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Mediterranean Bioconstructions Along the Italian Coast

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Abstract

Marine bioconstructions are biodiversity-rich, three-dimensional biogenic structures, regulating key ecological functions of benthic ecosystems worldwide. Tropical coral reefs are outstanding for their beauty, diversity and complexity, but analogous types of bioconstructions are also present in temperate seas. The main bioconstructions in the Mediterranean Sea are represented by coralligenous formations, vermetid reefs, deep-sea cold-water corals, *Lithophyllum byssoides* trottoirs, coral banks formed by the shallow-water corals *Cladocora caespitosa* or *Astroides calycularis*, and sabellariid or serpulid worm reefs. Bioconstructions change the morphological and chemico-physical features of primary substrates and create new habitats for a large variety of organisms, playing pivotal roles in ecosystem functioning. In spite of their importance, Mediterranean bioconstructions have not received the same attention that tropical coral reefs have, and the knowledge of their biology, ecology and distribution is still fragmentary. All existing data about the spatial distribution of Italian bioconstructions have been collected, together with information about their growth patterns, dynamics and connectivity. The degradation of these habitats as a consequence of anthropogenic pressures (pollution, organic enrichment, fishery, coastal development, direct physical disturbance), climate change and the spread of invasive species was also investigated.

The study of bioconstructions requires a holistic approach leading to a better understanding of their ecology and the application of more insightful management and conservation measures at basin scale, within ecologically coherent units based on connectivity: the cells of ecosystem functioning.

1. INTRODUCTION

Marine bioconstructions, or bioherms (Schuhmacher and Zibrowius, 1985), are elevated structures made of living benthic organisms (bio constructors) that overgrow the remnants (usually skeletons or shells) of their predecessors. Bioconstructions of various shapes and sizes are found along depth gradients ranging from the sea surface to the deep sea; some are ephemeral and last only a few seasons or years, whereas others persist for centuries or even millennia.

Bioconstructors modify primary (i.e. geological) substrates and provide secondary (i.e. biogenic) substrates for new bioconstructors and for non bioconstructors who simply inhabit them. Darwin (1842) first described the formation of tropical coral reefs, but biogenic formations are also present in nontropical seas. Erect benthic organisms are habitat formers since they modify primary substrates with their presence, but most of them do not build permanent formations and must renew with each generation (Jones et al., 1994). Bioconstructions, instead, are the result of centuries or even millennia of biological activities: their destruction can be almost irreversible, so they require the greatest attention in any conservation measures.

The European Union (EU) Habitats Directive 92/43/EEC (European Community, 1992) identified just a few marine habitats deserving protection at Community level, including *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows and “reefs”. The category “reefs” comprises both biogenic and geogenic formations that arise from the sea bed (European Commission, 2007, 2013). Rhizomes of *Posidonia* meadows grow on each other, entrap sediments and elevate the substrate, thus creating a bioconstruction type which might be referred to as being a simple subcategory of “reefs”. Both *Posidonia* meadows and biogenic “reefs”, as bioconstructions, promote high levels of biodiversity and enhance ecosystem functioning.

In the Mediterranean Sea, the richest European basin in terms of biodiversity, conservation priorities through the Natura 2000 network have been mostly devoted to *Posidonia* meadows (e.g. Boudouresque et al., 2009), with limited initiatives towards other types of bioconstructions. As a result, our understanding of the status and trends of most Mediterranean bio constructions is inadequate and often confined to few species, whose role is more presumed than quantitatively demonstrated. Recent studies show that human pressures are having critical effects on the distribution of various types of bioconstructions, causing their degradation, fragmentation and loss,

and the studies have shown this to occur from the shallow to the deep sea (Kružić, 2014; Piazzì et al., 2012; Teixidó et al., 2013; and references therein; Terrón Sigler et al., 2016a; Vorberg, 2000).

The management of bioconstructions, just as that of all components of natural capital, is based on three pillars:

- (a) *Patterns*—assessing the distribution of habitats and their conservation status.
- (b) *Processes*—understanding the drivers that determine the patterns and identifying stressors and their impacts.
- (c) *Measures*—enforcing management actions based on solid scientific evidence.

