Project for the preparation of a Strategic Action Plan for the Conservation of the Biodiversity in the Mediterranean Region (SAP BIO)

The coralligenous in the Mediterranean Sea

Definition of the coralligenous assemblage in the Mediterranean, its main builders, its richness and key role in benthic ecology as well as its threats





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RAC/SPA - Regional Activity Centre for Specially Protected Areas 2003

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Idealized representation of a typical coralligenous community (According to a drawing by Zabala, in Ros et al, 1985)



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1.DESCRIPTION

1.1- A coralligenous definition!

There is no real consensus amongst scientists studying the benthic communities in the Mediterranean Sea on what a coralligenous is. In this revision we will consider the coralligenous as a hard bottom of biogenic origin mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions. Although it is more extended in the circalittoral zone, it can also develop in the infralittoral zone, provided that light is dim enough to allow the growth of the coralline algae that make the buildup; therefore, infralittoral coralligenous concretions always develop in almost vertical walls, deep channels, or overhangs, and occupy reduced surfaces.

The sciaphilic communities developing near the sea level, in sites of heavy hydrodynamism, usually below the biogenic rim of the coralline alga Lithophyllum lichenoides (Boudouresque & Cinelli, 1976), are not considered in this revision, although they can exhibit small buildups of coralline algae. Other algal dominated communities thriving in the circalittoral zone such as rhodolith beds (Basso & Tomaselli, 1994) or Cystoseira zosteroides assemblages (Ballesteros, 1990) are not considered here, as the coralline algal concretion is reduced or almost nil.

Equally, some facies of the coralligenous, included into the name "precoralligenous" by several authors (e.g. Pérès & Picard, 1964; Gili & Ros, 1985; Ros et al., 1985); are avoided in this revision, upless they refer to sciaphilic communities without a basal buildup of coralline algae.

Therefore, the presence of a bioherm of coralline algae grown at low irradiance levels and in relatively calm waters is the main criterion on which we base our definition the coralligenous. This bioherm is always very complex in structure and allows the development of, in fact, several kinds of communities (Laborel, 1961; Laubier, 1966) ranging from those dominated by living algae (upper part of the concretions), suspension feeders (lower part of the concretions, wall cavities, and overhangs of the buildup), borers (inside the concretions), and even soft-bottom fauna (in the sediment deposited in cavities and holes). Therefore, the coralligenous has to be considered more like a submarine landscape or a community puzzle than as a single community.

2. HISTORY AND MAIN STUDIES

2.1- General and faunal studies

Marion (1883) firstly used the word coralligenous ("coralligène" in French) to describe the hard bottoms that fishermen from Marseilles called "broundo", which range between 30 and 70 meters depth, between seagrass meadows of Posidonia oceanica and coastal muddy bottoms. "Coralligène" means "producer of coral" and is related to the abundance of the red coral (Corallium rubrum) in this type of bottoms. 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 has been included in the bionomical descriptions of the Mediterranean sea bottoms since the end of the nineteenth century.

Feldmann (1937) thoroughly described the algal composition of the coralligenous from Banyuls and identified the main calcareous algae making the coralligenous buildup. He also made observations on the animals contributing to the buildup, and on the 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, showing its high microspatial variability and describing the environmental factors which allow its development.

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

Pérès & Picard (1958) characterized the coralligenous communities from the northeastern Mediterranean, defining an aspect with several warm water species and without several other species that dominate coralligenous buildups in the western Mediterranean.

Laborel (1960, 1961) also expanded the study of the coralligenous 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). Laborel (1960) also gave the first quantified lists of algal and animal species obtained by SCUBA diving.

Pérès & Picard (1964) summarized the knowledge on the coralligenous, defined the notion of precoralligenous and simplified the categories of Laborel (1961) by distinguishing two coralligenous types: the coralligenous over littoral rock and the bank or platform coralligenous, according to the original substrate (rock or sediment) where the buildup was initiated. They proposed an evolutive series relating the different biocenosis of the circalittoral zone in the Mediterranean and suggested the coralligenous as the climax biocenosis of this zone. They also referred to the word precoralligenous as a facies with a great development of erect, non-calcareous, sciaphilic algae and with a low cover of invertebrates. A summarized English version of Pérès & Picard (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 the coralligenous concretions in the region of Nice and Monaco, east of Marseilles.

Gamulin Brida (1965) made the first bionomical studies on the coralligenous in the Adriatic Sea and concluded that it is biogeographically very similar to the coralligenous from the northwestern Mediterranean, with a great abundance of big bryozoans, gorgonians and alcyonarians.

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

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

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

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

Gili & Ros (1984) reviewed the coralligenous communities of the Medes islands, in the northeast coast of Spain, and made an accurate evaluation of the total surface occupied by the coralligenous in this marine reserve (Gili & Ros, 1985). Detailed species lists of most vegetal and animal groups of coralligenous from singular areas in the Spanish Mediterranean can also be found in Ballesteros et al. (1993) and Ballesteros & Tomas (1999).

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

2.2. Algal studies

Feldmann (1937) was the first who unequivocally described the algal composition of the coralligenous, differentiated these bottoms from the deep water algal beds of Cystoseira spinosa and Cystoseira zosteroides, and identified the main calcareous algae making the coralligenous buildup. The algal community growing in the coralligenous received the name of Pseudolithophyllum expansum-Lithophyllum hauckii association.

SCUBA diving was first applied to the study of the algal flora of the coralligenous by Giaccone (1965), who made some "rélevés" of the coralligenous and defined it as a particular plant association, the Pseudolithophyllo-Halimedetum platydiscae in the zone of Palermo (Sicily). Giaccone & de Leo (1966) also studied by SCUBA diving the coralligenous and precoralligenous of the Gulf of Palermo by using the phytosociological method of Braun Blanquet. They distinguished both types of communities and named them Association of Lithophyllum expansum and Lithothamnion philippi (coralligenous) and 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).

Boudouresque (1970) studied with an accurate methodology the macroalgal communities of the coralligenous a detailed and exhaustive work on the sciaphilic benthic communities in the western Mediterranean (Boudouresque, 1971). SCUBA sampling and further sorting and identification in the aboratory were used. Augier et al. (1971) used this method to study the algal sciaphilic communities in the island of Port-Cros (France).

Boudouresque (1973) proposed to avoid the use of the terms coralligenous and precoralligenous, which have a physiognomical value but lack bionomical or phytosociological entity, and joined all the sciaphilic algal settlements under relatively sheltered conditions in one association (Peyssonnelietum rubrae), with two subassociations, corresponding to the assemblages developing in the infralittoral zone (Peyssonnelietum aglaothamnietosum) or in the circalittoral zone (Peyssonnelietum rodriguezelletosum). He reported the high biodiversity of these assemblages and defined the ecological group of algae characteristic of the coralligenous concretions (CC or Rodriguezellikon).

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

Boudouresque (1980) and Coppejans & Hermy (1986) made significant contributions to the study of the algal assemblages of the coralligenous in Corsica.

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

Giaccone et al. (1994) made a phytosociological revision of the sciaphilic assemblages described from the Mediterranean. According to this revision, most phytobenthic coralligenous assemblages are to be included in the Order Lithophylletalia, where two associations are distinguished: the Lithophyllo-Halimedetum tunae described by Giaccone (1965) and the Rodriguezelletum strafforellii described by Augier & Boudouresque (1975).

Phytobenhic assemblages growing in coralligenous concretions from vertical walls and overhangs in the infralittoral zone have to be included in the Order Rhodymenietalia, and belong most of the times to the association Udoteo-Peyssonnelietum squamariae described by Molinier (1960) from Corsica, which seems to be identical to the association of Peyssonnelia squamaria described by Feldmann (1937) from the Mediterranean Pyrenees.

3.ENVIRONMENTAL FACTORS AND DISTRIBUTION

3.1. Light

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

According to Ballesteros (1992) the coralligenous is able to develop at irradiances ranging from 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. Similar ranges are given by Ballesteros & Zabala (1993) which situate the lower light limit for the growth of Mediterranean corallines around 0.05% of the surface irradiance. These values agree with those obtained by Laubier (1966) in the coralligenous of Banyuls, at 32 meters depth, where he reported light levels of 1.8-2.6% of surface irradiance at noon in September.



Gorgoneans at ca 50 m depth; dim light area. © RAC/SPA

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

3.2. Nutrients, POC and DOC

Dissolved nutrients in seawater at coralligenous depths follow the annual pattern described for coastal Mediterranean waters, with highest values in winter and lowest values in summer. Mean annual water nitrate concentration near the coralligenous concretions at 18 and 40 meters depth in Tossa (northwestern Mediterranean) is around 0.6 μ mol t^1 , with

peaks of 1.5 µmol t¹ in winter and undetectable levels in summer (Ballesteros, 1992). Similar values are reported for a station in Cabrera, at 50 meters depth (Ballesteros & Zabala, 1993). However, these values are much lower than those reported from stations situated close to river mouths, such as the coralligenous from the Medes islands, where mean annual values are close to 1 µmol t¹ (Garrabou, 1997). Phosphate concentrations are much lower and are always below 0.1 µmol t¹ in Tossa and Cabrera (mean concentrations around 0.04 µmol t¹ or lower) (Ballesteros, 1992; Ballesteros & Zabala, 1993), or always below 0.2 µmol t¹ in Medes islands (mean concentrations around 0.13 µmol t¹) (Garrabou, 1997). The coralligenous seems to be adapted to these low nutrient concentrations in seawater, as increased nutrient availability greatly affects the specific composition, inhibits coralligenous construction and increases its destruction rates (Hong, 1980).

Mean annual particulate organic carbon (POC) of 387 μ g C t¹ are reported for the near-bottom planktonic community around the Medes islands at 15 meters depth (Ribes et al., 1999a), although winter and spring values were much higher (500 to 800 μ g C t¹). Dissolved organic carbon (DOC), reported also by Ribes et al. (1999a) from the same site, amounts to 2560 μ g C t¹, peaking in spring and summer. Ribes et al. (1999a) concluded that the detrital fraction was the dominant component of the total organic carbon in the near-bottom planktonic community throughout the year, which could be explained by the importance of run-off particles in Medes islands, but also by the input of organic matter by macroalgal (and seagrass) production, and by the activity of benthic suspension feeders in removing microbial organisms from the plankton. However, other studies are necessary in this topic because Medes islands are strongly affected by continental inputs of DOC and POC, which is not usually the case for most of Mediterranean coastal areas (mainly in islands or in the southern part).

3.3. Hydrodynamism

Flowing currents dominate at depths where the coralligenous develops (Riedl, 1966), but hydrodynamism generated by waves is very significative even at depths of 50 meters (Ballesteros & Zabala, 1993; Garrabou, 1997) for wave heights bigger than 1 meter. Rates of year round average in water motion in a coralligenous community in Medes islands between 25 and 35 meters depth is of 40 mg CaSO₄ hour⁻¹, that is, one order of magnitude lower than water motion at 2 meters depth (Garrabou, 1997). Nevertheless, and due to the intricated morphology of the coralligenous, the hydrodynamism can greatly differ from the various microenvironments, in a way similar to that reported for the light levels (Laubier, 1966).

3.4. Temperatures

Most of the organisms living in the coralligenous can withstand the normal seasonal range of temperatures that exhibit Mediterranean waters. Although Pérès & Picard (1951) stated that the coralligenous displays a relative stenothermy, Laubier (1966) described an annual temperature range from 10 to 23°C in the coralligenous of Banyuls. Ballesteros (1992) reported more or less the same temperatures for the coralligenous developing at 20 and 40 meters depth in Tossa de Mar between the end of November and the end of June (13 to 16°C), but differences of up to 9 degrees in summer, when the thermocline is

situated around 35 meters depth; however peak temperatures of 22°C are detected at the end of August at 40 meters depth.

In the Balearic islands, where the coralligenous is restricted to waters below 40 meters depth, water temperature ranges between 14.5 and 17°C for most of the year, but puntual 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 the coralligenous 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 meters and that is seldomly found between 50 and 70 meters, but only in seamounts (Sorelles and Mazarilles bancs, North west Tunisian coasts) or upwelling systems (Ballesteros, Ramos et al, unpublished data). Moreover, recent large scale mortality events of benthic suspension feeders thriving in the coralligenous have been attributed to unusual long-lasting periods of high temperatures during the summer (Perez et al., 2000; Romano et al., 2001), and autumn (Ben Mustapha & El Abed, 2001). These authors recorded a 22°C thermoclin up to 60 m depth, which affected the latter coralligenous of Zembra Marine Parc and the Cap Bon area (Tunisia). although the ultimate cause of these mortalities is still unclear (high temperatures, low food availability, pathogens and physiological stress?).

3.5. Salinity

The relatively shallow and coastal coralligenous of Banyuls displays salinity ranges between 37 and 38 per thousand (Laubier, 1966), but salinity variations of coralligenous 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). According to Laborel (1961) best developed formations are those found on the Aegean Sea, although best studied banks are those of the northwestern Mediterranean area, and being so, most of the data presented here comes from this area.

