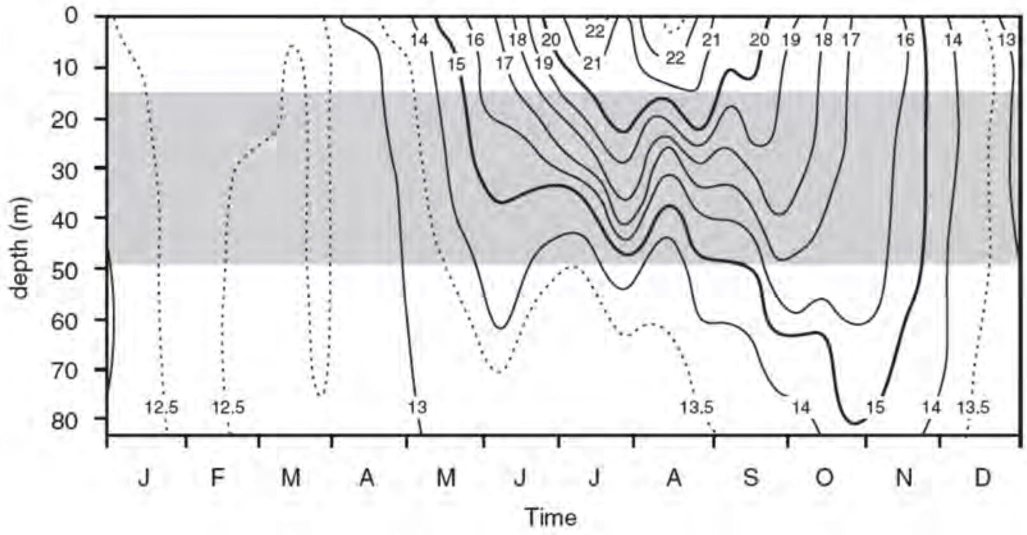

Figure 9. Average seawater temperatures for a depth of between 0 and 80 m off the Medes Islands (July 1973-December 1977). (Redrawn after Pascual & Flos, 1984).

Figure 10. CO_2 vents at 40 m depth in Columbretes Islands (Spain) hold dense populations of kelp *Laminaria rodriguezii* (Photo by E. Ballesteros).

Figure 11. Mortality of *Paramuricea clavata* colonies in a warming event at 42 m depth in Imperial Islet (Cabrera, Balearic Islands), year 2007 (Photo by E. Ballesteros).

3.5. Salinity

The relatively shallow and coastal coralligenous communities of Banyuls and the Medes Islands display salinity ranges between 37 and 38 per thousand (Laubier, 1966; Pascual & Flos, 1984), although salinity variations for coralligenous assemblages from insular areas should be lower.

3.6. Geographical distribution

Coralligenous buildups are common all around the Mediterranean coasts, with the possible exception of those of Lebanon and Israel (Laborel, 1987) (but see Spanier *et al.*, 2006; Ramos Esplà *et al.*, 2014). According to Laborel (1961), the best developed formations are those found in the Aegean Sea, although the most widely studied banks are those of the northwestern Mediterranean; therefore, most of the data presented here comes from this area. Giaccone (2007) and Ingrosso *et al.* (2018) mention Italian localities with coralligenous habitats and Falace *et al.* (2015) predict different tegnùe habitats in the northern Adriatic based on information on environmental parameters across the northern Adriatic basin. Martin *et al.* (2014) produced the first Mediterranean basin-scale map of “likely to occur” coralligenous outcrops (and maërl beds), which may help to guide future surveys devoted to their description and mapping.

3.7. General depth distribution

The minimal depth for the formation of coralligenous concretions depends on the amount of irradiance reaching the sea bottom. In vertical slopes in the area around Marseilles this minimal depth reaches -20 m, but it is much lower in other zones like the Gulf of Fos, where coralligenous communities are able to grow in shallower waters (-12 m) because of the high turbidity of the water related to the Rhône mouth. This minimal depth is displaced to deeper waters in insular areas like Corsica or the Balearic Islands, where water transparency is very high (Ballesteros & Zabala, 1993). However, coralligenous concretions can appear in very shallow waters if light conditions are dim enough to allow a significant development of coralline algae (Laborel, 1987; Sartoretto, 1994); this may even occur in the clearest waters like those around Cabrera, where a coralligenous buildup can be found at a depth of only 10 m in a cave entrance (Martí, 2002).

The depth distribution (Figure 12) of coralligenous assemblages in sub-horizontal to horizontal bottoms for different Mediterranean areas is as follows:

- Banyuls region (France): 20-40 m depth (Feldmann, 1937; Laubier, 1966)
- Marseilles region (France): 20-50 m (Laborel, 1961; Hong, 1980)
- Medes Islands (Spain): 20-55 m (Gili & Ros, 1984)
- Tossa de Mar (Spain): 20-60 m (Ballesteros, 1992)
- Naples (Italy): 45-70 m (Bacci, 1947)
- Cabrera (Spain): 50-100 m (Ballesteros *et al.*, 1993)
- Corsica (France): 60-80 m (Laborel, 1961)
- Sardinia (Italy): 60-140 m (Simeone *et al.*, 2014)
- Apulia (Italy): 10-100 m (Ingrosso *et al.*, 2018)
- Liguria (Italy): 25-100 m (Ingrosso *et al.*, 2018)
- Thyrrenian Seamounts (Italy): 60-120 m (Bo *et al.*, 2011)
- Northeastern Mediterranean: 70-90 m (Laborel, 1961)
- Aegean Islands: 56-114 m (Georgiadis *et al.*, 2009)
- Siculo-Tunisian region: 90-120 m (Laborel, 1961)
- Southeastern Mediterranean: 100-120 m (Laborel, 1961)

Figure 12. Coralligenous bank at Es Blancall, -40 m (Tossa de Mar, Spain) (Photo by E. Ballesteros).

3.8. Mapping

Distributional data on coralligenous concretions are essential in order to implement management measures for their conservation (García *et al.*, 2014). In a first approach, the fishermen’s knowledge can be used to make a rough cartography or at least to know the areas where coralligenous is present (Traganos *et al.*, 2014). Fishery maps are in little agreement with recent cartographies due to errors in positioning, but presence/absence data is useful for planning new surveys (Canessa *et al.*, 2017). Tentative maps can also be obtained by summarizing all the bibliographic information (Coppo & Diviaco, 2009; Cánovas-Molina *et al.*, 2016a). However, detailed sea bottom cartographies can only be made by using side scan sonar (SSS), subbottom profiler and multibeam echosounders, ground-truthing with direct scuba sampling, beam trawls, grabs, box-corers, underwater drop camera systems, benthic landers, remote operated vehicles (ROVs), or manned submersibles (Georgiadis *et al.*, 2009; Coppo *et al.*, 2009; Canese *et al.*, 2009; Barberà *et al.*, 2012; Astruch *et al.*, 2012; CARHAMB’AR, 2013; Ambroso *et al.*, 2013; Bonacorsi *et al.*, 2014; Blouet *et al.*, 2014; Marchese *et al.*, 2014; Chimienti *et al.*, 2014; Grinyó *et al.*, 2018; D’Onghia *et al.*, 2018; Santin *et al.*, 2018). The rigid cavernous framework of coralligenous outcrops yield intermediate to high backscatter in the SSS images (Bracchi *et al.*, 2014, 2015, 2017) and it is possible to distinguish between different geomorphological structures (blocks, ridges, platforms).

The accuracy of the available cartographies is a result of the different methods used in each particular study and the precision in positioning. Thus, the cartographic methods that have been used in every particular study are necessary in order to appropriately apply the resulting cartography to management issues. First, cartographies were produced mainly in Marine Protected Areas or other sites of special interest and were not supported by extensive SSS and multibeam surveys. However, some of these maps, involving mainly scuba diving, are still useful for management purposes in small MPAs (Gili & Ros, 1985). Amongst the earliest published information on the distribution of coralligenous assemblages we can report the cartographies of Medes islands (Gili & Ros, 1985), Nueva Tabarca (Ramos, 1985), Columbretes islands (Templado & Calvo, 2002) or Alboran Island (Templado & Calvo, 2006). Belsher *et al.* (2005) provide an accurate cartography of the sea bottom at the National Park of Port-Cros made using SSS, aerial photography, video images, scuba diving and grabs, but they are not able to distinguish between coralligenous assemblages and other rocky bottoms. Without being exhaustive, more recent cartographies at different scales and with different accuracy levels include those of Minorca Channel (Spain) (Barberà *et al.*, 2012), Cap de Creus (Spain) (Sardá *et al.*, 2012), some Balearic Islands MPAs (Spain) (Ballesteros *et al.*, 2013), Cap Trois Fourches (Morocco) (Bazairi *et al.*, 2013) and Jbel Moussa (Morocco) (Bazairi *et al.*, 2016), Rachgoun island (Algeria) (Ramos- Esplà *et al.*, 2016), Platamuni and Ratac (Montenegro) (Torchia *et al.*, 2016a), Cap Negro-Cap Serrat (Tunisie) (Torchia *et al.*, 2016c; Bouafif *et al.*, 2019), some sites in Lebanon (Ramos-Esplà *et al.*, 2014), Slovenia (Lipej *et al.*, 2016), Apulia region (Bracchi *et al.*, 2017), Port Cros National Park (Astruch *et al.*, 2012), several zones in Corsica (France) (Bonacorsi *et al.*, 2014; Pergent-Martini *et al.*, 2014) and Sardinia (Italy) (Rovere *et al.*, 2013; Simeone *et al.*, 2014).

The habitat mapping of the seafloor is very costly, mainly because of ground-truthings. Predictive spatial modelling is an alternative to produce benthic habitat maps based on complete acoustic coverage and a comparatively low number of sea truths (Vasallo *et al.*, 2018). A large-scale probabilistic model of the presence of three habitat types of tegnùe reefs in the northern Adriatic basin was developed using 9 variables (Falace *et al.*, 2015). Similarly, distribution of five coralligenous habitats recognized from the MPA of Tavolara-Punta Coda Cavallo (Sardinia) was driven by distance from coast, depth and lithotype, allowing the predictive cartography of these habitats (Vasallo *et al.*, 2018). Zapata Ramírez *et al.* (2014, 2016) used remote sensing and distribution modelling techniques to map the distribution of coralligenous bioconcretions with acceptable accuracy and to discriminate between main habitats in Portofino MPA (Liguria, Italy).

Anthropogenic pressures are related to the ecological quality of the habitats and they also deserve to be mapped as a starting point for improvement of the management of coralligenous habitats and other marine ecosystems. Holon *et al.* (2014) have created MEDTRIX, a general cartographic database for marine ecology and anthropogenic pressures along the Mediterranean coast that includes data on presence/absence of coralligenous outcrops and their diversity. Based on this database Holon *et al.* (2015) provide a first fine-scale cartography of impacts of ten anthropogenic pressures along the French Mediterranean coasts between 0 and 80 m, and thus covering a significant area of coralligenous assemblages.

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4. Structure

4.1. Coralligenous types : Structure and habitats

The morphology and inner structure of coralligenous concretions depend greatly on depth, topography, and the nature of prevailing algal builders (Laborel, 1961). Two main morphologies can be distinguished (Pérès & Picard, 1964; Laborel, 1987): banks and rims.

Banks are flat buildups with a variable thickness that ranges from 0.5 to several (3-4) metres. They are mainly built over more or less horizontal substrates, and have a very cavernous structure—plenty of holes (Laborel, 1987)—that often leads to a very typical morphology (it has been compared to a Gruyère cheese). These banks are sometimes surrounded by sedimentary bottoms, and Pérès & Picard (1952) argued that they developed from the coalescence of rhodoliths or maërl (coralligène de plateau). However, it is highly probable that these buildups have almost always grown upon rocky outcrops (Got & Laubier, 1968; Laborel, 1987; Bracchi *et al.*, 2014). Recent investigations in northern Corsica have found coralligenous outcrops with a circular shape growing on subhorizontal bottoms around 105-130 m depth that have been called coralligenous atolls (Bonacorsi *et al.*, 2012). Measuring 20-25 m of diameter, the different observed typologies could correspond to different evolutionary stages in relation to bioconstruction and erosion (Pergent-Martini *et al.*, 2014). The columnar coralline algae build-ups found in south-eastern Sicily (Di Geronimo *et al.*, 2002) also correspond to coralligenous banks. Tegnùe or trezze reefs from the northern Adriatic Sea can also be considered biogenic banks overgrowing rocky outcrops (Stefanon, 2000; Casellato & Stefanon, 2008).

Rims develop in the outer part of marine caves and on vertical cliffs, usually in shallower waters than banks. The thickness of rims is also variable and ranges from 20-25 cm to more than 2 metres; thickness increases from shallow to deep waters (Laborel, 1987) (Figure 13).

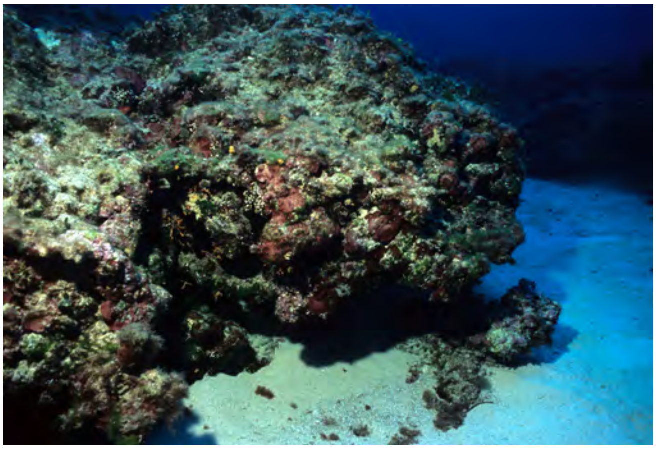

Figure 13. Coralligenous rim at Cavalleria, -38 m (Menorca, Spain) (Photo by E. Ballesteros).

Internal coralligenous 3D complexity can be evaluated by using X-ray computed microtomography in order to estimate its porosity (Pica *et al.*, 2014) or make 3-D reconstructions of coralline algae and detect bioeroders and other organisms (Bressan *et al.*, 2009).

In shallow water the main algal builder is *Mesophyllum alternans*, which builds flat or slightly rounded banks or rims with a foliaceous structure. As the water deepens, other corallines *(Lithophyllum stictaeforme, Lithophyllum cabiochae, Neogoniolithon mamillosum)* become important builders. Shallow water banks are generally covered with populations of green algae *Halimeda tuna* and *Flabellia petiolata (Lithophyllo-Halimedetum tunae)*, which can be so dense that they hide the calcareous algae (Figure 14). However, at greater depths the density of these erect algae decreases, and corallines dominate the community *(Rodriguezelletum strafforellii)*.

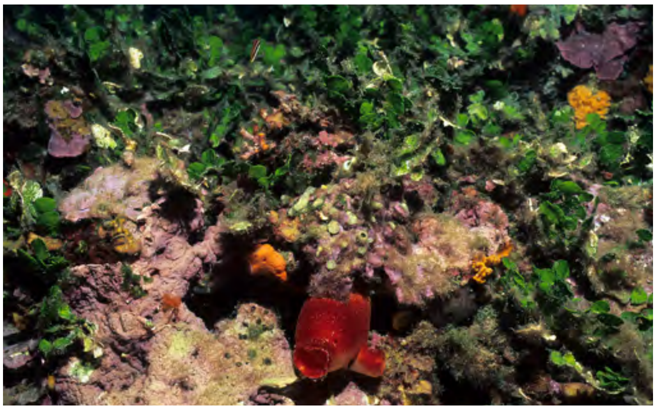

Figure 14. Shallow water coralligenous bank (Tossa de Mar, Spain) (Photo by E. Ballesteros).

Holes and cavities within the coralligenous structure always sustain a complex community dominated by suspension feeders (sponges, hydrozoans, anthozoans, bryozoans, serpulids, molluscs, tunicates) (Figure 15).

Figure 15. Cavity within a coralligenous assemblage at Columbretes Islands (Spain), -25 m (Photo by E. Ballesteros).

Boring sponges can occupate up to 25% of the small coralligenous cavities (Pica *et al.*, 2014). The smallest crevices and interstices of the coralligenous buildup have an extraordinarily rich and diverse vagile endofauna of polychaetes and crustaceans, while a lot of animals—attached or unattached—cover the main macroalgae and macrofauna, swarm everywhere, from the surface to the cavities or inside the main organisms, and thrive in the small patches of sediment retained by the buildup.

According to Hong (1982) four different categories of invertebrates can be distinguished with respect to their position and ecological significance in the coralligenous structure:

- fauna contributing to buildup, which help develop and consolidate the framework created by the calcareous algae. Several bryozoans, polychaetes (serpulids), corals and sponges constitute this category. They comprise 24% of the total species number.
- cryptofauna colonising the small holes and crevices of the coralligenous structure. They represent around 7% of the species, including different molluscs, crustaceans and polychaetes.
- epifauna (living over the concretions) and endofauna (living inside the sediments retained by the buildup), which represent a great number of species (nearly 67%).
- eroding species, accounting for only around 1%.

4.2. Algal builders

Coralline algae are the main coralligenous builders (Laborel, 1961; Laubier, 1966; Sartoretto, 1996). The taxonomy of this group of algae is very difficult and the nomenclature of the species is constantly changing. Due to their great importance in the construction of coralligenous concretions we will consider here a number of issues regarding the taxonomical status and current nomenclature of the main species.

The main algal building species, according to Sartoretto (1996) and several other authors (*e.g.* Feldmann, 1937; Pérès & Picard, 1964; Boudouresque, 1970; Hong, 1980; Ballesteros, 1991b), has repeatedly been identified as *Mesophyllum lichenoides* (Ellis) Lemoine. However, Cabioch & Mendoza (1998) reported the most common species of the genus *Mesophyllum* growing in coralligenous assemblages to be a different species and named it *Mesophyllum* alternans (Foslie) Cabioch & Mendoza (Figure 16). Although present in the Mediterranean Sea, *Mesophyllum lichenoides* does not seem to contribute to coralligenous buildup (Cabioch & Mendoza, 1998). Therefore, it is likely that some or most of the reports of *Mesophyllum lichenoides* as a coralligenous builder actually refer to *Mesophyllum alternans* (Cabioch & Mendoza, 1998).

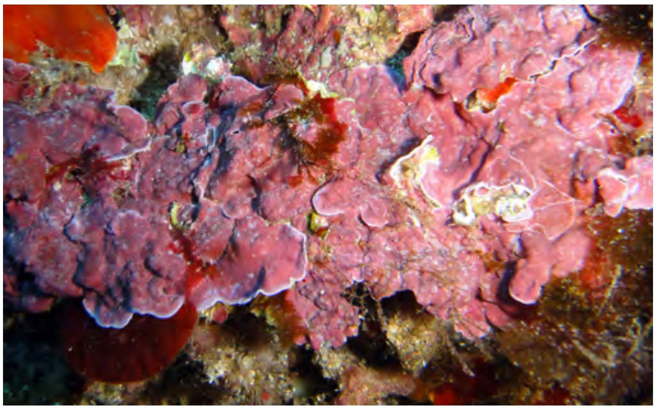
Figure 16. Algal coralligenous builder *Mesophyllum alternans* (Photo by E. Ballesteros).

Pseudolithophyllum expansum (*sensu* Lemoine) has been identified by most authors as being the second most common coralline alga in coralligenous concretions. However, Boudouresque & Verlaque (1978) identified another species, similar to *Pseudolithophyllum expansum*, and described it as *Pseudolithophyllum cabiochae*. Later, studies by Woelkerling (1983), Athanasiadis (1987), Woerkerling *et al.* (1993) and Furnari *et al.* (1996) shed some light (but also added further confusion) regarding the name to be applied to the alga called *Pseudolithophyllum expansum* and/or *Pseudolithophyllum cabiochae* by Mediterranean phycologists and marine biologists. The last review by Athanasiadis (1999a) suggested that *Pseudolithophyllum* should not be regarded as a different genus to *Lithophyllum* and that the two species growing in coralligenous communities should be named *Lithophyllum stictaeforme* (Areschoug) Hauck [= *Lithophyllum frondosum* (Dufour) Furnari, Cormaci & Alongi; = *Pseudolithophyllum expansum* (Philippi) Lemoine; = *Lithophyllum expansum* sensu Lemoine] (Figure 17) and *Lithophyllum cabiochae* (Boudouresque & Verlaque) Athanasiadis (Figure 18).


Figure 17. Algal coralligenous builder *Lithophyllum stictaeforme* (Photo by E. Ballesteros).


Figure 18. Algal coralligenous builder *Lithophyllum cabiochae* (Photo by E. Ballesteros).

Moreover, Woelkerling (1983) recognized the lectotype of *Lithophyllum expansum* Philippi (non Lemoine) as a *Mesophyllum* and considered it to be a heterotypic synonym of *Mesophyllum lichenoides*. However, a recent study by Cabioch & Mendoza (2003) showed that the lectotype of *Lithophyllum expansum* Philippi is specifically different from *Mesophyllum lichenoides*, *Mesophyllum alternans* and other Mediterranean species of this genus. They named it *Mesophyllum expansum* (Philippi) Cabioch and Mendoza (Figure 19) and it corresponds to the taxa usually identified as *Mesophyllum lichenoides* var. *agariciformis* (Pallas) Harvey by Mediterranean phycologists.

Figure 19. Algal coralligenous builder *Mesophyllum expansum* (Photo by E. Ballesteros).

As a result of all this confusion we are unable to determine the extent to which *Mesophyllum expansum* contributes to coralligenous buildup, although it is likely to make a significant contribution, at least in some places. Another species, *Mesophyllum macroblastum* (Foslie) Adey, has been reported for the coralligenous concretions in Corsica (Cabioch & Mendoza, 2003), and a fifth species (*Mesophyllum macedonis* Athanasiadis) (Athanasiadis, 1999b) may also be present in the coralligenous buildups of the Aegean Sea. According to Marc Verlaque (personal communication), three species of the genus *Mesophyllum* co-exist in the coralligenous communities off Marseille (*M. alternans, M. expansum, M. macroblastum*), suggesting a much greater biodiversity of coralligenous-building algae than expected. However, more research is needed in Mediterranean species of this genus since Peña *et al.* (2015) did not collect *M. alternans*, neither *M. lichenoides* from the western Mediterranean, but found another species, *Mesophyllum sphaericum*, growing as rhodoliths in maërl beds but also as epilithic crusts between 20 and 50 m depth.

The alga identified by Feldmann (1937) as *Lithophyllum hauckii* (Rothpletz) Lemoine, a very common coralline in the coralligenous buildups of the Banyuls region, should be named *Neogoniolithon mamillosum* (Hauck) Setchell & Mason (Hamel & Lemoine, 1953; Bressan & Babbini-Benussi, 1996) [= *Spongites mamillosa* (Hauck) Ballesteros] (Figure 20).

Figure 20. Algal coralligenous builder ***Neogoniolithon mamillosum*** (Photo by E. Ballesteros).

Although not a coralline alga, it should also be pointed out that authors prior to 1975 identified the calcareous *Peyssonnelia* growing in coralligenous communities as being *Peyssonnelia polymorpha* (Zanardini) Schmitz. Boudouresque & Denizot (1975) described a similar species, *Peyssonnelia rosa-marina* Boudouresque & Denizot (Figure 21), that is more common than *P. polymorpha* and which also contributes to coralligenous buildups. Therefore, reports of *Peyssonnelia polymorpha* prior to the description of *P. rosa marina* should probably be regarded as referring to this latter species or to both entities.

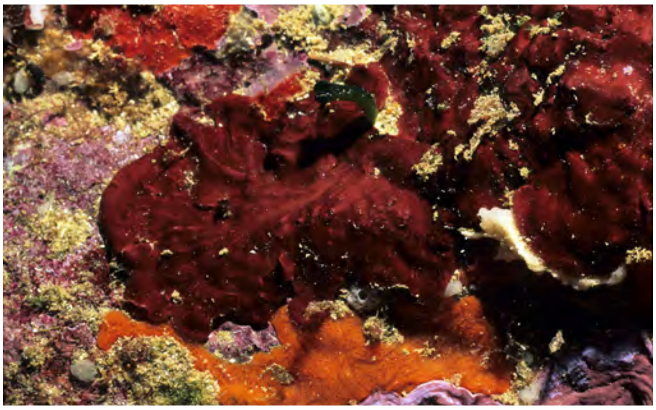

Figure 21. Algal coralligenous builder *Peyssonnelia rosa-marina* (Photo by E. Ballesteros).

Feldmann (1937) identified the four main calcareous algae responsible for the coralligenous buildups in the region of Banyuls: *Lithophyllum stictaeforme* (as *Pseudolithophyllum expansum*), *Neogoniolithon mamillosum* (as *Lithophyllum hauckii*), *Mesophyllum* cf. *alternans* (as *Mesophyllum lichenoides*) and *Peyssonnelia rosa-marina* f. *saxicola* (as *Peyssonnelia polymorpha*). The same species have also been reported for coralligenous concretions studied in several areas close to the Gulf of Lions (e.g. Boudouresque, 1973; Ballesteros, 1992). It seems that these species are almost always the same, with the possible exception of *Lithophyllum stictaeforme* which seems to be substituted by *Lithophyllum cabiochae* in several areas of the Mediterranean that are warmer than the Gulf of Lions (e.g. Corsica, Balearic Islands, eastern Mediterranean).

Hong (1980) reports three species as being the main coralligenous builders in the region of Marseilles: *Lithophyllum cabiochae, Mesophyllum alternans* and *Neogoniolithon mamillosum*. *Peyssonnelia rosa marina* is also very abundant. Other calcareous species contributing to buildup are *Archaeolithothamnion mediterraneum, Lithothamnion sonderi* and *Peyssonnelia polymorpha*.

According to Sartoretto *et al.* (1996), *Mesophyllum alternans* (as *Mesophyllum lichenoides*) is the main algal building species for both ancient and recent coralligenous constructions in the northwestern Mediterranean. *Mesophyllum alternans* is a highly tolerant species in terms of light, temperature and hydrodynamism, and is currently the dominant species in shallow waters. In some areas, *Peyssonnelia rosa-marina* and *Peyssonnelia polymorpha* may also be the dominant species, and build a very cavernous, highly bioeroded coralligenous concretion. In deep waters *Lithophyllum cabiochae* is the main calcareous alga in the region of Marseilles and Corsica, but its cover can vary from one geographical area to another. For example, the encrusting algal cover in deep water coralligenous concretions in Marseilles is limited to a few isolated small living thalli that seem insufficient to allow current renewal of the coralligenous construction. In contrast, these deep concretions are luxuriant in Corsica, as evidenced by the accumulation of living thalli of *Lithophyllum cabiochae*.

The identification of the species present in the algal framework of coralligenous blocks from 7,700 years ago to the present has shown that no species changes have occurred (Sartoretto *et al.*, 1996). The study by Sartoretto *et al.* (1996) in the Marseilles region and Corsica identified five Corallinaceae and one Peyssonneliaceae: the non-geniculate corallines *Mesophyllum alternans* (as *M. lichenoides*), *Lithophyllum* sp. (as *Titanoderma* sp., probably *Lithophyllum pustulatum* v. *confinis*), *Lithophyllum cabiochae-stictaeforme* (discrimination between *Lithophyllum cabiochae* and *Lithophyllum stictaeforme* is uncertain in fossil material), *Lithothamnion* sp., the geniculate coralline alga *Amphiroa verruculosa*, and, finally, *Peyssonnelia* sp. *Mesophyllum alternans* is also the main algal builder in the coralligenous concretions of the Mediterranean Pyrenees (Bosence, 1985), along with *Lithophyllum* and *Titanoderma* (quoted as *Pseudolithophyllum* and *Tenarea* in Bosence's paper). *Peyssonnelia polymorpha* and *Peyssonnelia rosa-marina* f. *saxicola* may also be abundant in the coralligenous concretions of the Mediterranean Pyrenees, the northeast coast of Spain, and the Balearic Islands (Bosence, 1985; Ballesteros, 1992; Ballesteros *et al.*, 1993). However, even if *Peyssonnelia* is abundant as a living encrusting alga, it is almost completely absent from the fossil record (Bosence, 1985; Sartoretto, 1996). Carbonate content of the *Peyssonnelia* species is lower than the average carbonate content in corallines (Laubier, 1966; Ballesteros, 1992), and calcification in the form of aragonite rather than calcite prevents a good fossilization of these species (James *et al.*, 1988). However, these and other species of *Peyssonnelia* usually have a basal layer of aragonite that may contribute to the consolidation of coralligenous concretions when mixed with the physico-chemical precipitations of $CaCO_3$ (Sartoretto, 1996).

4.3. Animal builders

Coralligenous animal builders were studied by Hong (1980) in the region of Marseilles. He found a total of 124 species contributing to buildups, which account for around 19% of the total number of species reported in the coralligenous concretions of Marseilles. The most abundant animal group are the bryozoans, accounting for 62% of species, followed by the serpulid polychaetes with 23.4%. The large bryozoan *Pentapora fascialis* has an important bioconstruction role in some northern Adriatic build-ups (Lombardi *et al.*, 2009). Minor contributors are the cnidarians (4%), molluscs (4%), sponges (4%), crustaceans (1.6%) and foraminifers (0.8%). However, Laborel (1987) considers foraminifer *Miniacina miniacea* (Figure 22) to be the most important animal builder. Hong (1980) distinguished three different types of animal builders: those contributing directly to buildup, and which are relatively large; those with a reduced buildup activity due to their small size; and those which agglomerate carbonate particles. The first group includes the bryozoans *Schizomavella spp.* (Figure 23), *Onychocella marioni, Cribilaria radiata, Pentapora fascialis, Entalophoroecia deflexa, Celleporina caminata, Myriapora truncata* (Figure 24) *Brodiella armata and Turbicellepora coronopus, several serpulids (Serpula vermicularis, Serpula concharum, Spirobranchus polytremma)* (Figure 25), the molluscs *Vermetus* sp., *Serpulorbis arenarius* (Figure 26) and *Clavagella melitensis*, and the scleractinians *Hoplangia durotrix, Leptopsammia pruvoti* (Figure 27), *Caryophyllia inornata* and *Caryophyllia smithii*. Among the second group, Hong (1980) reports some small bryozoans such as *Crassimarginatella maderensis* and *Mollia patellaria*,

Figure 22. Animal coralligenous builder *Miniacina miniacea* (Foraminifera) (Photo by E. Ballesteros).

serpulids like *Hydroides* spp., *Filogranula* spp., and *Spirorbis* spp., the cirripeds *Verruca strömia* and *Perforatus perforatus*, and the foraminifer *Miniacina miniacea*. In terms of the "agglomerative" animals, he reports sponges such as *Geodia* spp., *Spongia virgultosa* (Figure 28) and *Faciospongia cavernosa*, the bryozoans *Beania* spp., and the alcyonarian *Epizoanthus arenaceus*.

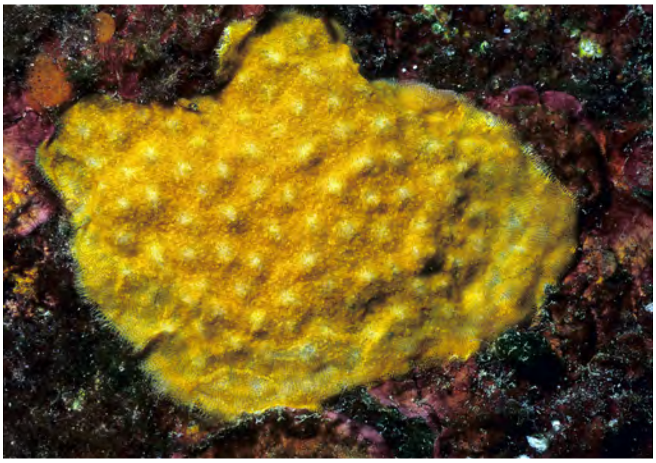

Figure 23. Animal coralligenous builder *Schizomavella mamillata* (Bryozoa) (Photo by E. Ballesteros).

Figure 24. Animal coralligenous builder *Myriapora truncata* (Bryozoa) (Photo by E. Ballesteros).

Figure 25. Animal coralligenous builder *Serpula vermicularis* (Polychaeta) (Photo by E. Ballesteros).

Figure 26. Animal coralligenous builder *Serpulorbis arenarius* (Mollusca) (Photo by E. Ballesteros).

Figure 27. Animal coralligenous builder *Leptopsammia pruvoti* (Cnidaria) (Photo by E. Ballesteros).

Figure 28. Animal coralligenous agglomerative species *Spongia virgultosa* (Porifera) (Photo by E. Ballesteros).

4.4. Bioeroders

Feldmann (1937) described the abundance of several organisms that erode calcareous concretions, in particular the excavating sponge *Cliona viridis* (Figure 29), the bivalve *Lithophaga lithophaga* and several annelids. Hong (1980) listed eleven bioeroders in the coralligenous communities of Marseilles: four different species of sponges of the genus *Cliona*, three species of molluscs, two species of polychaetes of the genus *Polydora*, and two sipunculids. According to Cerrano *et al.* (2012) the coralligenous concretion is cyclically renewed by the action of boring sponges, whose boring activity result in a characteristic limestone that is deposited below the coralligenous concretions (Cerrano *et al.*, 2001; Calcinai *et al.,* 2001).

Figure 29. Animal coralligenous bioeroder *Cliona viridis* (Porifera) (Photo by E. Ballesteros).

According to Sartoretto (1996), the organisms that erode coralligenous concretions are similar to those eroding other marine bioherms such as the trottoir of *Lithophyllum byssoides* or the coral reefs. Three types of eroding organisms can be distinguished: browsers, microborers and macroborers.

The only browsers in the coralligenous concretions are sea urchins (Laubier, 1966), as the only important Mediterranean fish grazing on algae (*Sarpa salpa*) do not usually thrive in coralligenous communities. *Sphaerechinus granularis* (Figure 30) is an important biological agent that substantially erodes coralligenous concretions (Figure 31), although local variations in sea urchin abundance and individual size greatly influence the amount of calcium carbonate eroded annually. Another sea urchin commonly found in coralligenous communities is *Echinus melo* (Figure 32).

Figure 30. Coralligenous browser *Sphaerechinus granularis* (Echinoidea) (Photo by E. Ballesteros).

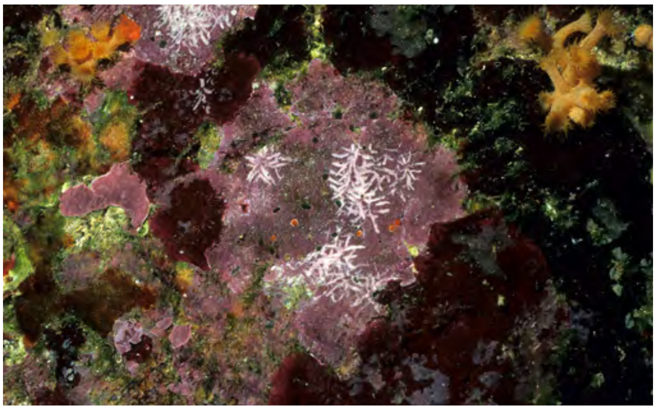

Figure 31. Browsing marks of *Sphaerechinus granularis* over *Lithophyllum stictaeforme* (Photo by E. Ballesteros).

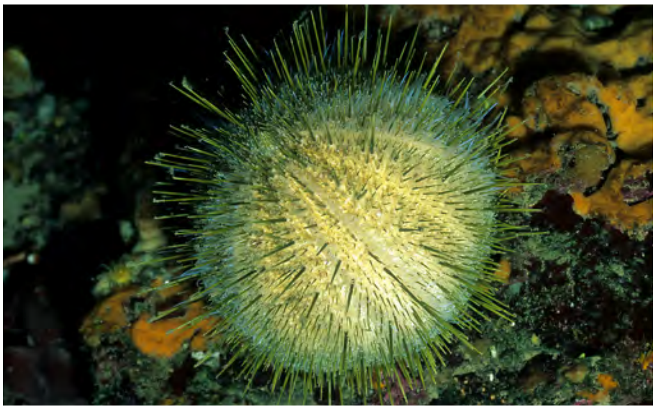

Figure 32. Coralligenous browser *Echinus melo* (Echinoidea) (Photo by E. Ballesteros).

The proportion of calcareous algae in its digestive content ranges from 18 to 50% of the total (Sartoretto, 1996), and it preys mainly on sponges, bryozoans and serpulid polychaetes. Given the low densities of this sea urchin in coralligenous communities (1 to 3 individuals in 25 m^{-2}), Sartoretto (1996) concludes that the bioerosional role of *Echinus melo* is very limited.

Microborers include blue green algae (cyanobacteria), green algae and fungi (Hong, 1980). Three green algae (*Ostreobium quekettii*, *Phaeophila* sp. and *Eugomontea* sp.) and four cyanobacteria (*Plectonema tenebrans, Mastigocoleus testarum, Hyella caespitosa* and *Calothrix* sp.), together with some unidentified fungi, seem to be the main microborers in coralligenous communities. Diversity is higher in shallow waters, while, according to colonization studies conducted by Sartoretto (1998), it is restricted to only one species (*Ostreobium*) in deep waters (-60 m).

Macroborers comprise molluscs (*Lithophaga lithophaga, Gastrochaena dubia, Petricola lithophaga, Hyatella arctica*), sipunculida (*Aspidosiphon mülleri, Phascolosoma granulatum*), polychaetes (*Dipolydora* spp., *Dodecaceria concharum*) and several excavating sponges (Sartoretto, 1996; Martin & Britayev, 1998). Among perforating sponges commonly found in coralligenous communities, some of them excavate mainly in *Corallium rubrum* and other calcareous cnidaria (*Aka labyrinthica, Scantilletta levispira, Dotona pulchella* ssp. *mediterranea, Cliona janitrix*), while others, such as *Pione vastifica*, *Cliona celata*, *Cliona amplicavata*, *Cliona schmidtii* and *Cliona viridis* can be found in a wide range of calcareous substrates (coralline algae, bivalves, madreporids, etc.) (Rosell & Uriz, 2002). *Cliona viridis* is the most powerful destructive sponge of calcareous substrates (Rosell *et al.*, 1999), and is also the most abundant excavating sponge in coralligenous communities (Uriz *et al.*, 1992a). Based on a single sample of a coralligenous outcrop measuring around 25 dm^3 of volume, Calcinai *et al.* (2007) found 7 boring sponges, being *Stoeba plicata* and *Geodia conchilega* the ones that were found deeper in the concretion. Sponges *Jaspis johnstoni* and *Stoeba plicata* were key species as bioeroders of the coralligenous concretion, while *Cliona janitrix* was the boring sponge more abundant in the red coral, *Corallium rubrum* (Calcinai *et al.*, 2007). Encrusting sponges and Sipunculida become more abundant in polluted coralligenous environments (Hong, 1983).

4.5. Assemblages

The final result of the builders and eroders of coralligenous concretions is a very complex structure, in which several microhabitats can be distinguished. Environmental factors (e.g. light, hydrodynamism, and sedimentation rates) can vary by one to two orders of magnitude in parts of the same buildup situated as close as one metre from each other. This great environmental heterogeneity allows several different assemblages to co-exist in a reduced space (Federghini *et al.*, 2000; Abiatti *et al.*, 2009). For practical purposes we will distinguish those situated in open waters (from horizontal to almost vertical surfaces) from those situated in overhangs and cavities. We will not discuss here the assemblages of macroborers (as the only available data have already been commented on), nor the assemblages thriving in the patches of sediment between or inside coralligenous build-ups (as there is no quantitative data on them). We will consider here mainly the descriptions made by sample collecting, although this methodology is almost forgotten in the current coralligenous descriptions, being replaced by visual sampling methods, both direct or indirect (Kipson *et al.*, 2011; Deter *et al.*, 2012; Piazzi *et al.*, 2014a). Still image acquisition has been identified as the most effective data gathering system in coralligenous environments (Zapata-Ramírez *et al.*, 2013) although its accuracy is lower than traditional sampling methods based on collection (Sant *et al.*, 2017).

Algae, both encrusting corallines and green algae, usually dominate in horizontal to sub-horizontal surfaces (Figure 33), although their abundance decreases with depth or in dim light. Phycologists have distinguished two main communities according to the light levels reaching coralligenous concretions. In shallower waters *Mesophyllum alternans* usually dominates in the basal layer and *Halimeda tuna* in the upper stratum, with an important coverage of other algae (*Peyssonnelia* spp., *Flabellia petiolata*) (Figure 34).

Figure 33. Green and red macroalgae dominate horizontal to subhorizontal surfaces in shallow coralligenous banks (Photo by E. Ballesteros).

Figure 34. Shallow coralligenous outcrop dominated by *Halimeda tuna* and *Mesophyllum alternans* (Sa Muladera, Tossa de Mar, -25 m) (Photo by E. Ballesteros).

This plant association has received the name of *Lithophyllo-Halimedetum tunae* and has been described in detail by Ballesteros (1991b). Algal biomass ranges between 1200 and 2100 gdw m^{-2}, while percentage coverage ranges from 180 to 400%. The number of species is very high (average of 76 species in 1024 cm^2) and average diversity is 2.5 bits ind^{-1}. Its bathymetric distribution ranges from a depth of 12-15 m to 30-35 m in the Gulf of Lions, but it can reach depths below 50 m in the clear waters of seamounts and insular territories of the western and eastern Mediterranean. This association develops at irradiances ranging from around 2.3 to 0.3 W m^{-2}, which correspond, respectively, to 3 and 0.4% of the surface irradiance. Other rélevés are described in Marino *et al.* (1998).