This study focuses on the most important biogenic habitats along the 8500 km of the Italian coast, covering a large portion of the habitat diversity of the whole Mediterranean basin. Our aims are to: (1) give an agreed definition of bioconstruction; (2) review the existing distributions of marine bioconstructions along the Italian coasts; (3) investigate the potential for assessing connectivity of marine bioconstructions using different approaches (e.g. genetic analyses, beta diversity and biophysical models); (4) provide information about the age of some bioconstructions by radiocarbon dating; (5) assess the effects of common human pressures; and (6) propose new areas of critical ecological importance to be included in protection priorities.

Based on this knowledge, recommendations for future research are proposed, together with guidelines for the conservation of coastal bioconstructions.

2. PATTERNS

2.1 What Is a Bioconstruction?

In the scientific literature bioconstructions are also called “biogenic reefs” and this has generated several, commonly rather sterile, nomenclatural controversies. Boero (2017a), for instance, commented on the recent discovery of a new biogenic reef in front of the Amazon River delta (Moura et al., 2016), mostly built by crustose coralline algae, just like Mediterranean coralligenous bio constructions (Ballesteros, 2006) that, however, was uncited.

The term “bioconstruction” was first used in marine and coastal geology usually referring to a limestone structure of biogenic origin that has been built up by modular and sediment binding organisms including macroalgae, corals, bryozoans and stromatoporoids (Fox, 2005). While describing a Silurian reef in Indiana (USA), Carozzi and Zadnik (1959) introduced the term “bioconstructed limestone” in geology, and the word “bioconstructed” was

used to differentiate limestones and dolomites from dolomitic calcarenites. Carozzi (1961) subsequently used the term “bioconstruction” for a stroma toporoid reef of the Upper Devonian in Alberta (Canada).

Jones et al. (1994, 1997) further integrated the term “bioconstruction” with the definition of “physical ecosystem engineers” for species that create, modify or maintain habitats by causing physical changes in biotic and abiotic materials or structures that, directly or indirectly, modulate the availability of resources to other species.

Only low diversity (mono or oligotypic) bioconstructions can be found in the Mediterranean, as in all temperate areas, whereas high diversity (polytypic) reefs are typical of tropical seas (Bianchi, 2002; Cocito, 2004; Sheppard et al., 2017). In some Mediterranean reefs the engineer species are either one (as in *Cladocora* reefs) or two (as in the *Dendropoma–Neogoniolithon* intertidal reefs), but rich species assemblages contribute to the construction of some coralligenous reefs.

Bianchi (2002) proposed two processes leading to biogenic reef formation: gregarism, in which individuals derived from different larvae or spores settle side by side, as in polychaete worms and vermetid molluscs, or modularity/coloniality, based on asexual reproduction (vegetative multiplication), as in cnidarians. Clonal organisms grow bigger than individual ones (Jackson, 1977), and their biogenic reefs are formed by aggregations of clonal formations, i.e., by the gregarism of modular organisms. The most conspicuous biogenic reefs are produced by the activity of skeleton producing organisms such as calcareous algae, oysters and corals. Other biogenic reefs may be produced by sand binding and cementing activities of some organisms, as in the case of sabellariid worm reefs or stromatolites formed by cyanobacteria. Calcareous sediments deriving from algae, mollusc shells, echinoderms spines, sponge spicules and other skeletal debris often fill the spaces within the reef framework and become consolidated in various ways. Sponges, zoanthids and certain colonial ascidians can bind reef materials together, becoming a sort of connective tissue. Organisms that grow as calcareous sheets can act as biological cementing agents, building permanent bonds that cause the strong adhesion of loose calcareous sediments to the reef frame. Beneath the living reef, the material has a marble like consistency. The mechanisms that produce such diagenetic cement are numerous and partially unclear, but the process is thought to include also a biological component derived from microbial activity or from organic compounds produced by reef organisms (Macintyre and Marshall, 1988; Scoffin, 1992).