3.7- Depth distribution

The minimal depth for the formation of coralligenous concretions depends on the amount of irradiance reaching the sea bottom. In vertical slopes from the area of Marseilles this minimal depth reaches -20 meters, but it is much lower in some zones, like the Gulf of Fos, where the coralligenous is able to grow in shallower waters (-12 meters) 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) and Zembra, Fratelli and Ia Galite (Ben Mustapha, data not published).

Nevertheless, coralligenous concretions can appear in very shallow waters if light conditions are dim enough to allow a great development of coralline algae (Laborel, 1987;

Sartoretto, 1994), even in the most clear waters, like those of Cabrera island where a coralligenous buildup can be found at only 10 meters depth in a cave entrance (Marti, 2002).

Depth distribution of the coralligenous in subhorizontal to horizontal bottoms for different Mediterranean areas

| Mediterranean sector | Depth | References |
|-----------------------------|--------------------|--|
| Banyuls region: | 20-40 meters depth | (Feldmann, 1937; Laubier, 1966) |
| Marseilles region: | 20-50 meters | (Laborel, 1961; Hong, 1980) |
| Medes islands: | 20-55 meters | (Gili & Ros, 1984) |
| Tossa de Mar: | 20-60 meters | (Ballesteros, 1992) |
| Naples: | 45-70 meters | (Bacci, 1947) |
| Cabrera: | 50-100 meters | (Ballesteros et al., 1993) |
| Corsica: | 60-80 meters | (Laborel, 1961) |
| Northeastern Mediterranean: | 70-90 meters | (Laborel, 1961) |
| Aegean islands: | 90-110 meters | (Laborel, 1961) |
| Siculo-Tunisian region: | 90-120 meters | (Laborel, 1961) |
| Cap Farine - Ile Cani | Higher to 60 m | Ben Mustapha & al, 2003 Ben Mustapha & El Abed, |
| Cap Bon – Zembra | 40 à 70 m | 2001, Ben Mustapha, not published |
| Southeastern Mediterranean: | 100-120 meters | (Laborel, 1961) |

4.Structure -

4.1.

Coralligenous types : Structure and habitats

Morphology of coralligenous buildups

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

Banks are flat buildups with a variable thickness that ranges between 0.5 and several (3-4) meters. They are mainly built over more or less horizontal substrates, and they have a very cavernous structure, plenty of holes (Laborel, 1987), which 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) expressed the opinion that they developed from the coalescence of rhodolithes or maërl ("coralligène de plateau"). Nevertheless, it is highly probable that these buildups grew almost always, upon rocky outcrops (Got & Laubier, 1968; Laborel, 1987) as the case of the coralligenous from Hallouf and Greco bancs from the eastern bassin off the Tunisian coasts (Ben Mustapha data not published).

Rims develop in the outer part of marine caves and on vertical cliffs, usually at shallower waters than banks. Thickness of the rims is also variable and range from 20-25 cm to more than 2 meters, thickness increasing from shallow to deep waters (Laborel, 1987).

In shallow water the main algal builder is Mesophyllum alternans, which builts flat or slightly rounded banks or rims with a foliaceous structure. As the water deepens, other corallines (Lithophyllum stictaeforme, Lithophyllum cabiochae, Neogoniolithon mamillosum) became 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, as it was recorded from the Hallouf banc (Ben Mustapha, data not published). However, at greater depths the density of these erect algae decreases and corallines dominate the community (Rodriguezelletum strafforellii).

Holes and cavities within the coralligenous structure always bear a complex community dominated by suspension feeders (sponges, hydrozoans, anthozoans, bryozoans, serpulids, molluscs, tunicates). The smallest crevices and interstices of the coralligenous buildup have an extraordinarily rich and diverse vagile endofauna of polychaetes and crustaceans, whilst 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 into the small patches of sediment retained by the buildup.

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

- 1. A fauna contributing to the buildup, helping and consolidating the framework created by the calcareous algae. Several bryozoans, polychaetes (serpulids), corals and sponges constitute this category. They include 24% of the total species number.
- 2. A cryptofauna colonising the small holes and crevices of the coralligenous. They represent around 7% of the species, being different molluscs, crustaceans and polychaetes its representatives
- 3. The epifauna (living over the concretions) and endofauna (living inside the sediments retained by the buildup), which represent a great number of the species (nearly 67%).
- 4. The eroding species, accounting only for a rough 1%.

4.2. Algal builders

Coralline algae are the main coralligenous builders (Laborel, 1961; Laubier, 1966; Sartoretto, 1996). Taxonomy of this group of algae is very difficult and the nomenclature of the species is in constant change. Due to its great importance in the construction of the coralligenous we will make here some considerations regarding the taxonomical status and current nomenclature of the main species.

The main building algal species, according to Sartoretto (1966) and several authors, has been repeatedly identified as Mesophyllum lichenoides (Ellis) Lemoine. However, Cabioch & Mendoza (1998) identified it as a different species and named it Mesophyllum alternans (Foslie) Cabioch & Mendoza. Therefore, probably all the reports of Mesophyllum lichenoides as a coralligenous builder have to be referred to Mesophyllum alternans (Cabioch & Mendoza, 1998).

Pseudolithophyllum expansum (sensu Lemoine) has probably been identified by most authors as being the second most common coralline alga in the coralligenous. Nevertheless, Boudouresque & Verlaque (1978) identified another species, similar to Pseudolithophyllum expansum, and described it as Pseudolithophyllum cabiochae. Later, works by Woelkerling (1983), Athanasiadis (1987), Woerkerling et al. (1993) and Furnari et al. (1996) have added some light (but also much confusion) on the name to be applied to the alga called "Pseudolithophyllum expansum" and/or 'Pseudolithophyllum cabiochae" by Mediterranean phycologists and marine biologists. The last revision by Athanasiadis (1999) suggested that Pseudolithophyllum can not be recognized as a genus different to Lithophyllum and that the two species growing in the coralligenous communities should be named Lithophyllum stictaeforme (Areschoug) Hauck [= Lithophyllum frondosum (Dufour) Furnari, Cormaci & Alongi; = Pseudolithophyllum expansum (Philippi) Lemoine; =Lithophyllum expansum sensu Lemoine] and Lithophyllum cabiochae (Boudouresque & Verlaque) Athanasiadis.

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].

Although not a coralline alga, it is worthy to say that authors before 1975 have identified the calcareous Peyssonnelia growing in the coralligenous as Peyssonnelia polymorpha (Zanardini) Schmitz. Boudouresque & Denizot (1975) described a similar species, Peyssonnelia rosa-marina Boudouresque & Denizot, more frequent than P. polymorpha, and which also inhabits the coralligenous concretions. Therefore reports of Peyssonnelia polymorpha before the description of P. rosa marina should probably be referred to this last species or to both entities.

Feldmann (1937) identified the four main calcareous algae making the coralligenous buildups in the region of Banyuls: Lithophyllum stictaeforme (as Pseudolithophyllum expansum), Neogoniolithon mamillosum (as Lithophyllum hauckii), Mesophyllum alternans (as Mesophyllum lichenoides) and Peyssonnelia rosa-marina f. saxicola (as Peyssonnelia polymorpha). The same species have been reported from coralligenous concretions studied



in several areas close to the Gulf of Lions (e.g. Boudouresque, 1973; Ballesteros, 1992). It seems that these species are always nearly the same, with the possible exception of Lithophyllum stictaeforme which seems to be substituted bv Lithophyllum cabiochae in several areas of the Mediterranean, warmer than the Gulf of Lions (e.g. Corsica, islands, Eastern Balearic Mediterranean?).

The main calcareous algae making the coralligenous buildups: Lithophyllum sp. A.Bouajina©RAC/SPA

Hong (1980) reports three species as 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 the buildup are Archaeolithothamnion mediterraneum, Lithothamnion sonderi (?) and Peyssonnelia polymorpha.

According to Sartoretto et al. (1996) Mesophyllum alternans is the main building algal species both from ancient and recent coralligenous constructions in the Northwestern Mediterranean. Mesophyllum alternans is a high tolerant species regarding light, temperature and hydrodynamism and it is the actual dominant species in shallow waters. In some areas, Peyssonnelia rosa-marina and Peyssonnelia polymorpha can also be the dominant species, building a very cavernous, highly bioeroded coralligenous. In deep waters Lithophyllum cabiochae is the main calcareous alga in the region of Marseilles and Corsica, but its cover can vary amongst geographical areas. For example, the encrusting algal cover in deep water coralligenous concretions in Marseilles is limited to a few isolated small living thalli which 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 7700 years to present times shows that no species changes have occurred (Sartoretto

et al., 1996). Five Corallinaceae and one Peyssonneliaceae are distinguished in the work by Sartoretto et al. (1996) from the Marseilles region and Corsica: 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 Peyssonnelia sp.. Mesophyllum alternans is also the main algal builder in the coralligenous concretions in the Mediterranean Pyrenees (Bosence, 1985), together with Lithophyllum and Titanoderma (quoted as Pseudolithophyllum and Tenarea in Bosence's paper). Peyssonnelia polymorpha and Peyssonnelia rosa-marina f. saxicola can also be abundant in the coralligenous concretions from the Mediterranean Pyrenees, the northeast coast of Spain, and the Balearic islands (Bosence, 1985; Ballesteros, 1992; Ballesteros et al., 1993).

Nevertheless, even if Peyssonnelia is abundant as a living encrusting alga, it is almost absent in the fossil record (Bosence, 1985; Sartoretto, 1996). Carbonate content of the Peyssonnelia species is lower than average carbonate content in the corallines (Laubier, 1966; Ballesteros, 1992) and the calcification in the form of aragonite instead of calcite prevents a good fossilization of these species (James et al., 1988). Nevertheless these and other species of Peyssonnelia usually have a basal layer of aragonite which may contribute to the consolidation of the coralligenous concretions when mixed with the physico-chemical precipitations of CaCO₃ (Sartoretto, 1996).

4.3. Animal builders

Coralligenous animal builders are studied by Hong (1980) from the region of Marseilles. He found a total number of 124 species contributing to the buildups, which account for a rough 19% of the total number of species reported in the coralligenous of Marseilles. The most abundant animal group are the bryozoans, accounting for 62% of the species, followed by the serpulid polychaetes, with the 23.4% of the species. Minor contributors are the cnidarians (4%), molluscs (4%), sponges (4%), crustaceans (1.6%) and foraminifers (0.8%). However, Laborel (1987) considers foraminifer Miniacina miniacea as being the most important algal builder.

The bryozoan Myriapora truncata; one of the main animal builders of the coralligenous. D.Cebrian



Hong (1980) distinguished three different types of animal builders: those directly contributing to the buildups, which are relatively big; those with a reduced buildup activity because of their small sizes; and those, which agglomerate carbonate particles. Amongst the first group, there are the bryozoans Schizomavella spp., Onychocella marioni, Cribilaria radiata, Entalophoroecia deflexa, Celleporina caminata, Myriapora truncata, Brodiella armata and Turbicellepora coronopus, several serpulids (Serpula vermicularis, Serpula concharum, Spirobranchus polytremma), the molluscs Vermetus sp., Serpulorbis arenarius and Clavagella melitensis, and the scleractinians Hoplangia durotrix, Leptopsammia pruvoti, Caryophyllia inornata and Caryophyllia smithii. Amongst the second group, Hong (1980) reports some small bryozoans like Crassimarginatella maderensis and Mollia patellaria, serpulids like Hydroides spp., Filogranula spp., and Spirorbis spp., the cirripeds Verruca strömia and Balanus perforatus, and the foraminifer Miniacina miniacea. Amongst the "agglomerative" animals, he reports some sponges like Geodia spp., Spongia virgultosa and Faciospongia cavernosa, the bryozoans Beania spp., and the alcyonarian Epizoanthus arenaceus.

4.4. Bioeroders

Feldmann (1937) described the abundance of several organisms that erode the calcareous concretions, in particular the excavating sponge Cliona viridis, the bivalve Lithophaga lithophaga and several annelids. Hong (1980) made a list of 11 bioeroders in the coralligenous of Marseilles: 4 different species of sponges of the genus Cliona, 3 species of molluscs, two species of polychaetes of the genus Polydora and two sipunculids. According to Sartoretto (1996), the organisms that erode the coralligenous are similar to those eroding other marine bioherms such as the "trottoir" of Lithophyllum lichenoides or the coral reefs. Three types of eroding organisms can be distinguished: browsers, microborers and macroborers.