In deeper waters or lower irradiances, the density of *Halimeda tuna* decreases and other calcareous algae become dominant (*Lithophyllum stictaeforme, Neogoniolithon mamillosum, Peyssonnelia rosa marina*) (Figure 35). Other common algae are members of the family Delesseriaceae and other laminar red algae (*Kallymenia, Gloiocladia, Sebdenia, Rhodophyllis, Predaea*),

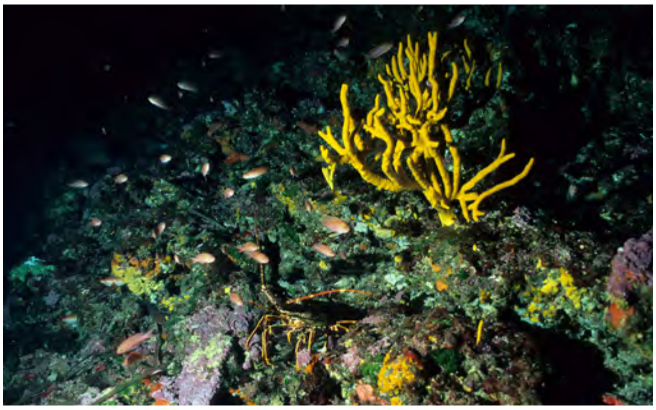

Figure 35. Deep water algal-dominated coralligenous rim (Scandola, Corsica, -45 m) (Photo by E. Ballesteros).

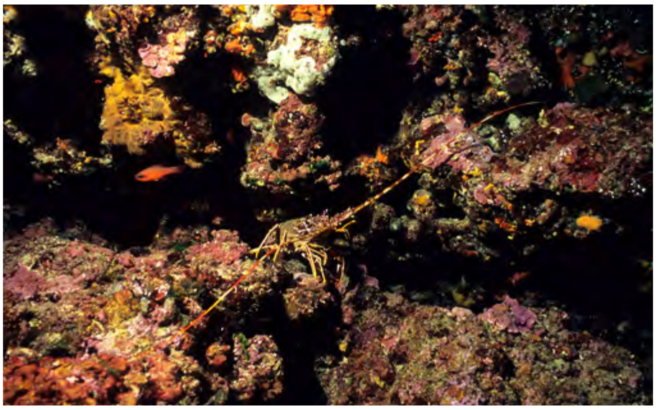

Figure 38. Detail of a deep water algal-dominated coralligenous rim (-50 m, Scandola, Corsica) (Photo by E. Ballesteros).

as well as the encrusting green alga *Palmophyllum crassum*. These assemblages correspond to the *Rodriguezelletum strafforellii* of Augier & Boudouresque (1975), which may be identical to the algal assemblage described by Feldmann (1937) for coralligenous concretions from the Mediterranean Pyrenees (Figures 36, 37, 38). Quantified species lists can be found in Boudouresque (1973), Augier & Boudouresque (1975), Ballesteros (1992), and Marino *et al.* (1998). Algal biomass averages 1600 g m^{-2} and percentage cover 122%, mostly corresponding to encrusting algae and, around 90%, corresponding to corallines; the number of species is low (38 species in 1600 cm^2 or lower) (Ballesteros, 1992).

Animal assemblages of these two plant associations can differ greatly from one to the other, as well as between sites and geographical areas. The abundance of suspension feeders mainly depends on average current intensity and availability of food (plankton, POC, DOC). In the richest zones (e.g. Gulf of Lions, Marseilles area) gorgonians can dominate the community (Figures 39, 40), but in very oligotrophic waters (e.g. Balearic Islands, eastern Mediterranean), sponges, bryozoans

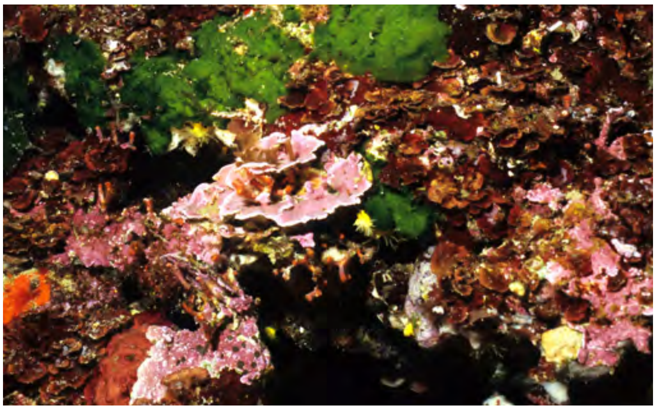

Figure 36. Detail of a deep water algal-dominated coralligenous bank at -42 m (Columbretes Islands, Spain) (Photo by E. Ballesteros).

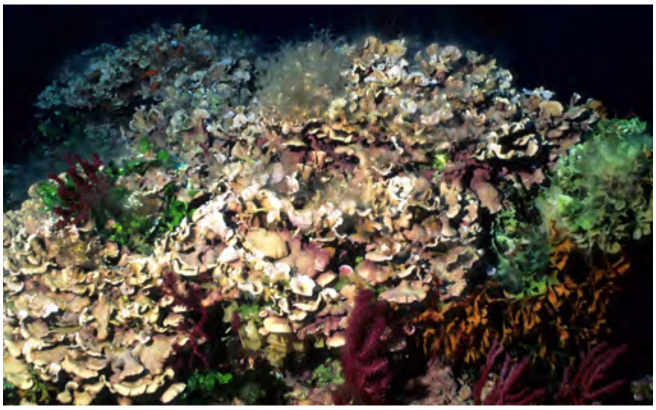

Figure 37. Detail of a deep water algal-dominated coralligenous assemblage with *Mesophyllum expansum* at a seamount (-39 m, Columbretes Islands, Spain) (Photo by E. Ballesteros).

Figure 39. Deep-water, animal-dominated coralligenous assemblage with *Paramuricea clavata* (Scandola, Corsica, -45 m) (Photo by E. Sala).

Figure 40. Deep-water, animal-dominated coralligenous assemblage with *Paramuricea clavata* (Medes Islands, Spain, -40 m) (Photo by E. Ballesteros).

and small hexacorals are the dominant suspension feeders (Figures 41,42). The only available quantified biomass data on invertebrate assemblages are those of True (1970) gathered from the Marseilles area, and these results are summarized below.

Figure 41. Deep-water, animal-dominated coralligenous assemblage with small invertebrates (***Crambe crambe, Hacelia attenuata***) (Cabrera, Balearic Islands, -45 m) (Photo by E. Ballesteros).

Figure 42. Detail of a deep-water, animal-dominated coralligenous assemblage with small invertebrates (Cabrera, Balearic Islands, -60 m). More evident species are sea star ***Hacelia attenuata***, tunicate ***Halocynthia papillosa*** and sponge ***Crella pulvinar*** (Photo by E. Ballesteros).

True (1970) studied an assemblage dominated by *Eunicella cavolini* (Figure 43). He reports a basal layer of encrusting algae accompanied by erect algae (total biomass of 163 g dw m^{-2}). *Eunicella cavolini* is the most abundant species (up to 304 g dw m^{-2}), followed by the bryozoans *Pentapora fascialis* (280.1 g dw m^{-2}), *Turbicellepora avicularis* (49.1 g dw m^{-2}), *Celleporina caminata* (22.3 g dw m^{-2}) and *Myriapora truncata* (19.9 g dw m^{-2}). Other less abundant species include unidentified Serpulidae, anthozoans *Alcyonium coralloides, Alcyonium acaule, Leptopsammia pruvoti,* and *Caryophyllia smithii*, tunicates *Microcosmus polymorphus* and *Halocynthia papillosa*, foraminifer *Miniacina miniacea*, sponges *Chondrosia reniformis* and *Axinella damicornis* and other bryozoans (*Adeonella calveti, Beania hirtissima, Sertella* spp., *Schizomavella* spp. and *Cellaria salicornioides*). The number of collected invertebrate species amounted to 146 in 7500 cm^2, with a total weight of invertebrates close to 1563 g dw m^{-2}. The main biomass corresponded to the phylum Bryozoa, closely followed by Cnidaria, and, with much lower values, Annelida, Porifera, Chordata (tunicates), and Mollusca.

Figure 43. Coralligenous wall dominated by ***Eunicella cavolini*** and ***Halimeda tuna*** (Garganellu, Corsica, -25 m) (Photo by E. Ballesteros).

Another assemblage studied by True (1970) is that dominated by *Paramuricea clavata* (Figure 44). Populations of *Paramuricea clavata* are abundant in steep rocky walls, but they also grow in horizontal to sub-horizontal surfaces if light levels are very low. The basal layer of the community can be mainly occupied by algae (usually attributable to *Rodriguezelletum strafforellii* association) or by other suspension feeders (sponges and bryozoans). The *relevés* of True (1970) do not report any algae. *Paramuricea clavata* has a total biomass of 746 g dw m^{-2}, followed by the cnidarians *Caryophyllia smithii* (326.3 g dw m^{-2}) and *Hoplangia durotrix* (188.1 g dw m^{-2}), the bryozoan *Celleporina caminata* (119.6 g dw m^{-2}), the anthozoan *Leptopsammia pruvoti* (54.9 g dw m^{-2}), the bryozoans *Adeonella calveti* (32.8 g dw m^{-2}) and *Turbicellepora avicularis* (31.4 g dw m^{-2}), and red coral (*Corallium rubrum*, 16.9 g dw m^{-2}). Other less abundant species include unidentified Serpulidae, sponges *Ircinia variabilis* (*fasciculata* in True, 1970), *Spongia officinalis, Sarcotragus spinosula, Cacospongia scalaris, Petrosia ficiformis, Aplysina cavernicola, Erylus euastrum* and *Agelas oroides*, the bryozoan *Sertella septentrionalis*, the alcyonarian *Parazoanthus axinellae*, molluscs *Pteria hirundo, Serpulorbis arenarius, Lithophaga lithophaga* and *Anomia ephippium*, and tunicates *Microcosmus*

Figure 44. Coralligenous assemblage dominated by ***Paramuricea clavata*** (Imperial Islet, Cabrera, Balearic Islands, -60 m) (Photo by E. Ballesteros).

polymorphus and *Polycarpa pomaria*. The number of collected invertebrate species amounts to 111 in 7500 cm^2, with a total weight of 3175 g dw m^{-2}. The main biomass corresponds to the phylum Cnidaria, followed by Annelida, Bryozoa, Porifera, Mollusca and Chordata.

Gili & Ballesteros (1991) described the species composition and abundance of the cnidarian populations in coralligenous concretions around the Medes Islands that are dominated by the gorgonian *Paramuricea clavata*. Total cnidarian biomass amounted to 430 g dw m^{-2}, with thirteen species of hydrozoans and nine species of anthozoans found in an area of 5202 cm^2. Species contributing the most to the total biomass of the taxocenosis were the anthozoans *Paramuricea clavata, Leptopsammia pruvoti, Parazoanthus axinellae, Caryophyllia inornata, Caryophyllia smithii, Alcyonium acaule* and *Alcyonium coralloides*, the hydrozoans *Sertularella gaudichaudii* and *Halecium tenellum* also being abundant.

Overhangs and big cavities of coralligenous assemblages have a different species composition to that found in open waters (Figure 45). Algae are usually completely absent because light is very reduced. However, some thalli of encrusting corallines, *Peyssonnelia* spp. and *Palmophyllum crassum*, can occasionally be found. There are no *relevés* for this kind of habitat reported in the literature except for those of True (1970), which, in fact, do not come from a coralligenous buildup but from a semi-dark zone dominated by red coral in a cave (Grotte de l'île Plane). This assemblage is worth describing as it is very similar to those developing in the overhangs of coralligenous constructions in the northwestern Mediterranean, or in coralligenous communities situated in very deep waters.

Figure 45. Overhang with an assemblage dominated by *Corallium rubrum* (Palazzu, Corsica, -32 m) (Photo by E. Ballesteros).

The assemblage of red coral described by True (1970) is dominated by the cnidarians *Corallium rubrum* (2002 g dw m^{-2}), *Caryophyllia smithii* (303 g dw m^{-2}), *Hoplangia durotrix* (54.1 g dw m^{-2}) and *Leptopsammia pruvoti* (52.4 g dw m^{-2}), the sponges *Petrosia ficiformis* (241.5 g dw m^{-2}) and *Aplysina cavernicola* (27.9 g dw m^{-2}), the bryozoan *Celleporina caminata* (100.5 g dw m^{-2}), and unidentified Serpulidae (232.4 g dw m^{-2}). Other abundant species are the sponges *Ircinia variabilis, Spongia officinalis, Aaptos aaptos* and *Ircinia oros*, the molluscs *Chama gryphoides* and *Anomia ephippium*, and several unidentified bryozoans. The total number of identified invertebrate species is 63 in 7500 cm^2, with a total biomass of 3817 g dw m^{-2}. The dominant phylum is largely the Cnidaria, although Porifera, Annelida and Bryozoa are also abundant.

The classification of the assemblages/communities/habitats found in the coralligenous outcrops is a pending issue. The only widely accepted classification proposed by the Barcelona Convention (UNEP/MAP/RAC-SPA, 2006) has been incorporated into the EUNIS classification system (Davies *et al.* 2004). Giaccone (2007) gives a list of the Mediterranean habitats from the Barcelona Convention that are included into the coralligenous environment. However, the current list is not complete according to some opinions (e.g. Templado *et al.*, 2012) and countries like Spain have adopted more complex and accurate habitat classification systems, which are also in accordance with EUNIS. Another initiative for habitat characterisation has ben proposed by the project CIGESMED (David *et al.*, 2014).

It should be remembered that most of the information presented in this chapter, if representative at all, reflects the biomass and species composition of several assemblages of coralligenous buildups from the Gulf of Lions, which are different to those reported from other sites of the western Mediterranean (e.g. Balearic Islands; Ballesteros *et al.*, 1993) or the eastern Mediterranean (Pérès & Picard, 1958; Laborel, 1960). Therefore, these data cannot be extrapolated to the entire Mediterranean coralligenous assemblages.

4.6. Food web

There is almost no information available about the food web structure of coralligenous ecosystems. Ruitton *et al.* (2014) propose a conceptual model of functional structure with different compartments from the coralligenous outcrop itself (builders, non-building macrophytes and suspension feeders, bioeroders, browsers and grazers, predators, detritus feeders, top predators, benthic particulate organic matter) and from the surrounding pelagic ecosystem (planktivorous teleosts, plankton, pelagic particulate organic matter, pelagic microbial loop, dissolved inorganic carbon). However, first data on the food web structure based on stable isotope analyses is not provided until the study of Belloni *et al.* (2019), who analyze 78 compartments or species in a coralligen ecosystem near Marseille, between 30 and 40 m depth. Particulate organic matter, mainly composed by plankton, is the main energy fuelling the food web, followed by benthic organic matter and some macrophytes. Abundant macroalgae such as *Codium* spp., *Flabellia petiolata*, *Palmophyllum crassum* or *Sphaerococcus cornopifolius* do not seem to provide any source of organic matter to higher trophic levels. Three levels of consumers are identified (suspension feeder invertebrates, invertivores and piscivorous teleosts). Several suspension feeders (cnidarians, bryozoans, tunicates) are hardly consumed but they seem to play an important role in particulate organic matter transfer. There is an urgent need of further studies to validate the preliminary data of Belloni *et al.* (2019) with the aim to provide a general trophic functioning model of the coralligenous habitats.

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5. Biodiversity

According to Boudouresque (2004a), coralligenous assemblages constitute the second most important hot spot of species diversity in the Mediterranean, after the *Posidonia oceanica* meadows. However, the number of species that thrive in these coralligenous assemblages due to the coralligenous' rich fauna (Laubier, 1966), complex structure (Pérès & Picard, 1964; Ros *et al.*, 1985), and the paucity of studies, is probably higher than any other Mediterranean seascape. In fact, coralligenous assemblages are one of the preferred diving spots for tourists due to the great diversity of organisms (Harmelin, 1993; Ingrosso *et al.*, 2018). Divers are astonished by the high number of species belonging to taxonomic groups as diverse as sponges, gorgonians, molluscs, bryozoans, tunicates, crustaceans or fishes. Moreover, there are innumerable organisms living in these coralligenous communities that go unnoticed by diving, and even without a careful sorting of samples (De Jode *et al.,* 2019). For example, in a sample of 370 g dw of *Mesophyllum* from a small coralligenous concretion in southern of Spain, García-Raso (1988) found 903 specimens of crustaceans, molluscs and polychaetes; other organisms from different groups (picnogonida, nematoda, echinoderms, sipunculida, sponges, tunicates, small fishes, such as Gobiidae and Bleniidae, as well as hydrozoans and bryozoans) were also abundant, but not quantified.

Laubier (1966) was the first author to emphasize the great biodiversity of coralligenous communities and listed 544 invertebrates from coralligenous assemblages in the region of Banyuls. Later, in an exhaustive survey of coralligenous communities around Marseilles, Hong (1980) listed a total of 682 species, while several authors (in Ros *et al.*, 1984) report 497 species of invertebrates in the coralligenous assemblages of the Medes Islands.

Our estimates of the species richness found in coralligenous communities give a very conservative number of 1775 invertebrates (Table I). Boudouresque (1973) has estimated that at least 315 species of macroalgae can thrive in Mediterranean sciaphilic communities (the coralligenous being the most widespread community) and Piazzi *et al.* (2009) show the high algal diversity found in coralligenous assemblages. Finally, there are no estimates of the number of fish that can be found in coralligenous communities, due to the high mobility of most species of this group, but our estimates based on available literature regarding the biology of Mediterranean fish (e.g. Whitehead *et al.*, 1984-1986; Corbera *et al.*, 1996; Mayol *et al.*, 2000) range between 110 and 125 species. However, all the biodiversity estimates seem to underestimate the biodiversity of coralligenous assemblages (De Jode *et al.,* 2019) because metabarcoding approaches give far higher number of Molecular Operational Units.

It is very difficult to mention all the species found to date in coralligenous communities, as the existing taxonomic literature is huge and contains many synonyms; this makes it impossible for a non-specialist in most of the groups to come up with an accurate number of the reported species. Nevertheless, we have attempted to make a first, and very conservative, estimate of the total number of species, which amounts to some 2,200 (Table I), although it is an underestimation of the existing biodiversity. A first step toward increased knowledge of the biodiversity present in coralligenous communities would be to obtain a more accurate estimate of which species have been found and their number. An initiative devoted to index the Mediterranean biodiversity named IndexMed (David *et al.*, 2016), has began with the species found in coralligenous assemblages in the frame of CIGESMED project.

Regarding the distribution of species according to depth it seems that shallow coralligenous assemblages are more functionally and phylogenetically diverse than deep ones (Doxa *et al.*, 2016), the taxonomic beta diversity peaking between 50 and 70 meters. Coralligenous platforms also increase the diversity of the macrobenthic assemblages thriving in nearby sedimentary bottoms (Appolloni *et al.*, 2017).

Group	Totals	References
Algae	315	1
Protozoans	61	2,3
Sponges	>300	7,22,23
Hydrozoans	55	2,4,5,8
Anthozoans	43	2,4,5,6,19
Scyphozoans	1	2,3
Turbellarians	3	2,3
Nemerteans	12	2
Polychaetes	191	9
Sipunculids	3	2,3
Echiurids	2	2
Chitons	14	21
Gastropods	357	21
Bivalves	137	21
Cephalopods	3	6
Scaphopods	1	21
Mites	6	2
Pycnogonids	15	3
Copepods	54	2
Ostracods	10	2
Cirripeds	3	2,3
Phyllocarids	1	3
Mysids	7	3
Cumaceans	12	20
Tanaidaceans	2	2,3
Isopods	14	2,3
Amphipods	100	10
Decapods	56	11,12
Brachiopods	8	13
Pterobranchs	1	2
Bryozoans	171	14
Crinoids	2	15
Ophiuroids	17	2,15
Echinoids	14	2,3,4,5,6,15,16
Asteroids	8	2,15,16
Holoturioids	9	2,3,4,5,6,15,16
Tunicates	82	17
Fishes	110	18,19

Table 1. Approximate number of species reported from coralligenous communities.
Compiled from [1] Boudouresque (1973), [2] Laubier (1966), [3] Hong (1980), [4] Ros ***et al.*** (1984), [5] Ballesteros ***et al.*** (1993), [6] Ballesteros & Tomas (1999), [7] Longo ***et al.*** (2017), [8] Llobet ***et al.*** (1991a), [9] Martin (1987), [10] Bellan-Santini (1998), [11] Garcia-Raso (1988), [12] Garcia-Raso (1989), [13] Logan (1979), [14] Zabala (1986), [15] Tortonese (1965), [16] Munar (1993), [17] Ramos (1991), [18] Whitehead ***et al.*** (1984-86), [19] Ballesteros (unpublished data), [20] Sezgin ***et al.*** (2009), [21] Poursanidis & Koutsoubas (2015), [22] Bertolino ***et al.*** (2013a) [23] Bertolino ***et al.*** (2013b).

The next section describes the main findings reported for each taxonomic group.

5.1. Taxonomic groups

• Algae

At least 315 species of macroalgae thrive in deep-water Mediterranean sciaphilic communities (Boudouresque, 1973), and most of them are found in coralligenous concretions. The algal assemblages found here show high biodiversity, with an average of 40 algal species in 600 cm².

Boudouresque (1973) defined the ecological group of algae characteristic of coralligenous concretions (CC or *Rodriguezellikon*), which -after his own review (Boudouresque, 1985)- comprises 28 species (e.g. *Rodriguezella* spp., *Aeodes marginata, Gloiocladia repens, Chondrymenia lobata, Gulsonia nodulosa, Polysiphonia elongata, Neogoniolithon mamillosum*) (Figure 46).

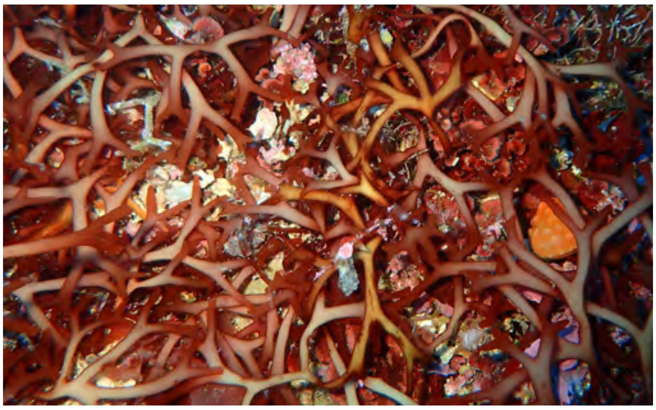

Figure 46. *Gloiocladia repens*, a characteristic and sometimes dominant erect red alga in coralligenous environments (Photo by E. Ballesteros).

However, coralligenous communities are never dominated by this group of species, but rather by other species with a more depth-related widespread distribution, examples being the encrusting corallines *Mesophyllum alternans, Lithophyllum stictaeforme,* and *Lithophyllum cabiochae*, the green algae *Palmophyllum crassum, Flabellia petiolata, Halimeda tuna* and *Valonia macrophysa*, some brown algae such as *Dictyota dichotoma, Dictyopteris polypodioides, Spatoglossum solierii, Zonaria tournefortii, Halopteris filicina, Phyllariopsis brevipes, Zanardinia typus,* and *Laminaria rodriguezii,* and a large number of red algae (several species of *Peyssonnelia, Kallymenia, Halymenia, Sebdenia, Predaea, Eupogodon, Myriogramme, Neurocaulon foliosum, Acrodiscus vidovichii, Osmundaria volubilis, Phyllophora crispa, Rhodymenia ardissonei, Acrosorium venulosum, Rhodophyllis divaricata, Hypoglossum hypoglossoides, Polysiphonia banyulensis, Plocamium cartilagineum, Sphaerococcus coronopifolius, Erythroglossum sandrianum,* and *Aglaothamnion tripinnatum*) (Boudouresque, 1973, 1985; Ballesteros, 1992, 1993).

The algal component of coralligenous communities is largely constituted by Mediterranean endemics, which quantitatively represent between 33 and 48% of the total flora (Boudouresque, 1985).

Coralligenous communities are rather rich in algal species, although this richness is lower than that found in photophilic or moderately sciaphilic communities (Ballesteros, 1992). Ballesteros (1991b) reports 90 species of macroalgae from the coralligenous assemblages of Tossa de Mar, where *Mesophyllum alternans* and *Halimeda tuna* dominate, but only 38 in the coralligenous communities from a deep-water site (Ballesteros, 1992). Piazzi *et al.* (2004) found small differences between algal assemblages of coralligenous habitats along the coast of Tuscany (Italy). However, algal populations in coralligenous habitats differ greatly on geographical scales across the whole Mediterranean (Boudouresque, 1973) and this is the main reason why, even if the species diversity in one site is rather constant, the overall algal richness of coralligenous habitats —on a Mediterranean-wide scale and covering all depths where it grows— can be huge.

• Protozoans

Fifty-four species of Foraminifera are listed by Hong (1980) in the check-list of species from the coralligenous communities of Marseilles, although none of these species seems to be characteristic of coralligenous habitats. *Miniacina miniacea* is the most abundant species, and other common species include *Massilina secans, Planorbulina mediterranensis, Elphidium crispum* and *Triloculina rotunda*. Laubier (1966) reports six species of Folliculinidae living as epibionts of bryozoans.

• Sponges

Coralligenous communities are very rich in sponges, which grow mainly in the more sciaphilic environments but also in more exposed areas. There are also some species (Clionidae) that are active bioeroders and which excavate the coralline framework. The number of species reported from different well-studied areas is 26 species from Banyuls (Laubier, 1966), 78 species from Marseilles (Hong, 1980), 48 species from the Medes Islands (Bibiloni *et al.*, 1984), 74 species from Cabrera (Ballesteros *et al.*, 1993), and 24 species from Tossa (Ballesteros & Tomas, 1999). The list of sponges reported in all these studies (along with those of True, 1970 and Rosell & Uriz, 2002) amounts to 142 different species. According to Hong (1980) the following species are characteristic of coralligenous biocoenoses: *Axinella damicornis, Acanthella acuta, Hymedesmia pansa, Agelas oroides* (Figure 47), *Dictyonella pelligera, Haliclona mediterranea, Spongionella pulchella* and *Faciospongia cavernosa*. Other abundant sponges (Laubier, 1966; True, 1970; Hong, 1980; Bibiloni *et al.*, 1984; Ballesteros *et al.*, 1993; Ballesteros & Tomas, 1999) are: *Cliona viridis, Clathrina clathrus, Oscarella lobularis, Chondrosia reniformis, Phorbas tenacior, Geodia cydonium, Aaptos aaptos, Pleraplysilla spinifera, Dysidea avara, Terpios fugax, Spongia virgultosa, Spongia agaricina, Spongia officinalis, Ircinia variabilis, Ircinia oros, Axinella verrucosa, Axinella polypoides, Diplastrella bistellata, Petrosia ficiformis, Hexadella racovitzai, Cacospongia scalaris,* *Dictyonella obtusa, Erylus euastrum, Hippospongia communis, Reniera cratera, Reniera fulva, Reniera mucosa, Spirastrella cunctatrix, Spongosorites intricatus* and *Hemimycale columella.*

Figure 47. *Agelas oroides* is a dominant sponge in coralligenous assemblages from the Eastern Mediterranean (Photo by E. Ballesteros).

The coralligenous communities from the eastern Mediterranean seem to be very rich in sponges (Pérès & Picard, 1958), as they are almost devoid of alcyonarians and gorgonians. Most abundant species have already been cited above, but we can highlight those of the genus *Axinella* (*A. polypoides, A. damicornis, A. verrucosa*), *Agelas oroides* and *Petrosia ficiformis* (Pérès & Picard, 1958).

Bertolino *et al.* (2013a) record 133 sponge taxa in coralligenous environments at four sites of the Ligurian Sea while Longo *et al.* (2017) record up to 153 taxa of sponges in coralligenous habitats from Apulia (Italy). Total number of sponges from these environments has been calculated in 273 (Bertolino *et al.*, 2013a) although a more reliable number should exceed 300 species (Bertolino *et al.*, 2013b; Bertolino *et al.*, 2017a,b). Both Pica *et al.* (2014), Calcinai *et al.* (2015) and Longo *et al.* (2017) point out that research has to be focused in cryptic species living at increasing depths since there are more species and biomass of sponges inside the coralligenous concretions than outside.

• Hydrozoans

Laubier (1966) reports sixteen hydrozoans from the coralligenous communities of Banyuls, whereas no list of these organisms is present in the study by Hong (1980). Gili *et al.* (1993) report 44 species of hydrozoans from the coralligenous and precoralligenous communities of the Medes Islands. According to Laubier (1966) and Gili *et al.* (1984, 1989) some species of hydrozoans are common on deep-water rocky bottoms and coralligenous assemblages: *Nemertesia antennina, Eudendrium rameum, Filellum serpens, Dynamena disticha, Clytia hemisphaerica, Hebella scandens, Sertularella polyzonias, Sertularella gayi, Sertularella ellisi, Sertularella crassicaulis, Laomedea angulata,* and *Cuspidella humilis.*

The only detailed study of hydrozoans found on coralligenous assemblages is that of Llobet *et al.* (1991a), who report 35 species of hydroids living on the thalli of *Halimeda tuna* in the coralligenous concretions of Tossa de Mar (northwestern Mediterranean). Llobet *et al.* (1991a) classify the most abundant hydrozoans into three categories on the basis of their horizontal zonation on the thalli. The hydroids common on the proximal articles (oldest) are relatively large and present throughout the year (*Eudendrium racemosum, Eudendrium capillare, Halecium tenellum* and *Kirchenpaueria echinulata*). Those common on the medial articles (*Campalecium medusiferum, Halecium pusillum, Hydranthea margarica, Phialella quadrata, Campanularia everta* and *Filellum serpens*) are smaller and often occur in dense monospecific patches. Finally, those common on the distal articles (*Campanularia raridentata, Clytia hemisphaerica, Sertularia distans, Sertularella polyzonias* and *Aglaophenia pluma*) are present for only short periods and are highly opportunistic. This zonation seems to reflect interspecific niche selection, enabling successful competition for space with other hydroids, algae and bryozoans.

• Anthozoans

Studies by Laubier (1966), True (1970), Hong (1980) and Gili *et al.* (1984, 1989) report several species of anthozoans (Figure 48) from coralligenous habitats (up to 44 in Gili *et al.*, 1993). The commonest species are *Parazoanthus axinellae, Leptopsammia pruvoti, Alcyonium coralloides, Alcyonium acaule, Paramuricea clavata, Eunicella singularis, Eunicella cavolinii, Rolandia rosea, Corallium rubrum, Telmatactis elongata, Maasella edwardsii, Monomyces pygmaea, Hoplangia durotrix, Caryophyllia inornata, Caryophyllia smithii, Clavularia ochracea, Cornularia cornucopiae* and *Epizoanthus arenaceus*. *Madracis pharensis* is especially abundant in the coralligenous outcrops from the eastern Mediterranean (Laborel, 1960). Gori *et al.* (2017) recently added new species of anthozoans found in the depth range 50-70 m.

Figure 48. *Madracis pharensis* is a very common anthozoan in coralligenous assemblages from the Eastern Mediterranean (Photo by E. Ballesteros).

• Scyphozoans

The only species reported (Hong, 1980) is *Nausitoë punctata*, living inside several massive sponges.

• Turbellarians

Laubier (1966) reports three turbellarians from the coralligenous communities of Banyuls, all very rare.

• Nemerteans

Nemerteans live endolithically in concretions. According to Pruvot (1897) and Laubier (1966), who report up to twelve species in the coralligenous communities of Banyuls, they are rather common. *Drepanophorus crassus, Tetrastemma coronatum, Micrura aurantiaca* and *Micrura fasciolata* are the most abundant.

• Nematodes

Nematodes are the most abundant microscopic metazoans in marine sediments and are present in the sediments retained in coralligenous assemblages, as well as in the endofauna of concretions and the epifauna of algae and sessile invertebrates. However, there are no studies dealing with this group of organisms in coralligenous assemblages.

• Polychaetes

Polychaetes are extremely abundant in coralligenous communities. Martin (1987) reported a total of 9,195 individuals present in twenty samples of 400 cm^2 collected from coralligenous communities dominated by *Mesophyllum alternans* and *Lithophyllum stictaeforme* from the Catalan coast (northwestern Mediterranean). This means an average of 460 worms per sample and a density of more than one individual per cm^2. He found 191 different species, with a dominance of Syllidae (31% of the total). The number of species per sample was very high, ranging between 71 and 32 for macrofauna (>0.4 mm) and between 55 and 27 for microfauna (<0.04 mm). Diversity of the samples was also very high, averaging 4.54 bits ind^{-1} for macrofauna and 4.34 bits ind-1 for microfauna (Shannon-Weaver index). According to Martin (1987), coralligenous assemblages are a very suitable habitat for polychaetes as the high structural complexity of the concretions allows the coexistence of several species in a reduced space.

The first checklist of polychaetes collected from coralligenous communities and studied by a specialist is that of Bellan (1964), who reported 70 different species in coralligenous communities.

Laubier (1966) carefully studied the assemblages of polychaetes in two coralligenous stations in the region of Banyuls. He reported 130 different species, *Lepidasthenia elegans, Kefersteinia cirrata, Xenosyllis scabra,* and *Typosyllis variegata* being the most abundant. According to his observations, and those of Bellan (1964), the polychaetes inhabiting coralligenous concretions are mainly ubiquitous species, although he distinguished two main groups: microfauna and macrofauna. Microfauna comprise three ecological groups: psammophilic species (e.g. *Xenosyllis scabra, Eurysillis tuberculata, Trypanosyllis coeliaca*), limic species (e.g. *Scalibregmidae, Sclerocheilus minutus*), and the strictly endogean species, which are the most 'characteristic' of coralligenous habitats (e.g. *Pholoe minuta, Chrysopetalum caecum, Eulalia tripunctata, Sige microcephala, Opisthodonta morena, Syllides longocirrata,* and so on). Among the macrofauna he distinguished four ecological groups: polychaetes living inside sponges (e.g. *Lepidasthenia elegans, Eunice siciliensis, Amphitrite variabilis*), the species living in small crevices and holes, like most Serpulidae and Terebellidae, as well as *Eunice torquata*, the big vagile polychaetes living over or inside coralligenous holes (e.g. *Lepidonotus clava, Harmothoe aerolata, Pontogenia chrysocoma, Trypanosyllis zebra*) and, finally, the excavating species of the genus *Dipolydora* and *Dodecaceria concharum*.

Hong (1980) also produced a long list of polychaetes inhabiting the coralligenous communities of Marseilles, reporting a total number of 109 species. He distinguished some characteristic species such as *Haplosyllis spongicola, Trypanosyllis coeliaca, Platynereis coccinea, Eunice torquata, Lumbrinereis coccinea* and *Potamilla reniformis.*

According to Martin (1987), who studied polychaete fauna in the coralligenous communities from the Catalan coast, the most dominant and constant species are *Filograna implexa, Spirobranchus polytrema, Polydora caeca, Pomatoceros triqueter, Syllis truncata, Nereis pelagica, Syllis gerlachi, Haplosyllis spongicola, Serpula concharum, Anaitides muscosa* and *Dodecaceria concharum.*

However, the most conspicuous species growing in coralligenous communities are not usually the most abundant, but rather the large and very apparent species of serpulids (True, 1970): *Salmacina dysteri, Serpula vermicularis, Serpula concharum, Sabella pavonina* (Figure 49), *Myxicola aesthetica*, *Sabella spallanzani*

Figure 49. *Sabella pavonina* is a common tubiculous worm in sediment-rich coralligenous assemblages (Photo by E. Ballesteros).

and *Protula* spp. (Ballesteros & Tomas, 1999). Rosso & San Filippo (2009) report 11 species of Serpuloideae contributing to the build up of coralligenous banks in the Avola region (SE Sicily). *Serpula vermicularis, S. concharum, Pomatoceros triqueter, Janua pagenstecheri, Placostegus crystallinus* colonise upward exposed algal thalli, while *Janita fimbriata, Semivermilia crenata, S. cribata* and *Josephella marenzelleri* appear in shadow surfaces or cavities (Rosso & San Filippo, 2009).

• Sipunculids

Always endolithic, the most abundant species of sipunculid is *Phascolosoma granulatum*, which, along with *Aspidosiphon mülleri*, is also a very active bioeroder (Sartoretto, 1996). Laubier (1966) reports a third species in the coralligenous community of Banyuls: *Golfingia minuta*.

• Echiurans

Bonellia viridis, very common in coralligenous communities, is an important detritus feeder. Laubier (1966) reports another, extremely rare species from the coralligenous community of Banyuls.

• Molluscs

Molluscs are extremely abundant in coralligenous communities. They support highest diversity than adjacent soft bottoms (Urra *et al.* 2012), but lower than other rocky bottoms (Donnarumma *et al.*, 2008). Martin *et al.* (1990) reported a total of 897 individuals in twenty samples of 400 cm^2, equivalent to an average of 45 species per sample and more than one mollusc per 10 cm^2. They report a very high number of species given the reduced area they sampled: 131. The number of species per sample ranged between 5 and 33. Average diversity for all the samples was 3 bits ind^{-1} (Shannon-Weaver index). Salas & Hergueta (1986) also reported a very high diversity, with an average of 22.7 species per sample.

The number of species reported in studies devoted to the coralligenous communities of a small geographic area are always high: 69 species in Banyuls (Laubier, 1966), 142 species in Marseilles (Hong, 1980), 108 species in the Medes Islands (Huelin & Ros, 1984) or 117 species (Urra *et al.*, 2012) in a coralligenous bottom of the Alboran Sea. According to these authors, and to Martin *et al.* (1990), the most common and constant species are the chiton *Callochiton achatinus*, the prosobranchs *Acmaea virginea, Calliostoma zizyphinum, Alvania lineata, Alvania cancellata, Setia semistriata, Setia tenera, Chauvetia minima, Chauvetia mamillata, Hinia incrassata, Fusinus pulchellus, Fusinus rostratus, Raphitoma linearis, Clanculus corallinus, Rissoina bruguierei, Triphora perversa, Muricopsis cristatus, Calyptraea chinensis* and *Bittium reticulatum*, the opisthobranchs *Odostomia rissoides, Diaphorodis papillata, Limacia clavigera, Cadlina laevis, Hypselodoris fontandraui, Chromodoris luteorosea, Chromodoris purpurea, Dendrodoris grandiflora, Duvaucelia striata, Peltodoris atromaculata, Glossodoris gracilis, Glossodoris tricolor, Polycera quadrilineata, Flabellina affinis* (Figure 50) and *Dondice banyulensis*, and the bivalves *Arca barbata, Striarca lactea, Musculus costulatus, Kellia suborbicularis, Lithophaga lithophaga, Coralliophaga lithophagella, Anomia ephippium, Pteria hirundo, Chlamys multistriata, Chama gryphoides, Lima lima* and *Hiatella arctica*. Some species are associated with the dominant species such as *Neosimnia spelta* (Figure 51) with gorgonians (Urra *et al.*, 2012).

Figure 50. *Flabellina affinis* is a common opisthobranch found in coralligenous assemblages where hydroids of the genus *Eudendrium* are abundant, as it feeds on them (Photo by E. Ballesteros).

Figure 51. The gastropod *Neosimnia spelta* feeds on gorgonians (Photo by E. Ballesteros).

Cephalopods are also present in coralligenous communities, although they are usually not reported in lists. Both *Octopus vulgaris* and *Sepia officinalis* are regularly present. *Loligo vulgaris* eggs are frequently seen in late winter and early spring in some coralligenous platforms.

According to Poursanidis & Koutsoubas (2015) more than 511 species of molluscs have been recorded so far from coralligenous formations, the majority of which belong to the class Gastropoda (357 species) followed by Bivalvia (137 species), Polyplacophora (14 species), Cephalopoda (2 species) and Scaphopoda (1 species). Carnivores are the dominant functional group, followed by filter feeders (Urra *et al.*, 2012).

• Mites

Mites are always rare in coralligenous communities. Laubier (1966) reports six species from Banyuls.

• Pycnogonids

Up to fifteen species of pycnogonids are reported by Hong (1980) from the coralligenous communities of Marseilles. *Achelia echinata, Rynchothorax mediterraneus, Tanystylum conirostre* and *Callipallene spectrum* seem to be the most common, although they are always rare. Only one species is reported by Laubier (1966) from Banyuls, and two species by Munilla & De Haro (1984) from the Medes Islands.

• Copepods

The fauna of copepods has been carefully studied by Laubier (1966) in one station from the coralligenous communities of Banyuls. He reports up to 54 species. *Ectinostoma dentatum, Harpacticus littoralis, Tisbe furcata, Thalestris rufoviolescens, Phyllothalestris mysis, Dactylopodia tisboides, Diosaccus tenuicornis, Amphiascus minutus, Amphiascus cinctus,* and *Laophonte cornuta* are extremely abundant. There are several copepods that live as parasites of different invertebrates: polychaetes, sponges, echinoderms, molluscs, cnidarians and tunicates (Laubier, 1966 and references therein).

• Ostracods

Although several species of ostracods are present in coralligenous communities (Laubier, 1966; Hong, 1980), no study has been devoted to this group. Laubier (1966) reports more than ten unidentified species in the 'endogean' microfauna.

• Cirripeds

The barnacles *Balanus perforatus* and *Verruca strömia*, in coralligenous walls and crevices, and *Acasta spongites,* an endobiont of several sponges (e.g. *Dysidea, Ircinia*), have been identified in coralligenous communities (Laubier, 1966; Hong, 1980, Carbonell, 1984).

• Phyllocarids

Only one species has been cited by Hong (1980) in the coralligenous communities of Marseilles.

• Mysids

Hong (1980) reports seven mysids from the coralligenous communities of Banyuls and Bakir & Katagan (2005) report four mysids from the coralligenous banks of Markiz Island (Turkey).

• Cumaceans

Three cumaceans are reported from coralligenous communities, and are always rare (Laubier, 1966; Hong, 1980), while Sezgin *et al.* (2009) report twelve species of cumaceans from 17 stations in coralligenous formations and Bakir & Katagan (2005) report ten species from the coralligenous banks of Markiz Island (Turkey).