2.2 Mediterranean Bioconstructions: Biodiversity and Distribution Along the Italian Coasts

Marine bioconstructions are common throughout the Mediterranean Sea, but complete cartographic data on their distribution are a major knowledge gap. The distribution of marine bioconstructions along the Italian seas reported here has been assembled from 468 documents (peer reviewed articles; international, national and regional reports; grey literature) reporting spatial information (e.g. maps or detailed acoustic mapping). Spatial information was also obtained from unpublished in situ observations from various sources. All records have been validated and georeferenced. When digital spatial information was not available, it was created by digitizing image maps or by extracting spatial information from the text, based on expert knowledge. The ArcGIS 10.1 software by ESRI (Environmental System Resource Institute, <https://www.esri.com/>) was used to integrate all the data into a geodatabase and to generate the distribution maps.

Included in the proposed definition of bioconstruction are the mattes of *P. oceanica* (i.e. the woody structures created by the rhizomes of this sea grass) since the new rhizomes grow over the old ones, raising seafloor and making it stable for thousands of years (Bianchi, 2002). Thus it is worthwhile to include the distribution of *Posidonia* meadows (Fig. 1) due to the key ecological role of this habitat in the Mediterranean Sea (Boudouresque and Meinesz, 1982), in order to provide a complete picture of the main marine bioconstructions of Italian seas. However, *Posidonia* meadows are still usually considered as a distinct habitat from “reefs” and are treated further here in only a limited way.

Bioconstructors comprise a wide range of organisms: calcareous algae, sponges, corals, vermetids, oysters, mussels, polychaetes (serpulids and sabellariids), barnacles, bryozoans and other noncalcified organisms such as cyanobacteria and diatom biofilms (Goldberg, 2013; Wood, 1999). The Mediterranean Sea hosts important biogenic structures (Relini, 2009) and the main ones considered here are as follows:

- *Lithophyllum byssoides* concretions/trottoirs
- *Astroides calycularis* formations/reefs
- Coralligenous assemblages
- *Cladocora caespitosa* formations/reefs
- Vermetid reefs
- Sabellariid reefs
- Cold water coral frameworks
- Serpulid reefs, including biostalactites

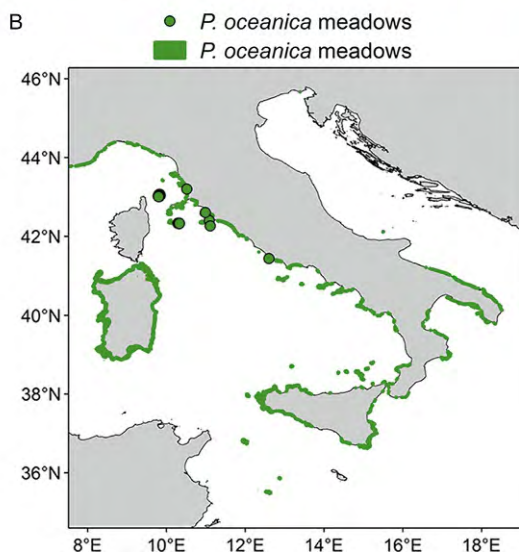
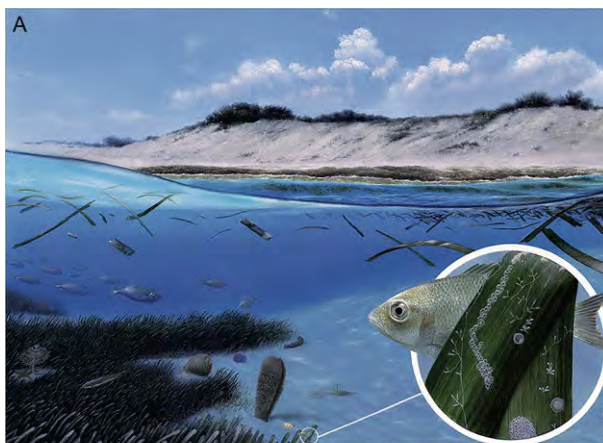