Browsers are restricted to sea urchins in the Mediterranean (Laubier, 1966), as the only important fish grazing on algae (Sarpa salpa) do not usually thrive in the coralligenous communities. Sphaerechinus granularis is an important biological agent which substantially erodes the coralligenous, 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 the coralligenous is Echinus melo. The proportion of calcareous algae in



the digestive content ranges between 18 and 50% of the total (Sartoretto, 1996) and it mainly predates on sponges, bryozoans and serpulid polychaetes. Given the low densities of this sea urchin in the coralligenous (1 to 3 individuals in 25 m⁻²), Sartoretto (1996) concludes that the bioerosional role of Echinus melo is very low. Microborers include blue green algae (Cyanobacteria), green algae and fungi (Hong, 1980). Three green algae (Ostreobium quekettii, Phaeophila sp. and Eugomontea sp.) and 4 Cyanobacteria (Plectonema tenebrans, Mastigocoleus testarum, Hyella caespitosa and Calothrix sp.),

Sphaerechinus granularis is an important biological agent, which substantially erodes the coralligenous. A.Bouajina©RAC/SPA

together with some unidentified fungi, seem to be the main microborers in the coralligenous. Diversity is higher in shallow waters, whilst it is restricted to only one species (Ostreobium) in deep waters (-60 m), according to colonization studies made by Sartoretto (1998).

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). Amongst perforating sponges common in the coralligenous, some of them are excavating mainly in Corallium rubrum and other calcareous cnidaria (Aka labyrinthica, Scantilletta levispira, Dotona pulchella ssp. mediterranea, Cliona janitrix), whilst others can be found in a wide range of calcareous substrates (coralline algae, bivalves, madreporids, etc.) like Pione vastifica, Cliona celata, Cliona amplicavata, Cliona schmidtii and Cliona viridis (Rosell & Uriz, 2002). Cliona viridis is the most powerful destructive sponge of calcareous substrates (Rosell et al., 1999) and it is the most abundant excavating sponge in the coralligenous (Uriz et al., 1992).

The encrusting sponges and the Sipunculida become more abundant in polluted coralligenous environments (Hong, 1983).

4.5. Assemblages

A Complex structure

The final result of the builders and eroders of the coralligenous is a very complex structure, where several microhabitats can be distinguished. Environmental factors (e.g. light, hydrodynamism, sedimentation rates) can be one to two orders of magnitude different amongst places of the same buildup situated only at one meter of each other. These high environmental heterogeneity allows the coexistence of several different assemblages in a reduced space. 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 report on the assemblages of macroborers (as the only available data has been already commented), nor on the assemblages thriving in the sediment patchess between nor inside the coralligenous buildups (as there is no quantitative data on them).

Algae, both encrusting corallines and green algae, usually dominate in horizontal to subhorizontal surfaces, although its abundance decreases with depth or dim light conditions. Phycologists have distinguished two main communities according to the light levels reaching the coralligenous. 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). This plant association received the name of Lithophyllo-Halimedetum tunae, and was thoroughly described by Ballesteros (1991b). Algal biomass ranges between 1200 and 2100 gdw m², 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 12-15 meters to 30-35 meters depth in the Gulf of Lions, but it can reach depths below 50 meters in the clear waters of seamounts and insular territories of the Western Mediterranean and the Eastern Mediterranean. This association develops at irradiances ranging approximately from 2.3 to 0.3 W m⁻², which respectively correspond to 3 and 0.4% of the surface irradiance. Other "rélevés" can be found 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). Other common algae are members of the family Delesseriaceae and other laminar red algae (Kallymenia, Fauchea, Sebdenia, Rhodophyllis, Predaea), and 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 from the coralligenous concretions by Feldmann (1937) from the Mediterranean Pyrenees. 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 90% corresponding to corallines; the number of species is low (38 species in 1600 cm² or lower) (Ballesteros, 1992).

Animal assemblages of these two plant associations can greatly differ among both associations, among sites and among 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, but in very oligotrophic waters (e.g. Balearic islands, eastern Mediterranean), sponges, bryozoans and small hexacorals are the dominant suspension feeders.

The only available quantified biomass data of invertebrate assemblages is that of True (1970) from the zone of Marseilles. Thus, we will summarize here his results.

True (1970) studied an assemblage dominated by Eunicella cavolini. He reports a basal layer of encrusting algae accompanied also 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 Parerythropodium 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 cm², 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 very lower values, Annelida, Porifera, Chordata (tunicates), and Mollusca.

Another assemblage studied by True (1970) is that dominated by Paramuricea clavata. Populations of Paramuricea clavata are abundant in steep rocky walls, but they also

grow in horizontal to subhorizontal surfaces if light levels are very reduced. 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 m², 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 the 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 polymorphus and Polycarpa pomaria. The number of collected invertebrate species amounts to 111 in 7500 cm², 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 dominated by the gorgonian Paramuricea clavata from the Medes islands. Total cnidarian biomass amounted 430 g dw m⁻², with 13 species of hydrozoans and 9 species of anthozoans found in an area of 5202 cm². 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 Parerythropodium coralloides, with the hydrozoans Sertularella gaudichaudii and Halecium tenellum being also abundant.

Overhangs and big cavities of the coralligenous have a different species composition from that found in open waters. Algae are usually completely absent because light is very reduced. Nevertheless, some thalli of encrusting corallines, Peyssonnelia spp. and Palmophyllum crassum can occasionally be found. There are no "relevés" of this kind of habitat published in the available literature, but 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). We will describe this assemblage, as it is very similar to those developing in the overhangs of the coralligenous constructions in the northwestern Mediterranean or in the coralligenous situated in very deep waters.

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 sponges Ircinia variabilis, Spongia officinalis, Aaptos aaptos, and Ircinia oros, molluscs Chama gryphoides and Anomia ephippium, and several unidentified bryozoans. The total number of identified invertebrate species is 63 in 7500 cm², with a total biomass of 3817 g dw m². The dominant phylum is largely the Cnidaria, but also abundant are Porifera, Annelida and Bryozoa.

We may take into account that most of the invertebrate data presented in this chapter, if representative at all, reflects the biomass and the species composition of several assemblages of the coralligenous buildups of the Gulf of Lions, which are different to that 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, this data can not be extrapolated to the entire Mediterranean coralligenous assemblages.

5.Biodiversity -

The coralligenous high biodiversity

Coralligenous assemblages are one of the preferred diving spots for tourists due to the high diversity of organisms. Divers are amazed by the high number of species belonging to taxonomic groups as diverse as sponges, gorgonians, molluscs, bryozoans, tunicates, crustaceans or fishes. Moreover, there is a huge amount of organisms living in the coralligenous that cannot be observed by diving, nor without a careful sorting of the samples. For example, in a sample of 370 g dw of Mesophyllum alternans from a small coralligenous concretion in the South of Spain, García-Raso (1988) found 903 specimens of Crustaceans, Molluscs and Polychaetes; other organisms from other groups (Picnogonida, Nematoda, Echinoderms, Sipunculida, Sponges, Tunicates, small fishes -Gobiidae and Bleniidae-, Hydrozoans, and Bryozoans) were also abundant although non quantified.

Laubier (1966) is the first author that emphasizes the high biodiversity of the coralligenous and lists 544 invertebrates from the coralligenous at the region of Banyuls. Later, Hong (1980), in an exhaustive survey of the coralligenous of Marseilles lists a total of 682 species, whilst several authors (in Ros et al., 1984) report 497 species of invertebrates in the coralligenous of the Medes islands. Our estimates of the species richness found in the coralligenous give a very conservative number of 1241 invertebrates (table I). In one sample of 1m², Romdhane & al (data not yet published) listed 35 algal species and 93 animal species in the coralligenous from a littoral vertical cliff from the gulf of Tunis.

Boudouresque (1973) has estimated that at least 315 species of macroalgae can thrive in Mediterranean sciaphilic communities (the coralligenous being the most widespread community). Finally, there are no estimates of the number of fishes that can be found in the coralligenous, due to the high mobility of most of the species of this group, but our estimates based on available literature on the biology of Mediterranean fishes (e.g. Whitehead et al., 1984-1986; Corbera et al., 1996; Mayol et al., 2000) range between 110 and 125 species.

Table I. Approximative number of species reported from the coralligenous (several authors).

| | Group | Totals | Refe | erences |
|--|--|-------------------------------|-------------|-----------------------------|
| | Algae | 315 | | 1 |
| | Protozoans | 61 | | 2,3 |
| | Sponges | 142 | 2,3,4,5,6,7 | |
| | Hydrozoans | 55 | | 2,4,5,8 |
| | Anthozoans | 43 | 2,4 | 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 | 7 | | 3 |
| | Prosobranchs | 61 | | 3 |
| | Opistobranchs | 33 | | 3 |
| | Bivalves | 41 | | 3 |
| | Cephalopods | 3 | | 6 |
| | Mites | 6 | | 2 |
| | Pycnogonids | 15 | | 3 |
| | Copepods | 54 | | 2 |
| | Ostracods | 10 | | 2 |
| | Cirripeds | 3 | | 2,3 |
| | Phyllocarids | 1 | | 3 |
| | Mysids | 7 | | 3 |
| | Cumaceans | 3 | | 2,3 |
| | 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 | | ,5,6,15,16 |
| | Tunicates | 82 | | 17 |
| | Fishes | 110 | | 18,19 |
| | | Referen | | |
| 1 Boudouresque (19 2 Laubier (1966) | • | osell & Uriz bet et al. (1 | (2002) | 14 Zabala (1 15 Tortones |
| 3 Hong (1980) | | • | 17710) | |
| 0, , | | artin (1987) allan Santini | (1000) | 16 Munar (1 |
| • • | Ros et al. (1984) 10 Bellan Santini (1998) 17 Ramos (1991) | | | |
| 5 Ballesteros et al. (1 | • | iarcia Raso | • • | 18 Whitehea |
| 6 Ballesteros & Tom | ias (1999) 12 G | iarcia Raso | (1989) | 19 Ballester |

13 Logan (1979)

data)

You will find next, it follows an account of the main knowledge acquired for each taxonomic group.

5.1. Taxonomic groups

5.1.1. Algae

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

Boudouresque (1973) defined the ecological group of algae characteristic of the coralligenous concretions (CC or Rodriguezellikon), which -after his own revision-(Boudouresque, 1985) is constituted by 28 species (e.g. Rodriguezella spp., Aeodes marginata, Fauchea repens, Chondrymenia lobata, Gulsonia nodulosa, Polysiphonia elongata, Neogoniolithon mamillosum).

Listing problems

It is very difficult to mention all the species found in the coralligenous up to now, due to the huge existing taxonomic literature and the high number of synonyms, that makes it impossible for a non specialist of most of the groups to render an accurate number of the reported species. Nevertheless, we have attempted to make a first, very conservative, estimate of the total number of species, which amounts to some 1666 (table I). A first step to the increase of the knowledge of the biodiversity existing in the coralligenous must try to give a more accurate estimate of the species found in the coralligenous their number.

However, the coralligenous is never dominated by this group of species, but by other species with a more depth-related widespread distribution such as 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 membranacea, Spatoglossum solierii, Zonaria tournefortii, Halopteris filicina, Phyllariopsis brevipes, Zanardinia prototypus, and Laminaria rodriguezii, and a large amount 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, banyulensis, Plocamium cartilagineum, Sphaerococcus coronopifolius, Polysiphonia Erythroglossum sandrianum, and Aglaothamnion tripinnatum) (Boudouresque, 1973, 1985; Ballesteros, 1992, 1993).

In the banc Hallouf, ongoing investigations (Ben Mustapha, data not yet published), allows the presence of a dense covert of pheophycae algae; under which thrives an important coralligenous. The pheophycae are mainly represented by Dictyota membranacea, Sargassum hornschuchii, Sargasum valgarae and Zonaria tournefortii. Rhodophycae were represented by a much important list of species, occuring in the low

strata; due to their smaller size in general: Fauchea repens, Galaxaura oblongata, Ptilophora mediterranea, Phyllophora nervosa, Vidalia volubilis, Chondrymnea lobata, Sebdenia dichotoma, Halarchnion ligatum, Halymenia sp, Peysonela rosa-marina, Peysonella rubra, Litophylum expansum et Litothamnium sp.While Chlorophycae were a minority with two dominating species: Flabellia petiola and Caulerpa racemosa. A third species, with sciaphic affinity, was also recorded is some stations :Palmophyllum crassum.

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

The coralligenous community is 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 of Tossa de Mar dominated by Mesophyllum alternans and Halimeda tuna, but only 38 in the coralligenous from a deep water site (Ballesteros, 1992). However, algal populations in the coralligenous greatly differ amongst sites (Boudouresque, 1973) and this is the main reason that, even if the species richness in one site is rather low, the overall algal richness of the coralligenous is huge.

5.1.2. Protozaons

54 species of Foraminifera are listed by Hong (1980) in the check-list of species from the coralligenous of Marseilles. None of this species seems to be characteristic of the coralligenous. Miniacina miniacea is the most abundant species. Other common species are Massilina secans, Planorbulina mediterranensis, Elphidium crispum, and Triloculina rotunda. Laubier (1966) reports six species of Folliculinidae living as epibionts of bryozoans.