• Tanaidaceans

Tanais cavolini and *Leptochelia savignyi* are rather common among the 'endogean' microfauna of coralligenous concretions (Laubier, 1966; Hong, 1980). Bakir & Katagan (2005) report two species from the coralligenous banks of Markiz Island (Turkey).

• Amphipods

A noteworthy number of amphipods have been sampled in coralligenous communities. Although Laubier (1966) only reports twelve species from the coralligenous communities of Banyuls, a list of 49 species is given by Hong (1980) in Marseilles, and forty species are reported by Jimeno & Turon (1995) in an extensive survey of the concretions by *Mesophyllum alternans* along the coast of Catalonia (northwestern Mediterranean). Sezgin *et al.* (2009) report 62 species of amphipods from 17 stations and Bakir & Katagan (2005) report 51 species from the coralligenous banks of Markiz Island (Turkey).

Coralligenous assemblages harbour a certain number of amphipods from photophilic algal communities, together with reophobic and sciaphilic species, which are linked to the presence of hydroids, sponges and bryozoans. Bellan-Santini (1998) lists 44 species from the coralligenous community (below 35 m depth), to which another 56 species collected from sciaphilic communities with *Flabellia petiolata* and *Halimeda tuna* have to be added. Therefore, a total number of 100 species is probably a good estimate of the amphipods thriving in coralligenous communities.

According to the available literature, common species include *Maera inaequipes, Maera grossimana, Liljeborgia dellavallei, Leptocheirus bispinosus, Gitana sarsi, Amphilochus picadurus, Colomastix pusilla, Iphimedia serratipes,* and *Stenothoe tergestina*. In coralligenous communities with some erect algae, the following species are also abundant: *Orchomene humilis, Leptocheirus guttatus, Stenothoe dollfusi, Leucothoe venetiarum, Pseudoprotella phasma, Cressa cristata, Cressa mediterranea, Caprella acanthifera, Corophium sextonae, Dexamine thea, Leucothoe euryonyx, Aora spinicornis* and *Elasmopus vachoni*. Few species (*Harpinia ala, Tryphosella simillima, Uncionella lunata*) have been collected solely in coralligenous communities (Bellan-Santini, 1998).

• Isopods

Laubier (1966) and Hong (1980) report fourteen species from coralligenous communities. *Cymodoce truncata, Jaeropsis brevicornis, Paranthura nigropunctata, Synisoma* sp., *Gnathia maxillaris* and *Paragnathia formica* seem to be relatively common species. Bakir & Katagan (2005) report nine isopods from the coralligenous banks of Markiz Island (Turkey).

• Decapods

The density of decapods in coralligenous concretions is very high, the estimate being 170 individuals in 500 g dw of *Mesophyllum alternans* (García-Raso & Fernández Muñoz, 1987). The abundance of species is also noteworthy (Sezgin *et al.*, 2009) and Bakir & Katagan (2005) report up to 45 species. According to García-Raso *et al.* (1996), it is very difficult to distinguish characteristic species of the coralligenous community because the assemblages are very similar to those found in other communities where there is shelter (e.g. the rhizomes of *Posidonia oceanica*).

Alpheus dentipes, Athanas nitescens, Pilumnus hirtellus, Pisidia longicornis, Galathea bolivari, Cestopagurus timidus and *Thoralus cranchii* are considered to be the characteristic decapod crustaceans inhabiting the shallow coralligenous concretions of *Mesophyllum alternans* in the southwestern Mediterranean, along with, in certain areas, *Porcellana plathycheles, Synalpheus hululensis* and *Calcinus tubularis* (Garcia-Raso, 1988). The three species, which account for most of the biomass of the decapod crustaceans in the shallow coralligenous communities of the southwestern Mediterranean, use this environment in a different way. In *Pilumnus hirtellus*, the coralligenous habitat seems to be a recruitment place, where mainly juveniles are recorded. The whole life cycle of *Alpheus dentipes* develops in the coralligenous concretions, while in the case of *Synalpheus hululensis* the coralligenous habitat provides shelter for reproductive individuals (García-Raso & Fernández Muñoz, 1987).

Other species of decapoda frequently reported from coralligenous bottoms are *Alpheus ruber, Alpheus megacheles, Pilumnus spinifer, Pisa tetraodon, Galathea intermedia, Eurynome aspera, Macropodia czerniavskii, Inachus thoracicus, Processa macrophtalma, Periclimenes scriptus, Typton spongicola, Balssia gasti* and *Pisidia longimana* (Laubier, 1966; Hong, 1980; Carbonell, 1984; García-Raso, 1988). Other large decapods that are usually found in coralligenous communities are *Dromia personata, Palinurus elephas* (Figure 52), *Scyllarus arctus*, *Scyllarides latus* and *Homarus gammarus* (Corbera *et al.*, 1993).

In deep waters, the decapod fauna reported by García-Raso (1989) is different from that reported from shallow water coralligenous habitats. This author found a total of thirty species, with *Pilumnus inermis, Galathea nexa* and *Euchirograpsus liguricus* being the most abundant decapods in these kinds of bottoms from the southwestern Mediterranean.

Figure 52. The spiny lobster, *Palinurus elephas,* is often associated to coralligenous outcrops (Photo by E. Ballesteros).

• Brachiopods

Brachiopod species usually inhabit small crevices and interstices within the concretionary masses of the coralligenous assemblages. *Crania anomala, Argyrotheca cistellula, Argyrotheca cordata, Argyrotheca cuneata, Megathiris detruncata* and *Lacazella mediterranea* are the brachiopods most commonly reported from coralligenous communities (Laubier, 1966; Logan, 1979; Hong, 1980). Another two species, *Megerlia truncata* and *Platidia davidsoni*, which are more typical of the bathyal zone, are seldomly collected from coralligenous habitats (Vaissière & Fredj, 1963; Gamulin-Brida, 1967; Logan, 1979).

• Bryozoans

Bryozoans are very abundant in coralligenous communities. Reported species amount to 67 in Banyuls (Laubier, 1966), 133 in Marseilles (Hong, 1980), 113 in the Medes Islands (Zabala, 1984), 92 in Cabrera (Ballesteros *et al.*, 1993) and 60 in Avola, SE Sicily (Rosso & San Filippo, 2009). A tentative estimate of the total number of bryozoans that thrive in coralligenous bottoms according to the abovementioned studies is around 170 species.

According to Zabala (1986) four different aspects regarding the distribution of bryozoans can be distinguished in coralligenous communities. Here we report the main species according to the studies by Laubier (1966), Hong (1980), Zabala (1984, 1986) and Ballesteros *et al.* (1993). The flat surfaces of the coralligenous platform are dominated by *Pentapora fascialis* and *Myriapora truncata*, which have *Nolella* spp., *Aetea* spp., *Crisia* spp., *Scrupocellaria* spp., *Mimosella verticillata* and *Synnotum aegyptiacum* as epibionts. *Turbicellepora avicularis* (Figure 53) is very common overgrowing gorgonians, and *Chorizopora brongniartii, Diplosolen obelium, Tubulipora plumosa, Puellina gattyae* and *Lichenopora radiata* are common epibionts of other organisms. Other common species are *Beania magellanica, Beania hirtissima,*

Figure 53. Bryozoan *Turbicellepora avicularis* frequently grows on gorgonian branches (Photo by E. Ballesteros).

Mollia patellaria, Schizomavella auriculata, Cellepora pumicosa, Plagioecia spp., *Cellaria fistulosa* and *Cellaria salicornioides*. Coralligenous walls have the species reported above but also *Smittina cervicornis* (Figure 54), *Adeonella calvetii, Chartella tenella* (Figure 55), *Cribilaria innominata, Schizomavella* spp., *Parasmittina tropica, Sertella* spp., *Caberea boryi,* and *Spiralaria gregaria*.

Figure 54. Branching bryozoan *Smittina cervicornis* is a common species in northern Mediterranean coralligenous outcrops (Photo by E. Ballesteros).

Figure 55. Soft bryozoan *Chartella tenella* usually hangs on coralligenous walls (Photo by E. Ballesteros).

Cavities and overhangs of coralligenous outcrops reveal bryozoan fauna that is almost identical to that present in semi-dark caves, with several species already reported above, along with *Dentiporella sardonica, Brodiella armata, Turbicellepora coronopus, Rynchozoon bispinosum, Schizotheca serratimargo* (Figure 56), *Escharoides coccinea, Escharina vulgaris, Callopora dumerilii, Smittoidea reticulata, Cribilaria radiata, Hippomenella mucronelliformis, Crassimarginatella maderensis, Crassimarginatella crassimarginata, Buskea nitida, Celleporina* spp., *Prenantia inerma, Diaporoecia* spp., *Enthalophoroecia deflexa* and *Idmidronea atlantica*. A final group is constituted by species that appear mainly in deep-water coralligenous habitats, below 50 m depth, and these are composed by stenotherm species that are also very resistant to sedimentation: *Figularia figularis, Escharina dutertrei, Escharina porosa, Onychocella marioni, Omaloseca ramulosa, Buskea dichotoma, Escharella ventricosa, Enthaloporoecia gracilis, Schizoporella magnifica, Mecynoecia delicatula, Idmidronea coerulea and Hornera frondiculata* (Figure 57). Harmelin (2017a) describes two contrasting assemblages from Port-Cros National Park dominated by bryozoans. The first assemblage covers rocky and biogenic walls and is dominated by large, heavily calcified and massive species such as *Schizomavella mamillata, Parasmittina rouvillei, Schizomavella linearis, Dentiporella sardonica, Beania magellanica, Reteporella grimaldii, Schizomavella cornuta* and *Myriapora truncata*. The second assemblage establishes on leaves of the green alga *Flabellia petiolata* and hosts short-lived and thin colonies such as *Schizomavella halimedae,*

Figure 56. Erect bryozoan *Schizotheca serratimargo* can be extremely common in coralligenous overhangs from the Central Mediterranean Sea (Photo by E. Ballesteros).

Figure 57. Extremely fragile bryozoan *Hornera frondiculata* thrives in deep water coralligenous outcrops (Photo by E. Ballesteros).

Haplopoma impressum, Chorizopora brongnarti, Escharina vulgaris and *Escharoides coccinea.*

• Crinoids

Two crinoids have been reported from coralligenous habitats, the common *Antedon mediterranea* (Laubier, 1966; Ballesteros *et al.*, 1993) and *Antedon bifida* (Montserrat, 1984).

• Ophiuroids

According to the report by Tortonese (1965) and the lists of Laubier (1966), Hong (1980) and Montserrat (1984), up to seventeen species of ophiuroids have been reported from coralligenous communities. There are some species that can be considered as characteristic of these habitats, such as *Ophioconis forbesii, Amphiura mediterranea* and *Amphiura apicula* (Tortonese, 1965; Laubier, 1966). Other brittlestars live entangled to the gorgonians: *Astropartus mediterraneus* (Figure 58) and *Ophiacantha setosa*. The commonest species, however, are *Ophiothrix fragilis, Ophiopsila aranea, Amphiura chiajei, Amphiura filiformis, Amphipholis squamata,* and *Ophioderma longicaudum*. *Ophiocomina nigra*, despite being a typical species of soft bottoms, is usually found in the small cavities containing sediment within coralligenous communities.

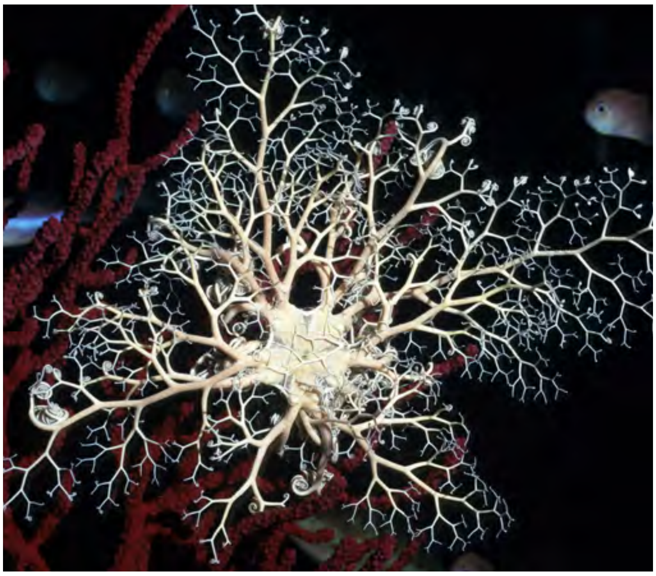

Figure 58. Brittlestar *Astropartus mediterraneus* lives entangled to gorgonians in deep waters (Photo by E. Ballesteros).

• Asteroids

Up to eight species of sea stars have been reported from coralligenous bottoms (Tortonese, 1965; Laubier, 1966, Munar, 1993). The most abundant species is the ubiquitous *Echinaster sepositus* (Figure 59). *Marthasterias glacialis* and *Hacelia attenuata* are also common, while *Ophidiaster ophidianus* is only found in the southern, warmer, areas of the Mediterranean.

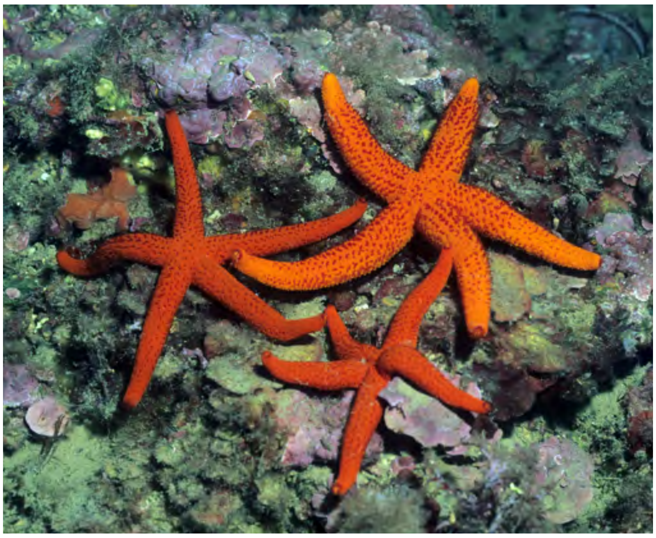

Figure 59. Seastar *Echinaster sepositus* is a common species in coralligenous assemblages (Photo by E. Ballesteros).

• Echinoids

Fourteen species of sea urchins are reported from coralligenous communities (Tortonese, 1965; Laubier, 1966; Hong, 1980; Montserrat, 1984; Munar, 1993). The most common species is *Sphaerechinus granularis* (Sartoretto, 1966), which is an important bioeroder. Also common in deep waters are *Genocidaris maculata* and *Echinus melo*. *Psammechinus microtuberculatus* is usually hidden inside the cavities of coralligenous outcrops. Juveniles of *Paracentrotus lividus* (and *Arbacia lixula*) are sometimes found but are never abundant. *Centrostephanus longispinus* (Figure 60) is more abundant in the warmer areas of the Mediterranean and usually lives within coralligenous crevices (Pérès & Picard, 1958; Laborel, 1960; Harmelin *et al.*, 1980; Francour, 1991). Finally, *Echinocyamus pusillus* is a ubiquitous and very small species that inhabits the small patches of sand and gravel inside the concretions.

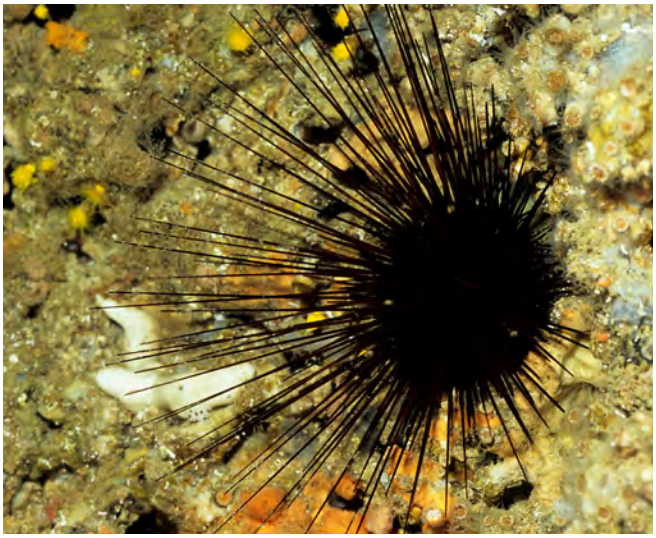

Figure 60. Needle spined sea urchin, *Centrostephanus longispinus*, lives in the crevices and small holes of deep water coralligenous outcrops (Photo by E. Ballesteros).

• Holothurioids

The most commonly observed species of sea cucumber is *Holothuria forskali* (Figure 61), which can be rather abundant in some coralligenous platforms (Laubier, 1966; Ballesteros & Tomas, 1999). However, the genus *Cucumaria* has several species that live endolithically (*C. saxicola, C. planci, C. kirschbergii, C. petiti*). Another four species typical of sandy and muddy habitats are also reported (Tortonese, 1965; Laubier, 1966; Montserrat, 1984): *Holothuria tubulosa, Holothuria mammata, Trachytyone tergestina* and *Stichopus regalis.*

Figure 61. Sea cucumber *Holothuria forskali* can be rather abundant in coralligenous banks (Photo by E. Ballesteros).

• Tunicates

Ramos (1991) describes a high species richness of ascidians in coralligenous communities, the families Didemnidae and Polyclinidae being especially present. In fact, around 70% of ascidian fauna is present in the coralligenous community (82 species). According to Ramos (1991), the most characteristic species of the coralligenous community are *Cystodites dellechiajei, Ciona edwardsii* and *Halocynthia papillosa*, although other abundant species include *Diplosoma spongiforme, Distaplia rosea, Trididemnum cereum, Trididemnum armatum* and *Polycarpa gracilis*. Other species that are often collected from coralligenous communities are *Distomus variolosus, Didemnum maculosum, Ecteinascidia herdmanni, Clavelina nana, Polysyncraton lacazei, Polysyncraton bilobatum, Polycarpa pomaria, Pyura* spp., *Microcosmus polymorphus, Microcosmus sabatieri, Styela partita, Eudistoma planum, Eudistoma banyulensis, Pseudodistoma cyrnusense, Aplidium densum,* and *Aplidium conicum* (Laubier, 1966; Hong, 1980; Turon, 1990; Turon, 1993). *Clavelina dellavallei* and *Rhodosoma verecundum* seem to be especially abundant in the coralligenous concretions from the Eastern Mediterranean (Pérès & Picard, 1958) (Figures 62-63).

Figure 62. Colonial tunicate *Pseudodistoma cyrnusense* is very common in Central Mediterranean coralligenous outcrops (Photo by E. Ballesteros).

Figure 63. Solitary tunicate *Clavelina dellavallei* is an epiphytic species, common in the Eastern Mediterranean (Photo by E. Ballesteros).

• Fish

The fish fauna from the coralligenous community includes a lot of fish covering a wide bathymetric range, such as *Epinephelus marginatus, Sciaena umbra, Coris julis, Dentex dentex, Symphodus mediterraneus, Symphodus tinca, Diplodus vulgaris, Apogon imberbis, Chromis chromis* or *Labrus merula*. However, there is a group of species that are characteristic of coralligenous communities. Some of these, like *Lappanella fasciata* or *Acantholabrus palloni*, are species restricted to deep waters (Sartoretto *et al.*, 1997), but others, such as *Anthias anthias* (Harmelin, 1990) (Figure 64), as well as (among the commonest species) *Gobius vittatus, Phycis phycis* and *Labrus mixtus* (Figure 65) (Garcia-Rubies, 1993, 1997), are easily observed during recreational diving. Other species are more abundant in coralligenous outcrops than in shallow waters, examples being *Serranus cabrilla, Spondyliosoma cantharus, Diplodus puntazzo, Ctenolabrus rupestris, Spicara smaris, Scorpaena scrofa* and *Symphodus doderleini*. Finally, *Conger conger, Muraena helena, Zeus faber, Scorpaena notata, Scyliorhinus canicula* and *Scyliorhinus stellaris* are also observed in the coralligenous habitat (Sartoretto *et al.*, 1997; Ballesteros, personal observation).

Figure 64. Swallowtail seaperch (*Anthias anthias*) make huge schools swimming over coralligenous bottoms (Photo by E. Ballesteros).

Figure 65. Cuckoo wrasse (*Labrus mixtus*) is usually observed when diving in coralligenous outcrops (Photo by E. Ballesteros).

The fish fauna inhabiting the small crevices of coralligenous concretions is probably related to cave dwelling fish, although data are very scarce. Hong (1980) reports juveniles of *Diplecogaster maculata* and *Gobius niger*. According to Patzner (1999), cryptobenthic species, such as *Thorogobius ephippiatus, Thorogobius macrolepis* (Figure 66), *Corcyrogobius liechtensteinii, Gammogobius steinitzii* and *Didogobius splechtnai*, which are usually observed in caves, may also be present in the small holes of deep-water coralligenous habitats. Another cave dwelling Gobiidae, *Speleogobius trigloides*, has been observed in deep coralligenous concretions from the Columbretes Islands (Spain) (Kersting & Ballesteros, pers. obs.).

Figure 66. *Thorogobius macrolepis* is a cryptobenthic fish that lives at the boundary between coralligenous and detritic bottoms and hides in tiny coralligenous holes (Photo by E. Ballesteros).

Gobius kolombatovici (Figure 67) lives in coralligenous environments, preferring the limits between the outcrops and the adjacent sedimentary bottoms (Kovacic & Miller, 2000; Francour & Mangialajo, 2005; Kersting & Ballesteros, pers. obs.). *Odondebuenia balearica* is another cryptobenthic fish that inhabits coralligenous communities, but which is rarely observed (Riera *et al.*, 1993).

Figure 67. Similar in habit and habitat to *Thorogobius macrolepis, Gobius kolombatovici* was described in year 2000 from Adriatic Sea coralligenous bottoms (Photo by E. Ballesteros).

Studies concerning the fish fauna of the coralligenous habitat have obtained slightly different results when performed in different areas (Bell, 1983; Harmelin, 1990; Garcia-Rubies, 1993, 1997; Ballesteros & Tomas, 1999). These differences should be related to biogeography or to differences in coralligenous rugosity. *Symphodus melanocercus*, for example, is a characteristic coralligenous species in Cabrera and other localities of the Balearic Islands, but it is a widespread species in terms of depth distribution in the northwestern Mediterranean (García-Rubies, 1993).

The fish diversity of coralligenous outcrops is affected by fishing. Areas protected from fishing host dense populations of large-sized target fish such as *Epinephelus marginatus, Sciaena umbra* or *Diplodus* spp., which are otherwise almost absent in open areas (Guidetti *et al.*, 2007).

The alpha-diversity of the fish populations from coralligenous bottoms in Port-Cros National Park is similar to the alpha-diversity of other shallow and rocky reefs or shallow seagrass meadows, but much higher than deep *Posidonia oceanica* meadows (Astruch *et al.*, 2018). Coralligenous habitats hold the largest number of individuals and biomass -mainly due to the high abundance of planktivorous fish- compared to other reefs and seagrass meadows (Astruch *et al.*, 2018). Piscivorous fish are also abundant in coralligenous environments.

Cardinali *et al.* (2009) provide a list of fish species observed in ROV transects over coralligenous banks in Calabria (Italy), between 30- and 150-meters depth; *Anthias anthias, Serranus cabrilla, Callanthias ruber* and *Lappanella fasciata* were some of the commonest species in a list of thirty-four.

Significant temporal variability at a diurnal scale has been detected for abundances of *Coris julis* in some areas, but no variability has been observed in *Diplodus vulgaris*, suggesting a species- and site-specific variability of fish abundances in shallow coralligenous outcrops (Witkowski *et al.*, 2016). However crepuscular periods are associated with sudden changes of abundances and behaviour (Witkowski *et al.*, 2016).

5.2. Endangered species

Although it is very difficult to determine the conservation status of any marine species living in the relatively deep waters where coralligenous communities develop, several approaches to endangered species have been taken.

According to Boudouresque *et al.* (1990), at least eight species of macroalgae that live in coralligenous communities can be considered as endangered: *Chondrymenia lobata, Halarachnion ligulatum, Halymenia trigona, Platoma cyclocolpa, Nemastoma dichotomum, Ptilophora dentata* (Figure 68), *Schizymenia dubyi, and Laminaria rodriguezii*. However, and according to our own observations, this list can be greatly extended by adding species such as *Aeodes marginata, Sphaerococcus rhizophylloides, Schmitzia neapolitana, Ptilocladiopsis horrida, Microcladia glandulosa, Rodriguezella bornetii, Rodriguezella pinnata* and *Lomentaria subdichotoma* (Ballesteros, unpublished data). Most of these species have coralligenous or maërl beds as their only habitats and seem to be very sensitive to pollution and increased sedimentation rates (Boudouresque *et al.*, 1990), two of the main threats to coralligenous assemblages. The case of *Laminaria rodriguezii* is especially relevant, as this species develops best in rhodolith beds, from where it has almost disappeared due to trawling activities; coralligenous bottoms now constitute its only refuge (Figure 69).

Figure 68. *Ptilophora dentata* is an Eastern Mediterranean endemism only collected so far from coralligenous environments (Photo by E. Ballesteros).

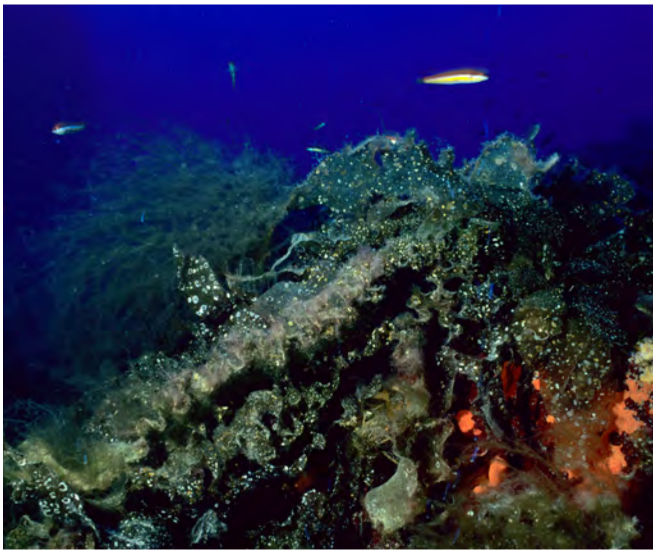

Figure 69. Some of the last refuges for kelp *Laminaria rodriguezii* are coralligenous outcrops (Photo by E. Ballesteros).

Several animals of coralligenous habitats are also considered to be at risk (Boudouresque *et al.*, 1991). Although none of them are in danger of extinction, local depletion of some species stocks may occur. Most of the endangered species have a great commercial value and this is the main reason for their increased rarity.

Among the anthozoans, red coral (*Corallium rubrum*) is exploited commercially in almost all Mediterranean countries, and its stocks have strongly declined in most areas, particularly in shallow waters (Weinberg, 1991). Gorgonians such as *Paramuricea clavata, Eunicella cavolinii* and *Eunicella singularis*, common in coralligenous communities but without commercial value, are pulled out inadvertently by recreational divers (Coma *et al.*, 2004; Linares *et al.*, 2007b). The black coral, *Savalia savaglia*, is a very rare species and can be a target for collection by divers, thus making the species even scarcer (Boudouresque *et al.*, 1991).

Some species of molluscs living in coralligenous communities are also threatened and protected by international conventions (Poursanidis & Koutsoubas, 2015). The edible rock-borer bivalve *Lithophaga lithophaga* is considered an endangered species (Boudouresque *et al.*, 1991) despite being extremely abundant. Harvesting by divers is only important in shallow waters and the reason behind calls for the species to be protected is actually an attempt to protect the shallow benthic communities in rocky shores dominated by macroalgae (Russo & Cicogna, 1991; Hrs-Brenko *et al.*, 1991), not the coralligenous bottoms themselves. Protection of the two species of fan mussels (*Pinna nobilis* and *Pinna rudis*) present in the Mediterranean has also been proposed (Boudouresque *et al.* 1991), as they have been decimated in northern Mediterranean areas by coastline modification, harvesting as souvenirs, anchoring, diving, sewage effluents and fishing activities (Vicente & Moreteau, 1991; Deudero *et al.*, 2015). *Pinna nobilis* mainly grows in seagrass meadows, and its presence in coralligenous communities is very unusual (Vicente & Moreteau, 1991). However, *Pinna rudis* (= *P. pernula*) is frequently seen in coralligenous habitats (Figure 70), at least in the warmer areas of the western Mediterranean (Ballesteros, 1998).

Figure 70. Rough fan mussel, *Pinna rudis*, is rather common in coralligenous outcrops from the central and southwestern Mediterranean (Photo by E. Ballesteros).

According to Templado (1991), neither of the two species of the genus *Charonia* that occur in the Mediterranean is threatened by extinction. *Charonia lampas* (Figure 71) is rare in the northern Mediterranean but rather common in the southwest, whilst *Charonia tritonis* variegata has been recorded in the eastern and southwestern Mediterranean. Both species are collected and used for decorative purposes, but Templado (1991) argues that indirect anthropogenic pressures (coastline development) are the main reason for its increased rarity, or even local extinction.

Figure 71. Trumpet shell, *Charonia lampas*, is an endangered gastropod once common on coralligenous bottoms (Photo by E. Ballesteros).

The sea urchin *Centrostephanus longispinus* is also considered an endangered species by Boudouresque *et al.* (1991), despite being a rare species in the northwestern Mediterranean, probably due to biogeographical reasons. No anthropic pressure has been proposed to explain its rarity.

The slipper lobster, *Scyllarides latus* (Figure 72), is highly appreciated gastronomically. The high market prices it obtains have stimulated increased fishing pressure, which has led to a dramatic decline in the abundance of this species in several areas of the Mediterranean (Spanier, 1991). It is more common

Figure 72. Slipper lobster *Scyllarides latus* hides in coralligenous outcrops and shallow caves (Photo by E. Ballesteros).

in the warmer Mediterranean areas (e.g. eastern Mediterranean, Balearic Islands), and less common in the colder ones.

The dusky grouper, *Epinephelus marginatus* (= *E. guaza*), is the main target species in spearfishing activities and its abundance has greatly decreased in several Mediterranean areas, mainly in the north (Chauvet, 1991). However, immature specimens and juveniles are very abundant in certain areas (e.g. Balearic Islands; Riera *et al.*, 1998) and, therefore, the species is only threatened in those places where there is no regular recruitment (e.g. northwestern Mediterranean). Moreover, the recovery of this species in marine protected areas has repeatedly been reported (Bell, 1983; Garcia-Rubies & Zabala, 1990; Francour, 1994; Coll *et al.*, 1999), as has reproduction (Zabala *et al.* 1997a, b), suggesting that adequate management can rapidly improve its situation in those areas where stocks continue to decline (Figure 73). Other groupers, such as *Epinephelus costae* (= *E. alexandrinus*), *Mycteroperca rubra* and *Polyprion americanus* (Riera *et al.*, 1998; Mayol *et al.*, 2000), are probably in a worse situation, as their population stocks are much lower than those of the dusky grouper.

Figure 73. Dusky groupers, *Epinephelus marginatus*, are common sights when diving in coralligenous outcrops from no-take protected areas (Photo by E. Ballesteros).

Sciaena umbra and *Umbrina cirrosa* are the two other fish considered as endangered in the review by Boudouresque *et al.* (1991). Both can live in coralligenous communities, the former being more abundant. Although both species are easily spearfished, *Sciaena umbra* stocks readily recover after fishing prohibition (Garcia-Rubies & Zabala, 1990; Francour, 1994).

Other species are not included in the list of Mediterranean endangered species by Boudouresque *et al.* (1991), although according to Mayol *et al.* (2000) they are exposed to major risk. This is the case of several small sharks inhabiting detritic and coralligenous habitats: *Scyliorhinus stellaris, Mustelus asterias, Mustelus mustelus, Squalus acanthias* and *Squalus blainvillei.* All these species were very common in fish catches by Balearic Island fishermen at the beginning of the twentieth century but are now extremely rare. Other species that can thrive in coralligenous communities and which are considered by Mayol *et al.* (2000) to be endangered are seahorses (mainly *Hippocampus ramulosus*, Figure 74), *Gaidropsarus vulgaris* and some cryptobenthic fish (*Didogobius splechtnai, Gammogobius steinitzii*). These are not commercial species and their increased rarity may be related to indirect effects of fishing (such as cascading effects), physical disturbances of trawling, or other unknown causes.

Figure 74. Long-snouted seahorse, *Hippocampus ramulosus*, is a very rare sight in coralligenous environments due to its widespread regression in the Mediterranean Sea (Photo by E. Ballesteros).

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6. Biotic relationships

6.1. Spatial interactions, herbivory, carnivory

Biotic relationships, both trophic ones and those related to spatial interactions, are a major force in structuring all ecosystems. In fact, the whole build-up of coralligenous concretions is affected by the interactions between encrusting corallines and other sessile, invertebrate builders (Figures 75, 76).

Figure 75. A thallus of *Lithophyllum* that overgrows red coral branches is in its turn overgrown by the colonial tunicate *Aplidium elegans* (Photo by E. Ballesteros).

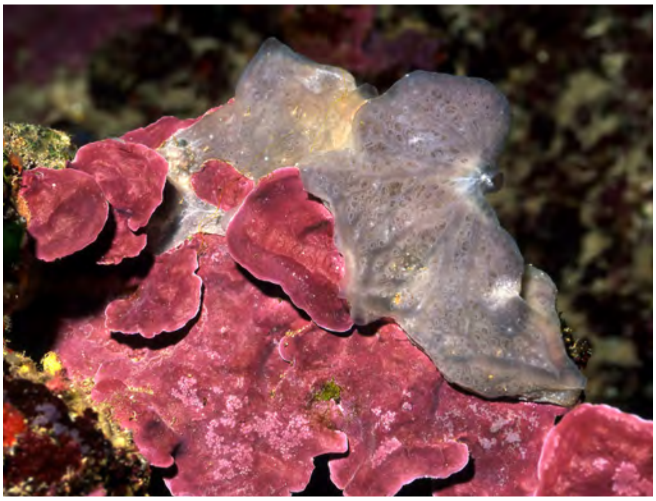

Figure 76. Encrusting sponge *Phorbas tenacior* overgrows encrusting coralline *Lithophyllum stictaeforme* (Photo by E. Ballesteros).

For example, the encrusting bryozoan *Schizomavella cornuta* is able to overgrow most invertebrates but is competitively inferior to the red alga *Lithophyllum stictaeforme* (Cocito & Lombardi, 2007). Interactions between sessile invertebrates are also the rule (Figures 77, 78). For instance, *Leptopsammia pruvoti* and *Corallium rubrum* tend to segregate one from the other at small distances suggesting that the spacing of *L. pruvoti* could be determined by the aggressive behaviour of *Corallium rubrum* (Giannini *et al.*, 2003). The final result (that is, what the concretion looks like) is not only related to which builder has been the most effective but also to how the borers (from sea urchins to excavating sponges and polychaetes) have modelled the build-up. Biotic relationships at this level are, therefore, crucial in building coralligenous assemblages.

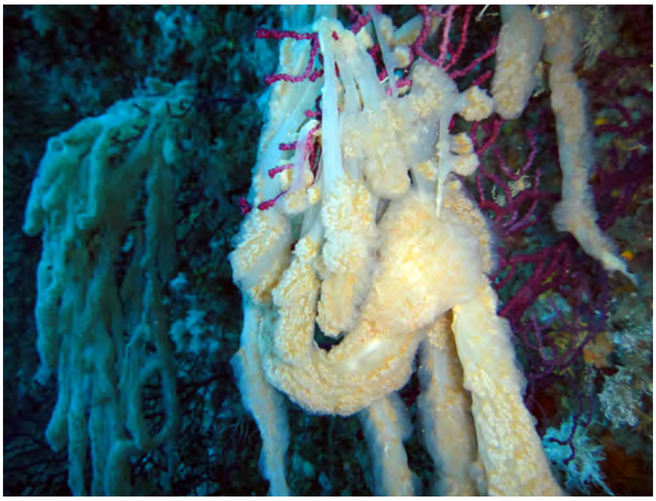

Figure 77. Huge *Aplidium proliferum* colonies overgrow gorgonians *Paramuricea clavata* at Jbel Moussa (Morocco) (Photo by E. Ballesteros).

Figure 78. Sponge *Hexadella topsenti* overgrows a bryozoan colony of *Hornera frondiculata* (Photo by E. Ballesteros).

Trophic relationships are especially interesting in coralligenous communities, as the main organisms are not easily edible. Most of them have skeletons that contribute to build-up, but which also deter feeding (Zabala & Ballesteros, 1989). Others may have chemical defences that make them unpalatable or even toxic (Martí, 2002). Most of the largest sessile invertebrates living in coralligenous communities do not feed directly upon other animals from the coralligenous assemblage but rather on the pelagic system; in fact, the largest part of the living biomass in coralligenous assemblages belongs to algae and suspension feeders (True, 1970; Zabala & Ballesteros, 1989), which suggests that herbivory and carnivory are not as important as in other marine Mediterranean environments. The low dynamism of coralligenous habitats (Garrabou *et al.*, 2002) also points in this direction.

However, both herbivory and carnivory are relevant to coralligenous communities. The sea urchin *Sphaerechinus granularis* is a major browser of encrusting corallines (Sartoretto & Francour, 1997), and several invertebrates (opisthobranchs, amphipods, copepods) are able to feed on the green alga *Halimeda* (Ros, 1978). Examples of carnivores include most of the fish that thrive in coralligenous communities, as well as most prosobranchs, echinoderms, vagile polychaetes and crustaceans. Although feeding by most animals is not selective, there are some noteworthy examples of animals that have a strong prey selection. These include the well-known cases of the opisthobranch *Peltodoris atromaculata*, which feeds on the sponge *Petrosia ficiformis* (Figure 79), and the other opisthobranchs such as *Flabellina affinis* and *Cratena peregrina* which feed mainly on hydrozoans of the genus *Eudendrium* (Figure 80) (Ros, 1978). Other interesting examples have recently been reported for copepods of the genus *Asterocheres*, which systematically feed on both rhagons and adult sponges by sucking the material produced at the ectosome of the sponge (Mariani & Uriz, 2001).

Figure 79. Dotted sea slug *Peltodoris atromaculata* feeds exclusively on sponge *Petrosia ficiformis* (Photo by E. Ballesteros).

Figure 80. Opisthobranch *Cratena peregrina* feeds on hydrozoans of the genus *Eudendrium* (Photo by E. Ballesteros).

6.2. Chemical ecology

The production of active substances in benthic organisms plays a major role in structuring benthic communities. Some of these substances act as a defence against consumers (e.g. unpalatable or repellent substances) while others mediate the interactions between species regarding the occupation of space (Martí, 2002). Sponges, bryozoans and tunicates are the taxa with the largest number of species having active substances (Uriz *et al.*, 1991). The lower side of coralligenous blocks, as well as semi-dark caves and overhangs, exhibits the highest percentage of active species of all the Mediterranean communities sampled by Uriz *et al.* (1991), suggesting that investment in production of allelochemicals plays an important role in space competition in coralligenous assemblages (Figure 81).

Figure 81. Coral *Leptopsammia pruvoti* inhibits growth of sponge *Clathrina clathrus* whether by trophic depletion of the surrounding waters, or by means of allelochemicals (Photo by E. Ballesteros).

6.3. Epibiosis, mutualism, commensalism, parasitism

There are innumerable relationships between species in coralligenous communities that can be described as ‘associations’, and these may or may not involve trophic transfer. Sometimes it is difficult to differentiate between them as the natural history of the species, or the benefits and costs of the components of the association, are unknown or not clearly understood. Our purpose here is not to review these associations, nor to mention all those which have been described for coralligenous communities, but to report some examples of epibiosis, mutualism, commensalism and parasitism that can give an idea of the complexity of the coralligenous community with respect to these kinds of relationships.

Epibiosis is a widespread phenomenon in benthic communities and coralligenous assemblages are an excellent example of the different strategies adopted by organisms to cope with this problem (True, 1970). Some basibionts tolerate different degrees of epibiosis and even almost complete overgrowth, whilst others have developed antifouling defences to avoid overgrowth. Both types of strategies can be displayed by species from the same zoological group living in coralligenous communities. For example, the ascidians *Microcosmus sabatieri* (Figure 82) and *Pyura dura* are usually completely covered by a wide array of epibionts, whilst *Halocynthia papillosa* and *Ciona edwardsi* are always free of overgrowing organisms (Ramos, 1991).

Figure 82. Tunicate ***Microcosmus sabatieri*** goes almost unnoticed, being overgrown by a wide array of organisms (Photo by E. Ballesteros).

Some epibionts are considered to select their hosts, whilst others are not selective. The anthozoan *Alcyonium coralloides* usually grows over the axes of gorgonians *(Eunicella, Paramuricea clavata)* (Figure 83), although it can also grow over other animals and seaweeds, or be attached to rubble or any other kind of substrate (Laubier, 1966; Gili, 1986). The anthozoan *Parazoanthus axinellae* prefers sponges of the genus *Axinella* (mainly *Axinella damicornis*) (Figure 84), but it can also grow over other sponges or over rock or encrusting corallines (Gili, 1986). The bryozoan *Turbicellepora avicularis* prefers the basal parts of the axes of gorgonians *Paramuricea clavata* and *Eunicella* spp. (Laubier, 1966; Zabala, 1986).

Figure 83. Anthozoan *Alcyonium coralloides* usually grows over the dead axes of gorgonians (Photo by E. Ballesteros).