Fig. 1 (A) *P. oceanica* meadow). (B) Distribution of *P. oceanica* along the Italian coast. Points represent data with no associated surface area and rectangles stand for polygons with a specific area characterized by the presence of *P. oceanica*. Boundaries of points and polygons of data layers are enhanced for illustrative purposes and do not reflect the real habitat extent. Panel (A): Alberto Gennari. Panel (B): EMODnet biology database; Belluscio, A., Panayiotidis, P., Gristina, M., Knittweis, L., Pace, M.L., Telesca, L., et al., 2013. Seagrass beds distribution along the Mediterranean coasts. Mediterranean Sensitive Habitats (MEDISEH) Final Report, DG MARE Specific Contract SI2.600741.

All these structures have a great importance in generating and maintaining marine biodiversity, since they increase spatial complexity and settlement opportunities (MacArthur and MacArthur, 1961; Rebele, 1994). Other Mediterranean bioformations, like rhodoliths and maërl beds, barnacles of

the upper intertidal belt, mussel and oyster beds and bryozoan reefs, host a great diversity of life, but they do not produce substantial bioconstructions and are not covered here.

2.2.1 *Lithophyllum byssoides* Concretions/Trottoirs

Lithophyllum byssoides (Lamarck) Foslie is a coralline red alga forming adherent crusts with a crinkled surface made of convoluted lamellae or finger like protrusions (Bressan et al., 2009; Verlaque, 2010). It is relatively common in the western and central Mediterranean, but it does not occur in the eastern most parts of the basin (Laborel, 1987). *L. byssoides* is one of the few genuinely intertidal Mediterranean algae; it occurs in a narrow vertical belt a few decimetres wide, located just above the mean sea level (Fig. 2A), forming large populations on rocky shores directly exposed to prevailing winds (Verlaque, 2010), covering either horizontal tidal notches (Antonioli et al., 2015) or overhangs. Under these conditions, numerous thalli of *L. byssoides* coalesce and form thick concretions that cover the surface of the rock, often protruding from it. Well developed concretions form step like or overhanging rims, which may protrude up to 2m from the colonized rocky surface. These rims are called *L. byssoides* “encorbellements” (corbels), when they protrude only a little, or “trottoirs” (sidewalks), when protruding greatly. At highly exposed sites they may be found up to 50 cm above the mean sea level, and as a result they form the uppermost bioconstructions on Mediterranean coasts. Living *L. byssoides* occurs only on the upper and outer surfaces of the rims; the remaining parts consist of very hard, multilayered materials formed by deposition processes that fill the interstices between the lamellae of the dead alga with a hardened sedimentary matrix (Verlaque, 2010). The overgrowth of notches gives the same aspect of the bioconstruction, but, in this case, the algae encrust a step of geological origin, protruding from its edge. Other algae are usually associated with a well developed rim of *L. byssoides* (e.g. *Chaetomorpha ligustica* (Kützinger) Kützinger (= *Chaetomorpha mediterranea* (Kützinger) Kützinger), *Palisada perforata* (Bory de Saint Vincent) Nam (= *Laurencia papillosa* (C. Agardh) Greville), *Pterocladia melanoidea* (Schousboe ex Bornet) Santelices (= *P. melanoidea* (Schousboe ex Bornet) E.Y. Dawson), *Lophosiphonia cristata* Falkenberg and *Taenioma nanum* (Kützinger) Papenfuss) (Bressan et al., 2009). The lower part of the rim is profusely colonized by sciaphilic algae and invertebrates that are similar to those living in clefts and caves (Laborel, 1987; Verlaque, 2010). Various types of bioeroders (sponges of the genus *Cliona*) and boring species (molluscs of the genus *Lithophaga*, etc.) are also present, reducing the stability of the rim by creating tunnels and cavities into the