5.1.3. Sponges

The coralligenous is very rich in sponges, growing mainly in the more sciaphilic environments, but also in the more exposed zones. There are also some species (Clionidae) that are active bioeroders and excavate the coralline framework. The number of species reported from different well-studied areas is of 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), 32 species from Zembra (Ben Mustapha & Sanchez Jerez, data not yet published) 24 species from Tossa (Ballesteros & Tomas, 1999). The list of sponges reported in all these works (and those of True, 1970 and Rosell & Uriz, 2002) amounts to 142 different species.

According to Hong (1980) the following species are characteristic of the coralligenous biocoenoses: Axinella damicornis, Acanthella acuta, Hymedesmia pansa, Agelas oroides, 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.

Coralligenous sponges from the eastern Mediterranean

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

In the ongoing study of Hallouf banc, located at 30 NM east of Monastir (Tunisia), Ben Mustapha (data not published) recorded the high frequency of the following species: Hippospongia communis, Cacospongia mollior, Ircinia dendroides, Ircinai fasciculata, Petrosia dura, Chalinella sp, Cliona sp, Chondrosia reniformis, Crambe crambe, Hamigera hamigera, Anchinoe sp, Acanthella acuta, Agelas oroides, Axinella damicornis, Axinella polypoides Hippospongia communis, Spongia officinalis, Spongia nitens, Cacospongia mollior, Fasciospongia cavernosa, Ircinia fasciculata, Ircinia spinosula, Ircinia chevreuxi, Sarcotragus muscarum. Dysidea fragilis.

Southerly, in the coralligenous of Greco banc, located at 35 NM east of Zarzis, Ben Mustapha & al (submitted) list the following main species Oscarella lobularis, Cliona viridis, Cliona celata, Chalinula. sp, Crambe crambe, Phorbas tenacior, Hemimycale columella, Hamigera hamigera et Petrosia ficiformis.

Finaly, the study of the coralligenous from the littoral rocky assemblages from the gulf of Tunis, (Romadhe & al, data not yet published) allowed an inventory of the sponge fauna, with the following species: Leucascandra sp, Sycon raphanus, Spirastrella cunctatrix, , Scopalina lophyropoda, Axinella damicornis, Hymeniacidon sanguinea, Chondria nucula, Caccospongia mollior, Hippospongia communis, Spongia officinalis, Ircinia fasciculata, Petrosia ficiformis, Aplysina aerophoba, Aplysinella sp. These last works, enrich the sponge list from the Tunisian coralligenous and precoralligenous, which included only 31 species from a total of 120 demopsonges hitherto recorded for all the Tunisian coasts (Ben Mustapha & al, 2002).

5.1.4. Hydrozoans

Laubier (1966) reports 16 hydrozoans from the coralligenous of Banyuls, and no list of these organisms is included in the work of Hong (1980). Gili et al. (1993) report 44 species of hydrozoans from the coralligenous and precoralligenous communities of the Medes islands, while from the gulf of Tunis, the coralligenous from a littoral vertical rock, included 7 species : Clytia johnstoni, Campanularia hincksi, Sertularella sp, Obelia sp, Orthopyxis calculata, Gonothyraea gracilis, Halecium halecinum (Romdhane et al , data not yet published). According to Laubier (1966), and Gili et al. (1984, 1989) some species of hydrozoans are common on deep-water rocky bottoms and the coralligenous: 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 on the hydrozoans of the coralligenous is that of Llobet et al. (1991a), who report thirty five 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 in 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 (Campanelaria everta and Filellum serpens) are smaller and often occurred in dense monospecific patches. And 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. These zonation seems to reflect interspecific niche selection, enabling successful competition for space with other hydroids, algae and bryozoans.

5.1.5. Anthozoans

Works by Laubier (1966), True (1970), Hong (1980) and Gili et al. (1984, 1989) report several species of anthozoans from the coralligenous (up to 44 in Gili et al., 1993). The commonest species are Parazoanthus axinellae, Leptopsammia pruvoti, Parerythropodium 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 specially abundant in the coralligenous outcrops from the eastern Mediterranean (Laborel, 1960).

The commonest species of Anthozoans presents on the coralligenous is Parazoanthus axinellae.A.Bouajina.©RAC/SPA



5.1.6. Scyphozoans

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

5.1.7 Tubellarians

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

5.1.8. Nemerteans

Nemerteans live endolithically in the concretions. According to Pruvot (1897) and Laubier (1966), who report up to 12 species in the coralligenous of Banyuls, they are rather common. Drepanophorus crassus, Tetrastemma coronatum, Micrura aurantiaca and Micrura fasciolata are the most abundant.

5.1.9. Nematodes

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

5.1.10. Polychaetes

Polychaetes are extremely abundant in the coralligenous. Martin (1987) reported a total of 9195 individuals present in twenty samples of 400 cm² collected in 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 cm². He found 191 different species, with a dominance of the Syllidae (31% of the total). The number of species per sample is very high, ranging between 71 and 32 for the macrofauna (>0.4 mm) and between 55 and 27 for the microfauna (<0.04 mm). Diversity of the samples is also very high, averaging 4.54 bits ind⁻¹ for the macrofauna and 4.34 bits ind⁻¹ for the microfauna (Shannon-Weaver index). According to Martin (1987), the coralligenous is 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 check-list of the polychaetes collected in the coralligenous and studied by a specialist is that of Bellan (1964), who reported 70 different species in the coralligenous communities.

Laubier (1966) carefully studied the assemblages of polychaetes in two coralligenous stations in the region of Banyuls. He reported 130 different species, being Lepidasthenia elegans, Kefersteinia cirrata, Xenosyllis scabra, and the most abundant Typosyllis variegata. According to his own observations and Bellan's (1964) the polychaetes inhabiting the coralligenous concretions are mainly ubiquitous species, although he distinguished two main groups: the microfauna and the macrofauna.

Amongst the microfauna there are 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" to the coralligenous (e.g. Pholoe minuta, Chrysopetalum caecum, Eulalia tripunctata, Sige microcephala, Opisthodonta morena, Syllides longocirrata, and so on). Amongst the macrofauna, he distinguished four ecological groups: polychaetes living

inside the sponges (e.g. Lepidasthenia elegans, Eunice siciliensis, Amphitrite variabilis), the species living in the small crevices and holes like most Serpulidae and Terebellidae, as well as Eunice torquata, the big vagile polychaetes living over or inside the 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 gave a long list of polychaetes inhabiting the coralligenous from 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 the 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 the coralligenous are not usually the most abundant; the big species of serpulids (True, 1970) are very apparent: Salmacina dysteri, Serpula vermicularis, Serpula concharum, Sabella pavonina, Myxicola aesthetica, Sabella spallanzani and Protula spp. (Ballesteros & Tomas, 1999). Romdhane et al (data not yet published) report 14 species from the coralligenous of a vertical littoral rock from the gulf of Tunis: Fabricia sabell, Maldanidaesp, Hydroïdes uncinata, Chrysopetalum debile, Hesione pantherina, Nematonereis unicornis, Syllis sp, Lagisca sp, Halla parthenopera, Eunice harassii, Eunice torquata, Nereis sp, Euphrosine foliosa et Leptonereis glauca

5.1.11. Sipunculids

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

5.1.12. Echiurans

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

5.1.13 Molluscs

Molluscs are extremely abundant in the coralligenous. Martin et al. (1990) reported a total number of 897 individuals in twenty samples of 400 cm², which means an average of 45 species per sample and more than one mollusc per 10 cm². They reported a very high number of species regarding the reduced area they sampled: 131. The number of species per sample ranged between 5 and 33. Average diversity for all the samples is 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.

Number of species reported in the 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), and 108 species in Medes islands (Huelin & Ros, 1984).

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, and Bittium reticulatum, the opisthobranchs Odostomia rissoides, Diaphorodis papillata, Limacia clavigera, Cadlina laevis, Hypselodoris fontandraui, Chromodoris luteorosea, Chromodoris purpurea, Dendrodoris grandiflora, Duvaucelia striata, Discodoris atromaculata, Glossodoris gracilis, Glossodoris tricolor, Polycera quadrilineata, Flabellina affinis 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.

In a 1 m² sample, Romdhane et al (data not yet published) report 27 species from the coralligenous of a littoral vertcal rock (gulf of Tunis) : Arca noae, Modiolus barbatus, Modiolarca subpicta, Chlamys varia, Anadara diluvii, Neopycnodonte cochlea, Coralliphaga lithophagella, Bittium latreilli, Bittium reticulatum, Alvania lactea, Alvania semistriata, Alvania cimex, Alvania lineata, Philbertia sp, Helicofusus sfaxianus, Clanculus cruciatus, Jujubinus monterosatoi, Trophonopsis richardi, Triphora perversa, Eulina incurva, Rissoa sp, Cythara taeniata, Murex trunchulus, Capulus hungaricus, Raphitoma echinata, Callochiton laevis, Chiton olivaceus.

Cephalopods are also present in the coralligenous although usually not reported in the 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. D.Cébrian

5.1.14. Mites

Mites are always rare in the coralligenous. Laubier (1966) reports 6 species from Banyuls.

5.1.15. Pycnogonids

Up to 15 species of picnogonids are reported from the coralligenous of Marseilles by Hong (1980). Achelia echinata, Rynchothorax mediterraneus, Tanystylum conirostre and Callipallene spectrum seem to be the most common, although always rare. Only one species

is reported by Laubier (1966) from Banyuls and two species by Munilla & De Haro (1984) from Medes islands.

5.1.16. Copepods

The fauna of copepods has been carefully studied by Laubier (1966) in one station from the coralligenous 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 which live as parasites of different invertebrates: polychaetes, sponges, echinoderms, molluscs, cnidarians and tunicates (Laubier, 1966 and references therein).

5.1.17. Ostracods

Although several species of ostracods are present in the coralligenous (Laubier, 1966; Hong, 1980), no study has been devoted to this group. Laubier (1966) reports more than 10 unidentified species in the "endogean" microfauna.

5.1.18. Cirripeds

Barnacles Balanus perforatus and Verruca strömia, in the coralligenous walls and crevices, and Acasta spongites, endobiont of several sponges (e.g. Dysidea, Ircinia), are reported from the coralligenous (Laubier, 1966; Hong, 1980, Carbonell, 1984).

5.1.19. Phyllocarids

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

5.1.20. Mysidis

Hong (1980) reports 7 mysids from the coralligenous of Banyuls.

5.1.21. Cumaceans

Three cumaceans are reported from the coralligenous, always rare (Laubier, 1966; Hong, 1980).

5.1.22. Tanaidaceans

Tanais cavolini and Leptochelia savignyi are rather common amongst the "endogean" microfauna of the coralligenous concretions (Laubier, 1966; Hong, 1980).

5.1.23. Amphipods

Amphipods are sampled in substantial numbers in the coralligenous. Although Laubier (1966) only reports 12 species from the coralligenous of Banyuls, a list of 49 species is given by Hong (1980) in Marseilles, and 40 species are reported by Jimeno & Turon (1995) in an extensive survey of the concretions by Mesophyllum alternans along the coasts of Catalonia (northwestern Mediterranean).
The coralligenous harbors a certain number of amphipods from the photophilic algal communities together with reophobic and sciaphilic species, linked to the presence of hydroids, sponges and bryozoans.

Bellan-Santini (1998) lists 44 species from the coralligenous community (below 35 meters depth), to which other 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 the coralligenous.

According to 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 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 only in the coralligenous (Bellan-Santini, 1998).

5.1.24. Isopods

Laubier (1966) and Hong (1980) report 14 species from the coralligenous. Cymodoce truncata, Jaeropsis brevicornis, Paranthura nigropunctata, Synisoma sp., Gnathia maxillaris and Paragnathia formica seem to be relatively common species.

5.1.25. Decapods

The density of decapods in coralligenous concretions is very high, being estimated in 170 individuals in 500 g dw of Mesophyllum alternans (García-Raso & Fernández Muñoz, 1987). 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 that found in other communities with the existence of 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 the characteristic decapod crustaceans inhabiting the shallow coralligenous concretions of Mesophyllum alternans in the southwestern Mediterranean, together 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 of the southwestern Mediterranean make a different use of this environment. In Pilumnus hirtellus, the coralligenous seems to be a recruitment place, where mainly juveniles are recorded. Alpheus dentipes develops all his life cycle in the coralligenous, whilst in Synalpheus hululensis the coralligenous gives shelter for the 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 decapods of big size that are usually found in the coralligenous are Dromia personata, Palinurus elephas, 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. He found a total of 30 species, with Pilumnus inermis, Galathea nexa and Euchirograpsus liguricus being the most abundant decapods in this kind of bottoms from the southwestern Mediterranean.

5.1.26. Pterobranchs

Only one pterobranch, Rhabdopleura normani, is reported by Laubier (1966) living as epibiont of bryozoans.