The number of species able to act as non-selective epibionts in coralligenous communities is huge, as most of the space is occupied and larvae usually have to settle over living animals or plants. Therefore, almost all sessile species can be epibionts (True, 1970) (Figure 85). Gautier (1962), for example, reviewed the epibiosis of bryozoans over bryozoans in coralligenous assemblages, and Nikolic (1960) reported up to eighteen species growing over *Hippodiplosia foliacea* in a coralligenous concretion in the Adriatic Sea. Of particularly interest are the observations by Laubier (1966) on some Heterotrichs (Protozoans) of the family Folliculinidae that live close to the zooid mouth of different species of bryozoans or even inside its empty zooids. Laubier (1966) reported up to six different species of Folliculinidae in the coralligenous communities of Banyuls living as epibionts of bryozoans.

Figure 84. Zoantharian *Parazoanthus axinellae* is usually a selective epibiont of sponge *Axinella damicornis* (Photo by E. Ballesteros).

Figure 85. Bivalve ***Pteria hirundo*** is a facultative epibiont of gorgonians and it is usually heavily epiphytized by other organisms (here by tube worms, encrusting sponge and ***Pycnoclavella*** sp.) (Photo by E. Ballesteros).

Damaged colonies of *Paramuricea clavata* following mass mortalitiy events are a suitable substrate for the colonization of epibionts (Harmelin & Marinopoulos, 1994). Three years after a mortality event in La Spezia (Italy), Cupido *et al.* (2007) recorded 24 taxa belonging to bryozoans, 8 sponges, 3 cnidarians, 4 algae, 1 tunicate and 1 serpulid. Most abundant bryozoans were *Beania magellanica, Schizobrachiella sanguinea, Rynchozoon* sp., *Schizomavella* spp., *Turbicellepora incrassata, Chartella* spp., *Margaretta cereoides, Reteporella grimaldii, Pentapora fascialis, Smittina cervicornis* and *Cellaria salicornioides* (Cupido *et al.*, 2007).

Mutualism has been reported, for example, in the case of the scyphozoan *Nausitoë punctata* and several horny sponges (Uriz *et al.*, 1992b). *Cacospongia scalaris, Dysidea avara* and *Dysidea fragilis* utilize the thecae of *Nausitoë punctata* as a substitute for skeletal fibres, presumably reducing metabolic costs associated with skeleton building. The scyphozoan should thus benefit from greater protection against predation and mechanical disturbance, trophic advantages (inhalant flow carries out small particles susceptible to capture by the scyphozoan), and chemical defence against predators, as the three species of sponges exhibit toxicity (Uriz *et al.*, 1992c).

Commensalism is one of the most common relationships in coralligenous communities. Most relationships are considered as commensalism as they lack unequivocal parasitic features. This could be the case of the polychaete *Eunice siciliensis* and the decapods *Alpheus dentipes* and *Typton spongicola*, which live as endobionts of the boring sponge *Cliona viridis* (Laubier, 1966). Another well-known example is that occurring between Cliona viridis and the likewise boring polychaete *Dipolydora rogeri* (Martin, 1996). The curious feature of this association is that it persists even when the sponge is massive and non-excavating. The feeding activity of the polychaete is favoured by the inhalant flow of the sponge and, moreover, the sponge offers physical protection to the worm when they are not embedded within the calcareous algae. The ability of the worm to manipulate relatively large particles (either to feed or to build its tubes) may favour the filtering activity of the sponge by cleaning the area around the inhalant papillae, thus preventing the collapse of their orifices (Martin & Britayev, 1998).

Polychaetes of the genus *Haplosyllis* are well-known commensalists (Martin & Britayev, 1998). Up to 200 specimens of *Haplosyllis spongicola* have been found in one cm^2 of sponge (Bacescu, 1971), and thus sponges merit the description of 'living hotels'. Another case is the polychaete *Haplosyllis depressa chamaeleon*, which lives exclusively as a commensal of the sea fan *Paramuricea clavata*, where it crawls above the living colonies (Laubier, 1960, 1966).

The barnacle *Acasta spongites* lives inside the sponge *Ircinia variabilis*, as well as other sponges (Laubier, 1966; Rützler, 1976; Uriz *et al.*, 1992b); it can be considered a case of parasitism as the cirriped settles into the inhalant oscula of the sponge, rendering it useless. Another barnacle, *Pyrgoma anglicum*, is quite often found living inside the anthozoan *Leptopsammia pruvoti* (Figure 86). Another example of parasitism in coralligenous communities is offered by the two boring spionid polychaetes *Dipolydora armata* and *Polydora hoplura* and the bryozoans *Dentiporella sardonica*, *Porella concinna, Brodiella armata* and *Schizomavella auriculata* (Laubier, 1959a, 1959b). The bryozoans are infested throughout their basal layer and polychaetes excavate galleries that reach the surface of the colony or modify the growth form of the bryozoan in such a way that the polychaete tubes are composed of host zooids. In both cases the bryozoan is stimulated to build calcareous formations around the end of the polychaete tubes, facilitating the feeding behaviour of the worm and protecting it (Laubier, 1966).

Figure 86. Barnacle *Pyrgoma anglicum* living inside the anthozoan *Leptopsammia pruvoti* can be considered a case of parasitism (Photo by E. Ballesteros).

6.4. Bacterial symbionts

Resident bacteria have a beneficial role in sponges (Bjork *et al.*, 2013) and gorgonian corals (La Rivière *et al.*, 2015). Microbial associates are hypothesized to contribute to the health and nutrition of their hosts in different ways by producing allelochemicals, acquiring nutrients or processing metabolic waste (Siegl *et al.*, 2008) and can be useful to survive in environmentally changing conditions (Ribes *et al.*, 2016). The so-called bacteriosponges contain dense and host-specific microbial populations that exceed by two to four orders of magnitude the microbial density of the surrounding water (Weisz *et al.*, 2008). Sponges harbouring high and low bacterial biomass in their tissues coexist in the coralligenous environment, allowing the sponge assemblage to utilize the suspended particulate and dissolved organic matter more efficiently than a single species population. This coexistence may at least partially explain the diversity and stability of dense and diverse sponge assemblages in the coralligenous and other habitats (Morganti *et al.*, 2017). While some species are host to rich microbiomes such as *Agelas oroides* and *Chondrosia reniformis* (Figure 87), others like *Dysidea avara* lack them (Ribes *et al.*, 2012). Sponges with similar eco-evolutionary features have similar bacterial phylogenetic communities; some of them show remarkably persistent bacterial communities over time while others show a large turn-over rate, similar to that observed in the bacterioplankton (Bjork *et al.*, 2013).


Figure 87. Sponge *Chondrosia reniformis* hosts a rich microbiome (Photo by E. Ballesteros).

Common octocorals in the coralligenous outcrops like *Eunicella* spp. and *Corallium rubrum* hold ancient and highly conserved associated microbiomes, whose composition seems to be regulated by the host depending on location and season (La Riviere *et al.*, 2015; van de Water *et al.*, 2018).
Bacteria of the genus *Endozoicomonas* dominate the microbiome of *Eunicella cavolini* (Bayer *et al.*, 2013).

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7. Processes

7.1. Growth and age of coralligenous concretions

The mean growth rate of pillars of *Mesophyllum alternans* (reported as *Mesophyllum lichenoides*) in La Ciotat (NW Mediterranean) has been estimated by radiocarbon dating to be 0.19 mm year^{-1} (Sartoretto, 1994), with a range of 0.11 to 0.26 mm year^{-1}. Coralligenous pillars from the Ionian Sea showed growth rates of 0.15 mm year^{-1} (Bertolino *et al.*, 2017b) and 0.27 mm year^{-1} (Di Geronimo *et al.*, 2002). Similar values of 0.16 mm year^{-1} over the last 640 years were obtained in a coralligenous block sampled at 15 m in the Natural Reserve of Scandola (Corsica) (Sartoretto *et al.*, 1996).

Ages obtained by radiocarbon dating of coralligenous concretions situated at depths between 10 and 60 m in the northwestern Mediterranean range from 640 ± 120 years BP to 7760 ± 80 years BP (Sartoretto *et al.*, 1996; Bertolino *et al.*, 2017a). They probably began to grow when the sea level was from 13 to 17 m lower than present (Sivan *et al.*, 2001). Internal erosion surfaces within the build-ups provide evidence of discontinuous development, probably related to favourable periods for carbonate deposition alternating with phases of partial destruction (Bertolino *et al.*, 2017a). The accumulation rate of the coralligenous constructions is very low (0.006 to 0.83 mm year^{-1}) and oscillates greatly according to depth and time period. The highest accumulation rates (0.20 to 0.83 mm year^{-1}) have been recorded for deep coralligenous concretions and correspond to a period between 8000 and 5000 years BP. After 5000 years BP, the only appreciable accumulation rates (0.11 to 0.42 mm year^{-1}) have been recorded for coralligenous concretions situated in relatively shallow waters (10 to 35 m depth), whereas the accumulation rates of concretions below a depth of 50 m is almost nil. Radiocarbon dating in bioherms from several localities in the Ligurian Sea indicate average growth rates ranging from 0.03 to 0.05 mm year^{-1} over 3000 years (Bertolino *et al.*, 2013). Thus, the development of these deep coralligenous formations occurred long time ago, when the depth of the overlying layer of water probably did not exceed 10-15 m, and since their period of settlement (8500 to 7000 years BP) the accumulation rate has progressively declined. This decrease in accumulation rates can no doubt be explained by the stable—but rather unfavourable—environmental conditions resulting from the decrease in irradiance related to increased water depth. It is also worth noting that the coralligenous concretions below a depth of 30 m in the Marseilles area are today inactive and almost devoid of living coralline algae. In contrast, those present in Corsica at a depth of 50 m and below (down to 65 m) are completely covered by living corallines and are in an active period of growth; this must be related to the clear waters present in Corsica (Figure 88).

Figure 88. Growth of coralligenous outcrops is still very active in Corsica (Palazzu, -50 m) (Photo by E. Ballesteros).

7.2. Carbonate production

Although there are no specific studies on the carbonate production of the coralligenous community on a yearly basis, Canals & Ballesteros (1997) estimated the carbonate production of the phytobenthos in the coralligenous and other communities from the continental shelf of the Balearic Islands, taking into account the standing crop of calcareous algae and their P/B ratios. The coralligenous community thriving in relatively shallow waters (with *Mesophyllum alternans* and *Halimeda tuna* as dominant algae) was the one with the highest production (around 465 g $CaCO_3$ m^{-2} year^{-1}). Production of deep-water coralligenous concretions dominated by *Lithophyllum cabiochae* was much lower (around 170 g $CaCO_3$ m^{-2} year^{-1}), but even this rate is much higher than average carbonate production for the Balearic shelf as a whole (100 g $CaCO_3$ m^{-2} year^{-1}). Net and gross organic carbon production of *Lithophyllum cabiochae* have been estimated at 3 and 7 µmol C cm^{-2} thallus d^{-1}, respectively, while net inorganic carbon production amounted to 3 µmol $CaCO_3$ cm^{-2} thallus d^{-1} (Martin *et al.*, 2013). Even if we still lack data from other species and areas, coralligenous habitats seem to be major carbonate producers in the Mediterranean Sea given their spread in the continental shelf (García *et al.*, 2014) (Figure 89).

Figure 89. Coralligenous habitats are major carbonate producers (Photo by E. Ballesteros).

The contribution of suspension feeders to the total carbonate production of coralligenous communities in the Balearic shelf—as well as in other Mediterranean areas—is practically unknown. However, estimates of the animal carbonate production in deep water (25-50 m depth) rocky bottoms from the Alboran Sea (southwestern Mediterranean), mainly dominated by big suspension feeders with calcareous skeletons (predominantly the coral *Dendrophyllia ramea*, the bryozoans *Pentapora fascialis, Smittina cervicornis* and *Myriapora truncata*, and polychaetes such as *Salmacina dysteri, Protula* sp. and other serpulids), are very high (around 660 g $CaCO_3$ m^{-2} $year^{-1}$) (Cebrian *et al.*, 2000) (Figure 90). Although the combination of highly productive calcareous animals in these bottoms is unusual in other Mediterranean areas, this figure can be considered as a top limit for animal carbonate production in the coralligenous habitat.

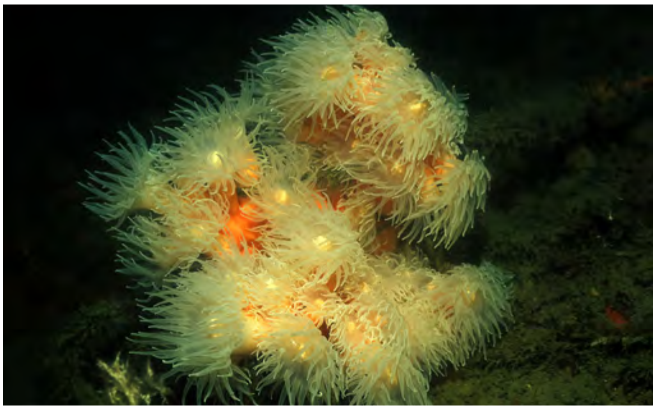


Figure 90. *Dendrophyllia ramea* is a major carbonate producer in Alboran Sea coralligenous bottoms (Punta de la Mona, Spain, -45 m) (Photo by E. Ballesteros).

7.3. Bioerosion

The most active browser in the coralligenous community is the sea urchin *Sphaerechinus granularis*, which accounts for a large part of the total coralligenous erosion. Sartoretto & Francour (1997) calculated an erosion rate ranging between 210 and 16 g $CaCO_3$ m^{-2} $year^{-1}$, with higher values in shallow waters and lower values in coralligenous concretions around 50 m depth. The bioerosional role of *Echinus melo* cannot be measured, but it is very low.

Among macroborers the Spionid polychaetes *Polydora* spp. and the mollusc *Hyatella arctica* are the only macrofauna that colonise experimental blocks after one year of exposure (Sartoretto, 1998). In this study, the total erosion caused by annelids and molluscs increases with the number of individuals but does not exceed 5.73 ± 0.77 g $CaCO_3$ m^{-2} at 20 m and 1.50 ± 0.99 g $CaCO_3$ m^{-2} at 60 m after one year of exposure. In natural communities macroborers are more abundant (excavating sponges, Sipunculida, perforating molluscs) and their absence in the experimental substrata may be due to their slow growth and to the high spatial and temporal variability of larval recruitment (Kleeman, 1973).

The comparative erosion rates produced by the three main types of eroding organisms (browsers, microborers and macroborers) have been estimated by Sartoretto (1996). Sea urchins account for roughly 95% of the total mass of $CaCO_3$ eroded. Bioerosion by micro- and macroborers accounts for the residual 5%, that of microborers being very low due to the great depths where coralligenous concretions develop and high sedimentation rates, two factors which prevent any significant development of microborers (Sartoretto, 1998). Bioerosion by macroborers is probably underestimated because the studies of Sartoretto (1998) do not take into account several organisms that are common in coralligenous communities, in particular the bivalve *Lithophaga lithophaga* and excavating sponges (Sartoretto *et al.*, 1996). The overall range of bioerosion observed in the coralligenous community is between 220 g $CaCO_3$ m^{-2} $year^{-1}$ in relatively shallow waters and 20 g $CaCO_3$ m^{-2} $year^{-1}$ at a depth of 60 m. This range is in agreement with the structure and age of coralligenous concretions situated below 50 m depth in the region of Marseilles (Sartoretto, 1996), and are at least one order of magnitude below the bioerosion experimentally estimated in coral reefs (Chazottes *et al.*, 1995).

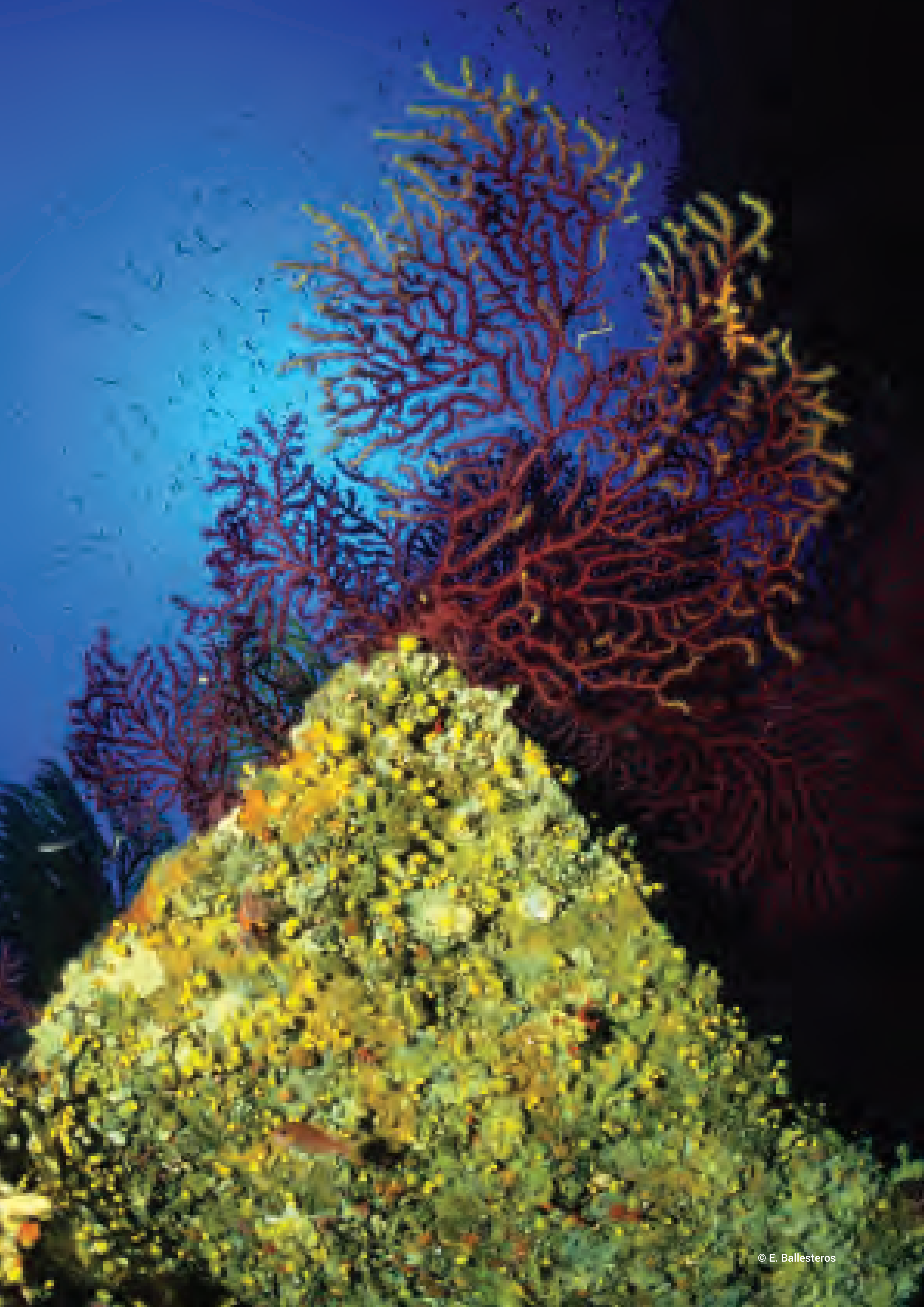
7.4. Sedimentation

The rugosity of coralligenous concretions promotes the deposition of particles that take part in the buildup of the coralligenous structure through complex processes of lithification (Marshall, 1983). However, high sedimentation rates can be a problem because sediment particles may cover the thalli of the encrusting corallines and make a screen against light (Laborel, 1961), as well as preventing the recruitment of new plants (Sartoretto, 1996). Not all the sediment particles deposited in the coralligenous structure are included in the concretion; indeed, many of them are eliminated by different browsers, while others are resuspended by currents, organisms and gravitation. The rugosity of different coralligenous types is different, as is the capacity for sediment retention. The amount of water movement is also important, and this usually decreases with depth. Studies conducted by Sartoretto (1996) in the Marseilles region conclude that around 9 kg m^{-2} $year^{-1}$ is retained in the coralligenous concretions situated at a depth of between 30 and 60 m, while the retention in shallow waters is much lower. However, daily sedimentation rates are extremely high in shallow waters (around 500 g m^{-2}) and much lower in deep waters (between 10 and 35 g m^{-2}) (Sartoretto, 1996).

The sediment that is finally incorporated into the coralligenous concretion by a process of lithification has a large calcareous component of organisms living in the coralligenous community (Laubier, 1966). Major contributors are coralline algae (57%), bryozoans (19%), molluscs (16%), corals and serpulids (3% each) (Laubier, 1966).

7.5. Carbon sink

There is no quantification of the relevance of the coralligenous and other Mediterranean calcareous biogenic frameworks as a marine carbon sink. Long-term carbon storage potential is obvious due to the calcareous accretion by coralline algae and calcareous macroinvertebrates. Coralline algae represent a yet unquantified but significant carbon store, whose potential carbon storage is similar to mangroves, saltmarshes and seagrass meadows (van der Heijden & Kamenos, 2015). This potential is even greater if we take into account that in calcareous-dominated shelf areas like those surrounding the Balearic Islands (Canals & Ballesteros, 1997) coralligenous and maërl beds cover almost 25% of the continental shelf (García *et al.*, 2014).



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8. Spatial variability

Coralligenous assemblages are very patchy and variability is present at different spatial scales (Figure 91), both in sessile and vagile assemblages (Abiatti *et al.*, 2009; Ponti *et al.*, 2018). Mobile macroinvertebrates show a high spatial variability at the scale of hundred of meters (Bedini *et al.*, 2014) while fish show a significant variability between locations (km) but not at a scale of hundreds of meters (Guidetti *et al.*, 2002).

Figure 91. Coralligenous assemblages are very patchy and variability is present at different spatial scales (Imperial Islet, Cabrera, -60 m) (Photo by E. Ballesteros).

Contributions by Ferdeghini *et al.* (2000), Acunto *et al.* (2001) and Piazzi *et al.* (2016), using photographic sampling, demonstrate the small-scale variability in algal assemblages from coralligenous communities, mainly due to the patchy distribution of calcareous algae and other dominant organisms. The structure of coralligenous assemblages mostly varied at the scale of meters while the structure was similar at larger scales (Piazzi *et al.*, 2016). Piazzi *et al.* (2004) carefully studied the algal composition of coralligenous banks developing in three different sub-tidal habitats (islands, continental shores and offshore banks), and reported high spatial variability at reduced scales but no major differences between assemblages at a habitat level, although those from the continental coasts were different from those developing in the islands (Piazzi *et al.*, 2009). Moreover, assemblages from the islands showed depth-related differences while those from continental coasts did not (Piazzi and Balata, 2011). Similar geographical differences in the specific composition between habitats are found in *Eunicella cavolini*-dominated assemblages (Sini *et al.*, 2014). However, *Paramuricea clavata*-dominated assemblages show a moderate spatial variability, with sites displaying high similarity even at large spatial scales (>100 km) (Casas-Güell *et al.*, 2015). In coralligenous habitats dominated by *Corallium rubrum*, the species composition and the morpho-functional groups differed consistently across several spatial scales, with the highest variability found at large spatial scales (>200 km) and the lowest at the scale of km (Casas-Güell *et al.*, 2016).

Different environmental factors account for the variability in the medium to large scale. Macroalgal variability in tegnùe reefs from the north Adriatic is related to the morphology of the outcrops, the depth and the distance from the coast (Curiel *et al.*, 2012). Depth seems to be the major vector of change in the substitution of calcareous algae by sponges at increasing depths (Deter *et al.*, 2012). In a study covering 120 coralligenous assemblages across France (Holon *et al.*, 2014) the observed spatial variability was explained at 28.8% by a model taking into account five physical environmental variables (surface temperature, turbidity, sediment percent cover, crevice percent cover and biological remains percent cover) and three spatial variables (longitude, latitude and depth). Spatial factors explained 19% of the variance while environmental factors accounted for the remaining variance.

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9. Dynamics

9.1. Seasonality and short-term dynamics

The study of dynamics for the whole coralligenous community was first assessed by Garrabou *et al.* (2002) using a photographic method to look for changes occurring in two monitored areas of coralligenous concretions covering 310 cm^2 over a period of two years. The rate of change observed averaged 10% $month^{-1}$, with very low to nil seasonality. Most of the area (>70%) remained almost constant throughout the two years of monitoring, showing no or few transitions, and this indicates the great persistence of the animals and plants that thrive in coralligenous communities (Figure 18). Casas-Güell *et al.* (2015) find almost no temporal changes in a five years period, whether in species composition nor in morpho-functional groups. The limited temporal variability of coralligenous reefs has been attributed to the reduced slow growth rates and slow mortality rates (Garrabou *et al.*, 2002; Virgilio *et al.*, 2006; Teixidó *et al.*, 2011) of the most abundant taxa and the reduced seasonality of environmental conditions (Virgilio *et al.*, 2006). However, Teixidó *et al.* (2011) point out that occasional mortality events and high recruitment pulses can occur (Garrabou *et al.*, 2009a; Linares *et al.*, 2018; Verdura *et al.*, 2019). Temporal variability is also reduced in tegnùe reefs (Abiatti *et al.*, 2009).

Other studies have been conducted with some compartments or species of coralligenous communities. In fact, most studies dealing with the biology of the main species in coralligenous communities (see chapter 'Functioning of outstanding and key species') have described the effects of seasonality, when this process exists.

In terms of benthic flora, Ballesteros (1991a) described the seasonal cycle of several phytobenthic communities from the northwestern Mediterranean, making a between-community comparison using the same parameters as descriptors. The coralligenous community with *Mesophyllum alternans* and *Halimeda tuna* had the lowest seasonality of all the subtidal communities studied, this being almost constant in autumn, winter and spring, but with peak productivity in summer, during which time there were higher biomass values than for the rest of the year. Piazzi *et al.* (2004) found significant seasonal differences that were mostly related to the disappearance of many turf species and the decrease in cover of most erect algae, principally foliose and corticated-terete forms, in winter. Although growth of coralline algae is almost constant throughout the year (Garrabou & Ballesteros, 2000), *Halimeda* growth occurs mainly in summer (Ballesteros, 1991c). In terms of structural changes in the community, two stages can be discerned over an annual cycle: the stage of diversified community, with a reduced coverage of *Halimeda* and other soft algae, and the stage of developed community, characterized by a high coverage of *Halimeda* (Ballesteros, 1991b). The shift from the diversified community stage to the developed community stage takes place through a production phase (early summer). A diversification phase can be distinguished in late autumn, when a sudden fall in *Halimeda* coverage is detected (Ballesteros, 1991b) (Figure 92).

Figure 92. The coralligenous assemblage dominated by *Halimeda tuna* and *Mesophyllum alternans* shows a moderate seasonality, with productivity peaking in summer (Photo by E. Ballesteros).

Most benthic hydrozoans exhibit a seasonal pattern, with reproduction in spring or autumn and growth from autumn to spring; most of them disappear during the summer, leaving only dormant basal stolons (Boero *et al.*, 1986). Epiphytic hydrozoans on *Halimeda tuna* decline in abundance in summer because of the death of old thalli of *Halimeda*, the growth of new thalli and apical articles on existing thalli, and possibly because of interspecific competition with epiphytic algae (Llobet *et al.*, 1991a).

Anthozoans exhibit a marked seasonality in all activities (Coma *et al.*, 1998a; Garrabou, 1999). According to Coma *et al.* (2002) respiration rates of *Paramuricea clavata, Dysidea avara* and *Halocynthia papillosa* vary two- to three-fold across the annual cycle, exhibiting a marked seasonal pattern but showing no daily cycle or significant day-to-day variability within months. The respiration rate of *Paramuricea* (a passive suspension feeder) does not correlate with temperature, but that of *Dysidea* and *Halocynthia* (active suspension feeders) increases with temperature. There is a low rate of new tissue synthesis during summer, together with the contraction of polyps and a low Q_{10}, which explains the low respiration rates of *Paramuricea* observed during the period of highest temperature. These low respiration rates support the hypothesis that energy limitations may underlie summer dormancy in some benthic suspension-feeding taxa in the Mediterranean (Figure 20).

Bryozoans inhabiting coralligenous outcrops show relatively low growth and relatively low temporal variability (Pacciardi *et al.*, 2004) although we have observed outstanding differences in the size and density of some erect calcareous bryozoans (*Reteporella grimaldii, Schizotheca serratimargo*) over the years in the coralligenous walls of Cabrera National Park (Ballesteros, pers. obs.) (Figure 93).

Figure 93. Bryozoan *Schizotheca serratimargo* can show outstanding differences in density and colony size over the years in coralligenous environments (Photo by E. Ballesteros).

There is growing evidence that seasonal patterns of activity and secondary production of suspension feeders in coralligenous assemblages are characterized by aestivation (Coma *et al.*, 2000). Several types of resting and resistance periods have been observed in several colonial ascidians in the warm season (Turon, 1992; Turon & Becerro, 1992). In the case of *Polysyncraton lacazei* the surface of the colonies is covered by a glassy pellicle and the siphonal apertures are sealed. This is interpreted as a rejuvenative phenomenon that extends the life span of the zooids (Turon, 1992). Some sponges also go through a resting, non-feeding period with cellular restructuring, mainly in summer. For example, some specimens of *Crambe crambe* appear to be covered by a glassy cuticle, obliterating the oscula and ostia after reproduction, from the end of August until the end of October (Turon *et al.*, 1999). These authors suggest that these resting stages develop not only in response to remodelling following reproduction, but also as an effect of water temperature abnormalities.
Mobile macroinvertebrates assemblages have been observed to change within a one year period (Bedini *et al.*, 2014). The decapod fauna also displays some seasonality (García-Raso & Fernández Muñoz, 1987), due to the intense recruitment of several species in late summer, and a progressive decrease in the density of individuals and an increase in their size from October to June. However, this seems not to be the case in molluscs (Urra *et al.*, 2012).

The fish fauna of coralligenous communities vary with time in spite of a fairly stable benthic environment (Guidetti *et al.,* 2002) and is also affected by seasonality (Garcia-Rubies, 1997), although its effect is of very minor importance. The number of species in fish counts along 50 m-long visual transects of the coralligenous bottoms around the Medes Islands slightly decreases in winter, and most fish seem to be less active than in summer (García-Rubies, 1997) (Figure 94).

Figure 94. Grouper *Epinephelus marginatus* is less active in winter (Photo by E. Ballesteros).

9.2. Changes in decadal time scales

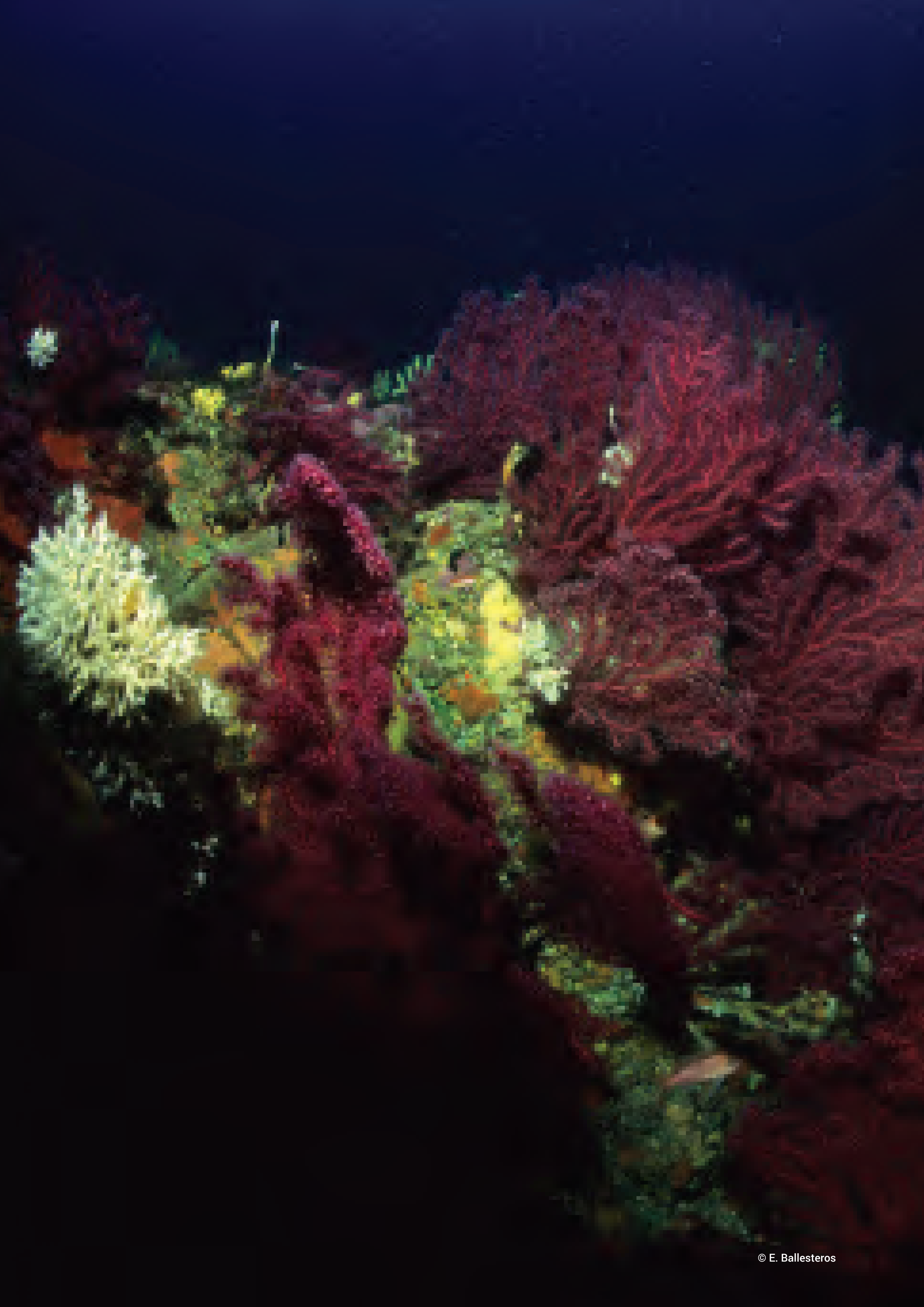
Photographic sampling has been used to detect changes at the scale of decades in coralligenous assemblages. The low mortality, slow growth, and usually low recruitment of most dominant species like sponges *Aplysina cavernicola, Chondrosia reniformis, Haliclona fulva, Scalarispongia scalaris, Petrosia ficiformis* and *Spirastrella cunctatrix* and anthozoans like *Alcyonium acaule, Leptopsammia pruvoti, Caryophyllia inornata* and *Corallium rubrum* prevent the existence of huge changes at decadal time scales if conditions remain stable (Teixidó *et al.*, 2005, 2009). When changes occur they seem to be related with an increase in human pressures (Roghi *et al.*, 2010; Gatti *et al.*, 2015a, 2017) such as increased sedimentation rates and water turbidity, mortality events related to warming, and invasive species. There seems to be a shift between 1980 and 1990 in Portofino reefs, when warming was fast and some species disappeared or got rarer, many finding refuge in deeper waters (Gatti *et al.*, 2017). However, introduced species increased in this study as also did some native ones like *Axinella verrucosa, Eunicella verrucosa, Leptogorgia sarmentosa* or *Salmacina dysteri,* which better stand the new environmental conditions (Gatti *et al.*, 2015a, 2017).

The comparison of the sponge diversity in a 25 years period (Bertolino *et al.*, 2015) using sets of photographs taken between 1987/1988 and 2012/2013 showed that the overall sponge coverage remained almost unchanged. Nevertheless, changes occurred at the species level, with increasing abundances in *Agelas oroides* and *Axinella* spp., and a drastic decrease in *Chondrosia reniformis*, *Phorbas tenacior*, *Acanthella acuta*, *Ircinia* spp., *Dysidea avara* and *Petrosia ficiformis* (Figure 95). No changes in the abundance of *Cliona viridis* and in the red encrusting sponges complex was noticed. The sampling of the same reefs at a time interval of about 40 years (Bertolino *et al.*, 2017b) showed a decrease by 45% of the species richness, which was higher in massive and erect sponges (67%) than in encrusting (36%), cavity dwelling (50%) or boring (25%) sponges, suggesting that the inner part of the bioconstructions was less affected by the variation in environmental conditions.

Figure 95. Encrusting sponge *Phorbas tenacior* is one of the species that has shown a drastic decrease during the last 25 years in Portofino coralligenous reefs (Photo by E. Ballesteros).

9.3. Changes at the level of centuries and millennia

Most species of sponges produce genera and/or species-specific spicules that remain embedded in the sediment filling the inner holes of the coralligenous concretions once the sponges die. The obtaining of corers including the whole thickness of a coralligenous build-up allows the recovery of the spicules through the entire life span of the concretion, which coupled with the age estimation of the different sections, allows the reconstruction of the sponge fauna along century and even millennia (Bertolino *et al.*, 2013, 2017a,b). Data from Ligurian reefs (Italy) show certain stability in sponge populations with time in the last 5000 years, with almost 50% of the assemblage remaining constant (Bertolino *et al.*, 2013). However, critical changes at generic level in diversity and abundance of sponges were observed at 500/250 year intervals, which could be related to different climatic periods and events that affected the Mediterranean area during the studied time span (Bertolino *et al.*, 2017a, b).



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10. Connectivity

Larvae of most coralligenous species studied so far often disperse only over short distances (Costantini *et al.*, 2007; Abiatti *et al.*, 2009), suggesting that populations should be strongly structured at different spatial scales, from meters to the whole Mediterranean. Species without larvae show higher levels of genetic structure than species with free-living larvae, but there are no significant differences between species with lecitotrophic or planktotrophic larvae (Cahill *et al.*, 2017). Habitat formers display a low dispersal capacity, a high retention rate an there is a weak effect of currents and fronts on their dispersal (Pascual *et al.*, 2017), showing a much higher structuring level than fish and other non-habitat former invertebrates (Calderón *et al.*, 2008; Maltagliati *et al.*, 2010; Schunter *et al.*, 2011; Ingrosso *et al.*, 2018) (Figure 96).

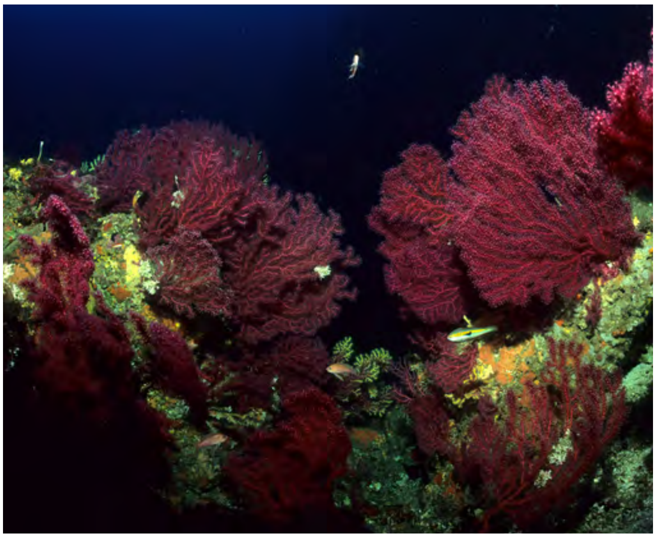

Figure 96. There is a consistent and highly significant genetic structuring among habitat formers of the coralligenous assemblages like *Paramuricea clavata* (Photo by E. Ballesteros).

Most genetic studies using mitochondrial and microsatellite markers concern cnidarians, sponges, echinoderms and tunicates, while there are no studies on bryozoans and polychaetes (Costantini *et al.*, 2017, 2018). Connectivity in coralligenous algal bioconstructors is almost nil but it is not expected to be very wide since they disperse by means of non-flagellate spores (Ingrosso *et al.*, 2018). The largest number of studies has been devoted to gorgonians (*Corallium rubrum, Paramuricea clavata, Eunicella* spp.) (Costantini *et al.*, 2007; Mokhtar-Jamaï *et al.*, 2011; Aurelle *et al.*, 2011; Abiatti *et al.*, 2014; Ledoux *et al.*, 2010, 2014a; Frleta-Valic *et al.*, 2014; Cannas *et al.*, 2015; Arizmendi-Mejía *et al.*, 2015; Pérez-Portela *et al.*, 2016; Costantini & Abiatti, 2016; Masmoudi *et al.*, 2016; Costantini *et al.*, 2016b; Cánovas-Molina *et al.*, 2018), and there is one study on the hexacoral *Leptopsammia pruvoti* (Goffredo *et al.*, 2009). In general there is a consistent and highly significant genetic structuring among populations (Figure 96). Further information at the species level is reported in the next chapter. There is a strong isolation and the level of structuring differs between phyla and species within phyla (Costantini *et al.*, 2018). Pelagic larval duration, however, does not appear to be a major driver of the structuring (Costantini *et al.*, 2018).

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11. Functioning of outstanding and key species

11.1. Coralline algae

Growth dynamics of two important coralligenous builders in the northwestern Mediterranean, *Mesophyllum alternans* and *Lithophyllum stictaeforme*, were studied in the bioconcretions of the Medes Islands marine reserve, in a steep wall situated at a depth of between 15 and 30 m (Garrabou & Ballesteros, 2000). Growth rates ranged from 0.16 month^{-1} for *Mesophyllum alternans* to 0.09 month^{-1} for *Lithophyllum stictaeforme*, with shrinkage rates being 0.09 and 0.04 month^{-1}, respectively. These growth rates are more than one order of magnitude lower than those reported for other Mediterranean and tropical coralline species, but similar to reports for crustose corallines in arctic and temperate waters. No seasonal pattern in growth or shrinkage was found for either species; however, seasonality in conceptacle occurrence was detected in *Lithophyllum stictaeforme*, with a high interannual variability. *Mesophyllum alternans* thalli frequently underwent fissions and fusions (almost one event during the two-year monitoring period for 50% of monitored plants), while they were rarely observed in *Lithophyllum stictaeforme* (Figure 97). These differences in growth, shrinkage, and fission and fusion events are interpreted as different growth strategies. *Mesophyllum alternans* has a more opportunistic strategy, growing faster and gaining area more rapidly, although it also loses area at higher rates. *Lithophyllum stictaeforme* has a more conservative strategy, it being more effective in maintaining the area acquired through its reduced growth rate (Garrabou & Ballesteros, 2000).