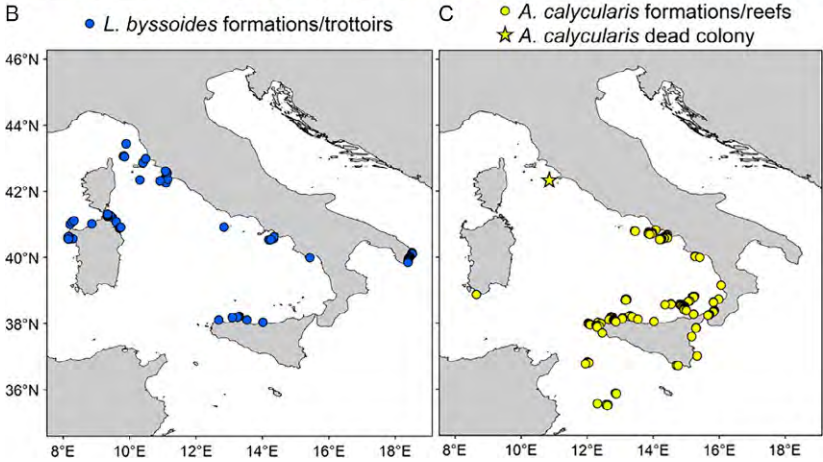


Fig. 2 (A) *L. byssoides* formations in the intertidal zone. The orange coral *A. calycularis* can also be found immediately below if the environmental conditions are suitable. (B) Occurrence and distribution of *L. byssoides* and (C) of *A. calycularis* along the Italian coast. Points represent data with no associated surface area. Boundaries of points of the data layers are enhanced for illustrative purposes and do not reflect the real habitat extent. Panel (A): Alberto Gennari.

bioconstruction. The polychaete *Spirorbis infundibulum* Harris & Knight Jones, 1964 is exclusive to this habitat (Bianchi, 1981).

L. byssoides is not rare along Italian shores. Most frequently, however, it occurs as separate, noncoalescing individual thalli. Build ups and large rims

occur on Tyrrhenian, Ionian and southern Adriatic shores (Fig. 2B), but have a circumscribed distribution, limited to stretches ranging from tens of metres to a few kilometres. When present, *L. byssoides* rims usually are not continuous along the shoreline but are best developed in inlets, crevices or other spots that provide partially shaded conditions and some shelter from wave action. A preference of this alga for calcareous rocks over granites and schists has been noted in some areas (Cossu and Gazale, 1997). In Italy, these bioconstructions reach their maximal extent in northwestern Sardinia, where rims can be wider than 2 m (Cossu and Gazale, 1997).

2.2.2 *Astroides calycularis* Formations/Reefs

The orange coral *Astroides calycularis* (Pallas, 1766) is an azooxanthellate dendrophylliid coral with a calcium carbonate exoskeleton, endemic to the Mediterranean Sea (Zibrowius, 1980, 1983; Fig. 2). It inhabits rocky shores from the surface to 50 m depth (Ocaña et al., 2000; Rossi, 1971) but is typically found in the shallow infralittoral zone (0–15 m depth), on vertical walls

or inside caves (Cinelli et al., 1977; Kružić et al., 2002; Zibrowius, 1978); in the latter habitat, it can exhibit great size and cover (Morri et al., 1994a). This scleractinian coral is considered a reef forming species (European Commission, 2013) since its bioconstructions cover up to 90% of some rocky areas in shallow waters (Goffredo et al., 2011) and host a rich invertebrate fauna. In the southern coast of the Iberian Peninsula, Terrón Sigler et al. (2014) found 81 macroinvertebrate species (mainly crustaceans, annelids and molluscs) associated with *A. calycularis* colonies.

A. calycularis mostly occurs in the south western part of the basin from the Straits of Gibraltar to Sicily (Terrón Sigler et al., 2016a). Musco et al. (2016) report a list of five hot spot areas, in the south western coast of the Italian peninsula, where *A. calycularis* reefs appear more developed (Fig. 2C), namely: (1) the Sorrento Peninsula and the islands of Ischia and Capri, (2) the Cilento coast, (3) the Strait of Messina and the Aeolian Islands, (4) the north western coast of Sicily and (5) Pantelleria and the Pelagie Islands in the Strait of Sicily. In the Adriatic Sea, the species is present with sparse

colonies along the Croatian coast only (Grubelić et al., 2004; Kružić et al., 2002); some sporadic records along the Italian side need confirmation. The northernmost record along the Italian coast is of a dead colony at Giglio Island (Bianchi and Morri, 1994). The northern limit of stable reef forming populations is at Ventotene (Pontine Islands), while the southern limit is in the Pelagie Islands (Musco et al., 2016).