5.1.27. Brachiopods

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

5.1.28. Bryozoans

Bryozoans are very abundant in the coralligenous. Reported species amount to 67 in Banyuls (Laubier, 1966), 133 in Marseilles (Hong, 1980), 113 in Medes islands (Zabala, 1984) and 92 in Cabrera (Ballesteros et al., 1993). A tentative estimate of the total number of bryozoans that thrive in the coralligenous bottoms according to the studies mentioned above is around 170 species. According to Zabala (1986) four different aspects regarding to the distribution of bryozoans can be distinguished in the coralligenous. Here we report the main species according to the works by Laubier (1966), Hong (1980), (Zabala, 1984, 1986) and Ballesteros et al. (1993).

The flat surfaces of the platform coralligenous 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 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, Mollia patellaria, Schizomavella auriculata, Cellepora pumicosa, Plagioecia spp., Cellaria fistulosa and Cellaria salicornioides.

Coralligenous walls have the species reported above but also Smittina cervicornis, Adeonella calvetii, Chartella tenella, Cribilaria innominata, Schizomavella spp., Parasmittina tropica, Sertella spp., Caberea boryi, and Spiralaria gregaria. In the gilf of Tunis (Korbous), the following 10 species have been reported form coralligenous littaoral wall from a 1 m² sampling: Crisia fistulos, Crisia oranensis, Caberia boryl, Annectocym sp, Synnotum

aegyptiacum, Aetea sp, Scrupocellaria reptans, Lichenopora radiata, Pherusella tubulosa, et Corallina balsaci (Romdhane et al, data not yet published)

Cavities and overhangs of the coralligenous bear a bryozoan fauna almost identical to that present in semi-dark caves, with several species already reported above, but also Dentiporella sardonica, Brodiella armata, Turbicellepora coronopus, Rynchozoon bispinosum, Schizotheca serratimargo, 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 last group is constituted by species that appear mainly in deep-water coralligenous, below 50 meters depth, which is composed by stenotherm species which 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.

5.1.29. Crinoids

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

5.1.30. Ophiuroids

According to the comments of Tortonese (1965) and the lists of Laubier (1966), Hong (1980) and Montserrat (1984), up to 17 species of crinoids were reported from the coralligenous. There are some species that can be considered as characteristic of the coralligenous such as Ophioconis forbesii, Amphiura mediterranea and Amphiura apicula (Tortonese, 1965; Laubier, 1966). Other brittlestars live entangled to the gorgonians: Astropartus mediterraneus and Ophiacantha setosa. The commonest species are, however, Ophiothrix fragilis, Ophiopsila aranea, Amphiura chiajei, Amphiura filiformis, Amphipholis squamata, and Ophioderma longicaudum. Ophiocomina nigra, although being a species typical of soft bottoms, is usually found in the small cavities with sediment of the coralligenous.

5.1.31. Asteroids



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

A. Bouajina © RAC/SPA

5.1.32. Echinoids

Fourteen species of sea urchins are reported from the coralligenous (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 the coralligenous. Juveniles of Paracentrotus lividus (and Arbacia lixula) can be found sometimes, never abundant. Centrostephanus longispinus is more abundant in the warmer areas of the Mediterranean and usually lives amongst the coralligenous crevices (Pérès & Picard, 1958; Laborel, 1960; Harmelin et al., 1980; Francour, 1991). Finally, Echinocyamus pusillus is an ubiquitous very small species that inhabits the small patches of sand and gravel inside the concretions.



The sea urchin Centrostephanus longispinus near the coralline algae Litophyllum sp and the sponges Chondrialla nucula et Suberites sp A. Bouajina © RAC/SPA

5.1.33. Holothurioids

The most commonly seen species of sea cucumber is Holothuria forskali, which can be rather abundant in some platform coralligenous (Laubier, 1966; Ballesteros & Tomas, 1999). Nevertheless, the genus Cucumaria has several species that live endolithically (C. saxicola, C. planci, C. kirschbergii, C. petiti). Other 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.

5.1.34. Tunicates

Ramos (1991) describes a high species richness of ascidians in the coralligenous community, with a high degree of presence of the families Didemnidae and Polyclinidae. In fact, around the 70% of the ascidian fauna is present in the coralligenous (82 species). According to Ramos (1991), the species more characteristic of the coralligenous 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 the coralligenous 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 specially abundant in the coralligenous concretions from the eastern Mediterranean (Pérès & Picard, 1958).

5.1.35. Fishes

The fish fauna from the coralligenous community includes a lot of fishes that can be considered of 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. Nevertheless, there is a group of species that are characteristic of the coralligenous.

Some of them like Lappanella fasciata or Acantholabrus palloni are species restricted to deep waters (Sartoretto et al., 1997), but others are easily observed in sport diving activities such as Anthias anthias (Harmelin, 1990), and (amongst the commonest species) also Gobius vittatus, Phycis phycis and Labrus bimaculatus (Garcia-Rubies, 1993, 1997). Other species are more abundant in the coralligenous than in shallow waters: 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 (Sartoretto et al., 1997; Ballesteros, pers. obs.).

The fish fauna inhabiting the small crevices of the coralligenous is probably related to cave dwelling fishes, although data is very scarce. Hong (1980) reports juveniles of Diplecogaster maculata and Gobius niger. According to Patzner (1999), cryptobenthic species usually observed in caves, can also be present in the small holes of the deep water coralligenous: Thorogobius ephippiatus, Thorogobius macrolepis, Corcyrogobius liechtensteinii, Gammogobius steinitzii and Didogobius splechtnai. Odondebuenia balearica is also a cryptobenthic fish inhabiting the coralligenous that is rarely observed (Riera et al., 1993).

Diplodus vulgaris swiming in mid water, on a coralligenous from a rocky substrate, with a sponge cover (incrusting) Phorbas sp and some colonies of Astroides calicularis. A. Bouajina © RAC/SPA



Works that dealt with the fish fauna of the coralligenous obtained slightly different results when carried out 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 regarding depth distribution in the northwestern Mediterranean (García-Rubies, 1993).

5.2. Endangered species

Although it is very difficult to know the conservation status of any marine species living in the relatively deep waters where the coralligenous develops, several approaches concerning the endangered species are already available.

Being so popular

Several animals of the coralligenous are also considered to be in a situation of risk (Boudouresque et al., 1991). In fact, none of them are in danger of extinction, although local depletion of the stocks of some species may occur. Most of the endangered species have a great commercial value and this is the main reason of their rarefaction. Amongst the anthozoans, the red coral (Corallium rubrum) is exploited commercially in almost all Mediterranean countries and its stocks have strongly declined in most areas, mainly in shallow waters (Weinberg, 1991). Populations of the gorgonians common in the coralligenous but without commercial value, such as Paramuricea clavata, Eunicella cavolinii or Eunicella singularis, are pulled out inadvertently by recreational divers (Coma et al., 2001). The black coral, Gerardia savaglia, is a very rare species, and can be a target for collection by divers, which can make the species even more scarce (Boudouresque et al., 1991) or can contribute to a disturbance of its habitat as it was recorded from Tabarka (Ben Mustapha, data not published). 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 northern parts (Chauvet, 1991). Nevertheless, immature and juveniles are very abundant in certain areas (e.g. Balearic Islands; Riera et al., 1998) and, therefore, the species is only threatened in the places where there is no regular recruitment (e.g. northwestern Mediterranean). Moreover, the recovery of this species in protected marine areas was repeatedly reported (Bell, 1983; GarciaRubies & Zabala, 1990; Francour, 1994; Coll et al., 1999), and so was reproduction (Zabala et al. 1997a, b), suggesting that an adequate management can rapidly improve its situation in the areas where stocks are still decreasing. In a probably worse situation are other groupers such as Epinephelus costae (= E. alexandrinus), Mycteroperca rubra or Polyprion americanus (Riera et al., 1998; Mayol et al., 2000), whose population stocks are much lower than those of the dusky grouper

According to Boudouresque et al. (1990), at least 8 species of macroalgae that live in the coralligenous can be considered as endangered: Chondrymenia lobata, Halarachnion ligulatum, Halymenia trigona, Platoma cyclocolpa, Nemastoma dichotomum, Ptilophora mediterranea, Schizymenia dubyi, and Laminaria rodriguezii. However, and according to our own observations, this list can be greatly increased with species such as Aeodes marginata, Sphaerococcus rhizophylloides, Schmitzia neapolitana, Ptilocladiopsis horrida, Microcladia glandulosa, Rodriguezella bornetii, Rodriguezella pinnata or Lomentaria subdichotoma (Ballesteros, unpublished data).

Most of these species have the coralligenous or the 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 of the coralligenous. The case of Laminaria rodriguezii is specially relevant, since it is a species that develops best in rhodolith beds, where it has almost disappeared because of trawling activities, and coraligenous bottoms constitute now its only refuge.

Some species of molluscs living in the coralligenous are also threatened. The edible lithophaga is considered an endangered rock-borer bivalve Lithophaga species (Boudouresque et al., 1991), although it is extremely abundant. Harvesting by divers is only important in shallow waters and the reason of the calls for protection of this species is, in fact, the protection of the shallow benthic communities in rocky shores dominated by macroalgae (Russo & Cicogna, 1991; Hrs-Brenko et al., 1991), not the coralligenous. The two species of fan mussels (Pinna nobilis and Pinna rudis) present in the Mediterranean were proposed for protection (Boudouresque et al. 1991), as they had been decimated in the northern Mediterranean areas by coastline modification and souvenir harvesting (Vicente & Moreteau, 1991). Pinna nobilis mainly grows in seagrass meadows, and its presence in the coralligenous is very unusual (Vicente & Moreteau, 1991). However, Pinna rudis (= P. pernula), is frequently seen in the coralligenous, at least in the warmer areas of the western Mediterranean (Ballesteros, 1998) as it is the case in Zembra Marine Parc (Ben Mustapha & Sanchez Jerez, data not yet published)

According to Templado (1991) none of the two species of the genus Charonia occurring in the Mediterranean is threatened by extinction. Charonia lampas is rare in the northern Mediterranean but rather common in the southwest, whilst Charonia tritonis variegata was recorded in the eastern and southwestern Mediterranean. Both species are collected and used for decoration purposes, but Templado (1991) thinks that indirect anthropogenic pressures (coastline development) is the main reason for its rarefaction and even, its local extinction.

The sea urchin Centrostephanus longispinus is also considered an endangered species by Boudouresque et al. (1991), although, in fact, it is a rare species in the northwestern Mediterranean, probably due to biogeographical reasons, as well as in Zembra Marine Parc and in Hallouf Banc, in the eastern Mediterranean (Ben Mustapha & Sanchez Jerez, data not yet published). No anthropic pressure has been claimed to explain its rarity.

The slipper lobster, Scyllarides latus, is very appreciated in gastronomy. The high market prices obtained for the slipper lobster stimulated increased fishing pressure which led to a dramatic decline in the abundance of this species in several areas of the Mediterranean (Spanier, 1991). It is more common in the warmer Mediterranean areas (e.g. Eastern Mediterranean, Balearic islands), being rarest in the colder ones.

Sciaena umbra and Umbrina cirrosa are the two other fishes considered as endangered in the review of Boudouresque et al. (1991). Both can live in the coralligenous, the former being more abundant. Both species are easily spearfished, but at least Sciaena umbra stocks easily recover after fishing prohibition (Garcia-Rubies & Zabala, 1990; Francour, 1994). Other species are not taken into account in the list of Mediterranean endangered species by Boudouresque et al. (1991), but according to Mayol et al. (2000) they are in a situation of major risk. This is the case of several small sharks inhabiting the detritic habitats and the coralligenous: Scyliorhinus stellaris, Mustelus asterias, Mustelus mustelus, Squalus acanthias and Squalus blainvillei All these species were very common in the fish catches by the Balearic islands fishermen at the beginning of the twentieth century, but are now extremely rare. Other species that can thrive in the coralligenous and that are considered as threatened by Mayol et al. (2000) are seahorses (mainly Hippocampus ramulosus), Gaidropsarus vulgaris and some cryptobenthic fishes (Didogobius splechtnai, Gammogobius steinitzii). These are not commercial species and their rarefaction may be related to indirect effects of fishing (cascading effects?), physical disturbances of trawling, or other unknown causes.

6.Biotic relationships -

6.1. Spatial interactions, herbivory, carnivory

Biotic relationships, both the trophical ones and those related to spatial interactions are a major force in structuring all ecosystems. In fact, all the building of the coralligenous concretion is affected by the interactions established between the encrusting corallines and other sessile, invertebrate, builders. The final result (that is, what the concretion looks like) is not only related to which builder was the most effective but also to how the borers (from sea urchins to excavating sponges and polychaetes) modelled the buildup. Biotic relationships at this level are, thus, crucial in the building of the coralligenous.