Figure 97. Fissions of thalli are rarely observed in coralligenous building alga *Lithophyllum stictaeforme* (Photo by E. Ballesteros).

It has been shown that *Lithophyllum cabiochae* shows algal necrosis in culture under elevated water temperature and these necrosis are facilitated if pCO_2 is higher than normal (Martin *et al.* 2009). *Lithophyllum cabiochae* survival in laboratory conditions depended both on irradiance and temperature, with longest survival (> 5 years) observed at 10-12°C and 20 µmols m^{-2} s^{-1}. Specimens died in less than half a year when subjected to 24-26°C and 75 µmols m^{-2} s^{-1}, explaining the ability of this species to survive at very low irradiances below the thermocline (Rodríguez-Prieto, 2016).

11.2. *Halimeda tuna*

Growth and production of a *Halimeda tuna* population from a coralligenous community (18 m depth) in the northwestern Mediterranean has been studied by Ballesteros (1991c). The production of new segments changed seasonally, being maximal in summer and minimal in winter (Figure 98), and this suggests that growth is mainly related to temperature and irradiance. The loss of segments seemed to be related to physical disturbances (storms) and herbivory. Annual production of *Halimeda tuna* was estimated at 680 g dw m^{-2}, equivalent to 114 g organic C m^{-2} year^{-1} and to 314 g $CaCO_3$ m^{-2} year^{-1}; the yearly P/B ratio was 1.87 year^{-1}. The epiphytic assemblage growing on the segments of *Halimeda tuna* also displayed high seasonality, with a maximum biomass and species richness in early summer. Values of growth and production reported in Ballesteros (1991c) emphasize the importance of *Halimeda tuna* as a producer both of organic matter and calcium carbonate in the coralligenous habitat. In fact, available data suggest that calcium carbonate production by *Halimeda* in shallow coralligenous concretions is similar to that of coralline algae (Canals *et al.*, 1988).

Figure 98. Production of new segments changes seasonally in *Halimeda tuna*, being maximal in summer and minimal in winter (Photo by E. Ballesteros).

11.3. Sponges

Garrabou & Zabala (2001) studied the growth dynamics of four demosponges (*Crambe crambe* and *Hemimycale columella* from a 'precoralligenous' community, and *Oscarella lobularis* and *Chondrosia reniformis* from a coralligenous community in the Medes Islands) and reported relatively slow growth dynamics with low growth and shrinkage rates. The coralligenous species had an average relative growth rate of 0.15 month^{-1} (*Oscarella*) and 0.022 month^{-1}

(*Chondrosia*), with shrinkage rates of 0.12 and 0.017 month^{-1}, respectively. Interspecific differences in growth, shrinkage, division and fusion rates were interpreted as evidence of distinct biological strategies aimed at persistence and the occupation of substratum. *Chondrosia reniformis* is conservative, with slow growth but great resistance to damage. *Crambe crambe* seems to enhance its rate of space occupation by a high division rate. *Hemimycale columella* grows quickly and shrinks at low rates, thus spreading rapidly over the substratum. *Oscarella lobularis* grows and shrinks rapidly, showing great growth.

The natural diet of *Dysidea avara*, a common sponge in coralligenous communities (Uriz *et al.*, 1992a) (Figure 99), has been studied by Ribes *et al.* (1999b). *Dysidea avara* obtained 85% of its ingested carbon from the fraction smaller than 5 µm (mostly procaryotes and pico- and nanoplankton) and 15% from the fraction larger than 5 µm (mostly phytoplankton). However, the partial contributions of the different groups varied seasonally, in accordance with the planktonic composition of the water column: during winter, phytoplankton was an important component of the total uptake (26%), whereas during the rest of the year it contributed less than 7% of the total uptake. This trophic plasticity may represent an advantage for the species because it attenuates the effects of seasonal fluctuations in the planktonic community. Moreover, the water transport rates of 63 ml g^{-1} min^{-1} and the high clearance rates for particles measuring 4 µm or less observed in *Dysidea avara* (Turon *et al.*, 1997) point to a significant grazing impact of sponges on the picoplankton in communities like the coralligenous, where *Dysidea avara* and other massive sponges are abundant (Laubier, 1966; Bibiloni *et al.*, 1984).

Figure 99. Sponge *Dysidea avara* obtains most of its ingested carbon from the planktonic fraction smaller than 5 µm, which means that it feeds mostly on prokaryotes and pico- and nanoplankton (Photo by E. Ballesteros).

11.4. Hydrozoans

The hydrozoan *Orthopyxis crenata*, a common hydroid growing on the alga *Halimeda tuna*, was most abundant from November to April, when three cohorts were identified (Llobet *et al.*, 1991b). During the rest of the year only two cohorts were identifiable, except in June and July when there was only one—juvenile—cohort. Reproduction took place from late October to early December, with recruitment occurring at the same time. In winter, colony sizes quintupled and tripled every 15 days, living a maximum of six weeks. The maximum abundance of hydroids in winter seems to be related to increased food availability, a decrease in competence by epiphytic algae and a decline in the turn-over rate of *Halimeda* (Ballesteros, 1991c). The strategy of *Orthopyxis crenata* and other hydroids is completely different to that of long-living anthozoans that are also common in coralligenous communities; the colonies survive for only a small number of weeks but asexual reproduction by the creeping stolons ensures colony survival beyond the life of *Halimeda* thalli, and perhaps indefinitely.

Coma *et al.* (1992) studied the life cycle of two similar species of hydrozoans living over the thalli of *Halimeda tuna* and also found that survival should be very long for each colony, due to the active asexual reproduction (by stolonisation in *Halecium petrosum*; by planktonic propagules in *Halecium pusillum*) that occurs throughout most of the year. Maximum life span of colonies was estimated to be only eight weeks, mean colony sizes increasing between three- and six-fold over consecutive two-week periods.

11.5. Red coral

Red coral is typically associated with the animal dominated communities growing in dim light conditions and which characterize smaller cavities, vertical cliffs and overhangs present in coralligenous concretions, although it also dwells on rocky outcrops and seamounts down to about one thousand meters (Costantini *et al.*, 2016b). Although it is essentially distributed in the western basin, it is also present in some areas of the eastern basin and the nearby Atlantic coast (Zibrowius *et al.*, 1984; Chintiroglou *et al.*, 1989; Aurelle *et al.*, 2011; Boavida *et al.*, 2016; Çinar *et al.*, 2018). The red coral can thrive in a wider range of depths given that environmental conditions are suitable (Figure 100).

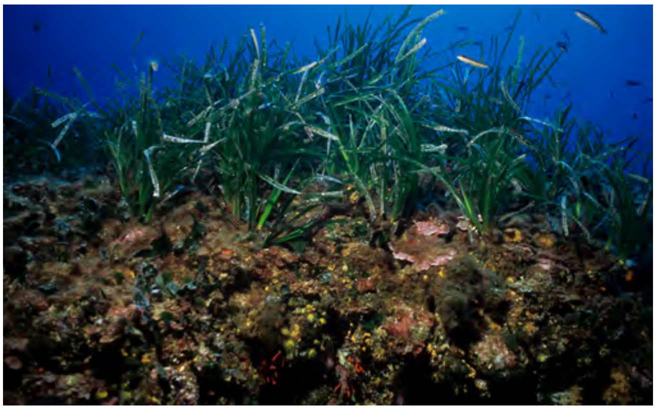

Figure 100. Red coral (*Corallium rubrum*) thrives in a wide depth range. Here it can be observed just below the deepest limit of seagrass *Posidonia* meadow, at -35 m in Cap de Cavalleria (Menorca) (Photo by E. Ballesteros).

In shallow waters it is a species mostly located in caves and in deep waters occurs in open areas, well below the deepest limits of the coralligenous outcrops.

Harvesting is the major source of disturbance in red coral populations (Santangelo *et al.*, 1993; Santangelo & Abbiati, 2001; Tsounis *et al.*, 2007; Rossi *et al.*, 2008; Montero-Serra *et al.*, 2014; Angiolillo *et al.*, 2016; Garrabou *et al.*, 2017; Jaziri *et al.*, 2017; Linares *et al.*, 2019), although large-scale mortality events have also been documented (Arnoux *et al.*, 1992; Garrabou *et al.*, 2001; Garrabou *et al.*, 2009a; Kruzic & Rodic, 2014; Bavestrello *et al.*, 2014; Linares *et al.*, 2019). Exposure of red coral colonies to 24ºC for 24 days caused a beginning of mortality only for colonies coming from deep waters, while exposure to 25°C for between 9 and 14 days caused generalized mortalities in deep and shallow colonies, indicating that colonies from shallow waters had greater thermotolerance to elevated seawater temperatures than the deep populations (Torrents *et al.*, 2008). However red coral colonies show a differential response to warm waters at a local scale, which might be explained by local adaptation or acclimatization (Haguenauer *et al.*, 2013). Recreational diving seems to have a limited impact on populations, but the potential risks of poaching and mechanical disturbance will increase in the near future with the predictable increase of diving (Garrabou & Harmelin, 2002) (Figure 101).

Figure 101. Big colonies of *Corallium rubrum* are extremely rare in shallow waters as they face the risk of being harvested by commercial divers or by poachers (Photo by E. Ballesteros).

According to Garrabou & Harmelin (2002), red coral has a high survivorship, with 60% of colonies reaching 22 years of age. Mortality is higher in juveniles, but partial mortality of colonies is higher in old colonies (Garrabou & Harmelin, 2002). Age at first reproduction is, on average, between 7 and 10 years, although the reproductive effort, i.e., the percentage of gravid polyps per colony, is higher in older colonies (Torrents *et al.*, 2005). Colonies are whether male or female, with genetic sex determination (Pratlong *et al.*, 2017). Male gonads develop within one year, whereas the maturation of female gonads takes two years (Vighi, 1972). Temperature appears as the main synchronizing factor of gonadal development within populations in Medes and Palos (Gori *et al.*, 2007). Planulae emission seems to be related to water temperature and lasts from May to October, according to each geographical area (Lacaze-Duthiers, 1864; Lo Bianco, 1909; Cerruti, 1921; Vighi, 1972; Santangelo *et al.*, 2003).

The brooding larvae of the red coral suggested that its dispersal capability was reduced (Weinberg, 1979; Abbiati *et al.*, 1993), which has been recently proved (Costantini *et al.*, 2007). Mean dispersal range of red coral ranges between 22 and 31 cm based on spatial genetic structure of the colonies (Ledoux *et al.*, 2010a; Costantini *et al.*, 2016b).

There is a high level of genetic structure at a regional scale, with heterogenous distribution from regional to sample levels (Costantini *et al.*, 2007; Ledoux *et al.*, 2010b, 2014a; Costantini *et al.*, 2016b). Populations from the Adriatic and North Africa are genetically different from those of the northern Western Mediterranean (Aurelle *et al.*, 2011). Populations from eastern and western Sardinia show a significant genetic differentiation (Cannas *et al.*, 2015). Depth has an important role in determining the patterns of genetic structure in *Corallium rubrum*, with a threshold in connectivity across 40-50 m depth (Costantini *et al.*, 2011, 2016b). Deep-water (55-120 m) populations of red coral show a high genetic similarity between the northern (Liguria, Tuscan Archipelago) and the southern (South Thyrrenian, Ionian) Mediterranean (Costantini & Abiatti, 2016). Thus, connectivity of shallow water populations is extremely limited and deep coral populations should not be considered as a source to recover shallow water populations, nor the reverse (Abiatti *et al.*, 2014; Ledoux *et al.*, 2014a,b).

Recruitment, when studied in experimental panels, is usually high at the beginning, subsequently decreasing (Garrabou & Harmelin, 2002; Bramanti *et al.*, 2005). However, differences in the results obtained by Harmelin & Garrabou (2002) and Bramanti *et al.* (2005, 2016) suggest there is high population variability in recruitment and colonization rates.

Red coral growth is strongly affected by intra- and interspecific interactions and stochastic events (Bavestrello *et al.*, 2009). Growth rates estimated by petrographic methods range from 1.57 to 0.91 mm year^{-1} for basal diameter (Garcia-Rodriguez & Massó, 1986; Abbiati *et al.*, 1992), but estimates decrease to 0.62 mm year^{-1} in mid-term (four-year) observations (Cerrano *et al.*, 1999; Bramanti *et al.*, 2005) and to 0.24 mm year^{-1} in long-term (twenty-two-years) studies (Garrabou & Harmelin, 2002; Bramanti *et al.*, 2014). A new technique for aging red coral developed by Marschal *et al.* (2005) suggests mean growth rates of around 0.35 mm year^{-1}, in close agreement with long-term observations. Growth rates in colony height have been estimated to be around 1.8 mm year^{-1} (Garrabou & Harmelin, 2002; Bramanti *et al.*, 2005). The average branching rate for each colony is 3.4 branches in 22 years (Garrabou & Harmelin, 2002).

In ancient times, red coral lived in relatively high-density populations with a large proportion of centuries-old colonies, even at shallow depths. Garrabou *et al.* (2017) provide demographic data on a recently discovered unexploited population of red coral in the MPA of Scandola (Corsica) (Figure 102), which shows the largest biomass (by more than 100-fold) reported to date, even in deep waters or in populations thriving in areas that have been protected for 30 years (Santangelo *et al.*, 2004, 2007, 2009; Tsounis *et al.*, 2007; Rossi *et al.*, 2008; Krucic & Popijac, 2009; Pedoni *et al.*, 2009; Angiolillo *et al.*, 2009, 2016; Linares *et al.*, 2010; Bramanti *et al.*, 2014). Harvested populations show about two-fold lower values on average, and up to four-fold lower values in colony size compared to non-harvested populations, reducing biomass and triggering a general simplification of affected populations (Montero-Serra *et al.*, 2014, 2015). Garrabou & Harmelin (2002) provide indisputable data on the longevity of colonies and the parsimonious population dynamics of *Corallium rubrum*. Current populations have shown a dramatic shift in their size structure, characterized by the absence of large colonies. Full recovery of shallow-water harvested populations may take several decades or even centuries (Garrabou & Harmelin, 2002; Tsounis *et al.*, 2007).

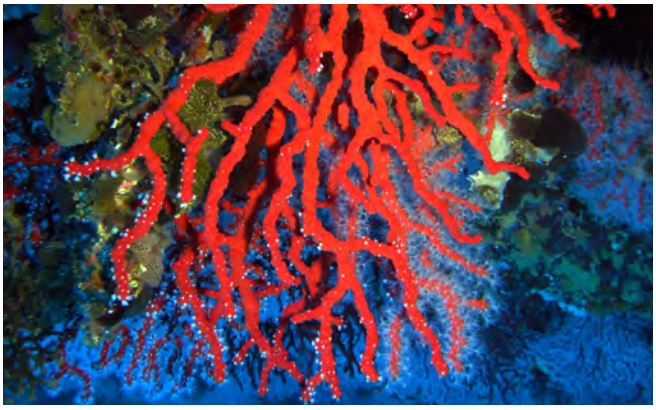
Figure 102. Colonies of an unexploited red coral population recently found in Scandola (Corsica) show a biomass and abundance several orders of magnitude greater than other examined populations studied so far, re-shifting the ecological baseline of this overexploited species (Photo by E. Ballesteros).

No sign of predation has been observed in monitored colonies of *Corallium rubrum* (Garrabou & Harmelin, 2002). In fact, predation appears to play a minor role in sessile, invertebrate-dominated communities (Garrabou *et al.*, 2002).

11.6. Soft gorgonians

Paramuricea clavata, Eunicella cavolini and *Eunicella singularis* are the commonest soft gorgonians in coralligenous bottoms (Figure 103). Growth of *Paramuricea clavata* has been monitored photographically over a two-year period (Coma *et al.*, 1998b). Based on growth-rate data, the largest colonies in the population (55 cm) were around 31 years old (Figure 104). On average, net production for all colonies was 75% of gross production. Gross production was 4.4 g afdw m^{-2} year^{-1}, while the P/B value was 0.11 year^{-1} and the turn-over time was nine years (Coma *et al.*, 1998a, b). Mistri & Ceccherelli (1994), in a study of *Paramuricea clavata* in the Straits of Messina (Italy), estimated a production of 3 g afdw m^{-2} year^{-1}, a P/B value of 0.13 year^{-1} and a turnover rate of 7.5 years. In *Eunicella cavolinii* Weinbauer & Velimirov (1995a, b) have estimated a production of 0.3 to 7.4 g afdw m^{-2} year^{-1}, a P/B around 0.24 and 0.32 year^{-1}, and a turn-over rate ranging from three to four years.


Figure 103. *Paramuricea clavata* and *Eunicella cavolini* are two common coralligenous-dwelling soft gorgonians (Photo by E. Ballesteros).


Figure 104. Largest colonies of *Paramuricea clavata* can exceed an age of 30 years (Photo by E. Ballesteros).

Mean increase in maximum height for *Paramuricea clavata* ranges from 1.8 to 2.7 cm year^{-1} (Weinberg & Weinberg, 1979; Mistri & Ceccherelli, 1984; Coma *et al.*, 1998a). Similar values have been obtained for *Eunicella singularis* (2.2 cm year^{-1}; Weinberg & Weinberg, 1979). Growth is lower in *Eunicella cavolinii* (0.85 to 1.14 cm year^{-1}: Velimirov, 1975; Weinbauer & Velimirov, 1995a).

Seasonality of growth in *Paramuricea clavata* requires long monitoring periods in order to be accurately detected, but available data suggest there is a high growth period in spring, this being consistent with the seasonal fluctuation in food sources (Coma *et al.*, 1998b).

The minimum age at first reproduction in *Paramuricea clavata* has been estimated to be around three to thirteen years on average (Coma *et al.*, 1995a; Bramanti *et al.*, 2016). Fecundity levels increase with colony size. Oogenesis in *Paramuricea clavata* lasts for

13-18 months and culminates with the release of mature eggs in June-July; reproduction is synchronous each year and as well as coinciding with increasing water temperature it is correlated with the lunar cycle (Coma *et al.*, 1995a). Food availability in *Paramuricea clavata* affects reproduction (Gori *et al.*, 2013) and helps to explain the spatial variability in the reproduction and energy storage of suspension feeders. Spawned eggs adhere to the outer surfaces of female colonies through the action of a mucous coating. Embryogeny and final maturation takes place among the polyps. On leaving the surface of the colonies, larvae immediately settle on the surrounding substrate. Even if fertilization rates are high, survivorship through the planulae and polyp stages is very low (Linares *et al.*, 2008b), which may help to explain the low recruitment rates observed in natural populations. There is a strict density-dependent control of recruitment operated by larger colonies in crowded populations (Bramanti *et al.*, 2016). Clonal propagation is not common (Pilczynska *et al.*, 2017), and maintenance of the populations is based on sexual reproduction (Coma *et al.*, 1995b).

Zooplankton (Nauplii, copepod eggs, other invertebrate eggs, calanoid copepods) accounts for an important share of the diet. Peak prey capture levels are recorded in spring and at the end of autumn; they fall off substantially in summer, when the proportion of colonies with contracted polyps is very high (Figure 105). The prey capture rate extrapolated to an annual cycle suggests that gorgonians play an important role in the flow of energy from plankton to the benthos; estimates from *Paramuricea clavata* populations situated in the Medes Islands indicate that this species can remove the equivalent of between 12 and 85 mg C m^{-2} day^{-1} from the zooplankton (Coma *et al.*, 1994). However, *Paramuricea clavata* has a broad and heterogenous diet that ranges from nanoeukaryotes (3.8 µm) to copepods (700 µm), and includes prey as diverse as ciliates, dinoflagellates, diatoms and suspended detrital organic matter (Ribes *et al.*, 1999c). Carbon of detrital origin accounts for roughly 48% of the total ingested carbon and shows a marked seasonal pattern, in which winter and spring are the seasons with the highest ingestion rates. The amount of carbon removed from the surrounding water is equivalent to 2.7 mg C m^{-2} day^{-1} from the living POC (including nanoeukaryotes, diatoms, ciliates and dinoflagellates) and 28.7 mg C m^{-2} day^{-1} from the detrital POC. No significant capture of dissolved organic matter or picoplankton has been observed. Ribes *et al.* (1999c) give an estimate of the partitioning of food sources that cover the energy needs of *Paramuricea clavata*, assuming data on ingestion rates observed in incubation chambers corrected by the effect of flow speed obtained from the literature. According to these authors, zooplankton and detrital POC make a similar contribution (about 48% each), with the living POC accounting for the remaining 4%, a figure that can probably be extrapolated to other gorgonians.

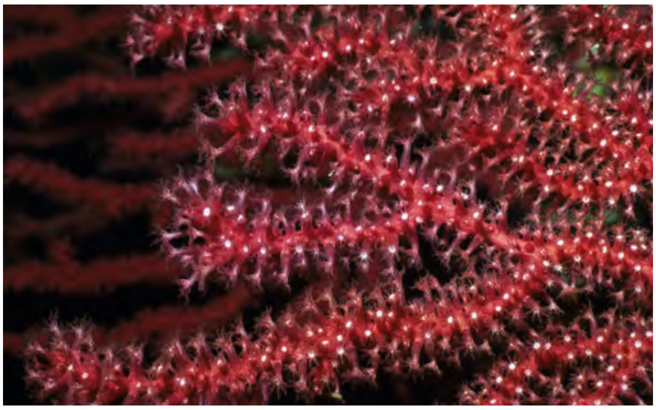

Figure 105. Peak prey capture in *Paramuricea clavata* is recorded in spring and at the end of autumn, when the proportion of colonies with extended polyps is very high (Photo by E. Ballesteros).

Metabolic activities of Mediterranean gorgonians are reduced in periods of high temperatures (>18ºC), with a decrease in open polyps and lower oxygen consumption (Previati *et al.*, 2010). *Paramuricea clavata* and *Eunicella cavolini* show first signs of necrosis after only three days at 25ºC but no such effects are observed in *Eunicella singularis* (Previati *et al.*, 2010). The zooxanthellae of *Eunicella singularis* (Figure 106) could provide an alternative source of energy when polyps are closed increasing its resistance to thermal stress (Previati *et al.*, 2010), at least for short-term periods. However, photosynthetic activity seems to collapse above 24ºC and bleaching occurs at 26ºC (Ezzat *et al.*, 2013), which explains the repeated summer mortality events of this species if heterotrophic nutrition is not able to meet basal metabolic requirements (Coma *et al.*, 2006, 2015). There is a different geographical and depth-related resistance capacity of *Eunicella singularis* to thermal stress in laboratory cultures. Unexpectedly, deep-water populations show a higher thermotolerance (Ferrier-Pagés *et al.*, 2009; Pey *et al.*, 2011).
As expected, though, populations from warmer areas show a slight increased thermotolerance, from 28 to 29ºC (Linares *et al.*, 2013).

Figure 106. The slightly brownish colour of *Eunicella singularis* is made by symbiotic zooxanthellae, which provide an alternative source of energy to the colony (Photo by E. Ballesteros).

The higher resistance of the colonies to thermal stress found in laboratory conditions than in the field suggests that food availability is playing an important role in assessing the thermotolerance of *Eunicella singularis*. Interestingly, *Eunicella cavolini* shows a lower thermotolerance in deep-water individuals, with highly resistant individuals present around 20 meters (Pivotto *et al.*, 2015).

Critical thermal thresholds triggering mortality in *Paramuricea clavata* depend on temperature and time. Short periods (2-5 days) of temperatures higher than 27ºC or one month at 24ºC are conditions triggering mortality (Crisci *et al.*, 2011). After one month of exposure at 25ºC, 97% of the colonies show tissue necrosis independently of localities (Crisci *et al.*, 2017) (Figure 107). However, the capacity of *Paramuricea clavata* to deal with thermal stress varies among individuals and populations, with very significant differences at a geographical (>500 Km) scale (Ledoux *et al.*, 2019).

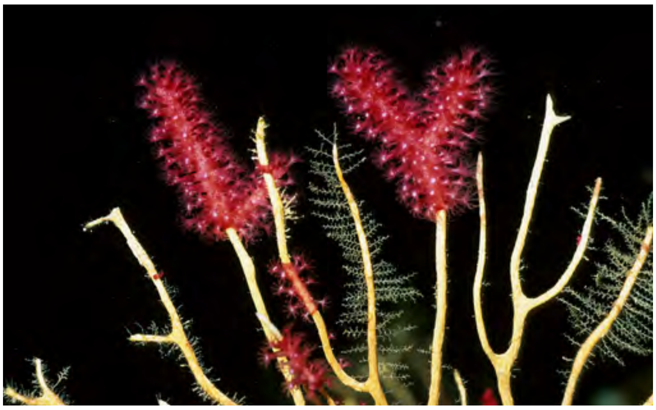

Figure 107. Most of the colonies of *Paramuricea clavata* show tissue necrosis after one month of exposure at 25ºC (Photo by E. Ballesteros).

Thermal stress also has important sublethal effects on the reproduction and the viability of early life stages of *Paramuricea clavata* (Linares *et al.*, 2014). Adults show a higher percentage of necrosis than juveniles, suggesting than reproduction makes them more vulnerable to thermal stress. Both male and female individuals show a similar percentage of tissue damage and a decrease in reproductive output, with reproduction in females being more impacted than in males (Linares *et al.*, 2008; Arizmendi-Mejia *et al.*, 2015b). These effects on reproduction seem to be a response to the injury itself, not a direct effect of thermal stress (Linares *et al.*, 2008). There is also a severe negative impact of thermal stress on the viability of embryos and larvae, resulting in reduced survivorship, abnormal embryonic development and impaired metamorphosis (Kipson *et al.*, 2012).

Main gorgonians inhabiting coralligenous concretions show different habitat preferences across the continental shelf (Gori *et al.*, 2011) (Figure 108). Distribution, depth limits and population structure can also change geographically (Linares *et al.*, 2007a; Gori *et al.*, 2011; Kipson *et al.*, 2015; Grinyó *et al.*, 2016; Pérez-Portela *et al.*, 2016; Sartoretto *et al.*, 2019; Benabdi *et al.*, 2019). For instance, *Eunicella cavolini* populations show contrasting differences in distribution depth limits and population structures across the Mediterranean Sea: Northwestern Mediterranean populations are characterized by dense populations dominated by small colonies (<20 cm), periodic recruitment, and low proportion of large gorgonians (>30 cm). Those from the central Adriatic displayed intermediate densities, with well-structured populations, and continuous recruitment. In the north Aegean, most populations presented low densities, high proportion of large colonies, but low number of small colonies, signifying limited recruitment (Sini *et al.* 2014, 2015).

Figure 108. Although gorgonians inhabiting coralligenous concretions show different habitat preferences, they can grow together (Photo by E. Ballesteros).

Eunicella singularis is more tolerant to a wide range of environmental conditions than *Paramuricea clavata* (Linares *et al.*, 2007a). Populations of both species also show contrasting size distribution patterns, with young individuals being dominant in *Eunicella singularis* and very scarce in *Paramuricea clavata* (Linares *et al.*, 2007a). These patterns suggest strong differences in the recruitment and general population dynamics. *Paramuricea clavata*, nor *Eunicella singularis*, displays a negative correlation between density and biomass with a slope close to -3/2, indicating that self-thinning is important in structuring the populations (Linares *et al.*, 2007a).

Growth in populations of *Paramuricea clavata* is far more sensitive to changes in survival rates than to growth, shrinkage or reproductive rates (Linares *et al.*, 2007b). Moreover, the slow growth and low mortality rates in stable conditions results in low damping ratios, which leads to low convergence to stable size structures (Linares *et al.*, 2007b). Demographic simulations to increasing mortalities show the fragility of the populations of *Paramuricea clavata*, which can be in severe decline and high risk of extinction when faced to medium to strong disturbances (Linares *et al.*, 2007b).

Paramuricea clavata is extremely sensitive to several kinds of direct and indirect anthropogenic disturbances like thermal anomalies (Cerrano *et al.*, 2000; Garrabou *et al.*, 2009a; Bramanti *et al.*, 2016), diseases (Bally & Garrabou, 2007; Vezzulli *et al.*, 2010, 2013), mucilaginous blooms (Kersting & linares, 2006; Schiaparelli *et al.*, 2007; Ponti *et al.*, 2018), anchoring (Bavestrello *et al.*, 1998), recreational and artisanal fishing (Markantonatou *et al.*, 2014), marine debris (Angiolillo *et al.*, 2015) and SCUBA diving (Harmelin & Marinopoulos, 1994; Coma *et al.*, 2004; Linares *et al.*, 2005; Linares & Doak, 2010; Tsounis *et al.*, 2012), which means that at least shallow-water populations are currently at risk of extinction (Linares *et al.*, 2009, 2017). Since *Paramuricea clavata* is living close to its upper thermal threshold in the Northwestern Mediterranean (Bensoussan *et al.*, 2010), warming can act as a driver for drastic changes in population structure and even long-term shifts in its bathymetrical distribution (Linares *et al.*, 2014) (Figure 109). In fact, shallow water populations of *Paramuricea clavata* are regularly subjected to natural disturbances, explaining the large sizes found in deep water places with regular water upwelling (Pérez-Portela *et al.*, 2016; Sartoretto *et al.*, 2019).

Figure 109. Massive mortalities triggered by thermal anomalies can have long lasting effects on *Paramuricea clavata* populations (Photo by Maite Vázquez-Luis).

Paramuricea clavata and other gorgonians are engineering species whose presence or absence affects the composition of sessile (Ponti *et al.* 2014, 2018; Gatti *et al.*, 2017; Verdura *et al.*, 2019) and vagile (Ponti *et al.* 2016; Valisano *et al.*, 2016) assemblages developing in the understory by changing some environmental conditions such as light and sedimentation rates (Valisano *et al.*, 2016). The abundance of calcareous builders like coralline algae and bryozoans is enhanced by the presence of gorgonians (Scinto *et al.*, 2009; Ponti *et al.*, 2018) (Figure 110). Disappearances of gorgonians may cause a shift from assemblages characterized by encrusting calcareous algae to filamentous and turf algae, decreasing the complexity and resilience of coralligenous bioconstructions (Ponti *et al.*, 2014; Linares *et al.*, 2018; Verdura *et al.*, 2019) (Figure 111). However, preliminary results do not show any consistent effect on the recruitment of bryozoans and other organisms in an experiment entailing presence and absence of *Paramuricea clavata* at three different regions of the Mediterranean Sea (Kipson *et al.*, 2019). Larval dispersal in *Paramuricea clavata* is restricted (Ledoux *et al.*, 2014) suggesting a very limited gene flow (Pérez-Portela *et al.*, 2016), which is corroborated by strong genetic differentiation between populations (Mokhtar-Jamaï *et al.*, 2013; Arizmendi-Mejía *et al.*, 2015a). However, small-scale spatial genetic structure is reduced, as a large amount of the mating is accomplished by males situated far away from the brooding female colonies (Mokhtar-Jamaï *et al.*, 2013). The low level of inbreeding because of multiple paternity of every brood enhances the genetic diversity of the populations (Mokhtar-Jamaï *et al.*, 2013). Nevertheless, there is a high level of genetic differentiation among populations at a western basin scale and also among populations of the same locality dwelling at different depths, which may be explained by both general and local oceanographic conditions (Mokhtar-Jamaï *et al.*, 2011). Populations in the Adriatic basin also show a significant pairwise differentiation at the local scale together with isolation by distance, revealing 4 regional clusters and a relatively high genetic diversity (Frleta-Valic *et al.*, 2014). Arizmendi-Mejía *et al.* (2015a) also show that genetic drift is strongly impacting the

Figure 110. Abundance of calcareous builders like coralline algae and bryozoans seems to be enhanced by the presence of gorgonians (Photo by E. Ballesteros).

Figure 111. Gorgonians die off may cause a shift on the understorey assemblage with an increase in turf and filamentous algae and an increase in the colonization of invasive species like *Caulerpa cylindracea* (Photo by Maite Vázquez-Luis).

smallest, most isolated populations.
For *Eunicella singularis* there is no genetic structuring of shallow water populations at the scale of 10 km but gene flow is restricted between shallow and deep populations, suggesting that deep-water populations will hardly act as a refuge to naturally recover shallow water populations after catastrophic events (Costantini *et al.*, 2016). Isolation by distance is also observed in *Eunicella cavolini*, both at the regional and local scales (Masmoudi *et al.*, 2016), although less pronounced than in other Mediterranean octocorals (Cánovas-Molina *et al.*, 2018). A low genetic differentiation is also present between deep and shallow in some populations but not in others (Masmoudi *et al.*, 2016; Cánovas-Molina *et al.*, 2018), suggesting the existence of different location-specific evolutionary histories.

11.7. Alcyonarians

The alcyonarian *Alcyonium acaule* (Figure 112) has a very slow growth, which is almost undetectable over a two-year period (Garrabou, 1999; Teixidó *et al.*, 2005). Recruitment is very low, this being the only method of population maintenance as there is no asexual reproduction (Garrabou *et al.*, 1999; Teixidó *et al.*, 2016). Mortality rates average 12.7% year^{-1}, with much higher mortalities in small colonies (Garrabou, 1999; Teixidó *et al.*, 2005). Contracted colonies are much more frequent in summer than in any other season (up to 80%) (Garrabou, 1999; Rossi, 2001). Sex ratio is 1:1 and colonies are already fertile when measuring 2-3 cm (Teixidó *et al.*, 2016). Spawning occurs once a year, mainly in July, at water temperatures higher that 20ºC (Teixidó *et al.*, 2016). Eggs are retained on the mother colony by mucous strings for a few days (Teixidó *et al.*, 2016), with larvae displaying low range dispersal and settlement near the parental colonies (Garrabou, 1999). Fertilization rates are high with blastulae developing after one day, planulae after 2-3 days and metamorphosis occurs after 8-22 days (Teixidó *et al.*, 2016). The survivorship of the recruits is moderate after two months (65-74%) (Teixidó *et al.*, 2016).

Figure 112. Sea fingers, *Alcyonium acaule*, are common components of coralligenous outcrops that show a very slow growth (Photo by E. Ballesteros).

11.8. Zoantharians

Growth and occupation of space by *Parazoanthus axinellae* (Figure 113) in coralligenous communities of the Medes Islands (northwestern Mediterranean) have been studied by Garrabou (1999). *Parazoanthus axinellae* has moderate growth dynamics (relative growth rate of 0.11 month^{-1} and a shrinkage rate of 0.09 month^{-1}) with non-significant differences over time, although growth rates peak during the summer to autumn period. Fission events are common, 29% of monitored colonies undergoing at least one fission event in two years. Fusion events were less frequent, with only 8% of colonies undergoing one fusion event in two years. Mortality rates average 9 % year^{-1}. The occupation of space in *Parazoanthus axinellae* seems to be based on spreading over the substrata at moderate rates, either by somatic growth or by fission. Most of the colonies (60%) were contracted in summer and mid autumn (Garrabou, 1999; Rossi, 2001).

Figure 113. Occupation of space in *Parazoanthus axinellae* seems to be based on spreading over the substrata by somatic growth (Photo by E. Ballesteros).

11.9. Scleractinians (*Leptopsammia pruvoti*)

Leptopsammia pruvoti is a common azooxanthellate solitary but aggregated scleractinian coral that usually inhabits crevices and overhangs in coralligenous environments across the Mediterranean Sea, reaching population densities of >17000 individuals m^{-2} (Goffredo *et al.*, 2005) (Figure 114). Polyps are dioecious, sexually mature when they reach 3 cm in length, and brood their larvae (Goffredo *et al.*, 2006). Sex ratio is 1:1 and fertilization occurs from January to April and planulation during May and June (Goffredo *et al.*, 2006). Maximum life span is 13 years and turnover time is 2.3 years, with most reproductive output coming from intermediate age classes (Goffredo *et al.*, 2010). Growth rate is homogenous and does not depend on seawater temperature (Caroselli *et al.*, 1992). Population age structures differ between populations, but no demographic characters correlated with temperature, indicating that other environmental conditions than temperature should modify size (Caroselli *et al.*, 2012). *Leptopsammia pruvoti* displays a high fecundity, short embryo incubation, small planula size and achieves sexual maturity relatively fast (Goffredo *et al.*, 2010), all characters indicating a rather accelerated dynamic for being an hexacoral. Its genetic structure indicates a deficit of heterozygosis, genetic differentiation occurring between patches within populations instead of among distant populations, and there is no correlation between genetic differentiation and geographical distance (Goffredo *et al.*, 2009). *Leptopsammia pruvoti* shows a significant decrease in organic matter, lipid and protein content of the tissue at high temperatures, with a slight increase in skeletal porosity under low pH conditions following one year of exposure (Movilla *et al.*, 2016).

Figure 114. The solitary coral ***Leptopsammia pruvoti*** makes aggregations of more than 10,000 individuals m^{-2} in coralligenous walls (Photo by E. Ballesteros).

11.10. Tunicates

Colonies of *Cystodites dellechiajei* (Figure 115), a very common ascidian in coralligenous communities (Ramos, 1991), exhibited restricted growth —or none whatsoever— over a two-year period in a vertical wall at a depth of 10-12 m in the northwestern Mediterranean (Turon & Becerro, 1992), although one of eleven colonies was able to grow actively. According to the authors' observations, only the individuals present in the most shaded microenvironments displayed active growth. Gonads were present in the population for most of the year. *Cystodites dellechiajei* shows a high relative biomass per unit area, low growth rates, high survival values (Turon & Becerro, 1992), and the presence of chemical defences (Uriz *et al.*, 1991), which would seem to indicate a very conservative life strategy.

Figure 115. Colonial ascidian *Cystodytes dellechiajei* exhibits restricted growth rates in coralligenous assemblages (Photo by E. Ballesteros).

Two solitary ascidian species common in coralligenous assemblages spawn in late summer and early autumn. Gamete release occurred after the period of highest temperature (September-October) in *Halocynthia papillosa* (Figure 116), while for *Microcosmus sabatieri* it occurred in October-November (Becerro & Turon, 1992). In order to explain the surprising fact of spawning after summer, a period of temperature and food limitation, Ribes *et al.* (1998) studied the natural diet and prey capture of the ascidian *Halocynthia papillosa* across an annual cycle. The natural diet included detrital organic matter, bacteria, *Prochlorococcus* and *Synechococcus*, protozoa and phytoplankton, with a mean size ranging from less than 1 µm to 70 µm. One specimen of *Halocynthia papillosa* weighing 0.25 g afdw was estimated to ingest an annual mean of 1305 µg C g afdw-1 h^{-1}. Carbon from detrital origin accounted for 92% of the total ingested carbon, while live carbon accounted for only 8%. Ingestion rates showed a marked seasonal pattern, with the highest ingestion of detrital particles in spring and the highest values of ingestion of live particles in summer and autumn. Ribes *et al.* (1998) hypothesize that live particles are of more significance in the species' diet than are particles of detrital origin, as the seasonal variation of ingested nitrogen from live particles explained 91% of the gonadal development variance for the year. Thus, living sestonic organisms, rather than detrital carbon, may be an essential source of nitrogen and other nutrients necessary for growth and reproduction in *Halocynthia papillosa*.

Figure 116. Solitary ascidian *Halocynthia papillosa* is a common species in coralligenous assemblages (Photo by E. Ballesteros).

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12. Disturbance

Natural ecosystems are affected by both natural and anthropogenic disturbances in response to various natural and human stressors. Sometimes it is not easy to know if the driver of a disturbance is mediated or not by a human stressor since the final effects on the whole ecosystem and their populations are the same or very similar. Very often stressors act together usually increasing (but also sometimes decreasing) their effects. The coralligenous environment is subjected to very different stressors, which can have serious impacts on its global structure, the species inhabiting the outcrops, and eventually putting some habitats at risk and causing severe ecological shifts.

Coralligenous habitats are very vulnerable to disturbances due to the longevities displayed by most of the engineering species (Teixidó *et al.*, 2011) and their low dispersal, strong isolation and high level of structuring (e.g. Costantini *et al.*, 2018). Mass mortalities, shifts from bioconstructors to turf-dominated assemblages, homogenization, loss of alpha and beta-diversity, increase in opportunistic/tolerant fast-growing species (stoloniferans, mussels, hydrozoans, erect macroalgae, serpulids, bryozoans) and disappearance of sensitive species are amongst the most observed impacts (Piazzi *et al.*, 2012, 2014, 2015, 2017; Di Camillo & Cerrano, 2015; Montefalcone *et al.*, 2017; Sartoretto *et al.*, 2017; Verdura *et al.*, 2019). Among the stressors or pressures that have been reported to impact the coralligenous assemblages we can mention trawling, artisanal and recreational fishing, harvesting, pollution (waste water discharges, aquaculture activities, diffuse), anchoring, alien species invasions, diving activities, blooming of mucilaginous and filamentous aggregates, increased sedimentation rates, marine debris, shipwrecks, catastrophic storms, diseases, warming and acidification (Ballesteros, 2006, 2009; Teixidó *et al.*, 2013; Cerrano *et al.*, 2014; Linares *et al.*, 2015; Holon *et al.*, 2015; Cánovas-Molina *et al.*, 2016a; Penna *et al.*, 2017; Bevilacqua *et al.*, 2018; Ingrosso *et al.*, 2018). Next we will report on the stressors acting over the coralligenous assemblages and their already observed or expected impacts.