2.2.3 Coralligenous Assemblages

According to Ballesteros (2006), a coralligenous reef is a hard substratum of biogenic origin that is mainly produced by the accumulation of calcareous encrusting corallines (red algae, Rhodophyta) growing under dim light conditions. It often develops on almost vertical walls, on gently sloping bottoms near the base of a wall and on overhangs, but it can also form platforms on the continental shelf (Fig. 3A and B). Recently, coralligenous atolls, whose origin is still unresolved, have been discovered between 100 and 130 m depth off the northern coasts of Corse (Bonacorsi et al., 2012).

Coralligenous formations consist of carbonatic bioherms whose thicknesses range from 25 cm to more than 2 m, and they can characterize the

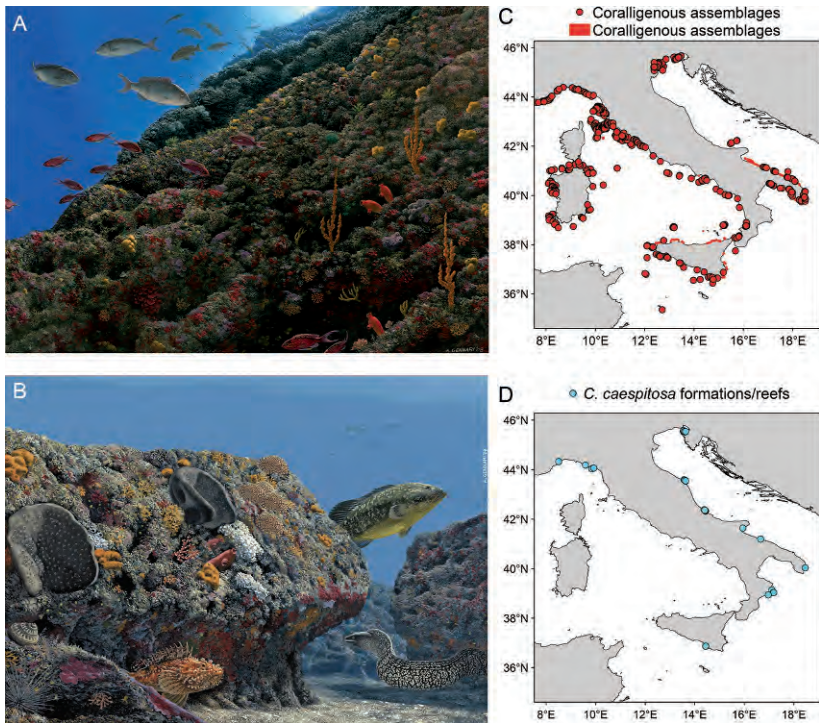


Fig. 3 The two main geomorphological categories of the coralligenous assemblages (A) rims and (B) banks. (C) Spatial distribution of coralligenous formations. (D) Distribution of the main banks of *C. caespitosa*. Points represent data with no associated surface area and rectangles stand for polygons with a specific area characterized by the presence of coralligenous assemblages. Boundaries of points and polygons of data layers are enhanced for illustrative purposes and do not reflect the real habitat extent. Panels (A) and (B): Alberto Gennari.