Trophic relationships are specially interesting in the coralligenous, as the main organisms are not easily edible. Most of them have skeletons which contribute to the buildup but also deter feeding (Zabala & Ballesteros, 1989). Others may have chemical defences which make them unpalatable or even toxic (Marti, 2002). Most of the biggest sessile invertebrates living in the coralligenous do not feed directly upon other animals from the coralligenous but on the pelagic system. In fact, the biggest part of the living biomass in the coralligenous belongs to algae and suspension feeders (True, 1970; Zabala & Ballesteros, 1989), which could suggest that herbivory and carnivory is not as important as it is in other marine Mediterranean environments. The low dynamism of the coralligenous (Garrabou et al., 2002) also points in that direction.



The sponge Petrosia dura grazed by a Nudibranch. D.Cebrian

However, both herbivory and carnivory, are not irrelevant in the coralligenous. 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 are furnished by most of the fishes thriving in the coralligenous, but also by most prosobranchs, echinoderms, vagile polychaetes and crustaceans. Although for most animals feeding is not selective, there are some noteworthy examples of animals having a strong prey selection. There are, for example, the well-known cases of the opisthobranch Discodoris atromaculata feeding on the sponge Petrosia ficiformis, or other opisthobranch Flabellina affinis feeding

mainly on hydrozoans of the genus Eudendrium (Ros, 1978). Other interesting examples have been recently furnished for copepods of the genus Asterocheres, which systematically feed both on rhagons and adult sponges by sucking the material produced at the ectosome of the sponge (Mariani & Uriz, 2001).

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) and others mediate the interactions between species regarding the occupation of space (Marti, 2002). Sponges, bryozoans and tunicates are the taxa with a 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, exhibit the highest percentage of active species of all Mediterranean communities sampled by Uriz et al. (1991), suggesting that investment in production of allelochemicals plays an important role in space competition in the coralligenous.

6.3. Epibiosis, mutualism, commensalism, parasitism

There is a huge amount of relationships between species in the coralligenous that can be described as "associations", involving or not 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. It is not our purpose to make a revision of these associations, not even to mention all those which have been described in the coralligenous, but to report some examples of epibiosis, mutualism, commensalism and parasitism, that can give an idea of the complexity of the coralligenous in this kind of relationships.

Epibiosis is a widespread phenomenon in benthic communities and the coralligenous is an excellent example of the different strategies adapted by the organisms to cope with this problem (True, 1970). Some basibionts tolerate different degrees of epibiosis and even nearly total 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 the coralligenous. For example, the ascidians Microcosmus sabatieri or Pyura dura are usually completely covered by a wide array of epibionts, whilst Halocynthia papillosa or Ciona edwardsi are always free of overgrowing organisms (Ramos, 1991).

Some epibionts are considered to select their hosts, whilst other are not selective. The anthozoan Parerythropodium coralloides usually grows over the axes of the gorgonians (Eunicella, Paramuricea clavata), although it can also grow over other animals, seaweeds, or be attached to rubble or any other kind of substrate (Laubier, 1966; Gili, 1986). The anthozoan Parazoanthus axinellae prefers the sponges of the genus Axinella (mainly Axinella damicornis) 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 the gorgonians Paramuricea clavata and Eunicella spp. (Laubier, 1966; Zabala, 1986).

The number of species that can act as non-selective epibionts in the coralligenous is huge, as most of the space is occupied, and larvae must usually settle over living animals or plants. Therefore, almost all sessile species can be epibionts (True, 1970). Gautier (1962), for example, reviewed the epibiosis of bryozoans over bryozoans in the coralligenous, and

Nikolic (1960) reported up to 18 species growing over Hippodiplosia foliacea in a coralligenous concretion on the Adriatic sea. Particularly interesting 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 of Banyuls living as epibionts of bryozoans.

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 benefit from a higher protection against predation and mechanical disturbance, trophic advantages (inhalant flow carries out small particles susceptible to be captured 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 relationship in the coralligenous. 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 also boring polychaete Dipolydora rogeri (Martin, 1996).

The curiosity of this association lies in the fact in that it even persists when the sponge is massive and non excavating. The polychaete has its feeding activity 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 cm² 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 and other sponges (Laubier, 1966; Rützler, 1976; Uriz et al., 1992b); this 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 not rare living inside the anthozoan Leptopsammia pruvoti.

Another example of parasitism in the coralligenous 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).

7.Processes -

7.1. Growth and age of corallinegous concretions

Mean growth rate of pillars of Mesophyllum alternans (as Mesophyllum lichenoides) in La Ciotat (NW Mediterranean) estimated by the radiocarbon dating method has been established in 0.19 mm year⁻¹ (Sartoretto, 1994) ranging from 0.11 mm year⁻¹ to 0.26 mm year⁻¹. Similar values of 0.16 mm year⁻¹ during the last 640 years have been obtained in a coralligenous block sampled at 15 meters in the Natural Reserve of Scandola (Corsica) (Sartoretto et al., 1996).

The age of the coralligenous buildups

Ages obtained by radiocarbon dating on coralligenous concretions situated at depths between 10 and 60 meters in the Northwestern Mediterranean range from 640 ± 120 years BP to 7760 ± 80 years BP (Sartoretto et al., 1996). Internal erosion surfaces within the buildups give evidence of discontinuous development. The accumulation rate of the coralligenous constructions is very low (0.006 to 0.83 mm year⁻¹) and greatly oscillates according to depth and time period. The higher accumulation rates (0.20 to 0.83 mm year⁻¹) were recorded for deep coralligenous 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) are recorded for coralligenous concretions situated in relatively shallow waters (10 to 35 meters depth), whereas the accumulation rates of coralligenous situated below 50 meters depth is almost nil.

Thus, the development of these deep coralligenous formations occurred a long time ago, when the depth of the overlying layer of water above the concretions did not probably exceed 10-15 meters, 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 the increase in water depth. It is also interesting to emphasize that the coralligenous concretions below 30 meters depth in the Marseilles area are nowadays inactive, almost devoid of living coralline algae. In contrast, those present in Corsica at 50 meters depth and below (down to 65 meters depth) are completely covered by living corallines and are in an active period of growth, which has to be related to the clear waters present in Corsica.

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 the

calcareous algae and their P/B ratios. The coralligenous thriving in relatively shallow waters (with Mesophylum alternans and Halimeda tuna as dominant algae) was the community with a highest production (around 465 g CaCO₃ m⁻² year⁻¹). Production of deep water coralligenous dominated by Lithophyllum cabiochae was much lower (around 170 g CaCO₃ m⁻² year⁻¹), but even this rate is much higher than average carbonate production for the overall Balearic shelf (100 g CaCO₃ m⁻² year⁻¹).

The contribution of suspension feeders to the total carbonate production of the coralligenous in the Balearic shelf -as well as in other Mediterranean areas- is mostly unknown. However, estimates of the animal carbonate production in deep water (25-50 meters depth) rocky bottoms from the Alboran Sea (southwestern Mediterranean) mainly dominated by big suspension feeders with calcareous skeletons (mainly 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 CaCO₃ m⁻² year⁻¹) (Cebrian et al., 2000). 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.

7.3. Bioerosion

The most active browser in the coralligenous is the sea urchin Sphaerechinus granularis which accounts for a great part of the total coralligenous erosion. Sartoretto & Francour (1997) calculated an erosion ranging between 210 and 16 g CaCO₃ m⁻² year⁻¹, with higher values in shallow waters and lower values in coralligenous concretions around 50 meters depth. The bioerosional role of Echinus melo can not be measured, but it is very low.

Amongst the macroborers, the Spionid polychaetes Polydora spp. and the mollusc Hyatella arctica are the only macrofauna colonising 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 it does not exceed 5.73 \pm 0.77 g CaCO₃ m⁻² at 20 meters and 1.50 \pm 0.99 g CaCO₃ m⁻² at 60 meters 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 larva recruitment (Kleeman, 1973).

The comparison of the erosion rates produced by the three main types of eroding organisms (browsers, microborers and macroborers) was estimated by Sartoretto (1996). Sea urchins account for roughly 95% of the total mass of CaCO₃ eroded. The bioerosion by micro and macro-borers accounts for the residual 5%, that of microborers being very low due to the great depths where the coralligenous develops and the high sedimentation rates, which avoids a high development of microborers (Sartoretto, 1998). Bioerosion by macroborers is probably underestimated because in the studies of Sartoretto (1998) several organisms that are common in the coralligenous are not taken into account, in particular the

bivalve Lithophaga lithophaga and excavating sponges (Sartoretto et al., 1996). Total ranges of bioerosion observed in the coralligenous range between 220 g CaCO₃ m⁻² year⁻¹ in relatively shallow waters and 20 g CaCO₃ m⁻² year⁻¹ at 60 meters depth. These ranges are in agreement with the structure and age of the coralligenous concretions situated below 50 meters 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 the coralligenous concretions promotes deposition of particles, which take part in the building up of the coralligenous structure through complex processes of lithification (Marshall, 1983). However, high sedimentation rates can be a problem because sediment particles can cover the thalli of the encrusting corallines making a screen against light (Laborel, 1961) but also preventing the recruitment of new plants (Sartoretto, 1996). Not all the sediment particles deposited in the coralligenous are included in the concretion; a great part of them is eliminated by different browsers and another is resuspended by the currents, organisms and gravitation.

The rugosity of the different coralligenous types is different and so it is the capacity of sediment retention. The amount of water movement is also important, and it usually decreases with depth. Studies made by Sartoretto (1996) in the Marseilles region conclude that around 9 kg m⁻² year⁻¹ are retained in the coralligenous concretions situated between 30 and 60 meters depth, whilst the retention in shallow waters is much lower. Nevertheless daily sedimentation rates are extremely high in shallow waters (around 500 g m²) 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 great calcareous component of organisms living in the coralligenous (Laubier, 1966). Major contributors are coralline algae (57%), bryozoans (19%), molluscs (16%), corals and serpulids (3% each) (Laubier, 1966).

8. Dynamics and seasonality

The study of dynamics for the whole coralligenous community is a very difficult task and it has not been studied until very recently. Garrabou et al. (2002) used a photographical method to look for the changes occurring in two monitored areas of coralligenous of 310 cm² along 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 through time showing none or few transitions in the two years of monitoring, indicating the high persistence of the animals and plants thriving in the coralligenous.

Other works applied to some compartments or species of the coralligenous communities. In fact, most of the studies dealing with the biology of the main species in the coralligenous (see chapter "Functioning of outstanding and key species") described the effects of seasonality, when it existed.

Regarding the benthic flora, Ballesteros (1991a) described the seasonal cycle of several phytobenthic communities from the northwestern Mediterranean, making a comparison amongst communities, using the same parameters as descriptors. The coralligenous with Mesophyllum alternans and Halimeda tuna has the lowest seasonality of all the subtidal communities studied, being almost constant in autumn, winter and spring, but having a peak productivity in summer, with higher biomass values than the rest of the year. Growth of coralline algae is almost constant through the year (Garrabou & Ballesteros, 2000) but growth of Halimeda mainly occurs in summer (Ballesteros, 1991c). Based on structural changes in the community, two stages can be discerned along 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 conversion of 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).

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 of apical articles on existing thalli, and possibly because of interspecific competition with epiphytic algae (Llobet et al., 1991a).

Anthozoans exhibit a marked decrease 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 through 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 (passive suspension feeder) do not correlate with temperature but that of Dysidea and Halocynthia (active suspension feeders) increases with temperature.

There is a low rate of synthesis of new tissue 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.

There is growing evidence that seasonal patterns of activity and secondary production of suspension feeders in the coralligenous 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 which 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 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 the resting stages develop not only in response of remodelisation following reproduction, but also as an effect of water temperature abnormalities.

The decapod fauna also displays a certain seasonality (Garcia-Raso & Fernández Muñoz, 1987), due to the intense recruitment of several species in late summer, and a progressive decrease in density of individuals and an increase in their size from October to June.

The fish fauna of the coralligenous is also affected by seasonality (Garcia-Rubies, 1997), although its effect is of very minor importance. The number of species in fish counts along 50m-long visual transects in the coralligenous bottoms in the Medes islands slightly decreases in winter, and most fishes seem to be less active than in summer.

9. Functioning of outstanding and key species -

9.1.- Coralline algae

Growth dynamics of two important coralligenous builders in the Northwestern Mediterranean, Mesophyllum alternans and Lithophyllum stictaeforme (as Lithophyllum frondosum) were studied in the bioconcretions of Medes islands marine reserve, in a steep wall situated between 15 and 30 meters depth (Garrabou & Ballesteros, 2000). Growth rates ranged between 0.16 month⁻¹ for Mesophyllum alternans and 0.09 month⁻¹ for Lithophyllum stictaeforme, with shrinkage rates being 0.09 and 0.04 month⁻¹ respectively. These growth rates are over an order of magnitude lower than those reported for other Mediterranean and tropical 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 over the 2 year monitoring period for 50% of the monitored plants), while they were rarely observed in Lithophyllum stictaeforme. 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, being more effective in maintaining the area acquired through its reduced growth rate (Garrabou & Ballesteros, 2000).