12.1. Warming

A warming trend is observed in the Mediterranean (Bethoux *et al.*, 1990; Vargas-Yañez *et al.*, 2008; Rivetti *et al.*, 2014) with coastal water temperature increases by 1 ºC in the last 30 years (Garrabou *et al.*, 2009a,b). Interannual variation has increased over this period for the water situated above 20 meters depth in Liguria (Parravacini *et al.*, 2015) causing thermal anomalies in shallow waters. Owing to climatic and hydrographic anomalies in the Ligurian Sea, the characteristic summer conditions of reduced resources, high water column stability and high temperatures (normally during July and August) lasted much longer than usual in the summer of 1999. This coincided with a mass mortality event of benthic suspension feeders over several hundred kilometres, affecting coralligenous communities situated at a depth of less than 40 m, where the temperature anomaly lasted for over a month (Perez *et al.*, 2000; Romano *et al.*, 2001) (Figure 117).

Figure 117. Impact of the temperature anomaly of summer 1999 in *Paramuricea clavata* colonies from Port-Cros National Park, France (Photo by E. Ballesteros).

The accumulated density decrease in *Paramuricea clavata* colonies four years after the mass mortality event accounts for around half the initial population at the Port-Cros National Park (France) (Linares *et al.*, 2005). Red coral populations thriving above a depth of 30 m were also affected (Garrabou *et al.*, 2001). This large-scale mortality event, together with other small-scale mass mortality events (Cerrano *et al.*, 2000), seems to be unequivocally related to seawater temperature increase and global warming (Romano *et al.*, 2000) (Figure 118).

Figure 118. Partial mortality of *Eunicella cavolini* in Fornells, Menorca, after the temperature anomaly of summer 1999 (Photo by E. Ballesteros).

Several episodes of suspension feeder mortality at the end of the twentieth century are also probably related to thermal anomalies (Bavestrello & Boero, 1986; Rivoire, 1991; Harmelin & Marinopoulos, 1994; Bavestrello *et al.*, 1994). Garrabou *et al.* (2009a) report 25 macroinvertebrates affected by the temperature anomaly of 2003, with highest impact in the Gulfs of Genoa and Naples, medium impact in Provence, Corsica and Sardinia and the lowest impact in Catalonia and the Balearic Islands. The species reported include gorgonians (*Paramuricea clavata, Eunicella cavolini, E. singularis, E. verrucosa, Leptogorgia sarmentosa, Corallium rubrum*), scleractinians (*Cladocora caespitosa, Balanophyllia europaea*), zoantharians (*Parazoanthus axinellae*), sponges (*Spongia officinalis, Ircinia dendroides, I. variabilis, I. oros, Agelas oroides, Crambe crambe, Cacospongia* sp., *Hippospongia communis, Petrosia ficiformis*), bryozoans (*Myriapora truncata, Reteporella* spp.) and bivalves (*Spondylus gaederopus, Lima* spp., *Arca* spp., *Ostrea edulis, Lithophaga lithophaga*). Other coralligenous species that have been reported to suffer extensive damage are the sponges *Chondrosia reniformis* (Di Camillo & Cerrano, 2015), *Aplysina cavernicola* (Kruzic & Rodic, 2014) and *Cliona viridis* (Foulquié *et al.*, 2019), the scleractinians *Madracis pharensis, Caryophyllia inornata* and *Leptopsammia pruvoti* (Kruzic & Rodic, 2014), the bryozoans *Pentapora fascialis, Reteporella beaniana* (Kruzic & Rodic, 2014, Harmelin, 2017b) and *Schizotheca serratimargo* (Ballesteros, personal observations), the tunicates *Pyura dura, Halocynthia papillosa* and *Microcosmus* spp. (Cerrano *et al.*, 2000) and the coralline red alga *Lithophyllum stictaeforme* (Cerrano *et al.*, 2000). Other mortality events related to warming in the western Mediterranean are described for *Paramuricea clavata* (Gambi *et al.*, 2006; Sbrescia *et al.*, 2008; Huete-Stauffer *et al.*, 2011; Linares *et al.*, 2018) (Figures 119, 120) and *Eunicella singularis/Eunicella cavolini* populations (Coma *et al.*, 2006; Turicchia *et al.*, 2018). Two large mass mortality events have been reported from the Adriatic during 2003 and 2012, when temperatures reached up to 6ºC above the average, affecting up to 30 species down to 40 m depth, mainly in the southern and central Adriatic (Kruzic & Rodic, 2014). Values of 28 °C in the Cres area and 30 °C in Mljet in 2009 were concomitant with moderate to severe mass mortalities of scleractinian corals and gorgonians down to 45 m (Kruzic *et al.*, 2016).

After 1999, positive thermal anomalies in shallow western Mediterranean waters became much more frequent (i.e. 2003, 2006, 2009, 2011, 2012) (Bensoussan *et al.*, 2010; Coma *et al.*, 2006; Kruzic & Rodic, 2014; Linares *et al.*, 2018) following a planetary trend (Frölicher *et al.*, 2018; Frölicher & Laufkötter, 2018). Summer conditions have increased by 40% from the 1970s (Coma *et al.*, 2009). Warmer waters coupled with reduced food resources result in biomass loss >35% and severe mortalities in laboratory conditions in *Paramuricea clavata* (Coma *et al.*, 2009) indicating that temperature anomalies are the underlying cause of the mass mortality episodes, with energetic constraints serving as a triggering mechanism (Coma *et al.*, 2009, 2015). Some suspension feeders might be able to withstand the normal duration of adverse summer conditions but not an anomalous prolongation of these conditions (Coma *et al.*, 2000; Coma & Ribes, 2003), resulting from an energy shortage of suspension feeders related to low food availability in summer.

Figure 119. Aspect of the shallowest (-38 m) population of *Paramuricea clavata* from Imperial Islet (Cabrera, Balearic Islands) before the summer thermal anomaly of 2007 (Photo by E. Ballesteros).

Figure 120. Aspect of the shallowest (-38 m) population of *Paramuricea clavata* from Imperial Islet (Cabrera, Balearic Islands) in autumn 2007 right after a thermal anomaly (Photo by E. Ballesteros).

Thermal anomalies mainly affect shallow waters (Bensoussan *et al.*, 2010; Rivetti *et al.*, 2014), causing massive mortalities in the upper distribution limits of the species and, thus, healthy populations remain only in deep waters (Linares *et al.*, 2005, 2017; Ponti *et al.*, 2014, 2018; Gatti *et al.*, 2017). Recovery of populations after a catastrophic mass mortality is not easy due to the low dispersal rate of most affected organisms (Abiatti *et al.*, 2009; Ledoux *et al.*, 2010a, 2014; Costantini *et al.*, 2007, 2016a, 2018), the low growth (Garrabou & Harmelin, 2002; Teixidó *et al.*, 2005; Linares *et al.*, 2007b), the fact that reproduction itself is also affected (Cerrano *et al.*, 2005; Linares *et al.*, 2008; Arizmendi-Mejía *et al.*, 2015b) and the existence of barriers that prevent colonization of shallow water outcrops by larvae from deep water populations (Costantini *et al.*, 2011). However, some populations of *Paramuricea clavata* show a slight recovery due to an increase in the recruitment rate (Cerrano *et al.*, 2005; Cupido *et al.*, 2012), coenenchyme regeneration and fragmentation of affected branches (Cerrano *et al.*, 2005). Clonal reproduction seems to be too low to play an important role in population recovery (Pilczynka *et al.*, 2017).

The mid- to long-term effects of these massive mortalities at the community level are much less documented. However, Coma *et al.* (2006) show that the delayed effects in the 1999 mass mortality event on *Eunicella singularis* exert a much greater impact than the immediate effects (Figures 121, 122). In a *Paramuricea clavata*-dominated coralligenous wall, these delayed consequences lead to important changes in species composition, structure and functioning, replacing a structurally complex habitat dominated by long-lived species, by a simplified habitat with lower species richness and diversity dominated by turf-forming species (Verdura *et al.*, 2019). In fact, gorgonians are known to affect the composition of vagile assemblages (Ponti *et al.*, 2016) and enhance the presence of calcareous builder organisms (Scinto *et al.*, 2009; Ponti *et al.*, 2018). Moreover, there are long-lasting effects on the densities, colony growth, colony shape, and population structure of the populations affected by mass mortality events (Cerrano & Bavestrello, 2008).

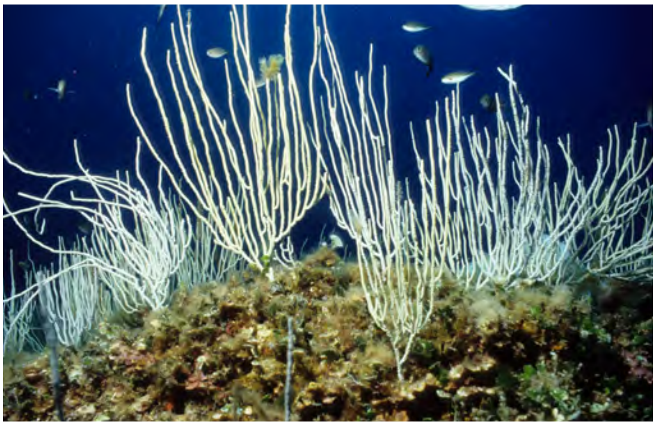

Figure 121. Aspect of the population of *Eunicella singularis* from Fornells (Menorca, Balearic Islands) in year 1990 (Photo by E. Ballesteros).

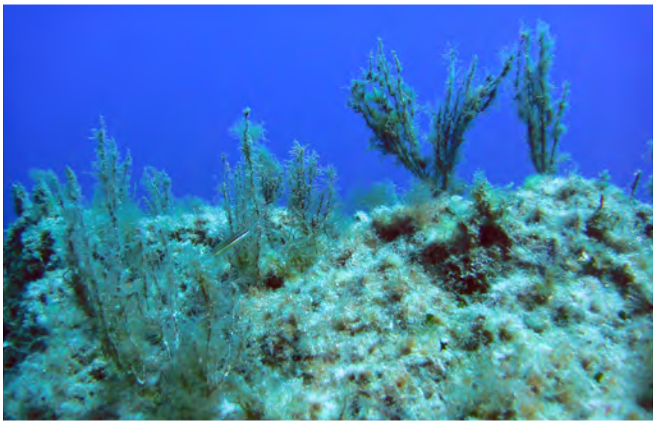

Figure 122. Aspect of the population of *Eunicella singularis* from Fornells (Menorca, Balearic Islands) in year 2004, four years after the occurrence of the 1999 and 2003 thermal anomalies (Photo by E. Ballesteros).

Most mass mortality events are unequivocally related to thermal anomalies (Rivetti *et al.*, 2014). However, warming cannot be blamed for a mass mortality episode affecting 80% of the largest colonies of *Corallium rubrum* along the Amalfi coast and the Gulf of Salerno, at a depth range between 80 and 100 m (Bavestrello *et al.*, 2014). The formation of local-down-welling currents, sudden activity of sulphur springs or local landslides increasing turbidity are natural processes that could trigger this mortality event (Bavestrello *et al.*, 2014). Other mass mortalities are the consequence of pathogens, filamentous or mucilaginous aggregates or anoxic events (Cerrano & Bavestrello, 2008).

Although thermal anomalies together with the food availability shortage typical of summer months seem to be necessary for most of these mortality events to occur, Bally & Garrabou (2007) found that inoculation of four bacterial isolates from diseased *Paramuricea clavata* colonies onto healthy colonies caused disease signs similar to those observed during the 2003 mortality event. The infection depended on elevated seawater temperatures in a range consistent with the field records during thermal anomalies. *Vibrio coralliilyticus* showed virulence to *Paramuricea clavata* (Bally & Garrabou, 2007) although Vezzulli *et al.* (2010) also found other species of *Vibrio* (*V. harveyi, V. splendidus*). Huete-Stauffer *et al.*, (2013) also found bacteria belonging to the genus *Vibrio* in a mass mortality event of *Paramuricea clavata* in Sardinia, but it did not seem the etiological cause of death. Latest research suggests that the interplay of environmental stressful events (high temperature, energy constrains) and microbial infections may be superimposed to compromise immunity and trigger mortality outbreaks (Vezzulli *et al.*, 2013) (Figure 123). In fact, 90% of the bacterial community associated to *Paramuricea clavata* in pristine locations was represented by the genus *Endozoicomonas* (Oceanospirillales), while samples collected in human impacted areas and during mass mortality events had higher bacterial diversity and abundance of disease-related bacteria such as *Vibrio* spp. (Vezzulli *et al.*, 2013).

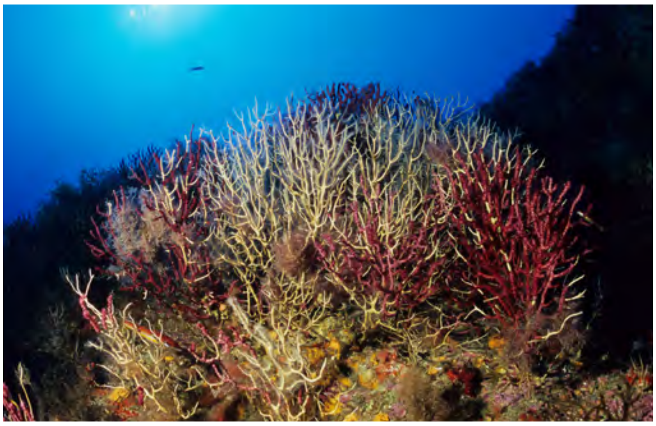

Figure 123. Latest research suggests that the interplay of environmental stressful events (high temperature, energy constrains) and microbial infections may trigger mortality outbreaks (Photo by E. Ballesteros).

Moreover, a shift in microeukaryotic communities associated to *Paramuricea clavata* from ciliates to apicomplexans has been observed when temperature changed from 18ºC to 25ºC (Ledoux *et al.*, 2019). Thus, it seems that high temperatures and energetic constrains affect the composition of the microbiome of *Paramuricea clavata*.

12.2. Diseases

Although diseases are natural processes that regulate population dynamics of several organisms (Boero, 1996), there is recent evidence of an increase in the frequency and intensity of mass mortality events, partially or totally related to diseases (Cerrano & Bavestrello, 2009). Here we report a list of diseases observed in organisms that inhabit coralligenous concretions, regardless of whether they are or not related to an anthropogenic pressure.

As it has been said already, diseases by pathogenic bacteria of the genus *Vibrio* seem to play an important role in mass mortality events of *Paramuricea clavata*, although they are not solely sufficient to trigger these outbreaks (Vezzulli *et al.*, 2013).

Warm water and the massive proliferation of a cyanobacterium attributed to the genus *Porphyrosiphon* have been hypothesized to be the main causes of a disease affecting *Parazoanthus axinellae* (Cerrano *et al.*, 2006).

At least since the year 1981 the bivalve *Spondylus gaederopus* (Figure 124) has been suffering frequent and recurrent mortalities that are not related to thermal anomalies (Meinesz & Mercier, 1983; Ballesteros, personal observations), which has been related to some viral, bacterial or fungal infection.

Figure 124. Bivalve *Spondylus gaederopus* undergoes frequent mortalities related to a recurrent disease (Photo by E. Ballesteros).

Recently, *Pinna nobilis* has suffered a mass mortality event in the western Mediterranean Sea (Vázquez-Luis *et al.*, 2017) caused by a haplosporidan parasite (Darriba, 2017; Catanese *et al.*, 2018) with a high spread potential (Cabanellas-Reboredo *et al.*, 2019) that can colonize also other Mediterranean areas and can put this species at the break of extinction.

Sphaerechinus granularis, one of the most common sea urchins in shallow coralligenous beds, suffers from the bald sea-urchin disease (Figure 125), a non-specific bacterial disease affecting to other echinoids, which causes conspicuous lesions on the body surface and may cause death (Höbaus *et al.*, 1981; Maes & Jangoux, 1984, 1985). Partial mortalities of coralligenous building algae *Mesophyllum alternans, Neogoniolithon mamillosum* and *Lithophyllum stictaeforme*, similar to the coralline white band syndrome and the coralline white patch disease have been observed along the Spanish Mediterranean coasts, apparently associated to high seawater temperatures (Hereu & Kersting, 2016) although not unequivocally (Hereu *et al.*, 2019).

Figure 125. *Sphaerechinus granularis* suffers from the bald sea-urchin disease, a non-specific bacterial disease affecting to echinoids (Photo by E. Ballesteros).

Finally, outbreaks of the viral encephalopathy and retenopathy disease have been observed affecting dusky groupers -mainly the dusky grouper, *Epinephelus marginatus*- in Italy (Marino & Azzurro, 2001; Vendramin *et al.*, 2013; Giacopello *et al.*, 2013), Tunisia (Haddad-Boubaker *et al.*, 2014), Algeria (Kara *et al.*, 2014) and the Balearic islands (Valencia *et al.*, 2019), as well as moray eels, *Muraena helena* (Valencia *et al.*, 2018). Infected individuals suffer from abnormal swimming, external wounds, reduced vision, neurological lesions and, finally, death (Figure 126).

Figure 126. A grouper *Epinephelus marginatus* affected by the viral encephalopathy and retinopathy disease in Cabrera (Balearic Islands) (Photo by E. Ballesteros).

12.3. Mucilaginous and filamentous algae

Blooming of mucilaginous and filamentous algal aggregates (Figure 127) can trigger important mortalities in gorgonians (Mistri & Ceccherelli, 1996; Giuliani *et al.*, 2005; Kersting & Linares, 2006; Schiaparelli *et al.*, 2007) since they entrap the aggregates and can suffocate the polyps. These events are specially important and recurrent in the northern Adriatic (Precali *et al.*, 2005) and in Liguria (Cánovas-Molina *et al.*, 2016a). The effects of such events involve not only partial colony necrosis of gorgonians but also a decrease in the abundances of encrusting coralline algae and bryozoans, an increase in turf algae and a decrease in alpha- and beta-diversity (Piazzi *et al.*, 2018). Whether these mucilaginous events are related to anthropic activities like eutrophication is not well understood (Ingrosso *et al.*, 2018). The organisms causing these events are probably different from one place to another, the mucilaginous aggregates from the northern Adriatic being probably different from the filamentous aggregates from the western Mediterranean. According to Sartoni & Sonni (1991) and Sartoni *et al.* (1995) three main species are involved, the Ochrophyta *Acinetospora crinita* and the Chrysophyta *Nematochrysopsis marina* and *Chrysonephos lewisii*, although other species such as the ochrophyta *Zosterocarpus oedogonium* have also been reported (Schiaparelli *et al.*, 2007).

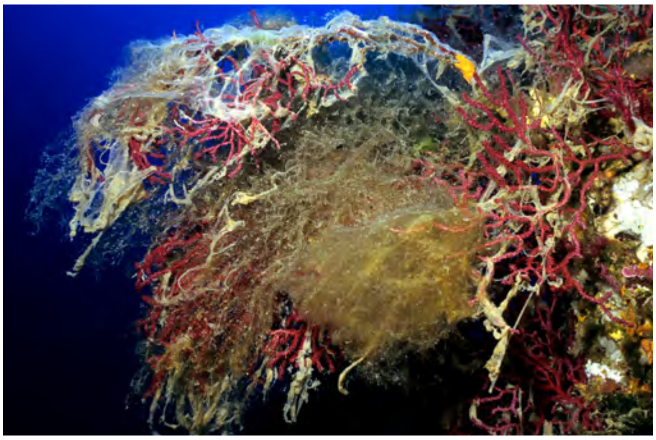

Figure 127. Gorgonians entrap filamentous aggregates involving partial colony necrosis (Photo by E. Ballesteros).

12.4. Pollution

Hong (1980) studied the effects of wastewater along three stations situated in a gradient of multisource pollution in the Gulf of Fos (Marseilles), and in an unpolluted reference zone. Biodiversity decreased from the reference station (310 species) to the most polluted zone (214 species), and mainly affected bryozoans, crustaceans and echinoderms; molluscs and polychaetes were largely unaffected. The number of individuals also decreased with increased pollution, as did the biomass of sponges and bryozoans, and the diversity of invertebrates (Shannon's index). However, the density of sipunculids increased with pollution.

Pollution also quantitatively decreases the number of infralittoral species in coralligenous communities and increases those species with a wide ecological distribution (Hong, 1980, 1983).

The abundances of the species responsible for build-up and those living in the coralligenous community decrease with the pollution gradient, both in terms of number and density of individuals. There are few data concerning the impact of various pollutants on the growth of coralline algae (Littler, 1976), although it is known that orthophosphate ions inhibit calcification (Simkiss, 1964). However, Hong (1980) observed that with increased pollution, large thalli of *Mesophyllum alternans* are replaced by Peyssonneliaceae, which have a much lower building capacity (Sartoretto, 1996). Moreover, the species that act as bioeroders (Figure 128) are more abundant in polluted areas (Hong, 1980). Thus, all the available evidence suggests that pollution accelerates the destruction of coralligenous assemblages and inhibits building activity.

Figure 128. . Bioeroders such as the boring sponge *Cliona viridis* become more abundant in polluted areas (Photo by E. Ballesteros).

Hong's (1980) main conclusions are that pollution (1) decreases species richness, (2) greatly increases the relative abundance of species with a wide ecological distribution, (3) almost eliminates some taxonomical groups, (4) decreases the abundance of the largest individuals of the epifauna and (5) inhibits coralligenous construction and increases its destruction rates. Piazzi *et al.* (2011) show that the structure of both mature and early successional macroalgal assemblages from coralligenous outcrops significantly vary between areas were nutrients are experimentally supplied than in untreated areas, early successional stages displaying stronger differences than mature assemblages.

The presence of coastal industries has been associated with an increased spatial heterogeneity and decreased diversity of coralligenous assemblages (Bevilacqua *et al.*, 2012). Cormaci *et al.* (1985) studied the deep-water phytobenthic communities developing over coralligenous concretions in the Gulf of Augusta, a site that is heavily polluted by both urban and industrial wastewater. Water turbidity seems to be the main factor causing degradation and homogenization of the phytobenthos. There is a slight decrease in the number of species (26 algal species sample^{-1}) when compared to similar sites and depths of unpolluted areas (30 to 38 algal species sample^{-1}) (Furnari *et al.*, 1977; Battiato *et al.*, 1979).

12.5. Fishing

High fishing pressure plays a major role in the degradation of hard bottom communities (Bavestrello *et al.*, 1998, 2014; Boudouresque *et al.*, 2017). Both traditional and recreational fishing have an effect on coralligenous communities, affecting target species but also erect species and the bioconstruction itself (Figures 129, 130).

Figure 129. Traditional fishing gear like trammel nets have an important direct mechanical damage on the fragile coralligenous outcrops (Photo by E. Ballesteros).

Figure 130. Fronds of endangered kelp *Laminaria rodriguezii* removed by a trammel net fishing for lobster on a coralligenous bottom (Photo by E. Ballesteros).

Besides the impact on target species there is a direct mechanical damage caused by fishing gear (Bavestrello *et al.*, 1998; Piazzi *et al.*, 2012; Enrichetti *et al.*, 2019a), whereas indirect effects involve increase in sediment load and resuspension as well as damage from ghost nets (Figure 131) and lost fishing lines (Bo *et al.*, 2009; Markantonatou *et al.*, 2014; Cau *et al.*, 2015; Ferrigno *et al.*, 2018a). Consoli *et al.*, (2018) show that 98% of litter in Mediterranean remote islands like those in the Straits of Sicily correspond to fishing lines, causing entanglement and coverage of organisms (30%) and damaging (15%) the fauna. Bo *et al.* (2014) report that 40% of ROV video frames show broken corals or other signs of fishing impacts.

Figure 131. Lost fishing nets damage engineering species and continue capturing fish and decapods for a long time (Photo by E. Ballesteros).

Trawling is probably the most destructive fishing method and is causing degradation of large areas of coralligenous concretions (Boudouresque *et al.*, 1990). García *et al.* (2014) report that 37% of coralligenous and maërl beds from the Balearic Islands are directly affected by bottom trawling. Trawling not only causes direct physical damage by breaking down the coralligenous structure and rolling the coralligenous blocks, but also negatively affects photosynthetic production of encrusting and erect algae by increasing turbidity and sedimentation rates when applied to adjacent sedimentary bottoms (Palanques *et al.*, 2001). Tegnùe reefs from the northern Adriatic are highly friable and are seriously threatened by this activity (Pranovi *et al.*, 2000).

Fishing leads to a significant decrease in mean specific number of fish species, producing changes in the composition of the community (Bell, 1983; Garcia-Rubies & Zabala, 1990). This effect is due not only to the nearly total absence of some fish, demonstrated in two species (*Epinephelus marginatus* and *Sciaena umbra*) that are extremely vulnerable to spearfishing (Figure 132), but also to the notable scarcity of other species (Garcia-Rubies, 1999). However, depth acts as a protective factor by limiting the effects of fishing, given the inherent difficulty in locating from the surface the coralligenous bottoms that are isolated from the coast (Garcia-Rubies, 1999). No cascading effects through overfishing have so far been detected in coralligenous communities, as they have been in shallow rocky bottoms (Sala *et al.*, 1998), although they may well exist as both densities and sizes of fish and lobsters have been greatly modified over the last one hundred years.

Figure 132. Groupers and other vulnerable fish rapidly recover after fishing prohibition (Photo by E. Ballesteros).

Whatever the case, populations of groupers and other vulnerable fish rapidly recover after fishing prohibition (Harmelin, 1991; Coll *et al.*, 1999; Harmelin & Robert, 2001) (Figure 133) and readily exhibit normal socio-behavioural patterns and reproductive success (Zabala *et al.*, 1997a, b).

Figure 133. Brown meagre, ***Sciaena umbra***, is extremely vulnerable to spearfishing (Photo by E. Ballesteros).

12.6. Red coral harvesting

Special trawling to collect precious red coral with what is known as the 'Italian Bar' or 'St. Andrew Cross' is highly destructive. Ortiz *et al.* (1986) report the capture of up to 50 kg of benthic fauna (mainly gorgonians) in order to collect 15 kg of living red coral in the Alboran Sea. The abovementioned device is so effective at destroying the seabed that it has also been used for scientific studies of fauna associated with red coral (Templado *et al.*, 1986; Maldonado, 1992).

Coral harvesting by divers or manned submersibles is not as destructive but changes completely the size structure of the populations, and the branching pattern and density of the colonies (Tsounis *et al.*, 2007; Montero-Serra *et al.*, 2014, 2015; Cattaneo-Vietti *et al.*, 2016). The maximum sustainable yield in the coralligenous bottoms of the Costa Brava (Spain) is reached at an age of first capture between 30 and 100 years, while current legislation allows harvesting of approximately 11 year-old colonies (Tsounis *et al.*, 2007). Maximum life span of 99 % of the colonies was 60 years at Portofino (Italy) and 40 years at Cap de Creus (Spain). According to measured annual growth rate of basal diameter (0.24 mm year^{-1}), the minimum harvestable size (7 mm basal diameter) was reached in 30–35 years, and the percentage of colonies above it was 6.7 % at Portofino and 2.1 % at Cap de Creus (Tsounis *et al.*, 2007).

Shallow (< 50 m) red coral populations are much more harvested than deep-water populations (Rossi *et al.*, 2008; Cattaneo-Vietti *et al.*, 2017) and are more exposed to mortality events (Garrabou *et al.*, 2009a) and to poaching of juvenile colonies (Tsounis *et al.*, 2007) (Figure 134). Since deep-water populations should not be considered as a plausible larval source for shallow water populations due to their extremely low connectivity (Costantini *et al.*, 2011), survival of shallow water red coral populations is at stake.

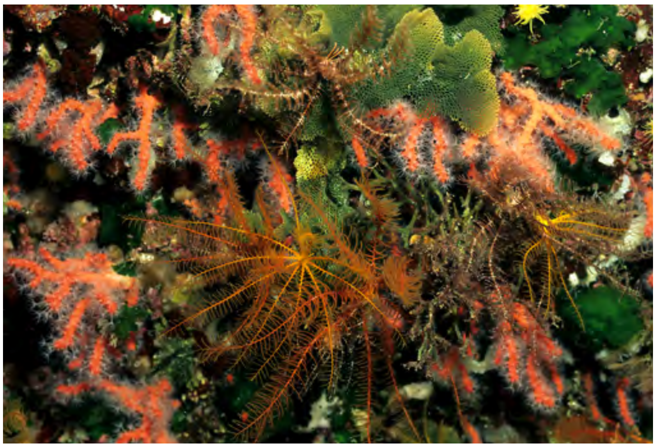

Figure 134. Shallow water populations of red coral are heavily harvested and are composed of small colonies (Photo by E. Ballesteros).

Creation of no-take MPAs is a good solution to protect red coral populations although poaching events always occur, even in the best surveyed places (Linares *et al.*, 2011, 2019). The development of molecular forensic methods and statistical analyses (Ledoux *et al.*, 2013, 2016) should help in the assignment of harvested colonies to their populations of origin, opening new instruments to struggle against poaching and illegal trade.

All this data suggest a non-sustainable exploitation of red coral which, together with the finding of a pristine population in Scandola (Corsica) (Garrabou *et al.*, 2017), suggest the need for a harvesting moratorium in most-harvested areas, the enforcement of no-take MPAs in areas with red coral populations and the establishment of much larger fishing minimum legal colony sizes (Garrabou *et al.*, 2017; Linares *et al.*, 2019).

12.7. Marine debris

Occurrence of marine debris in coralligenous outcrops is massive and widespread (Ingrosso *et al.*, 2018; Ruitton *et al.*, 2019). Ten per cent of ROV images in the deep waters of Cap de Creus have man-made objects (Sardá *et al.*, 2012). Litter concentrates over rocky bottoms (Melli *et al.*, 2015) affecting gorgonians, red coral, antipatharians and big sponges. Most litter objects present in coralligenous bottoms are long-lines and ghost nets. Ruitton *et al.* (2019) describe a protocol -Ghost Med- devoted to quantifying the impact of lost fishing gear in the French Mediterranean and propose tools for their removal.

12.8. Anchoring

Boat anchoring has a high destructive potential in coralligenous formations (Ballesteros, 2006) and it is an important cause of damage and mortality of *Paramuricea clavata* in Portofino Promontory (Bavestrello *et al.*, 1998).

12.9. Diver frequentation

The coralligenous community is one of the most popular sites for recreational diving in the Mediterranean (Boudouresque, 2004b; Chimienti *et al.*, 2017) due to its great variety of life and great visual appeal (Harmelin, 1993). Several studies have detected the direct impact of divers on the largest invertebrates of the coralligenous community. Sala *et al.* (1996) found that the large and fragile calcareous bryozoan *Pentapora fascialis* was present at all levels of exposure (from overhangs to epibiotic) in locations where diving was not allowed, whereas colonies were largely restricted to cryptic positions at diving locations in the Medes Islands marine reserve (Figure 135).

Figure 135. Fragile calcareous colonies of bryozoan *Pentapora fascialis* are good indicators for recreational diving stress on coralligenous environments (Photo by E. Ballesteros).

Density, colony diameter and colony height were also significantly lower at frequented than at unfrequented sites. Densities of colonies of the bryozoan *Pentapora fascialis* showed a significant decrease (50% in one year) after a diving site was opened in the marine protected area of the Medes Islands (Garrabou *et al.*, 1998). The impact was greater on boulders covered by coralligenous concretions than on vertical walls, probably as a result of the protection provided by the dense canopy of the gorgonian *Paramuricea clavata*. In fact, most erect calcareous bryozoans are good indicator species for recreational diving stress on coralligenous environments (Luna-Pérez *et al.*, 2009; Nuez-Hernández *et al.*, 2014). The number of species of erect bryozoans and the colony sizes of *Adeonella calveti, Myriapora truncata, Pentapora fascialis, Reteporella grimaldii*, and *Smittina cervicornis* decreases at increasing diving frequencies (Casoli *et al.*, 2016).

The tunicate *Halocynthia papillosa* is also very sensitive to the adverse effects of scuba diving (Luna-Pérez *et al.*, 2010). Individuals at frequently dived sites are smaller, less abundant, and occupy more cryptic positions than those present in non-dived localities.

High levels of recreational scuba diving (e.g. > 1000 visits site^{-1} year^{-1}) also appear to be greatly modifying the natural demographic parameters of *Paramuricea clavata* in the Medes Islands marine reserve and adjacent sites by means of a three-fold increase in adult mortality (Coma *et al.*, 2004) (Figure 136).

Figure 136. Gorgonian populations of *Paramuricea clavata* are highly sensitive to high levels of recreational scuba diving (Photo by E. Ballesteros).

This increase in adult mortality is due to toppling by divers, since annual mortality induced by overgrowth is almost similar in dived and non-dived sites, whereas annual mortality by toppling in high visitation areas ranges from 4.9 to 6.9% (1.5% in low visited sites). Non-intentional breaking of gorgonians *Paramuricea clavata* has also been reported by Harmelin & Marinopoulos (1994) from the coralligenous communities in Port-Cros National Park (France). Epibionts in *Paramuricea clavata* following tissue injury are more abundant if exposed to scuba diving than if this activity is forbidden. Reproductive success on walls and overhangs seem to be reduced by bubbles as they efficiently remove eggs brooded on colony branches (Tsounis et al 2012).

Warming-related mortalities have more significant effects on *Paramuricea clavata* than diving activities, but the combination of both disturbances can have large and lasting effects on the future viability of gorgonian populations (Linares *et al.*, 2010). Simulated reduction of diving effects dramatically increases the time to quasi-extinction for populations of *Paramuricea clavata* subjected to realistic frequencies of mass mortality events (Linares and Doak, 2010).

In conclusion, high frequencies of scuba diving might lead the coralligenous community to be dominated by erosion-resistant species, such as encrusting and massive organisms, rather than erect, articulate and foliose species (Garrabou *et al.*, 1998; Betti *et al.*, 2019). Therefore, human frequentation may affect the coralligenous community as a whole.

12.10. Catastrophic storms

Extreme storms have a deep physical impact on coralligenous outcrops. Teixidó *et al.* (2013) report a major shift immediately after a catastrophic -once every fifty years- storm in the Catalan coast, with changes in species richness, beta-diversity and cover of benthic species up to 58%. Species with fragile forms (e.g. bryozoans *Adeonella calveti* and *Myriapora truncata,* red algae *Lithophyllum stictaeforme* and *Peyssonnelia rosa-marina*, cnidarians *Paramuricea clavata* and *Parazoanthus axinellae*, and sponges *Dysidea avara* and *Clathrina clathrus*) (Figure 137) were the most impacted and cover losses ranged between 50 and 100%. On the contrary, other species such as sponges *Crambe crambe, Agelas oroides* or *Chondrosia reniformis* showed affections lower than 20%. The same storm caused a mean decrease of 13% in the density of colonies of *Paramuricea clavata* (Coma et al., 2012). Even if a large amount of coralligenous fish species were casted onto shore in beaches situated close to coralligenous bottoms (i.e. *Epinephelus marginatus, Anthias anthias*) (Garcia-Rubies *et al.*, 2012a,b) *in situ* fish counts before and after the storm did not detect any major effect on their populations.

Figure 137. Erect bryozoan *Adeonella calveti* was one of the most impacted species after a catastrophic storm hit Medes Islands MPA in December 2008 (Photo by E. Ballesteros).

According to Teixidó *et al.* (2013) the abrasion of the storm was not able to completely homogenize the substrate and small surviving patches of perennial species -mainly encrusting algae and clonal encrusting invertebrates- remained, favouring the recovery via vegetative regrowth one year after the storm.

Cocito *et al.* (1998) also found a high mortality of the bryozoan *Pentapora fascialis* after a severe winter storm in Tino Island (Liguria). The recovery of the population to pre-storm coverage required three and a half years (Cocito *et al.*, 1998).

12.11. Sedimentation

Increasing sedimentation is a major problem for rocky reefs (Airoldi, 2003). Anthropogenic changes to land cover (urbanization, forest loss, intensification of agriculture in steep slopes) may increase soil erosion and sediment deliveries in coastal waters, increasing turbidity and sedimentation (Mateos-Molina *et al.*, 2015). Shoreline alterations like coastal urbanization, construction of harbours and coastal defences and other coastal engineering works (e.g. beach regeneration) also modify significantly the sedimentary regimes (Ingrosso *et al.*, 2018). Trawling also increases turbidity and sedimentation rates (Palanques *et al.*, 2001) that can affect coralligenous concretions when performed in sedimentary bottoms situated nearby (Ballesteros, 2006).

High levels of sedimentation cause an important decrease in organism cover in coralligenous outcrops, changing also the community and its dynamics (Ferrigno *et al.*, 2018b) (Figure 138). According to Roghi *et al.* (2010) increased sedimentation rate is one of the major impacts responsible for the changes observed in coralligenous assemblages in Punta Mesco (Liguria) since 1937. The main stressor affecting the coralligenous shoals of Vado Ligure is also probably the high sedimentation rate (Gatti *et al.*, 2012). High levels of sedimentation can cause severe alterations in macroalgal coralligenous assemblages (Piazzi *et al.*, 2012) by enhancing the growth of turf-forming algae and encrusting invertebrates over erect and encrusting algae (Balata *et al.*, 2005). However, there are some species whose presence is enhanced by

Figure 138. High levels of sedimentation cause an important decrease in organism cover in coralligenous outcrops, changing also the community and its dynamics (Photo by E. Ballesteros).

high turbidity and sedimentation rates such as gorgonians *Leptogorgia sarmentosa* and *Eunicella verrucosa* (Carpine & Grashoff, 1975; Gatti *et al.*, 2012) (Figure 139).

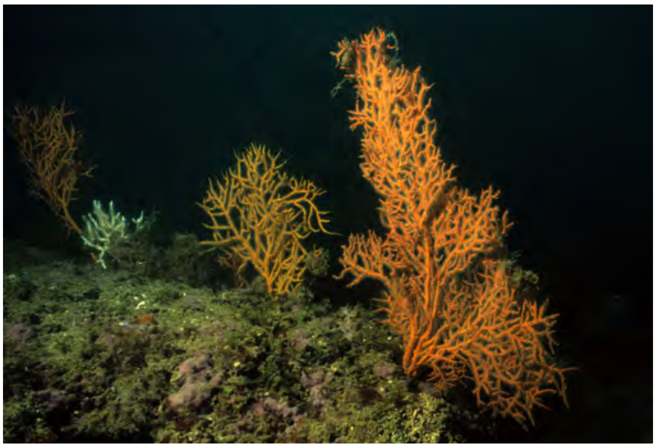

Figure 139. High turbidity and high sedimentation rates enhance the presence of some species of gorgonians such as ***Leptogorgia sarmentosa*** and ***Eunicella verrucosa*** (Photo by E. Ballesteros).

12.12. Invasive species

Some species introduced into the Mediterranean have become invasive (Boudouresque & Ribera, 1994; Boudouresque & Verlaque, 2002) and a number of them can thrive in, or are more or less adapted to, the coralligenous habitat. Currently, only introduced algal species are threatening coralligenous assemblages in some areas of the western Mediterranean. There is a lack of information in the impact of lessepsian species in the sessile coralligenous assemblages of the Eastern Mediterranean even if some reports show the importance of introduced fish (Spanier *et al.*, 2006).

Probably the most threatening alien species for the coralligenous community is the turf-forming red alga *Womersleyella setacea* (Figure 140) which is currently distributed along most of the Mediterranean basin (see Athanasiadis, 1997). This species grows abundantly in coralligenous (and other sublittoral) communities (Figure 141), forming a dense carpet, 1-2 cm thick, over the encrusting corallines that constitute the buildup (*Mesophyllum alternans, Lithophyllum cabiochae*, and others) (Ballesteros, 2004).

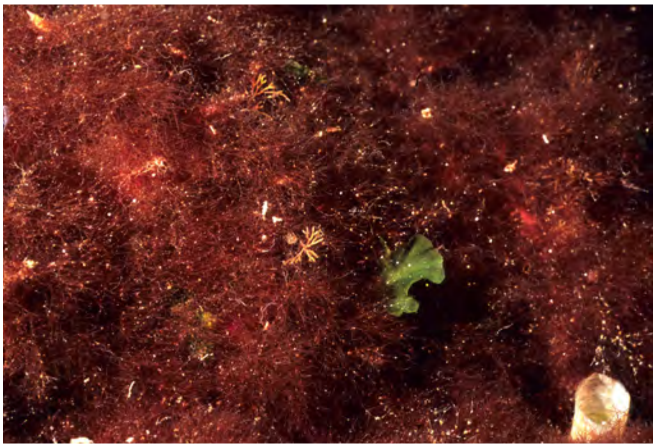

Figure 140. Filamentous red alga ***Womersleyella setacea*** is the most threatening alien species for coralligenous assemblages (Photo by E. Ballesteros)

Figure 141. Red carpet of invasive turf alga ***Womersleyella setacea*** covers a coralligenous rim in Scandola MPA, Corsica, at 40 m depth (Photo by E. Ballesteros).

Maximum biomass values reached by *Womersleyella setacea* amounts to 126 g dw m^{-2} at 30 m depth (Cebrian & Rodríguez-Prieto, 2012) and did not show any seasonal pattern but lower values are reported in spring. Although *Womersleyella setacea* can withstand a large range of environmental conditions its mid to long-term life requirements are dim light levels and low temperatures (Cebrian & Rodríguez-Prieto, 2012). The carpet of *Womersleyella setacea* undoubtedly decreases light availability to the encrusting corallines (avoiding or reducing photosynthesis and growth of these algae), increases sediment trapping (Airoldi *et al.*, 1995), excludes other macroalgae and turf algae by overgrowth and pre-emption (Piazzi *et al.*, 2002, 2007), inhibits recruitment of coralline algae and gorgonians (Ballesteros *et al.*, 1998; Linares *et al.*, 2014) and reduces juvenile survival of gorgonians (Cebrian *et al.*, 2012; Linares *et al.*, 2012, 2014) (Figures 142, 143).