Mediterranean rocky bottoms from 15 to 130m depth, depending on water transparency (Ballesteros, 2006; Martin et al., 2014). These build ups are mainly due to the activity of several encrusting calcareous algae (of the genera *Lithophyllum*, *Lithothamnion*, *Mesophyllum*, *Neogoniolithon* and *Peyssonnelia*) (Laborel, 1961; Laubier, 1966; Sartoretto et al., 1996) whose remains are cemented by microbial carbonates. Several species and/or assemblages can be associated with these biogenic red algal constructions (Boudouresque et al., 2015), namely: forests of the seaweed *Cystoseira zosteroides* (Turner) C. Agardh (Ballesteros et al., 2009); animal forests consisting of gorgonians, e.g., *Eunicella* spp. and *Paramuricea clavata* (Risso, 1826); large erect sponges such as *Axinella polypoides* Schmidt, 1862; bryozoans such as *Turbicellepora* spp. and *Pentapora fascialis* (Pallas, 1766); stands of crustose but not bioconstructing algae; turf and bushy macroalgae; and small sized sessile metazoans belonging mainly to sponges, cnidarians, serpulid polychaetes, bryozoans and ascidians (Boudouresque, 1973). The result is an extraordinary habitat with a great biodiversity. Ballesteros (2006) made a first estimate of the number of species associated with coralligenous formations, listing about 1670 species. However, this is probably an underestimated number because the complex structure of coralligenous assemblages and their highly diverse composition suggests that they host more species than any other Mediterranean habitat.

Light is an important driver in determining the distribution and assemblages of benthic organisms, together with water movement, sediment rates, substrate features and geographical area (Ballesteros, 2006). The main coralligenous geomorphological structures along the Italian coasts are on cliffs (Fig. 3A) and platforms (Fig. 3B). Coralligenous rims develop on vertical and subvertical cliffs between 10 and 50 + m depth, or surrounding the opening of submarine caves, often forming structures of considerable thickness. Coralligenous banks are flat structures developing over more or less horizontal substrata, between 15 and 100 + m depth. These platforms can be extensive and develop on both rocky substrates (Laborel, 1987) and coastal debris deposits, generally starting from the coalescence of rhodoliths together with sand and gravel (Basso et al., 2007).

Coralligenous assemblages are widespread along the Italian coast (Fig. 3C), with the exception of the sandy muddy seabed between the Po delta river and the Gargano Peninsula. Many mesophotic biogenic habitats are scattered on the northern Adriatic continental shelf. These structures, locally called *trezze* or *tegnùe*, are similar to coralligenous assemblages and their size ranges from a few to thousands square metres in the surface area, and they rise up to 4m in height from the surrounding sedimentary bottom

(Gordini et al., 2012). High concentrations of small and medium sized reefs are distributed off the lagoons of Venice and Grado Marano, and a larger reef system is located 3–5 km off Chioggia (Tosi et al., 2017). The high variability at different spatial scales of the benthic assemblages in the Adriatic mesophotic biogenic habitats, in relation to local abiotic features, distance from the coast and outcrops, has been highlighted for both phyto and zoobenthos (Curiel et al., 2012; Ponti et al., 2011).

The onshore–offshore gradient of coastal freshwater inputs is the main driver of nutrient dynamics in the northern Adriatic Sea, playing an important role also in structuring the assemblages of the outcrops. These assemblages occur in three main typologies based on the abundance of encrusting calcareous red algae, algal turfs, sponges and ascidians. Algal turfs, encrusting sponges (e.g. *Dictyonella incisa* (Schmidt, 1880) and *Antho* (*Antho*) *inconstans* (Topsent, 1925)) and bioeroders generally characterize large near shore reefs, strongly affected by riverine inputs. Encrusting calcareous red algae and colonial ascidians, e.g., *Polycitor adriaticus* (Drasche, 1883), dominate off shore reefs. Both algal turf and noncalcareous encrusting algae (e.g. *Peyssonnelia* spp.) are abundant, together with massive sponges (e.g. *Ircinia variabilis* (Schmidt, 1862), *Tedania* (*Tedania*) *anhelans* (Vio in Olivi, 1792) and *Chondrosia reniformis* Nardo, 1847) that occur on the outcrops (Falace et al., 2015; Fava et al., 2016; Ponti et al., 2011).