9.2. Halimeda tuna

9.2.1 The key role of Halimeda tuna



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. In fact, available data suggests that calcium carbonate production by Halimeda in shallow coralligenous concretions is similar to that of the coralline algae (Canals et al., 1988).

Halimeda tuna : important producer of organic matter and calcium carbonate.A.Bouajina© RAC/SPA

Growth and production of an Halimeda tuna population from a coralligenous community (18 meters depth) in the northwestern Mediterranean was studied by Ballesteros (1991c). The production of new segments changed seasonally being maximal in summer and minimal in winter, suggesting 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 CaCO₃ m⁻² year⁻¹, and the yearly P/B ratio amounted to 1.87 year⁻¹. The epiphytic assemblage growing on the segments of Halimeda tuna also displayed a high seasonality, with a maximum biomass and species richness in early summer.

9.3. 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 Medes Islands), indicating 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 for distinct biological strategies to persist and occupy 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., 1992), was studied by Ribes et al. (1999b). Dysidea avara obtained 85% of its ingested carbon from the fraction smaller than 5 μ m (mostly procaryotes and pico and nanoplankton) and 15% from the fraction larger than 5 μ m (mostly phytoplankton). However, the partial contributions of the different groups varied seasonally, following 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 μ m 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).

9.4. 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). 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, recruitment occurring at the same time. In winter, colony sizes quintuplicated and triplicated every 15 days, living a maximum of 6 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 are completely different to long-lived anthozoans also common in the coralligenous; the colonies survive for only a small number of weeks but asexual reproduction by the creeping stolons ensure colony survival beyond the life of Halimeda thalli, and perhaps indefinitely. Coma and 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) occurring throughout most of the year. Maximum life span of colonies was estimated to be only eight weeks, mean colony sizes increasing between three to sixfold over consecutive two week periods.

9.5. Red coral



Red coral is typically associated with the animal dominated communities growing in dim light conditions that characterize the smaller cavities. vertical cliffs and overhangs present in the coralligenous. It is essentially distributed in the western basin but it is also present in some areas of the eastern basin and African Atlantic coast (Zibrowius et al., 1984; Chintiroglou et al., 1989).

Red coral colonies thriving in a deep coralligenous. $\ensuremath{\mathbb{C}\mathsf{RAC}}\xspace/\ensuremath{\mathsf{SAP}}\xspace$

Harvesting is the major source of disturbance in red coral populations although large scale mortality events have also been documented (Arnoux et al., 1992; Garrabou et al., 2001). Sport diving activities seem 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, in press).

According to Garrabou & Harmelin (in press), red coral has a high survivorship, 60% of colonies reaching 22 years of age. Mortality is higher in juveniles, but partial mortality of colonies is higher in old colonies. Recruitment occurs in pulses but it is usually very low. Measured growth rates are 0.24 mm year⁻¹ for basal diameter and 1.78 mm year ⁻¹ for colony height. Average branching rate for each colony is of 3.4 branches in 22 years. Harvested populations show about 2-times lower values on average and up to 4-times lower values in colony size than in the non-harvested populations. Garrabou & Harmelin (in press) 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 last several decades or even centuries (Garrabou & Harmelin, in press).

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

9.6. Gorgonians

Growth of Paramuricea clavata has been monitored photographically for two years (Coma et al., 1998b). Based on growth rate data, the largest colonies in the population (55 cm) were around 31 years old. On average, net production for all colonies was 75% of gross production. Gross production was 4.4 g afdw m⁻² year⁻¹, the P/B value was 0.11 year⁻¹ and the turn-over time was 9 years (Coma et al., 1998a,b). Mistri & Ceccherelli (1994) estimated, for Paramuricea clavata in the Straits of Messina (Italy), a production of 3 g afdw m⁻² year⁻¹, a P/B value of 0.13 year⁻¹ and a turn-over rate of 7.5 years. In Eunicella cavolinii Weinbauer & Velimirov (1995a,b) 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 3 to 4 years.

Paramuricea clavata considered the most beautiful among Mediterranean gorgonians. ©RAC/SAP



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 needs longer monitoring periods to be unequivocally detected, but available data suggests that there is a high growth period in spring, which is 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 at around 7 to 13 years average (Coma et al., 1995a). 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 being synchronous each year and coinciding with increasing water temperature and correlating with the lunar cycle (Coma et al., 1995a). Spawned eggs adhere to the outer surfaces of the 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. The maintenance of the population 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. The prey capture rate extrapolated to an annual cycle suggests that gorgonians play an important role in the flow of energy from the 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).

Nevertheless, Paramuricea clavata has a broad and heterogenous diet that ranges from nanoeukaryotes (3.8 μ m) to copepods (700 μ m), including 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 where the seasons with the highest ingestion rates. The amount of carbon removed from the surrounding water is equivalent of 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, nor 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, there is a similar contribution of zooplankton and detrital POC (about 48% each), with the living POC accounting for the remaining 4%, a figure that can probably be extrapolated to other gorgonians.

9.7. Alcyonarians

Growth and occupation of space of two common alcyonarians in the coralligenous communities of Medes islands (northwestern Mediterranean) was studied by Garrabou (1999). Parazoanthus axinellae has a moderate growth dynamics (relative growth rate of 0.11 month⁻¹ and shrinkage rate of 0.09 month⁻¹), with non-significant differences over time, although growth rates peaked during summer to autumn periods. Fission events are common, 29% of monitored colonies undergoing at least 1 fission event in 2 years. Fusion events were less frequent, with only 8% of the colonies undergoing 1 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 by somatic growth and by fission. Most of the colonies (60%) were contracted in summer and mid autumn (Garrabou, 1999).

On the other hand, Alcyonium acaule has a very slow growth, which is almost undetectable over a two year period. Recruitment is very low, occurring in autumn, being the only way of population maintenance as there is no asexual reproduction. Mortality rates average 12.7% year⁻¹, with much higher mortalities in small colonies. Contracted colonies are much more frequent in summer than in any other season (up to 80%). Colonies of Alcyonium acaule are usually aggregated due to the retention of the eggs by the mucous

strings, implying a short-range dispersal for larvae and the settlement near the parental colonies (Garrabou, 1999).

9.8. Tunicates

Colonies of Cystodites dellechiajei, a very common ascidian in the coralligenous (Ramos, 1991), exhibited restricted growth or none whatsoever over a two year period in a vertical wall at 10-12 meters 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 the great part of the year. Cystodites dellechiajei shows a high relative biomass per unit area, low growth rates, high survival values (Turon & Becerro, 1992), and presence of chemical defences (Uriz et al., 1991) which seem to indicate a very conservative life strategy.

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, whilst it occurred in October-November for Microcosmus sabatieri (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 through an annual cycle. The natural diet included detrital organic matteer, bacteria, Prochlorococcus and Synechococcus, protozoa and phytoplankton, with a mean size ranging from less than 1 μ m to 70 μ m. One specimen of Halocynthia papillosa weighing 0.25 g afdw was estimated to ingest an annual mean of 1305 μ g C g afdw⁻¹ h⁻¹. Carbon from detrital origin accounted for 92% of the total ingested carbon, while live carbon accounted only for the 8%. Ingestion rates showed a marked seasonal pattern, with highest ingestion of detrital particles being in spring and highest values of ingestion of live particles being in summer and fall.

Ribes et al. (1998) hypothesize that live particles are of more significance in the diet of the species than 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, instead of detrital carbon, may be an essential source of nitrogen and other nutrients necessary for growth and reproduction in Halocynthia papillosa.

10.-Disturbances -

10.1. Large scale events

Several episodes of mortality of suspension feeders were detected in the northwestern Mediterranean (Rivoire, 1991; Cerrano et al., 2000; Perez et al., 2000, Ben Mustapha & El Abed, 2001). Here we report the existing data on the last large-scale mortality of suspension feeders that affected shallow water assemblages (10 to 40 meters depth) eastwards from Marseilles and in some other areas of the Central western Mediterranean (Minorca; Ballesteros, unpublished data).

Climatic events and mass mortality

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 kilometers, affecting the coralligenous communities situated above 40 meters depth, where the temperature anomaly lasted for more than one month (Perez et al., 2000; Romano et al., 2001, Ben Mustapha & El Abed, 2001).

Red coral populations thriving above 30 meters depth were also affected (Garrabou et al., 2001). This event of mortality, together with other large scale mass mortality events (Ben Mustapha &t Vacelet., 1991 ; Vacelet., 1991) or small-scale mass mortality events (Cerrano et al., 2000) recorded during the past decade in the Mediterranean suggest that they might be related to seawater temperature increase and global warming. 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, submitted) due to the energy shortage of suspension feeders related to the low food availability in summer.

If mass mortality events are related to the global warming trend, these events might occur again and become more frequent, which would induce profound changes in the coralligenous specific composition and structure. In fact, Paramuricea clavata, the suspension feeder more drastically affected in the summer 1999 mortality event (Perez et al., 2000), is completely absent above 40 meters depth in the warm Central Mediterranean waters of the Balearic islands (Ballesteros, unpublished data), which can be related to the longer duration of summer conditions in this area. However, the ultimate cause of these mortalities is still unclear, since the temperature anomaly can only have caused physiological stress which has triggered the development of some pathogenic agent that otherwise would have remained non-virulent.

10.2. Degradation by waste waters

Hong (1980) studied the effects of waste water along three stations situated in a gradient of multisource pollution in the Gulf of Fos (Marseilles) and in an unpolluted reference zone. Biodiversity decreases from the reference station (310 species) to the most polluted zone (214 species) and mainly affects bryozoans, crustaceans and echinoderms, molluscs and polychaetes being mostly unaffected. The number of individuals also decreases with increased pollution, as well as biomass of sponges and bryozoans, and diversity of invertebrates (Shannon's index). Nevertheless, the density of sipunculids increases with pollution.

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

The abundance of the species that make the buildup and those living in the coralligenous decrease with the gradient of pollution, both in number and in density of individuals. There is little data concerning the impact of various pollutants on the growth of coralline algae (Littler, 1976), although it is known that ortophosphate ions inhibit calcification (Simkiss, 1964). Anyway, 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 are more abundant in the polluted zones (Hong, 1980). Thus, all the available evidences, suggest that pollution accelerates the destruction of the coralligenous and inhibits the building activity.

Hong's (1980) main conclusions are that pollution (1) decreases the species richness, (2) highly increases the relative abundance of species with a wide ecological distribution, (3) almost eliminates some taxonomical groups, (4) decreases the abundance of the biggest individuals of the epifauna and (5) inhibits coralligenous construction and increases its destruction rates.

Cormaci et al. (1985) studied the deep water phytobenthic communities developing over coralligenous concretions in the Gulf of Augusta, a heavily polluted site both by 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).

10.3. Degradation by fishing

Trawling is probably the most destroying fishing method and it is causing degradation of large areas of coralligenous (Boudouresque et al., 1990; Ballesteros, unpublished data). Trawling not only has a direct physical damage by breaking 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). Special trawling to collect the precious red coral with the so-called "Italian Bar" or "Saint Andrew Cross" is highly destructive. Ortiz et al. (1986) report the capture of up to 50 kg of benthic fauna (mainly gorgonians) to collect 15 kg of living red coral in the Alboran Sea. This artifact is so effective in destroying the seabed that it was used to make scientific studies on the red coral associated fauna (Templado et al., 1986; Maldonado, 1992).

Traditional fishing and recreational fishing also have an effect on the coralligenous, but this mainly affects the target species. Fishing leads to a significant decrease in mean specific number of fish species, implying 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), extremely vulnerable to spear-fishing, but also to the notable scarcity of other species (Garcia-Rubies, 1999).

However, depth acts as a protective factor decreasing the effects of fishing, given the difficulty inherent in locating from the surface the coralligenous bottoms isolated from the coast (Garcia-Rubies, 1999). No cascading effects by overfishing have been already detected in the coralligenous, as they have been in shallow rocky bottoms (Sala et al., 1998), but they may exist, since densities and sizes of fishes and lobsters have been strongly modified in the last one hundred years.

Anyway, populations of groupers and other vulnerable fishes, rapidly recover after fishing prohibition (Harmelin, 1991; Coll et al., 1999; Harmelin & Robert, 2001), and they readily exhibit normal socio-behavioural patterns and reproductive success (Zabala et al., 1997a,b).

10.4. Degradation by diver frequentation

The coralligenous is one of the most popular sites for recreational diving in the Mediterranean due to its great variety of life and its great visual appeal. Some studies have detected direct impact of divers in the biggest invertebrates of the coralligenous. Sala et al. (1996) detected that the big and fragile calcareous bryozoan Pentapora fascialis was found at all levels of exposure (from overhangs to epibiotic) at locations where diving was not allowed, whereas colonies where almost restricted to cryptic positions at diving locations in the Medes islands marine reserve. 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 in boulders covered by coralligenous than in vertical walls, probably due to the protection provided by the dense canopy of the gorgonian Paramuricea clavata. Nevertheless, these high levels of recreational SCUBA diving (e.g > 1000 visits site⁻¹ year⁻¹) appear to be strongly modifying also 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 & Polà, 1999; Coma et al., 2001). This increase in adult mortality is due to toppling by divers, since annual mortality induced by overgrowth is almost similar between dived and undived sites, but toppling annual mortality in high visitation areas ranges from 4.9 to 6.9% (1.5% in low visited sites). Anchoring seems to have also a negative impact on the coralligenous although there are no studies where it is conveniently assessed.