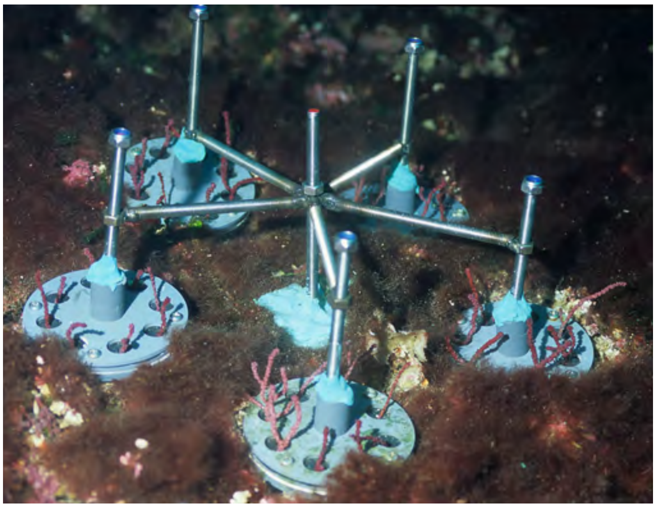

Figure 142. Experimental plates used by Cebrian ***et al.*** (2012) to assess the effect of ***Womersleyella setacea*** on recruits of ***Paramuricea clavata*** at 30 m depth in Scandola MPA (Photo by E. Ballesteros).

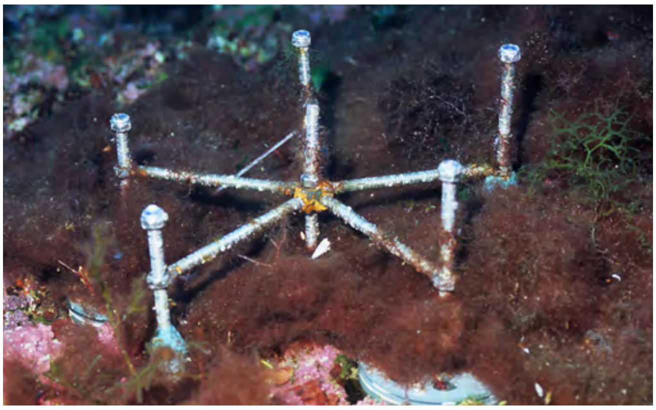

Figure 143. Same experimental plates of Figure 142 after 17 months, almost completely covered by a ***Womersleyella setacea*** carpet (Photo by E. Ballesteros).

Overgrowth by *Womersleyella setacea* also inhibited reproduction in six common coralligenous sponges (*Phorbas tenacior, Crambe crambe, Agelas oroides, Acanthella acuta, Axinella polypoides and Hymedesmia* sp.) (de Caralt & Cebrian, 2013). *Womersleyella setacea* is very successful at establishing itself and persisting from year to year (Airoldi, 1998); therefore, it may cause enormous damage to the entire coralligenous community. Indeed, the species richness found in sites invaded by *Womersleyella setacea* is lower than that observed in non-colonized sites (Piazzi *et al.*, 2002).

Another alien turf alga that is able to grow in deep waters is *Acrothamnion preissii*, which, nevertheless, has been mainly reported from maërl beds (Ferrer *et al.*, 1994) and the rhizomes of the seagrass *Posidonia oceanica* (Piazzi *et al.*, 1996). Although present in the coralligenous community of the Balearic Islands (Ballesteros, personal observation), it is never dominant in this environment and always grows together with *Womersleyella setacea*.

Caulerpa taxifolia is another species that can threaten the coralligenous community. Although mainly developing in relatively shallow waters (Meinesz & Hesse, 1991), it has been recorded down to a depth of 99 m (Belsher & Meinesz, 1995) and in some areas, such as Cap Martin (France), totally invaded the coralligenous community (Meinesz, 1999).

Caulerpa cylindracea, another invasive species that is quickly spreading in the Mediterranean (Piazzi *et al.*, 2005), is also able to grow in deep waters where coralligenous assemblages develop (Ballesteros, 2004; Cebrian & Ballesteros, 2009) (Figure 144). *Caulerpa cylindracea* represents a serious threat for Mediterranean coralligenous assemblages as it mostly affects encrusting organisms (Piazzi *et al.*, 2007), decreases species diversity (Piazzi *et al.*, 2012), reduces gorgonian recruitment and juvenile survival (Cebrian *et al.* 2012; Linares *et al.*, 2014) and decreases sponge cover but not sponge diversity (Baldacconi & Corriero, 2009). Although healthy *Paramuricea clavata* populations seem able to reduce the invasiveness of *Caulerpa cylindracea* (Ponti *et al.*, 2018), its colonization was not prevented in populations that suffered a massive mortality event (Linares *et al.*, 2018; Verdura *et al.*, 2019) (Figure 145). Because both *Caulerpa cylindracea* and *Womersleyella setacea* affect the viability of juvenile colonies of *Paramuricea clavata*, populations of this species invaded by these two species can be jeopardized (Cebrian *et al.*, 2012).

Figure 144. Green alga ***Caulerpa cylindracea*** overgrows coralligenous assemblages in Cabrera (Balearic Islands) (Photo by E. Ballesteros).

Figure 145. Alien species ***Caulerpa cylindracea*** colonizes a coralligenous assemblage dominated by ***Paramuricea clavata*** nine months after a mortality event in Imperial Islet (Cabrera, -42 m). Dead axes of ***Paramuricea clavata*** are heavily overgrown y tube-forming polychaete ***Salmacina dysteri***, ramified thin bryozoan ***Savignyella lafontii***, brown alga ***Dictyopteris*** and unidentified turf algae (Photo by E. Ballesteros).

Two other algal species that have been reported to behave as invaders in the Mediterranean are *Asparagopsis taxiformis* (Ballesteros & Rodríguez-Prieto, 1996) (Figure 146) and *Lophocladia lallemandii* (Patzner, 1998) (Figure 147). The two species are becoming increasingly abundant both in shallow bottoms and deep waters around the Balearic Islands. They have been found to a depth of 65 m in coralligenous bottoms with or without *Womersleyella setacea* (Cebrian & Ballesteros, 2007, 2010; Ballesteros, personal observations).

Figure 146. *Asparagopsis taxiformis* is an introduced red alga that rarely behaves as invader in coralligenous environments (Photo by E. Ballesteros).

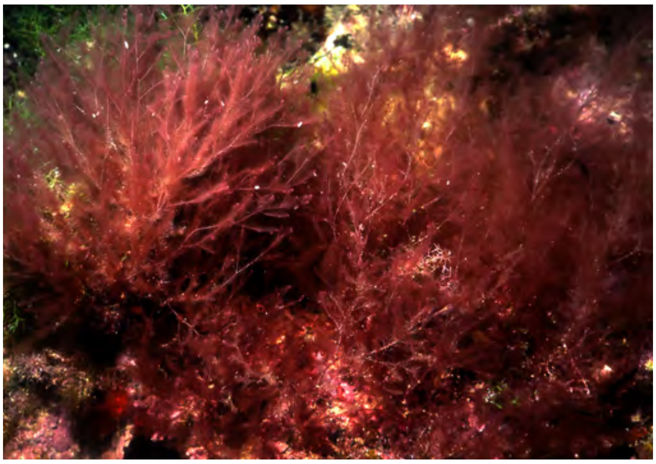

Figure 147. Although usually restricted to infralittoral rocky bottoms, invasive red alga *Lophocladia lallemandii* can occasionally be abundant over shallow coralligenous assemblages (Photo by E. Ballesteros).

The latest introduced algal species with invasive features in coralligenous assemblages is *Rugulopteryx okamurae*, whose proliferations are threatening several habitats around the rich waters of the Strait of Gibraltar (García-Gómez *et al.*, 2018; Sempere-Valverde *et al.*, 2019). It is still early to properly assess its effects on coralligenous assemblages, but its cover can attain up to 50% coverage in coralligenous outcrops.

Introduced fish from the Red Sea constituted only 11.6% of species composition in trammel net fishing in a shallow coralligenous reef off Haifa, Israel, but they contributed 46.2% of the fish abundance and 40.6% of the biomass in these samples. *Siganus luridas, S. rivulatus* and *Sargocentron rubrum* were the main contributors (Spanier *et al.*, 2006) (Figure 148). *Pomacanthus maculosus* (Bariche, 2009) and *Pterois miles* (Bariche *et al.*, 2013) are recent introductions from the Red Sea that have been observed in coralligenous bottoms. Unfortunately, there are no functional studies addressing the effects of these introductions in Eastern Mediterranean coralligenous outcrops.

Figure 148. Invasive rabbitfish *Siganus luridus* is the most abundant fish captured by trammel nets in Kas, Turkey (Photo by E. Ballesteros).

12.13. Acidification

CO_2 levels are increasing in the atmosphere and in the oceans, driving a drop of 0.1 pH units in acidity since the beginning of the industrial revolution in the oceans. It is predicted that at the end of the present century the drop in pH will represent an additional 0.3 units (IPCC, 2013). This increase in acidity will reduce the carbonate ion concentrations in the ocean, reducing the level of calcium carbonate saturation (Gattuso *et al.*, 2015). This reduction is expected to have important effects on organisms, mainly on those with calcareous skeletons such as coralline algae, corals, molluscs and bryozoans (Feely *et al.*, 2004; Gattuso *et al.*, 2013; Kroeker *et al.*, 2013) (Figure 149). Thus, it is expected that the coralligenous habitats whose structural framework in composed by calcareous organisms will be seriously affected. A meta-analysis by Zunino *et al.* (2017) predicts that acidification in the Mediterranean will increase fleshy algal cover by increasing photosynthetic activity of macrophytes and will reduce calcification both by algae and corals. We have to stress, though, that ocean acidification will have a future impact in the coralligenous and other calcium carbonate structures but given the current levels of CO_2 in the Mediterranean no anthropogenic effect of acidification is observed nowadays.

Figure 149. A partially dissolved skeleton of gastropod *Bolma rugosa* in the CO_2 vents of Columbretes Islands (Photo by E. Ballesteros).

Skeletons of coralline algae are made of high magnesium calcite, which is far more soluble than other forms of calcium carbonate (Andersson *et al.*, 2008; Kuffner *et al.*, 2008; Porzio *et al.*, 2011). Thus, coralline algae should respond to ocean acidification by decreasing net calcification, growth and reproduction (Basso, 2012). Elevated pCO_2 enhances *Lithophyllum cabiochae* death and the dissolution of dead skeletons is much higher at elevated pCO_2 conditions than under ambient pCO_2, suggesting that net dissolution of this important coralligenous builder will exceed net calcification by the end of this century (Martin & Gattuso, 2009). Moreover, high pCO_2 enhances algal necrosis when *Lithophyllum cabiochae* is exposed to high temperatures (Martin *et al.*, 2009). Photosynthetic efficiency is reduced under elevated pCO_2 in *Lithophyllum cabiochae* but calcification rate is maintained or even enhanced (Martin *et al.*, 2013). It seems that *Lithophyllum cabiochae* has the ability to buffer the medium against ocean acidification, enabling the deposition of magnesium calcite under elevated pCO_2 (Nash *et al.*, 2016), suggesting that coralline algae may be more resilient to ocean acidification than previously thought.

There are several described effects of ocean acidification in Mediterranean macroinvertebrates thriving in coralligenous bottoms. There are different species-specific abilities to use horizontal transmission to modify microbiomes in response to a lowered pH in sponges (Ribes *et al.*, 2016), which contribute to survivorship in a scenario of lowered pH. *Dysidea avara* is the more adaptable, followed by *Agelas oroides*, while *Chondrosia reniformis* has a null ability in acquiring new microbes and is severely affected by lowered pH (Ribes *et al.*, 2016).

The red coral, *Corallium rubrum*, has a magnesium calcite skeleton (Vielzieuf *et al.*, 2008). Biocalcification, skeletal growth rates and feeding activity of the polyps of *Corallium rubrum* are significantly reduced at pCO_2 scenarios predicted by the end of this century (Cerrano *et al.*, 2013; Bramanti *et al.*, 2013) suggesting a new stressor for this already threatened species. In contrast, the skeleton and calcification of the scleractinian coral *Leptopsammia pruvoti* remain unaffected when colonies are exposed to low pH (Movilla *et al.*, 2016).

Although bryozoans provided by a calcareous skeleton are resilient for short-term exposures to low pH values (Rodolfo-Metalpa *et al.*, 2009) skeleton corrosion occurs at medium term exposures (Lombardi *et al.*, 2011b). Corrosion is much higher when coupled to high temperatures (Rodolfo-Metalpa *et al.*, 2009) and the growth is reduced (Lombardi *et al.*, 2011a), although colonies seem to be able to respond to ocean acidification by adjusting resource allocation between zooids of different types (Lombardi *et al.*, 2011c). Thus, ocean acidification can severely affect the survival of bryozoans with high magnesium calcite skeletons.

The only direct observations of naturally occurring coralligenous outcrops under acidified conditions have been done by investigating CO_2 vents (Figure 150). In vents situated at 40 m depth in Columbretes islands (Spain) there is a replacement of coralligenous bioconstructions by kelp beds when pH decreases from 8.1 to 7.9 units (Linares *et al.*, 2015) (Figure 151). High magnesium calcite organisms such as coralline algae and bryozoans are completely absent near the vents; coralline algae are replaced by encrusting aragonite-calcifying algae (*Peyssonnelia rosa-marina*) (Linares *et al.*, 2015). ROV explorations in hydrothermal vents off Panarea island (Italy) at pH values around 6.2-7.0 units and 80 m depth show a wide coverage of red algae *Peyssonnelia* spp. and green algae *Flabellia petiolata*, together with sponges but also tube polychaetes and bryozoans (*Reteporella grimaldi*) (Esposito *et al.*, 2018). These two examples do not always agree with the effects on species when faced to low pH in the laboratory, but unequivocally show the potential of ocean acidification to change the seascapes dramatically.

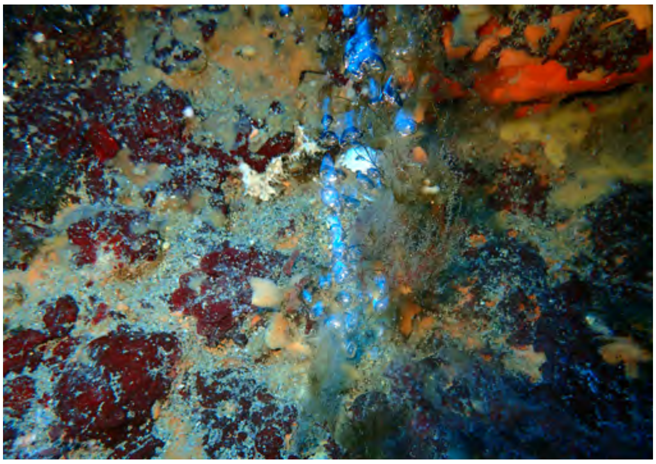

Figure 150. CO_2 vents related to volcanic activity are currently the only sites in the sea where to observe the effects of acidified conditions (Photo by E. Ballesteros).

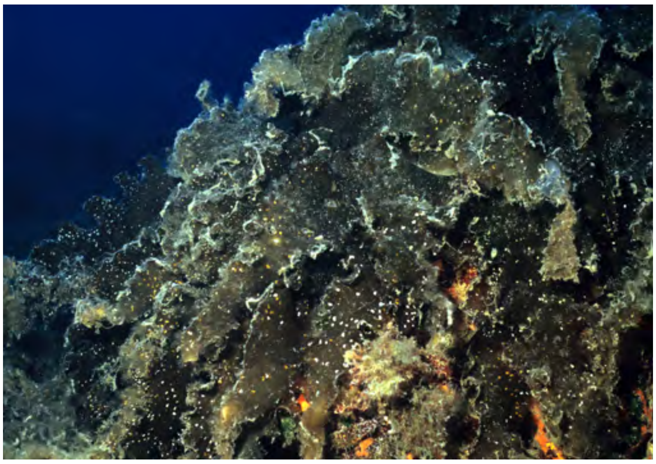

Figure 151. Kelp beds of endemic and threatened *Laminaria rodriguezii* substitute coralligenous outcrops near CO_2 vents at Columbretes Islands (Spain), -40 m depth (Photo by E. Ballesteros).

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13. Conservation issues

13.1. Criteria

Planning conservation measures at the Mediterranean level should ensure the best protection not only of species, function and genetic diversity (Giakoumi *et al.*, 2103) but also the different seascapes. Thus, it is necessary to consider different depth belts taking into consideration the different levels of diversity from taxonomic to phylogenetic (Doxa *et al.*, 2016) but also the different depth-related morphologies and assemblages. The occurrence of isolated breeding units and differences in genetic diversity among samples at scales of tens of meters suggest that strategies for conservation and restoration of coralligenous species and habitats should include a range of scales from the local to the regional level (Costantini *et al.*, 2007; Abiatti *et al.* 2009; Arizmendi-Mejía *et al.*, 2015).

13.2. Legislation

Several specific laws concerning the protection of the coralligenous habitat and some of the species thriving in it are in force in the European Union, although they do not concern non-EU countries. Destructive fishing is specifically prohibited over coralligenous and maërl beds in the European Union (Council Regulation No 1967/2006 concerning management measures for the sustainable exploitation of fishery resources in the Mediterranean Sea) and coralligenous bioconstructions host a species of interest listed in the Annexes of the EU Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora), such as the red coral (*Corallium rubrum*). However, coralligenous outcrops are not listed among the priority habitats and, thus, EU countries are not required to declare sites of community interest (SCis) to protect specifically the coralligenous environment. The EU Water Framework Directive (WFD; Council Directive 2000/60/EC establishing a framework for Community action in the field of water policy) aims to control the input of nutrients and chemicals into the water bodies, including the coastal zones in order to guarantee the water quality and indirectly, the quality of the freshwater and coastal marine ecosystems. However, the WFD does not protect habitats but use their species composition to assess the water quality, i.e. the water quality of a water body has to be good enough for maintaining the species and the functions of aquatic ecosystems, indirectly being a measure of protection. Finally, the EU Marine Strategy Framework Directive (MSFM; Council Directive 2008/56/EC establishing a framework of community action in the field of marine environmental policy) is the first encompassing piece of EU legislation specifically aimed at the protection of the marine environment and its natural resources (Figure 152). Its approach is ecosystem-based and its main goal is to achieve a good environmental status of EU marine waters by 2020. According to MSFD, a good environmental status is achieved when (i) the biodiversity is maintained, (ii) non-indigenous species do not adversely affect the ecosystem, (iii) population of commercial fish species are in good health, (iv) elements of food webs ensure long-term abundance and reproduction, (v) eutrophication is minimized, (vi) the sea floor integrity ensures the functioning of the ecosystem, (vii) possible hydrological alteration do not adversely affect the ecosystem, (viii) there are no effects of contaminants, (ix) seafood contaminants are below safe levels, (x) marine litter does not cause harm and (xi) introduction of energy (including noise) does not adversely affect the ecosystem. This directive encompasses all marine ecosystems and, thus, coralligenous reefs are included.


Figure 152. The EU Marine Strategy Framework Directive aims at achieving a good environmental status of coralligenous environments and all EU marine habitats by 2020 (Photo by E. Ballesteros).

At a national level, tegnùe outcrops, the northern Adriatic mesophotic biogenic habitats, have been granted the status of "Zona di Tutela Biologica" in Italy, a zone of biological protection, i.e. a regulated no-take zone, with a decree of the Italian Ministry of Agricultural, Forest and Forestry Policies (G.U. n. 193, 19/8/2002).

The only umbrella that includes all Mediterranean countries in their efforts to preserve the Mediterranean Sea is the Barcelona Convention, adopted in 1995 for the protection of the marine environment and the Mediterranean coastal regions. The Barcelona Convention is based on a Mediterranean Action Plan (MAP) that has given rise to seven protocols addressing specific aspects of conservation. The Protocol concerning Specially Protected Areas and Biological Diversity includes a list of endangered or threatened species (Annex II) (Figures 153, 154) and a list of species whose exploitation is regulated (Annex III) (Figures 155, 156), including several coralligenous species (http://web.unep.org/unepmap/5-specially-protected-areas-protocol-spa-and-biodiversity-protocol). This protocol also holds several Action Plans addressed to the protection of different taxa and ecosystems.

Figure 153. Brown cowry *Luria lurida* is an endangered species according to the Annex II of the SPA protocol (Photo by E. Ballesteros).

Figure 154. The threatened rough fan mussel, *Pinna rudis*, can be occasionally seen in coralligenous outcrops (Photo by E. Ballesteros).

Figure 155. *Spongia lamella* is present in the Annex III of the SPA protocol (Photo by E. Ballesteros).

Figure 156. Spiny spider crab, *Maja squinado*, is an endangered species whose exploitation is regulated according to the Annex III of the SPA protocol (Photo by E. Ballesteros).

The Action Plan concerning the coralligenous and other calcareous bioconcretions in the Mediterranean (UNEP-MAP-RAC/SPA, 2008) was adopted by the contracting parties in January 2008 and is specially devoted to coralligenous assemblages and maërl beds. The main actions undertaken by this Action Plan include: (i) to establish a reference list of species that are found in coralligenous outcrops, (ii) to help to the taxonomic identification of species constituting coralligenous and maërl assemblages through an inventory of taxonomic experts and researchers/institutions working in the field, (iii) to promote monitoring methods and (iv) to encourage the conservation of the coralligenous environment by creating MPAs, notably in international waters. Although not legally binding, this is the only initiative bringing together all the Mediterranean countries towards the knowledge and conservation of coralligenous outcrops.

13.3. Effective protection

As stated in the Coralligenous Action Plan, one of the main problems hindering the proper implementation of measures concerning the protection of coralligenous outcrops is the lack of relevant spatial data on these habitats (Georgiadis *et al.*, 2009; Martin *et al.*, 2014). The coverage of mapped seabed is recently expanding (in part due to the investment of the Coralligenous Action Plan) (see the "Mapping" section on this document). Moreover, basin-scale (non-detailed) cartographies like that of Giakoumi *et al.* (2013) and modelling tools can also be used to look for areas where to focus the searching efforts (Martin *et al.*, 2014) or to make predictive cartographies (Falace *et al.*, 2015; Zapata-Ramírez *et al.*, 2016; Vasallo *et al.*, 2018). However, effective protection should be based on the complete and accurate mapping of coralligenous habitats, including their morphology and information on species composition and assemblages (Ingrosso *et al.*, 2018).

Aside the protection for destructive fishing that has to be applied at the EU level, EU countries have the areas or Sites of Conservation Interest (SCI). Declared under the umbrella of the Habitats Directive, they have been created based mainly on the presence of *Posidonia* meadows, as this is the only marine habitat type of "special interest". However, most countries are currently turning their attention towards the "reef" habitat category (Fraschetti *et al.*, 2009), which includes coralligenous and tegnùe outcrops.

Nevertheless, at the Mediterranean level, the most widespread figure of protection is the creation of marine protected areas (MPAs) (Ingrosso *et al.*, 2019) (Figure 157). Creation of MPAs has been mainly oriented to the protection of exploited natural resources (fish and shellfish) but somehow they have also been designated to protect seascapes that are specially sensible and/or attractive for scuba divers (Fava *et al.*, 2008; Boero, 2017; Ingrosso *et al.*, 2019). Since coralligenous environments have a high aesthetic value (Harmelin, 2009; Tribot *et al.*, 2016; Chimienti *et al.*, 2017) and they host a large number of commercial coastal fish (Astruch *et al.*, 2018) they have been very often included in MPAs. Future efforts need to be focused on the designation of MPAs in areas harbouring well-developed coralligenous concretions in particular in places with low levels of anthropogenic impacts like the banks of the Sicily Channel (Altobelli *et al.*, 2017).

Figure 157. Marine protected areas (MPAs), the most widespread figure of protection in the Mediterranean, are an effective way of recovering vulnerable fish populations (Columbretes Islands, Spain) (Photo by E. Ballesteros).

13.4. Restoration

Natural recovery of coralligenous buildups could take centuries or even millenia due to the slow growth rates and the bioerosion calcareous encrusting macroalgae and macroinvertebrate carbonate builders, but natural recovery of engineering species populations like gorgonians can take "only" decades (Montero-Serra *et al.*, 2018) (Figure 157). Active restoration can be a good approach to foster the recovery of populations with slow growth rates and low recruitment rates as the required times to attain a full recovery can be shortened. Nevertheless, active restoration has been seldom used in coralligenous assemblages (Guarnieri *et al.*, 2019).

Transplanted explants of *Paramuricea clavata* and *Eunicella* spp. have been used for enhancing population recovery (Linares *et al.*, 2008; Fava *et al.*, 2010). Pruning techniques have also been used to increase the recovery of *Paramuricea clavata* affected by mass mortality events (Previati *et al.*, 2011). Methods based on recruitment enhancement in artificial substrates have been tested for the recovery of the populations of the precious red coral (Bramanti *et al.*, 2007; Benedetti *et al.*, 2011). Macroinvertebrate restoration protocols that are being developed in the frame of the EU MERCES (Marine Ecosystem Restoration in Changing European Seas) project (http://www.merces-project.eu/) are based on transplanting whether fragments or entire colonies from donor sites and on recruitment enhancing techniques and devices (Cerrano *et al.*, 1999; Cerrano *et al.*, 2018; Guarnieri *et al.*, 2019). A negative correlation between survival after transplanting and growth rates has been found: Slow-growing species will tend to require lower initial effort due to higher survival after transplanting but the time period required for full restoration will tend to be longer (Montero-Serra *et al.*, 2018). Moreover, due to the high genetic structure of the gorgonians inhabiting coralligenous outcrops, colony size, proximity and population size has to be taken into consideration for restoration purposes (Mokhtar-Jamaï *et al.*, 2013).

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14. Monitoring

14.1. Methods

Monitoring natural assemblages becomes necessary if we want to assess temporal changes. Accurate temporal studies of coralligenous algal assemblages may involve sample collection by scraping quadrats and analysing samples in the laboratory (Ballesteros, 1992; Piazzi *et al.* 2002, 2004; Sant *et al.*, 2017) because of the small size and difficult identification of species. However, the scraping method is destructive and does not allow the monitoring of the same benthic area through time.

The use of photoquadrats (Figure 159) is not so accurate and does not always give the same results (Cecchi *et al.*, 2014; Piazzi *et al.*, 2014b; Sant *et al.*, 2017). Photography, though, is very useful because it is non-destructive and reduces diving time and decompression stops (Cecchi *et al.*, 2014; Piazzi *et al.*, 2015; Sant *et al.*, 2017). Garrabou *et al.* (2002) used still photography taken in permanent quadrats through time to look for relative changes in the assemblages, a technique that can be notably improved when species are identified (e.g. Kipson *et al.*, 2011; Holon *et al.*, 2013). Photoquadrats are being used to estimate species presence/absence (e.g. Kipson *et al.*, 2011), to estimate semi-quantitative abundances (e.g. Cecchi *et al.*, 2014 ; Casas-Güell *et al.*, 2015 ; Montefalcone *et al.*, 2017), to make more precise estimates by means of stratified random points (Kohler & Gill, 2006; Deter *et al.*, 2012) or by shaping every species and calculating its abundance (e.g. Trygonis & Sini, 2012; Casas-Güell *et al.*, 2016; Sartoretto *et al.*, 2017; Sant *et al.*, 2017). Coralligenous environments have a high heterogeneity at different spatial scales (Peirano *et al.*, 2009; Piazzi *et al.*, 2014a) and special care has to be devoted in obtaining enough number of replicates for reaching a representative sampling area (Kipson *et al.*, 2011; Piazzi *et al.*, 2014a; Sant *et al.*, 2017), which changes according to every assemblage.

Figure 159. Photoquadrats are a useful, non-destructive, technique for the study of coralligenous assemblages (Photo by E. Ballesteros).

The use of ROVs or manned submersibles (Figure 160) is very useful in deep coralligenous banks and it is being used more and more frequently for monitoring purposes (e.g. Bo *et al.*, 2010; Bavestrello *et al.*, 2014; Ferrigno *et al.*, 2015, 2017a, 2018b; Cánovas-Molina *et al.*, 2016b; Altobelli *et al.*, 2017; Enrichetti *et al.*, 2019b; Salvati *et al.*, 2019).

Figure 160. Manned submersible Johnson Sea Link operating in Cabrera National Park (Balearic Islands) (Photo by E. Ballesteros).

The monitoring of engineering species can be performed *in situ* by labelling colonies along transects (e.g. Coma *et al.*, 2004; Linares *et al.*, 2007b) or by using quadrats (e.g. Sala *et al.*, 1996; Linares *et al.*, 2005, 2008) (Figure 161). Still photography of permanent plots (e.g. Garrabou & Ballesteros, 2000; Garrabou & Zabala, 2001; Garrabou & Harmelin, 2002) is also used, which extremely reduces

Figure 161. Density and height of engineering species like gorgonians can be measured *in situ* by using quadrats (Photo by J.C. Calvin).

diving time but requires long image analytical time. Recent technology improvements allow the obtaining of three dimension images by scuba, ccuba diving and ROVs, which have been already used to estimate *Paramuricea clavata* population structure (Pavoni *et al.*, 2013; Palma *et al.*, 2018). Photogrammetric surveys enable a non-destructive, rapid sampling, that coupled to an automated system can be used to cover wide areas (Palma *et al.*, 2018, 2019). The use of photogrammetry, photomosaic elaborations and 3D modelling may largely improve the quality and quantity of data and therefore the quality of the assessments (Zapata-Ramírez *et al.*, 2013).

Engineering species are only a compartment of the coralligenous outcrops and thus, if we restrict the monitoring to these species, we are monitoring populations and not the assemblage or the ecosystem. This is especially important when designing protocols compliant with the Marine Strategy Framework Directive, whose approach is ecosystemic.

14.2. Protocols

The adoption of standardized monitoring methodologies, although not necessary, is a step forward in the comparison of data obtained in different or the same sites by independent teams. Both the implementation of the Action Plan concerning the coralligenous and other calcareous bioconcretions and the Marine Strategy Framework Directive require the development of monitoring techniques and protocols.

Most protocols require scuba diving in relatively shallow coralligenous environments (Figure 162), ccuba (Closed Circuit Underwater Breathing Apparatus) diving in intermediate depths and the use of ROVs in deep waters. In the frame of the Coralligenous Action Plan, Pergent *et al.* (2015) describe the basis for monitoring coralligenous assemblages, which is further developed by Garrabou *et al.* (2014), Garrabou & Kipson (2014), Kipson (2014) and Kipson *et al.* (2014).

Figure 162. Sampling for cryptobenthic fish species at Columbretes islands (Spain) (Photo by D.K. Kersting).

The Croatian protocol (Garrabou *et al.*, 2014; Kipson *et al.*, 2014) uses photosampling, visual censuses for habitat structure and function (species composition, habitat complexity, bioconcretion, bioerosion) and assessment of natural and anthropogenic impacts whether using divers or ROVs (Figure 163). In France, the French monitoring network (RECOR) surveys coralligenous concretions by means of photoquadrats and anthropogenic pressures in 120 locations (Holon *et al.*, 2013). Ruitton *et al.* (2019) describe a protocol for the quantification of lost fishing gear in benthic assemblages. Other protocols, mostly addressed to furnish data for the assessment of the ecological quality of the coralligenous outcrops in the frame of several EU Directives, and involving all kind of methodologies, are summarized in the next chapter.

Figure 163. Visual censuses are frequently used in coralligenous assemblages for assessing species composition and habitat complexity (Photo by J.C. Calvin).

14.3. Ecological quality indexes

All monitoring protocols have the final aim of obtaining information about the status of the subject they are monitoring, whether they are populations, assemblages or ecosystems. The comparison of the information obtained at the same site in two different sampling times tells us about the changes that have taken place in that period and we can make a diagnosis of what is happening. When faced to conservation issues, monitoring protocols try to obtain the ecological status of the monitored subjects in order to know if they are improving or not. The ecological status can be based on a single descriptor (e.g. gorgonians, macroalgae...) or on several descriptors. If we want to obtain the ecological status of the whole habitat or the ecosystem we need to measure as many descriptors as possible or to focus only on those descriptors that provide the best information (ecological indicators). Descriptors are usually evaluated by different metrics and they are usually combined and weighed to obtain a multimetric index that can be used to make spatial and temporal comparisons. Even if indexes are not necessary to make comparisons, they are useful because values are visually simple. In fact, both the Water Framework

Directive and the Marine Strategy Framework Directive rely on indexes for the assessment of the ecological status. Several indexes for determining the ecological status have been recently developed following the advice of Harmelin (2009). All indexes are relatively recent, they need to be more widely applied and tested and they have to be compared. Moreover, some indexes are in constant evolution and improvement and thus it is too early to make evaluations or recommendations. However, it would be desirable to arrive in the future to some sort of consensus amongst Mediterranean scientists on the indexes to be applied and, if this is not possible, to start an intercalibration exercise between the different methodologies.

The Ecological Status of Coralligenous Assemblages index (ESCA) (Cecchi & Piazzi, 2010; Cecchi *et al.*, 2014) is a photography-based, WFD-compliant, multimetric index that combines the sensitivity level, the alpha diversity (taxa/groups number) and the beta-diversity (evaluated as the mean distance of all photographic samples from centroids calculated from a PERMDISP analysis; Anderson, 2006) of macroalgal coralligenous assemblages. A sensitivity level is assigned to every taxa/group (Figure 164) and the sensitivity level of each photograph is obtained by adding all the values of sensitivity level reported for all the taxa/group in the photograph. Reference sites are considered and an Ecological Quality Ratio (EQR, ranging from 0 to 1) are provided for each metric and site after averaging three years of sampling. The final EQR is the mean of the three EQRs. The ESCA index is tested in coralligenous assemblages from Tuscany and decreases at increasing nutrient concentrations in seawater, sedimentation rates and invasive species abundance (Cecchi *et al.*, 2014). The ESCA is also MSFD-compliant (Piazzi *et al.*, 2015) and when sessile macroinvertebrates are considered, the resulting index (named ESCA-TA) detects the levels of human pressure more precisely (Piazzi *et al.*, 2017a). ESCA index has recently been applied to assess the impacts of the salvaging of the Costa Concordia shipwreck (Penna *et al.*, 2017).

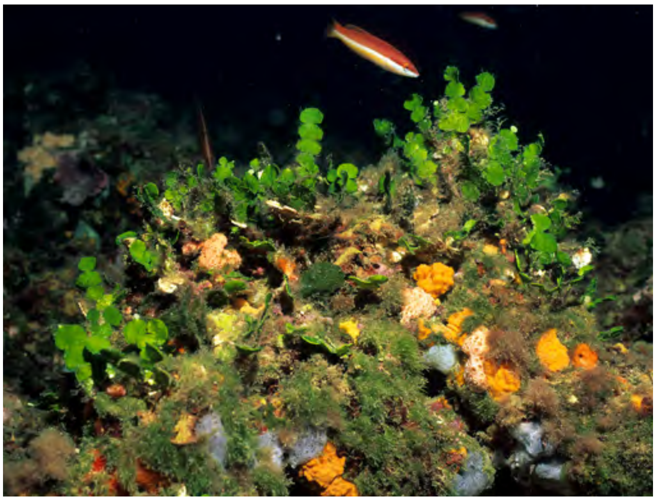


Figure 164. Green alga *Halimeda tuna* is one of the most sensitive species to disturbances according to ESCA index (Photo by E. Ballesteros).

The Coralligenous Assemblage Index, CAI (Deter *et al.*, 2012) is a WFD-compliant index, ranging from 0 to 1, with quality status established in five classes. It has been developed from a wide data set collected in the eastern French Mediterranean coast. *In situ* measures obtained by ccuba diving during a special monitoring included percent cover of visible sessile species (using photoquadrats) and gorgonian demographic features, and considered outcrop morphology, geographical orientation, principal current direction, and depth. After selection of the more appropriate descriptors, the final index is based in three selected metrics: Bryozoan percent cover, sludge percent cover and builder species percent cover. CAI is positively and significantly linked to water quality.

Gatti *et al.* (2012) describe a Rapid Visual Assessment method (RVA) (Parravacini *et al.*, 2010) using a seascape approach and integrating biological, mesological and geomorphological information. The outcrops are divided into three morphotypes and different mesologic parameters (e.g. slope, depth, elevation from the bottom). The biological characterisation distinguishes three layers (upper, intermediate and basal) and measures total cover, maximum height and percentage of epibiosis/necrosis for the upper layer, species richness, seasonal/perennial species ratio and number of species of erect bryozoans for the intermediate layer, and percentage cover of different groups of encrusting organisms, thickness and consistency of the calcareous layer and bioerosion. The results obtained for each of the nine descriptors are converted into quality scores from 1 (bad quality) to 3 (good quality) and the final ecological status is established in five classes, with the index ranging from 1 to 3. The RVA has been tested in the coralligenous off Vado Ligure (Gatti *et al.*, 2012) and between Marseille and Toulon (Gatti & Sartoretto, 2013), with satisfactory results.

The RVA method of Gatti *et al.* (2012) has evolved into the Coralligenous Assessment by ReefScape Estimation (COARSE) index (Gatti *et al.*, 2015) that has been tested in 21 stations from the PACA region (France), including stations subjected to high, moderate and low anthropogenic pressures. The most relevant difference from the RVA method concerns the descriptors from the intermediate layer, where seasonal/perennial species ratio is replaced by the number of erect calcified species, and the descriptor regarding the number of erect bryozoans is replaced the number of erect bryozoans but weighed by the sensitivity level of each species (Figure 165). The COARSE index is also calculated differently from the RVA index. The COARSE index is robust to observer biases and to the different level of anthropogenic pressures of the sampled sites. Final quality scores are an average of the quality scores of every layer and range from 1 to 3. However, as RVA, COARSE index is not totally compliant with MSFD because it still lacks the comparison with reference condition sites (Gatti *et al.*, 2015). COARSE and ESCA indexes have been applied to coralligenous reefs from sites affected by different human pressures (Piazzi *et al.*, 2017b), providing different but complementary information on the quality of the reefs. Casoli *et al.* (2017) apply a slightly modified COARSE index between 35 and 76 m depth to assess the impact of salvaging the Costa Concordia wreck, with easy and cost-effective application in deep waters.

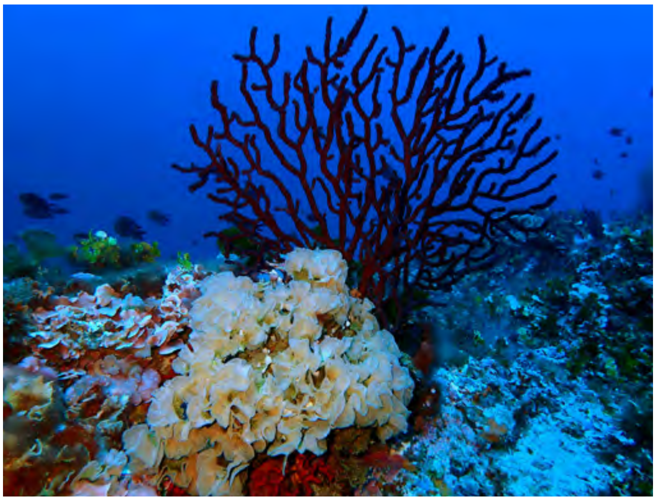


Figure 165. Erect bryozoans are sensitive species that are used in the estimation of COARSE index (Photo by E. Ballesteros).

The INDEX-COR approach (Sartoretto *et al.,* 2014, 2017) creates a multimetric index based both on photosampling and visual diving observations that integrates three variables: the sensitivity of taxa to organic matter and sediment input, the taxonomic richness and the structural complexity of the assemblages. Every taxon is assigned to a sensitivity level group (indifferent, opportunistic, tolerant and sensitive; Pinedo *et al.*, 2015) (Figure 166) and sample sensitivity is calculated according to a formula inspired from the MEDOCC index (Pinedo *et al.*, 2015).

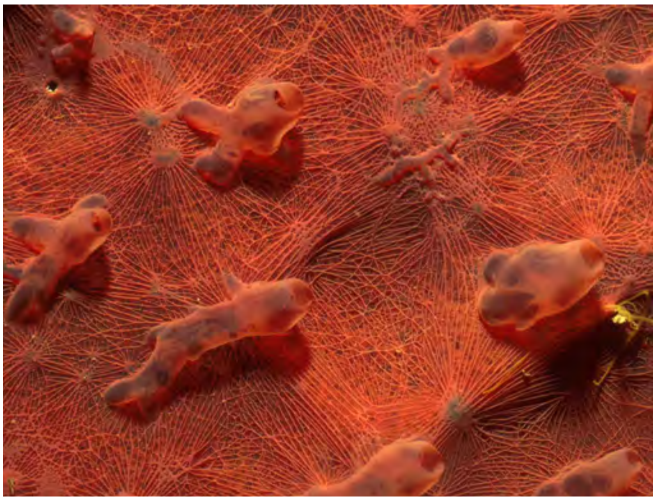


Figure 166. Sponge *Hexadella topsenti* is a sensitive species to organic matter and sediment input according to INDEX-COR (Photo by E. Ballesteros).

The structural complexity of the assemblages uses the categorization by Gatti *et al.* (2012) and obtains a score of “structure”. The three metrics are combined to obtain the IC index that ranges between 0 and 100. It provides effective discrimination on the conservation status of coralligenous habitats across the PACA region area (France) and is highly and significantly related with the pressure levels of the sites.

The Integrated Sensitivity Level of coralligenous Assemblages (ISLA) index (Montefalcone *et al.*, 2017) uses photoquadrats, where the cover values of each taxa (or morphological group) is classified into 8 classes of abundance according to Boudouresque (1971). Each taxon (or morphological group) has a sensitivity level to disturbance (SLD; estimated using biological traits) and a sensitivity level to stress (SLS; estimated using expert judgement). Both sensitivity levels are integrated into a single sensitivity level (ISL) that is finally scored along a numerical scale from 0 to 9, with lowest values corresponding to the most tolerant organisms and highest values to the most sensitive (Montefalcone *et al.*, 2017) (Figure 167). Abundances of each taxa/group are multiplied by their corresponding sensitivity levels and all the values are added to estimate an index for each photograph. An ecological quality ratio (EQR) is calculated as the ratio between the index and the value of the same index obtained in a reference site (Ballesteros *et al.*, 2007). The ISLA index has been successfully applied to a spatial gradient of stress and to a long-term data set obtained in the same site, being very effective in measuring the change experienced by coralligenous assemblages in both space and time (Montefalcone *et al.*, 2017).