Garrabou et al. (1998) conclude that abrasion by divers may affect other organisms of the coralligenous since it contains many sessile, long-lived organisms with fragile skeletons and slow growth rates that make them very prone to toppling disturbances. They suggest that diving might lead the coralligenous community to be dominated by erosion-resistant species, such as encrusting and massive organisms, instead of erect, articulate and foliose species. Therefore, human frequentation may affect the coralligenous community as a whole. Unfortunately, the paucity on data on turn-over rates of most organisms thriving on the coralligenous does not allow to quantitatively estimate its carrying capacity of divers (Sala et al., 1996).

10.5. Invasives species

Some introduced species in the Mediterranean have become invasive (Boudouresque & Ribera, 1994) and some of them can thrive on or are mainly adapted to the coralligenous habitat. At this moment only introduced algal species are threatening the coralligenous in some areas of the Mediterranean.

Probably the most dangerous alien species for the coralligenous community is the small red alga Womersleyella (Polysiphonia) setacea that is currently distributed along most of the Mediterranean basin (see Athanasiadis, 1997). This species grows abundantly in the coralligenous (and other sublitoral communities) forming a dense carpet, 1-2 cm thick, over the encrusting corallines that constitute the buildup (Mesophyllum alternans, Lithophyllum cabiochae, and others) (Ballesteros, pers. obs.). The carpet of Womersleyella setacea surely 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 by overgrowth and pre-emption (Piazzi et al., 2002), and inhibits recruitment of corallines and of other algal and animal species inhabiting the coralligenous (Ballesteros et al., 1998). Womersleyella setacea is very succesful in becoming established and in persisting from year to year (Airoldi, 1998), and, therefore, the potential damage of this alga to the entire coralligenous community can be huge. In fact, 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 at the Balearic islands (Ballesteros, pers. obs.), it is never dominant in this environment and always grows together with Womersleyella setacea.

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

Two other species that have been reported to act as invaders in the Mediterranean are Asparagopsis taxiformis (Ballesteros & Rodríguez-Prieto, 1996) and Lophocladia lallemandii (Patzner, 1998). Both species are becoming increasingly abundant both in shallow bottoms and deep waters in the Balearic islands. They have been found down to 50 meters depth in coralligenous bottoms with or without Womersleyella setacea (Ballesteros, pers. obs.).

11.CONCLUSIONS ON THE KNOWLEDGE OF THE CORALLIGENOUS COMMUNITIES

We have reviewed the present knowledge of the coralligenous buildups from different points of view. It is difficult to give a short list of conclusions because most of the chapters of this review already summarize a large amount of work.

The coralligenous, as described here, is a typical Mediterranean biogenic buildup basically made by coralline algae growing in dim light conditions and in relatively calm waters. It usually develops in the circalittoral zone but it can also thrive in the lower infralittoral zone if irradiance levels are low enough to allow the growth of the encrusting corallines which make the buildup.

Most of the available data comes from studies made in the Western Mediterranean. Almost nothing is known from Eastern Mediterranean buildups, which may be related to the greater depth where the coralligenous develops in this area (usually beyond the normal limit of scientific SCUBA diving) and to the lack of traditional marine research institutes.

The main distribution of the coralligenous is well-known at a large scale: it is common all around the Mediterranean coasts with the possible exception of those of Lebanon and Israel.

The knowledge on the environmental factors is rather poor, as the coralligenous is a highly heterogenous system and environmental parameters can strongly differ both at a geographical scale and at a microscale. However, even if more data is necessary, basic knowledge on light (irradiance), temperatures, nutrient concentrations and hydrodynamism is available. Irradiance seems to be the most critical factor for the development of the coralligenous concretions. Available data suggests 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 different 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 includes several assemblages due to its high heterogeneity. Algal asemblages develop in open waters and are dominated by several species of encrusting red algae. Mesophyllum alternans dominates in relatively shallow waters whilst Lithophyllum stictaeformis, Lithophyllum cabiochae and Neogoniolithon mamillosum are more abundant in deep waters. Two main different algal assemblages have been distinguished. Shallow water assemblages are rich in species of green algae. Animal assemblages greatly differ among sites and geographical areas. In open areas, mixed with algae, cnidarians dominate the assemblage (mainly gorgonians) in relatively eutrophic areas, and in more oligotrophic waters sponges and bryozoans dominate. In overhangs and big cavities the communities of suspension feeders are dominated by anthozoans, sponges and bryozoans. Some works have approached the study of the algal builders, the animal builders and, also, the

bioeroders. However, biomass data of the different species composing the assemblages is very scarce.

There is a considerable amount of work done in the biodiversity of the coralligenous. Probably much other data can be gathered if floristic and faunistic works are taken into account, as well as monographs of the different groups where comments on the ecological distribution of the species is present. A first estimate on the number of species thriving in the coralligenous is around 1666 (315 algae, 1241 invertebrates and 110 fishes). Works dealing with the coralligenous of certain areas give a number of species ranging between 500 and 700 species of marine invertebrates. Also important is the very high density of vagile fauna inhabiting the coralligenous, which can reach more than 3 invertebrates for each gram of coralligenous and, for example, a density of more than 1 polychaete worms per cm².

Some mediterranean endangered species live in the coralligenous, although none is exclusive of this environment.

Diversity being so great, the coralligenous harbours an intense connectivity amongst their inhabitants. Space competition is strong, the space is completely saturated by organisms, and epibiosis is extremely frequent. Alellochemicals must play an important role in space competition, as the coralligenous exhibits a very high percentage of chemically active species. Trophic relationships are also strong in the coralligenous, mainly amongst the 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 the coralligenous buildups, its carbonate production, and the bioerosion and sedimentation rates have merited very few studies, that, however, provide very valuable data. They point on the very low accumulation rates and its relationship with water depth and light availability, the important source of carbonate for the continental shelf that represent the coralligenous buildups, the relatively low bioerosion rates -at least in deep waters where the algal growth is the lowest-, and the relatively high sedimentation rates. Figures of accretion rates of up to 0.83 mm year⁻¹, with carbonate production (vegetal and animal) of up to 1000 g CaCO₃ m⁻² year⁻¹ and of bioerosion of up to 220 g CaCO₃ m⁻² year⁻¹ are reported. These values are always higher in shallow than deep waters.

Big animals and plants of the coralligenous are highly persistant and show low to nil seasonality regarding the occupation of space. Most of the area of the coralligenous remains unvariable after e.g. two years of monitoring. However, pulses of growth have been detected in some organisms such as the green alga Halimeda tuna or its epiphytic hydrozoans. Vagile invertebrates and the fish fauna also show a certain seasonality, mainly due to recruitment pulses and inactivity in winter. Several suspension feeders also exhibit some degree of physiological seasonality, with a decrease in activity in summer, probably related to the low food availability and high temperatures occurring at that season.

Some outstanding species inhabiting the coralligenous (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; tunicates Halocynthia papillosa, Cystodytes dellechiajei and Microcosmus sabatieri) have been carefully studied in order to know one or several of its

following features: growth rates, population dynamics, age, carbonate production, natural diets, prey capture, reproduction, spawning, and recruitment patterns.

Main perturbation roots

Five main causes of disturbance affecting the coralligenous assemblages have been distinguished:

- a. Large scale events, involving mass mortalities of suspension feeders, seem to be related to summer high water column stability and high temperatures, but their ultimate causes are still unclear; it has been suggested that they are related to the current global warming trend.
- b. Waste waters profoundly affect the structure of the coralligenous by inhibiting coralline algal growth, increasing bioerosion rates, decreasing species richness and densities of the biggest individuals of the epifauna, eliminating some taxonomical groups (e.g. most echinoderms, bryozoans and crustaceans) and increasing the abundance of highly tolerant species.
- c. Fishing is another cause of coralligenous degradation. Trawling is specially destructive as it physically destroys the coralligenous structure but also increases turbidity and sedimentation rates, which negatively affects algal growth and suspension feeding. Traditional as well as recreational fishing mainly affect target species, but most of them rapidly recover after fishing prohibition or after implementation of scientifically-guided fisheries management.
- d. Diver frequentation is another cause of recent degradation of the coralligenous but this kind of disturbance only affects, for the moment, very few areas situated at the most popular sites for recreational diving.
- e. Finally, invasive alien species are another cause of concern, as their number is increasing in all the Mediterranean. Specially dangerous for the coralligenous is the red turf alga Womersleyella setacea that forms a dense carpet over the encrusting corallines, inhibiting photosynthesis and growth of the main coralligenous builders.

12.Actions

12.1. Gaps in the scientific knowledge

Regarding the current state on the knowledge of the coralligenous it is easy to detect several gaps in the scientific knowledge that make it difficult to formulate some recommendations in order to protect the coralligenous:

1- There is a total lack of cartography of coralligenous bottoms all over the Mediterranean, with the exception of some extremely reduced spots situated mainly in marine parks or reserves. An (at least) approximate cartography and quantification of these bottoms are required.

2- It is highly recommended to make a list of all the organisms that have been found living in the coralligenous, in order to have a precise idea of the amount of biodiversity contained in this environment.

3- Almost nothing is known about the coralligenous concretions from the eastern Mediterranean. Special effort has to be made in the description and functioning of the coralligenous in this area.

4- Other studies related to the processes that take part in the buildup and the erosion of the coralligenous have to be made, as almost all existing information comes from one or two localities situated in the northwestern Mediterranean.

5- Understanding of the functioning of outstanding and key species is essential to the implementation of an adequate management of the coralligenous. These studies may to be enhanced, mainly for groups that are structurally important such as macroalgae, anthozoans, bryozoans and sponges.

6- The effect of disturbances in the coralligenous is very little known, and there is no data on the recovery capacity (with the exception of fish stocks after fishing prohibition) of this environment. The following subjects seem to be particularly important:

- a) Indirect impacts of trawling
- b) Impact of waste water dumping
- c) Effects of alien species invasion
- d) Causes of recent large scale mortality events

12.2. Recommendations for the coralligenous protection

In the light of the current knowledge, there are some recommendations that can be made in order to conserve (or even improve) the coralligenous environments. Most of these recommendations concern not only the coralligenous but most of the coastal benthic habitats, as waste water dumping, trawling and overfishing, and invasion by alien species are problems affecting the whole coastal area. Measures reducing these impacts may improve the overall quality of the marine coastal environment. Specific measures for the protection of the coralligenous that can be suggested are the following:

Recommendations

1- No waste water should be dumped over coralligenous bottoms, or its vicinity.

2- Trawling must be totally forbidden in areas with coralligenous outcrops and their vicinity, to avoid not only the physical damage of trawling over the coralligenous but also the indirect effects due to increased turbidity and sedimentation rates.

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

4- Correct management of traditional and recreational fisheries has to be implemented in order to prevent stock depletion of target fishes and crustaceans.

5- Diving pressure should be compatible with the normal functioning and conservation of the coralligenous.

6- There is an urgent need for relevant legislation on the introduction of alien species.

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The Regional Activity Centre for Specially Protected Areas (RAC/SPA) constitutes one of the institutional components of the Mediterranean Action Plan (MAP) of the United Nations Environment Programme (UNEP), coordinated under the supervision of the MAP Co-ordinating Unit. The Centre was set up in 1985 to assist Mediterranean countries in implementing the Protocol on specially protected areas and biological diversity. The Centre aims at assisting Mediterranean countries to establish and manage marine and coastal protected areas and to conserve biological diversity.

Among the Centre's activities is a project for preparing a **Strategic Action Plan for the Conservation of Marine and Coastal Biological Diversity in the Mediterranean Region** -SAP BIO Project - (1 January 2001 - 31 December 2003).

Starting from an assessment at national and regional level of the state of marine and coastal biodiversity, based on existing scientific data, and taking into account the Jakarta Mandate (developed within the framework of the Convention on Biological Diversity) and the Protocol on Specially Protected Areas and Biological Diversity, the SAP BIO Project aims at analysing the negative factors that affect marine and coastal biodiversity, or the lack of information, and identifying concrete remedial action. Integration of the actions decided on at national, sub-regional and regional level, along with detailed investment portfolios, involvement of stakeholders, and the development of approaches and principles, will become the Strategic Action Plan for Biodiversity. In addition to this strategy, which is the final document of the processes, within the framework of the SAP BIO Project, a series of national and regional reports is being prepared.

The present document is part of this series.



UNITED NATIONS ENVIRONMENT PROGRAMME Regional Activity Centre for Specially Protected Areas





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