Figure 167. The coral *Phyllangia americana mouchezi* has a sensitivity level to disturbance of 16 and a sensitivity level to stress of 5, with a final sensitivity level score of 6 according to ISLA index (Photo by E. Ballesteros).

The Ecosystem-Based Quality Index (EBQI) for coralligenous assemblages (Ruitton *et al.*, 2014) follows the ecosystem-based approach required by the MSFD and is compliant with this EU Directive. It is based on photoquadrats for the quantification of most ecological compartments (Deter *et al.*, 2012) except for teleosts and cephalopods, where visual counts are used (Figure 168). The EBQI encompasses the following compartments: Builders, non-calcareous macroalgae, filter- and suspension feeders, bioeroders, browsers and grazers, planktivorous teleosts, predatory teleosts, high level predators, cephalopods, benthic detritus, and detritivores (Figure 169). Compartments are balanced according to their relative weight in the functioning of the ecosystem (according to expert judgment) from 5 to 1. The scores are added up and final scores range between 0 (worst) and 10 (best). The EBQI is also associated to a confidence index in a similar way to other EBQI indexes (Personnic *et al.*, 2014; Thibaut *et al.*, 2017).

Figure 168. Visual counts of teleosts and cephalopods are used to obtain EBQI index (Photo by E. Ballesteros).

The Standardized Coralligenous Evaluation Procedure (STAR) (Piazzi *et al.*, 2019) integrates approaches already used by pre-existing indexes in a standardized method. This methodology involves ten main steps: (1) surveys are performed once a year in April-June; (2) substrate has to be vertical and depth around 35 m; (3) three areas of 4 m^2 have to be selected for each site; (4) ten photographs of 0.2 m^2 should be collected; (5) thichness of the calcareous layer should be measured with a hand-held penetrometer and six replicates per area; (6) size and percentage of necrosis and epibiosis of erect anthozoans has to be visually assessed; (7) sediment cover has to be estimated at each photograph; (8) percentage cover of each conspicuous taxa has to be estimated at each photograph and the overall sensitivity level (SL) has to be calculated by multiplying the value of the SL of each taxon/group for its abundance and then summing up the final values (Piazzi *et al.*, 2017a,b); (9) species number per photograph has to be counted; and (10) beta-diversity has to be evaluated as the mean distance of all photographic samples of each area from centroids calculated through PERMDISP (Anderson, 2006).

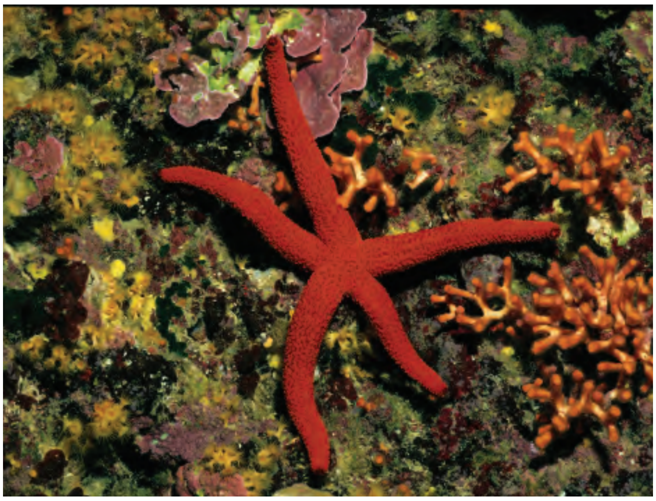


Figure 169. EBQI index is based on photoquadrats to quantify the different ecological compartments, except for teleosts and cephalopods that are measured visually *in situ* (Photo by E. Ballesteros).

The Mesophotic Assemblages Ecological Status index (MAES) (Cánovas-Molina *et al.*, 2016b) uses ROV photography and video to obtain data on three types of variables regarding the structure of the outcrops (number of visible taxa, basal layer coverage, density of erect species) (Figure 170), the condition of the dominant erect species (average height, % colonies with necrosis or epibiosis) and the visible human impact (density of marine litter). MAES considers reference conditions, which corresponds to the best values obtained for each metric. A simplified version of the MAES index (MAES-q), estimated with a lower number of variables, is also described (Cánovas-Molina *et al.*, 2016b). Final scores range from 6 to 18 (MAES) or from 6 to 12 (MAES-q). The index is applied in the Ligurian and Thyrrenian Seas with satisfactory results.

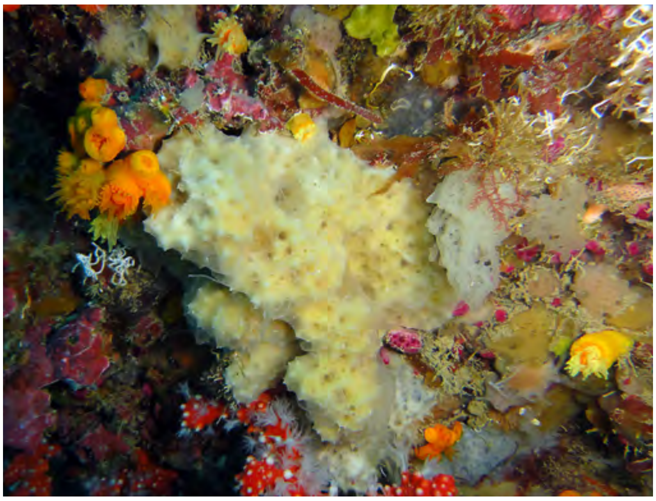


Figure 170. Number of visible taxa, basal layer coverage and density of erect species are variables that should be obtained when estimating MAES index (Photo by E. Ballesteros).

The Coralligenous Bioconstructions Quality Index (CBQI) (Ferrigno *et al.*, 2017) also uses video frames obtained by ROV and has been developed on the basis of MAES (Cánovas-Molina *et al.*, 2016b) and the Coral Condition Index (CCI; Ferrigno *et al.*, 2016). It takes into consideration three types of variables regarding the structure of the outcrops, the stressors and the abiotic factors. Structure is assessed measuring coralligenous cover, number of morphological groups and gorgonian density. The stress is quantified measuring percentage of necrosis or epibiosis (Figure 171), the cover or entanglement of fishing gear over organisms and the percentage of frames with fishing gear. The inclusion of abiotic factors in the index (depth, slope and substrate type) -the main difference with MAES- tries to buffer differences among sites due to environmental factors not related to anthropic pressures. The final index scores from 0 (bad) to 12 (optimum). The application of the CBQI to rocky cliffs, shoals and banks from the Gulf of Naples suggests that it could be a fast and easy method to assess coralligenous habitats quality in long-term monitoring programs.

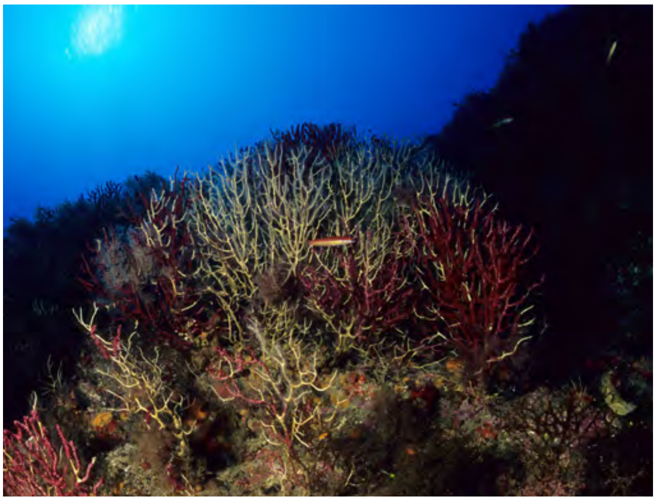


Figure 171. Percentage of necrosis and epibiosis of gorgonians is one of the measures of stress that must be assessed when estimating CBQI index (Photo by E. Ballesteros).

The Mesophotic Assemblages Conservation Status (MACS) (Enrichetti *et al.*, 2019) is a recent multi-parametric index that integrates three descriptors included in the Marine Strategy Framework Directive to define the environmental status (biological diversity, seafloor integrity, marine litter). The index includes two independent components, the Index of Status and the Index of Impact, each one involving six different metrics. The Index of Status targets conspicuous species diversity, basal layer and canopy composition, whilst the Index of Impact targets siltation level, canopy condition and marine litter occurrence. Data is also obtained by ROV video and has shown a high ability to disentangle natural from anthropogenic factors. It has been applied so far to Ligurian and Thyrrenian Seas.

The Ecological and Biological Value (EBV) (Altobelli *et al.*, 2017) has been applied to Sicily Channel seamounts -where coralligenous banks usually are an important ecosystem-. The EBV is based on the EBSA criteria for identifying significant areas requiring protection (Taranto *et al.*, 2012) and uses the presence of indicators (mainly sensitive/vulnerable habitats), naturalness and depth (Altobelli *et al.*, 2017) (Figure 172), as well as major threats (fishing gears, debris, invasive species, mining). Data is obtained from bibliographic resources and scientific surveys (mainly using ROVs). Indicators are weighed into 3 scores based on their relevance for EBSA purposes and threats are weighed into five scores specific for each indicator. Final index is obtained with the quotient between the indicator value and the threat value of each seamount, the highest quoted being those requiring conservation priority. Altobelli *et al.* (2017) detect several seamounts (Graham, Pantelleria Vecchia and Nereo) that are serious candidates for the creation of MPAs.

Figure 172. Presence of sensitive habitats and naturalness are criteria for identifying significant areas requiring protection according to EBV index (Photo by E. Ballesteros).

14.4. Citizen science and web platforms

Citizen science can be defined as the participation of non-scientific volunteers in the obtaining of the data according to some kind of protocols, under the coordination and control of professional scientists. It is a field that is growing fast and is being applied in a wide range of marine research (Goffredo *et al.*, 2010; Thiel *et al.*, 2014). Several initiatives have emerged in the Mediterranean Sea (Cerrano *et al.*, 2017; Di Camillo *et al.*, 2018; Ponti *et al.*, 2019), some of them related to invasive species, where the large coverage of volunteers is extremely useful for monitoring their spread (e.g. Zenetos *et al.*, 2013; Bodilis *et al.*, 2014; Cerrano *et al.*, 2017). Even if diving in the deep waters where coralligenous habitats develop requires advanced diving skills, the great number of people that dive in the Mediterranean and the attractiveness of coralligenous environments for scuba diving (Harmelin, 2009; Rodrigues *et al.*, 2016; Thierry de Ville d'Avray *et al.*, 2019) makes it an interesting target for the implementation of citizen science projects (Figure 173).

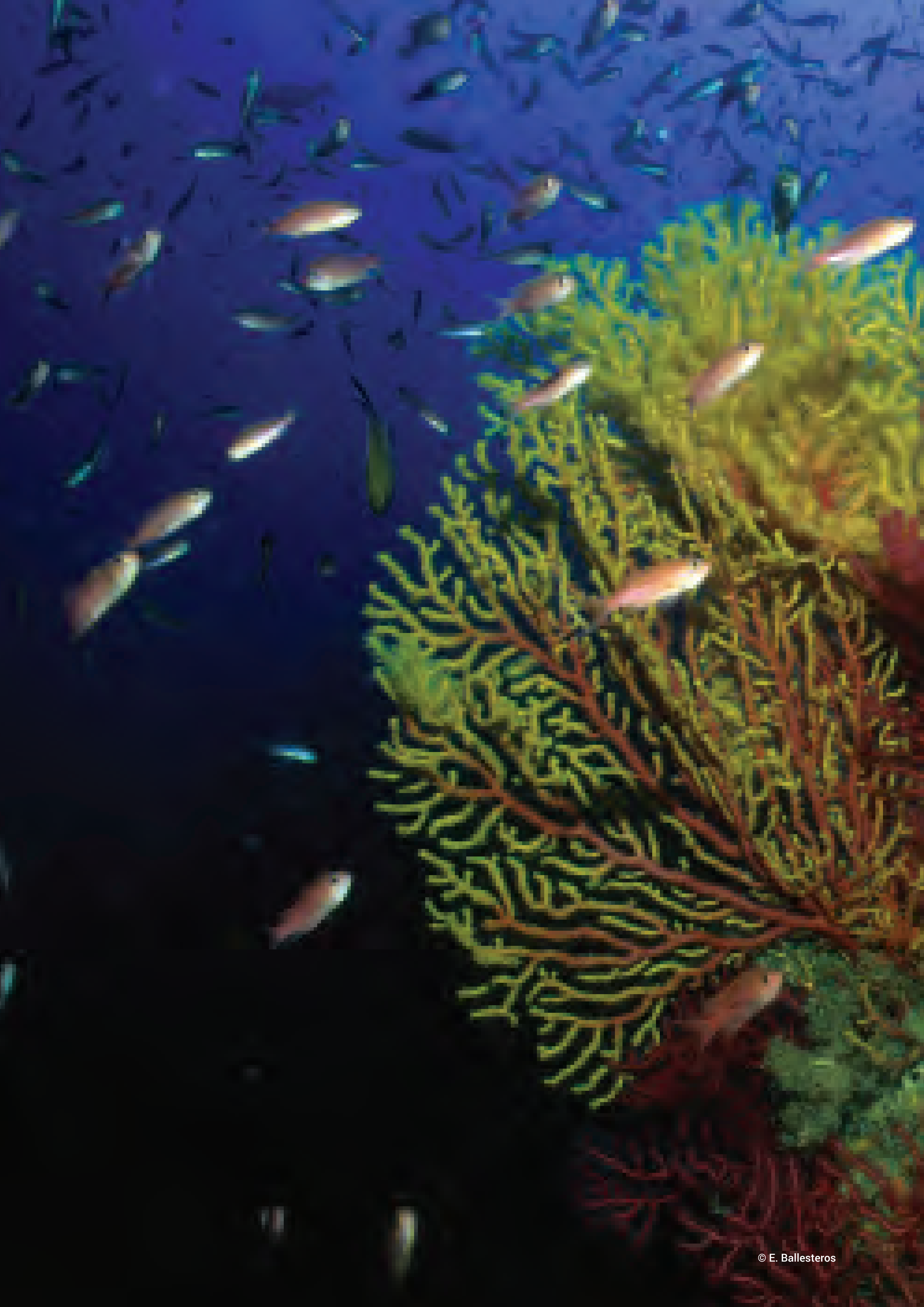
Probably, the first citizen science project related to coralligenous environments, the "Operazione Oro Rosso", related to *Corallium rubrum*. The project aimed at collecting information on the geographic, bathymetric distribution and health status of red coral populations along the Italian coast (Bramanti *et al.*, 2011). It consisted in answering a questionnaire which provided partial but significant information on the required items. The Reef Check Italia U-CEM protocol offers a 1-day intensive training course to volunteers

Figure 173. Attractiveness of coralligenous environments for scuba diving makes them an interesting target for the implementation of citizen science projects (Photo by E. Ballesteros).

that allows them to perform independent observations on invasive species, threatened species, ecosystem engineers, species sensitive to climate change and species commercially exploited (Cerrano *et al.*, 2017). These data are transferred by the volunteers to a online database (RCMed) that is afterwards used for monitoring by scientists (Cerrano *et al.*, 2017). The online platform "Seawatchers" (http://www.observadoresdelmar.es) has the special project "Warning Corals" whose goal is to obtain information on the distribution, conservation status and reproduction of the main Mediterranean gorgonians (Figure 174). Other platforms are iNaturalist (www.inaturalist.org) and other networks indexed by the Global Biodiversity Information Facility (GBIF, www.gbif.org) (Ponti *et al.*, 2019).

To our knowledge, at present, there are two web platforms that exclusively deal with coralligenous habitats and species: ERAnet, a website where amateur observers can provide data on topographic features, conspicuous species and pressures affecting coralligenous habitats (Gerovasileiou *et al.*, 2016), and CORMedNet (cormednet.medrecover.org), which aims to gather information on distribution, population dynamics and genetics of key species dwelling in coralligenous assemblages (Ponti *et al.*, 2019). Ruitton *et al.* (2019) use citizen science to obtain information on lost fishing gear by means of an online data recovery form (https://www.mio.univ-amu.fr/ghostmed/en/form/).

Figure 174. Inform about processes like gorgonian reproduction is one of the goals of the citizen science project "Warning Corals" from the online platform "Seawatchers" (Photo by E. Ballesteros).



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15. Natural capital and Ecosystem services

Natural capital is the value of resources and services provided by Nature and can be quantified economically. Ecosystem services include any kind of service that human beings obtain from the existence and functioning of ecosystems (Constanza *et al.*, 1997). Goods and services provided by ecosystems have a value that can be explored not only in economic terms but also in terms of the work done by the biosphere for its generation and maintenance (Franzese *et al.*, 2017). Coralligenous outcrops are rated first in an assessment of the value of heterotrophic natural capital of Mediterranean habitats (Franzese *et al.*, 2017), confirming its importance at the Mediterranean level (Figure 175).

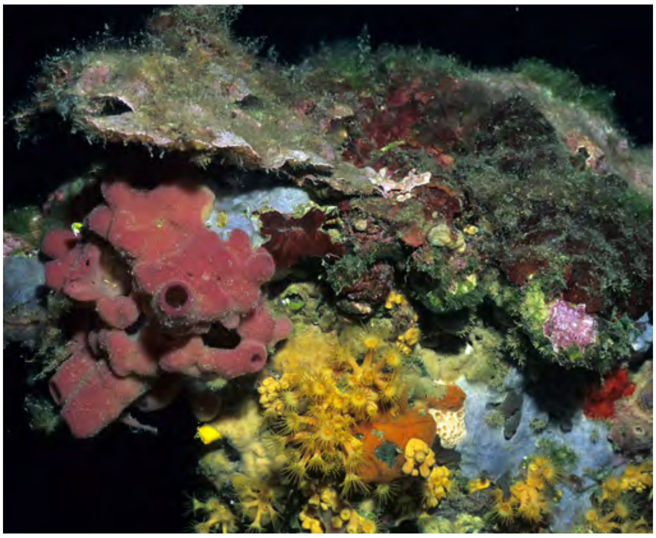


Figure 175. Coralligenous outcrops are rated first in an assessment of the value of heterotrophic natural capital of Mediterranean habitats (Photo by E. Ballesteros).

Even if coralligenous habitats are not very well known among non-divers, there is a general awareness that they sustain a high biodiversity (Figure 176) and that they provide important environmental services (Tonin & Lucaroni, 2017).

Figure 176. There is a general awareness that coralligenous outcrops sustain a high biodiversity (Photo by E. Ballesteros).

Main ecosystem services provided by coralligenous outcrops include food, diving sites, angling and spearfishing, research and inspiration (Thierry de Ville d'Avray, 2019). Moreover, it provides supporting ecosystem services such as habitat and refuge for hundreds of species and also it is an essential habitat for juveniles (Thierry de Ville d'Avray, 2019) (Figure 177).

Figure 177. Juveniles of spiny lobsters, *Palinurus elephas*, hide in coralligenous concretions (Photo by E. Ballesteros).

The source of food items obtained in coralligenous bottoms is huge since they are home to highly valued species (i.e. lobsters, groupers, scorpion fish, breams) but we still do not know of any proper economic assessment (Figure 178).

Figure 178. Number of food items provided by coralligenous bottoms is huge since they are home to highly valued species like *Dentex dentex* (Photo by E. Ballesteros).

In contrast, the importance of coralligenous bottoms to generate revenues for diving operations has been reported. An economic impact of €4.7 M in 2014 has been estimated in Apulia (Italy) (Chimienti *et al.*, 2017). Local extinction of gorgonians has the highest negative effect on diving utility of the coralligenous outcrops (Rodrigues *et al.*, 2016). In fact, the value of coralligenous outcrops when referred to diving operations is related to its beauty. Green algae (*Flabellia petiolata*), gorgonians (*Eunicella cavolini, Paramuricea clavata*), scleractinian corals (*Leptopsammia pruvoti*), sea urchins and bryozoans (*Myriapora truncata*) are the groups of organisms with the highest aesthetic scores in a study based in online surveys of aesthetic perception in coralligenous photographs (Tribot *et al.*, 2016). Moreover, species richness and functional richness show a positive effect on aesthetic value (Tribot *et al.*, 2016). The perception of divers about the beauty of these biogenic formations is so high that more than 50% of them were willing to pay for restoration actions (removal of marine debris) in tegnùe habitats (Tonin, 2018). Since landscapes/seascapes perceived as aesthetic are more likely to be protected, their conservation will probably enhance biodiversity, which in turn will probably improve ecosystem functioning and services, ultimately reinforcing the aesthetic experience (Tribot *et al.*, 2018) in a virtuous loop linking aesthetic value, conservation and biodiversity. In short, the beauty of coralligenous environments can be widely used to enhance the social background for conservation priorities, not only for the coralligenous itself but, in general, for benthic Mediterranean ecosystems (Figure 179).

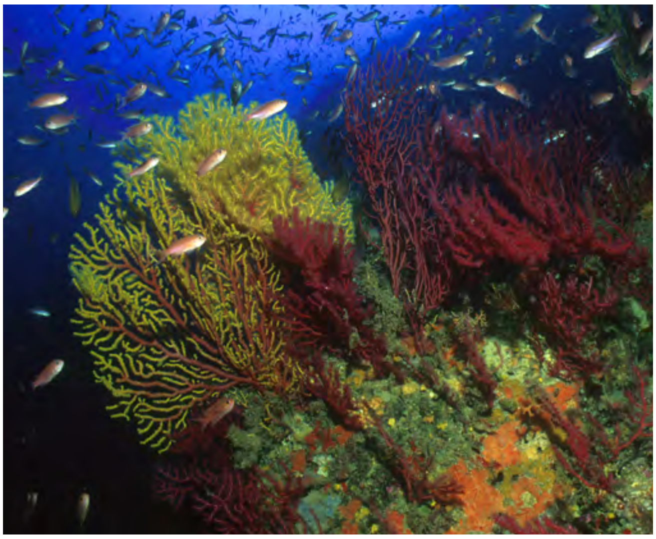
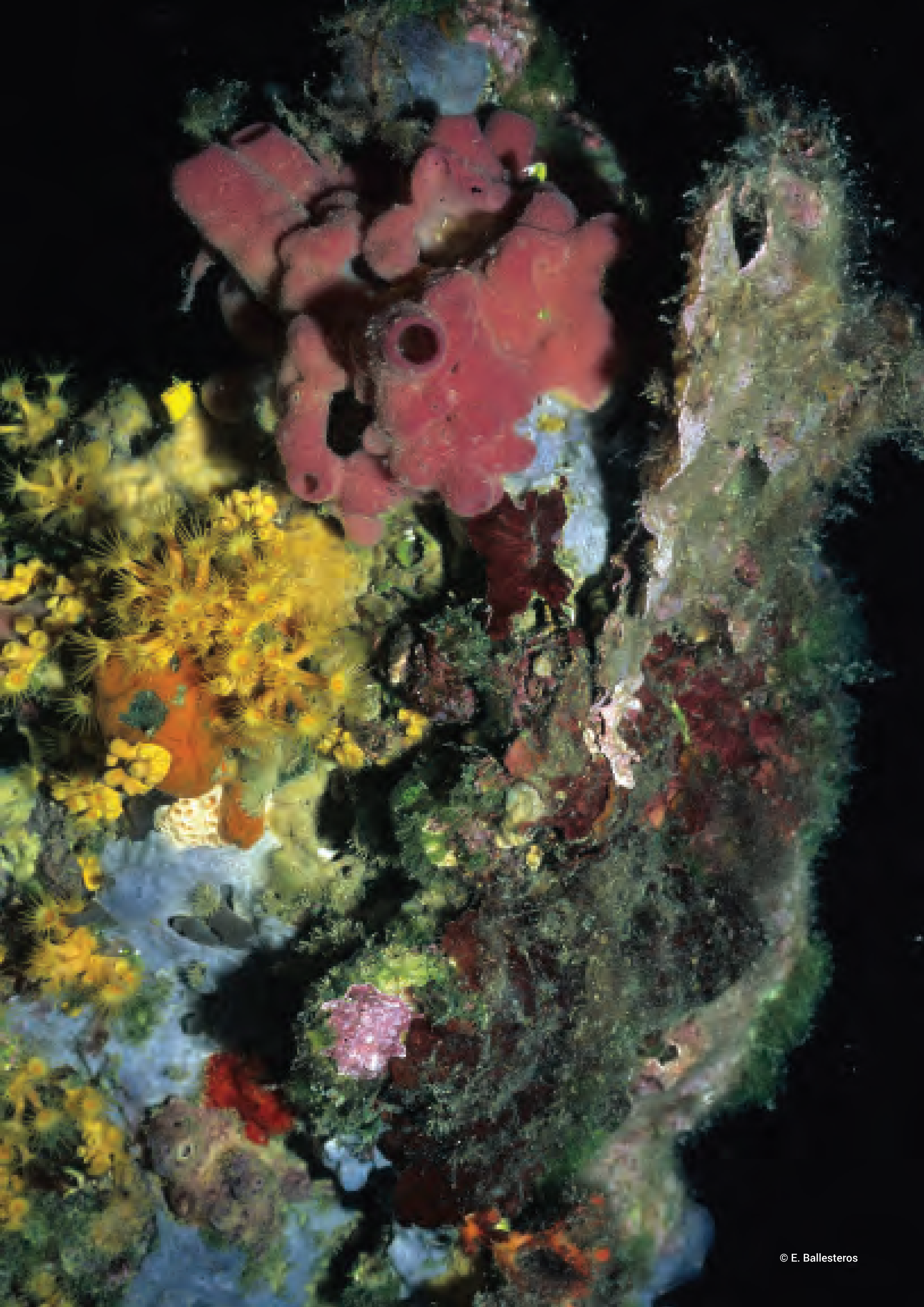


Figure 179. Beauty of coralligenous environments can be widely used to enhance the social background for conservation priorities (Photo by E. Ballesteros).



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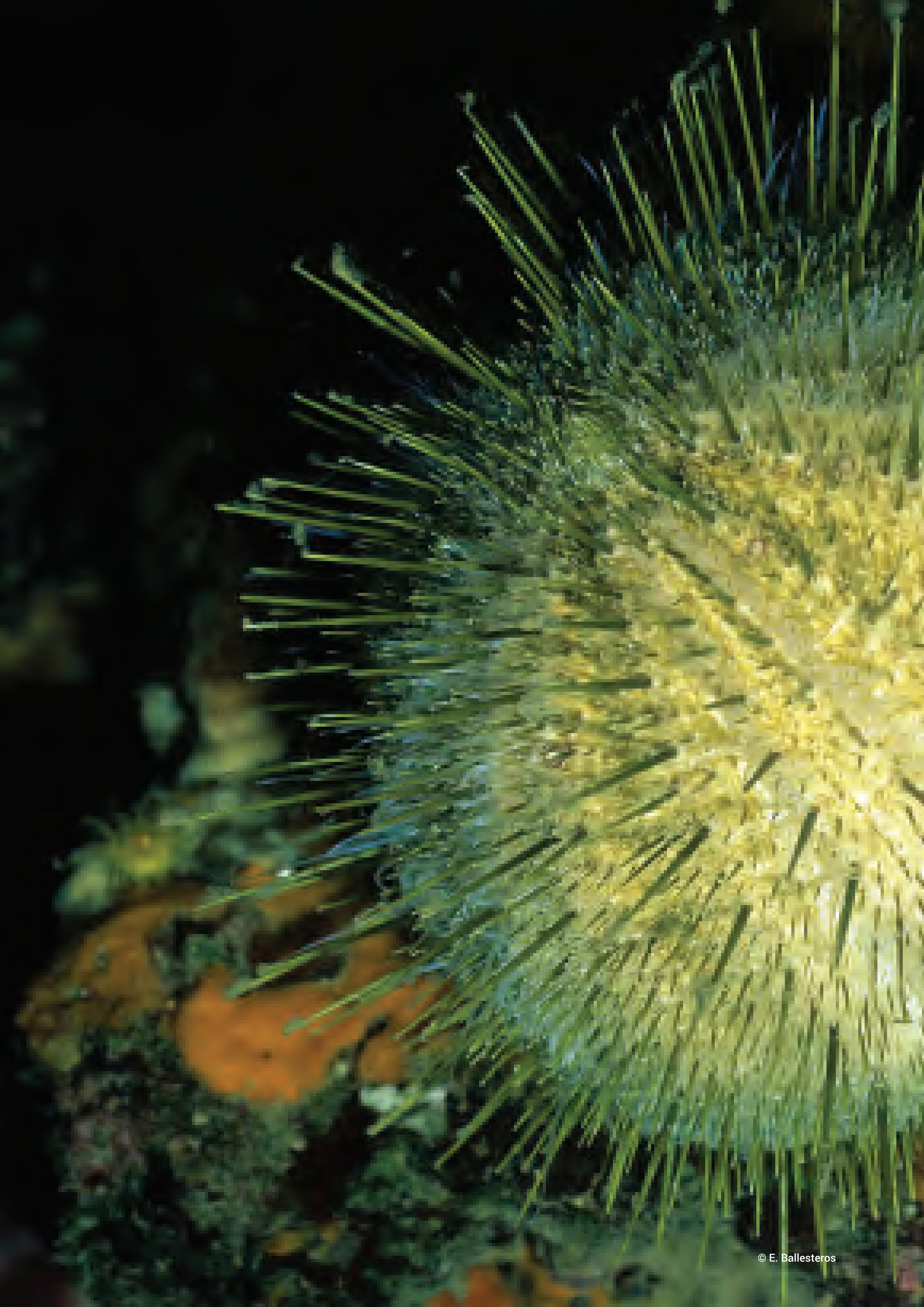

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16. Conclusions regarding current knowledge on coralligenous communities

The coralligenous habitat, as described here, is a typical Mediterranean biogenic build-up that basically comprises coralline algae growing in dim light conditions and in relatively calm waters. Although it usually develops in the circalittoral zone it can also thrive in the lower infralittoral zone if irradiance levels are low enough to allow the growth of the encrusting corallines responsible for build-up.

Most of the available data come from studies conducted in the western Mediterranean. Knowledge about Eastern Mediterranean build-ups is increasing thanks to exploring actions mainly undertaken by RAC/SPA.

The main distribution of coralligenous communities has been well documented on a large scale: it is common all around the Mediterranean coasts, with the possible exception of sites situated close to the Nile delta. The Northern Adriatic has a special kind of build-ups called tegnùe that slightly differ from typical coralligenous outcrops.

Knowledge about environmental factors is rather poor, as the coralligenous habitat is a highly heterogeneous system and environmental parameters can differ greatly at large geographical scales and at small, within-habitat scale. However, even though the obtaining of more data is necessary, basic knowledge of light (irradiance), temperatures, nutrient concentrations and hydrodynamism is available. Irradiance seems to be the most critical factor for the development of coralligenous concretions. Available data suggest that light levels must range between 1.3 MJ m^{-2} $year^{-1}$ and 50-100 MJ m^{-2} $year^{-1}$, that is, between 0.05% and 3% of the surface irradiance.

Two main morphologies can be distinguished: banks, which are built over more or less horizontal substrates, and rims, which develop in the outer parts of marine caves and vertical cliffs.

The coralligenous habitat includes several assemblages due to its high heterogeneity. Algal assemblages develop in open waters and are dominated by several species of encrusting red algae. *Mesophyllum* spp. dominate in relatively shallow waters while *Lithophyllum stictaeforme*, *Lithophyllum cabiochae* and *Neogoniolithon mamillosum* are more abundant in deep waters. Two main algal assemblages have been distinguished. Shallow water assemblages are rich in species of green algae, while deep-water assemblages have a poorer algal flora, with some encrusting and foliaceous red algae. Animal assemblages differ greatly among sites and geographical areas. In open areas, mixed with algae, cnidarians dominate the assemblage (mainly gorgonians) in relatively eutrophic areas, while in more oligotrophic waters sponges and bryozoans dominate. In overhangs and big cavities suspension-feeder communities are dominated by anthozoans, sponges and bryozoans. Some research has been devoted to the study of algal and animal builders, as well as bioeroders. However, biomass data for the different species composing the assemblages is very scarce. Data on food web structure is almost nonexistent although preliminary results show that coralligenous outcrops are mainly fueled by the pelagic environment.

A considerable amount of research has been done on the biodiversity of coralligenous concretions. Much more data could probably be gathered by taking into account floristic and faunistic studies, as well as monographs from the different groups that contain comments on the ecological distribution of species. A first estimate on the number of species thriving in coralligenous communities is around 2100 (315 algae, 1775 invertebrates and 110 fishes). Studies dealing with the coralligenous communities of certain areas give the number of species as ranging between 500 and 700 species of marine invertebrates. Also important is the very high density of vagile fauna that inhabits coralligenous outcrops, which can reach more than three invertebrates per gram of coralligenous concretion and, for example, a density of more than one polychaete worm per cm^2.

Some endangered Mediterranean species live in the coralligenous habitat, although none is exclusive to this environment.

As coralligenous diversity is so great, the coralligenous habitat reveals an intense connectivity among its inhabitants. Space competition is strong, as the space is completely saturated by organisms, and epibiosis is extremely frequent. Alellochemicals must play an important role in space competition, as coralligenous communities exhibit a very high percentage of chemically active species. Trophic relationships are also strong in coralligenous communities, particularly among vagile species, as most of the sessile invertebrates have skeletons that deter feeding. Several examples of mutualism, commensalism and parasitism have been reported.

Growth of coralligenous build-ups, carbonate production, and bioerosion and sedimentation rates have merited very few studies, although those published have presented very valuable data. They indicate (i) very low accumulation rates and their relationship to water depth and light availability, (ii) important source of carbonate for the continental shelf represented by coralligenous build-ups, (iii) relatively low bioerosion rates, at least in deep waters where algal growth is the lowest, and (iv) relatively high sedimentation rates.

Accretion rates of up to 0.83 mm year^{-1}, carbonate production (vegetal and animal) of up to 1000 g $CaCO_3$ m^{-2} year^{-1}, and values for bioerosion of up to 220 g $CaCO_3$ m^{-2} year^{-1} have been reported. These values are always higher in shallow than in deep waters.

Large animals and plants of coralligenous assemblages are highly persistent and show low to nil seasonality in terms of space occupation. Most of the area covered by a coralligenous community remains unchanged after, for example, two years of monitoring. However, growth pulses have been detected in some organisms such as the green alga *Halimeda tuna* or its epiphytic hydrozoans. Vagile invertebrates and fish fauna also show a degree of seasonality, mainly due to recruitment pulses and inactivity in winter. Several suspension feeders also exhibit some physiological seasonality, with decreased activity in summer, probably related to the low food availability and high temperatures that occur during this season. Decadal changes can be, however, important and are usually driven by anthropic pressures, but also by natural events like exceptional storms. The scarce data available on changes at the scales of centuries and millennia detects critical shifts at intervals of 250-500 years, which can be related to climatic periods.

The connectivity amongst coralligenous outcrops seems to be lower than in other assemblages growing at shallower waters. Larvae of most coralligenous engineering species show very reduced ranges of dispersal.

Some outstanding species inhabiting coralligenous assemblages (algae *Mesophyllum alternans, Lithophyllum stictaeforme* and *Halimeda tuna*; sponges *Hemimycale columella, Crambe crambe, Chondrosia reniformis, Dysidea avara* and *Oscarella lobularis*; hydrozoans *Orthopyxis crenata, Halecium petrosum* and *Halecium pusillum*; anthozoans *Paramuricea clavata, Eunicella cavolinii, Eunicella singularis, Corallium rubrum, Alcyonium acaule, Parazoanthus axinellae, Leptopsammia pruvoti*; tunicates *Halocynthia papillosa, Cystodytes dellechiajei* and *Microcosmus sabatieri*) have been carefully studied in order to determine one or several of the following features: growth rates, population dynamics, age, carbonate production, natural diets, prey capture, reproduction, spawning, and recruitment patterns.

Several stressors affecting coralligenous assemblages have been distinguished:

a) Warming, involving mass mortalities of suspension feeders.

b) Diseases, which can also lead to mortality outbreaks on suspension feeders, herbivores, macroalgae and fish.

c) Blooms of mucilaginous and filamentous algae.

d) Pollution, which profoundly affects the structure of coralligenous communities by inhibiting coralline algal growth, increasing bioerosion rates, decreasing species richness and densities of the largest individuals of the epifauna, eliminating some taxonomical groups (e.g. most echinoderms, bryozoans and crustaceans), and increasing the abundance of highly tolerant species.

e) Fishing, both for its effect on target species and on the habitat structure. Trawling is especially destructive, for not only physically destroying the coralligenous structure but by increasing turbidity and sedimentation rates. Traditional, as well as recreational, fishing mainly affect target species.

f) Red coral harvesting, whose full recovery has been estimated to take several decades or even centuries.

g) Marine debris, that concentrates over rocky bottoms and affects big suspension feeders.

h) Anchoring, which has a high destructive potential.

i) Diver frequentation, affecting, at the moment, very few areas situated at the most popular sites for recreational diving.

j) Catastrophic storms, which have a very low recurrence but huge effect.

k) Sedimentation related to changes in land cover and coastal engineering works.

l) Invasive alien species, whose numbers are increasing throughout the Mediterranean.

m) Acidification, which at the moment is not relevant but its effects can be very important in the mid-term future according to most predicted scenarios of carbon emissions.

Several legislations concern the protection of coralligenous assemblage at the level of the countries bordering the Mediterranean and at the UE level. The Barcelona Convention is the only conservation umbrella involving all Mediterranean countries, although it is not legally binding for the contracting parties. In the frame of the Barcelona Convention, the Action Plan concerning the coralligenous and other calcareous bioconcretions, adopted in 2008, is mainly devoted to the protection of the coralligenous habitats. However, the lack of relevant spatial data on coralligenous outcrops hinders the implementation of any measure of protection, which is currently only guaranteed by the creation of Marine Protected Areas.

The restoration of coralligenous environments should take centuries or even millennia, and active methodologies devoted to the recovery of engineering species have recently emerged.

Several monitoring protocols are being adopted by different organisations, countries and research teams, most of them involving scuba or ccuba diving but also ROVs or manned submersibles. Compelled by the urgency to meet the requirements of WFD and MSFD, we have witnessed the creation of several indexes that measure the ecological value or the ecological quality of coralligenous outcrops.

Ecosystem services provided by coralligenous outcrops include food, diving sites, research and inspiration and the natural capital of coralligenous environments is rated first -together with seagrass *Posidonia* meadows- in Mediterranean marine habitats.

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17. Actions

17.1. Gaps in scientific knowledge

In terms of the current state of scientific knowledge about the coralligenous habitat it is easy to detect several gaps that make it rather difficult to make recommendations for protecting coralligenous assemblages:

1. Even if mapping of coralligenous and other important habitats has recently increased, there still is a lack of cartography for most coralligenous bottoms across the Mediterranean. New efforts addressing cartographies and quantification of these bottoms are required.

2. Although compilations on the species found in coralligenous outcrops have been performed for some taxonomic groups (e.g. sponges, molluscs), there still is a profound lack of knowledge for other, very important groups of organisms. So, there is a need to spread these checklists to obtain a precise idea of the amount of biodiversity contained in this environment.

3. Special efforts have to be made as regards the description and functioning of coralligenous communities in the eastern Mediterranean. Further studies regarding the food web structure are urgently needed.

4. Further studies dealing with the processes involved in the build-up and erosion of coralligenous assemblages must be conducted, as almost all the existing information comes from scattered localities situated in the northwestern Mediterranean. Mid (decadal) to long-term (centuries) dynamics of coralligenous outcrops must be addressed if we want to truly understand the functioning and the persistence of these environments.

5. An understanding of the functioning of outstanding and key species is essential in order to implement an adequate management strategy for the coralligenous habitat. Most of the present studies concern a reduced number of species (mainly gorgonians) and they have to be expanded to organisms of other taxonomical groups.

6. The knowledge on the effects of disturbances in coralligenous assemblages is very uneven. Although a lot of research is currently devoted to stressors such as mass mortalities related to warming, diseases, and acidification, other important stressors are quite forgotten (sedimentation, pollution, invasive species).

17.2. Recommendations for protecting coralligenous communities

In light of current knowledge, there are a number of recommendations that can be made in order to conserve (or even improve) coralligenous environments. Most of these recommendations concern not only the coralligenous habitat, but most coastal benthic habitats, as wastewater dumping, trawling and overfishing, and invasion by alien species are problems that affect the whole of the coastal area. Measures to reduce these impacts may improve the overall quality of the marine coastal environment. Specific measures aimed at protecting the coralligenous environment might include the following:

1. No wastewater dumping should be allowed over coralligenous bottoms, nor in their vicinity.

2. Trawling must be completely prohibited in areas with coralligenous outcrops and their vicinity, the aim being to avoid not only the physical damage caused by trawling over coralligenous assemblages but also the indirect effects due to increased turbidity and silting.

3. Any other anthropic activity involving an increase in water turbidity and/or sediment removal (e.g. coastline modification, beach regeneration) should be avoided in the vicinity of coralligenous outcrops.

4. Correct management of traditional and recreational fisheries must be implemented in order to prevent stock depletion of target fish and crustaceans. Red coral harvesting needs more restricted legislation and enforcement.

5. The impact of diving must be compatible with the normal functioning and conservation of the coralligenous environment. Anchoring has to be completely prohibited over coralligenous outcrops.

6. There is an urgent need for suitable legislation concerning dumping of plastic and other debris in the marine environment, the introduction of alien species and carbon emissions.

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