The Apulian coralligenous region has been known for decades (Parenzan, 1983; Sarà, 1966, 1968; Sarà and Pulitzer Finali, 1970) and it represents a key element of the seascape, covering about 38% of the seafloor between 10 and 100 m depth (Bracchi et al., 2017). Here, coralligenous banks are predominant and these show the maximum spatial dominance both in the 10–40 m and in the 70–90 m depth ranges. At shallower bathymetric intervals (10–40 m depth), these formations occur both as coralligenous constructions *sensu stricto* and in mosaic form with *Posidonia* meadows (Bracchi et al., 2017). Also, the Apulian coralligenous region shows high spatial variability at different scales, highlighting the patchy and complex nature of these assemblages (Terlizzi et al., 2007). Several processes might generate the observed variability. These include disturbance (Airoldi, 2000; Connell, 2005), topographic heterogeneity (Archambault and Bourget, 1999), pre and postsettlement biological interactions (Hunt and Scheibling, 1997; Sebens, 1986) and different patterns of growth (individual vs modular organisms: Jackson, 1977).

In the Ligurian Sea there are different typologies of coralligenous bio constructions likely due to the different geomorphology of the coast; biological assemblages are similarly diverse, and some still need to be described

in detail (Canessa et al., 2017; Cánovas Molina et al., 2013, 2014, 2016). The western and eastern coasts followed different formation patterns, leading to two major geological systems (Cattaneo Vietti et al., 2010). Along the eastern coast, coralligenous formations develop mainly on vertical cliffs with parallel series of horizontal rims, from 25–30 m to 80–100 m depth. Along the western side, vertical cliffs are not so common and the coast has a different geomorphology, with a wider sandy platform. The Western Ligurian Riviera has been poorly studied and rarely characterized due to its patchy distribution of isolated rocky outcrops and their limited extent.

Sardinia hosts a notable variety and abundance of coralligenous formations due to the complexity of the coast and to the shape of the sublittoral slope. In the Marine Protected Area (MPA) of Tavolara Punta Coda Cavallo five typologies were recognized: (i) enclaves within infralittoral assemblages on vertical walls, either carbonatic or granitic; (ii) on limestone pinnacles between 25 and 40 m depth; (iii) on granite inselbergs and other erosional remnants from 38 to 56 m depth; (iv) organogenic platforms at 42–44 m; and (v) on beach rocks at 27, 40 and 54 m (Bianchi et al., 2007). Five major coralligenous communities have been recognized and mapped: (1) association with *C. zosteroides*; (2) facies with *A. polypoides*; (3) facies with *Eunicella cavolini* (Koch, 1887); (4) facies with *Eunicella singularis* (Esper, 1791); and (5) facies with *P. clavata* (Vassallo et al., 2018). Other rare and endangered species "typical" of the coralligenous populations can be found along the Sardinian coast, such as the exuberance of the Mediterranean red coral *Corallium rubrum* (Linnaeus, 1758) whose populations dwell on steep rocky walls free from sediments (Cau et al., 2015a, 2016). Dense *E. cavolini* facies have been documented along with rich and diverse animal forests dominated by gorgonian and black corals dwelling both in rocky outcrops arising from soft bottoms of the continental shelf and in submarine canyons dissecting the Sardinian continental margin, at a depth range comprised between 100 and 180 m (Bo et al., 2015; Cau et al., 2015b, 2017a,b). This condition, together with the existence of a nursery area for catsharks within the coral ramifications and the occurrence of a meadow of the now rare soft bottom alcyonacean *Isidella elongata* (Esper, 1788) in small surviving muddy enclaves, indicates that this ecosystem have to be considered a pristine Mediterranean deep sea coral sanctuary that would deserve special protection (Cau et al., 2017c).

Distribution of coralligenous formations along the Campania coast has been investigated since the end of XVIIIth century, mostly for economic reasons (red coral banks exploitation, Cattaneo Vietti et al., 2016). More

recently, Appolloni et al. (2018) published a comprehensive map of coralligenous habitats in the Gulf of Naples. Most of the present studies have been performed by means of remotely operated vehicles (ROVs) so as to assess the status of deep assemblages associated to offshore shoals, and the effects of fishery pressures (Ferrigno et al., 2017).

Deep surveys carried out along the Calabrian coast through ROV revealed a mixed assemblage of the black coral *Antipathella subpinnata* (Ellis & Solander, 1786) and the sea fans *P. clavata* and *E. cavolini* from 50 to 100 m depth in the Favazzina area. The extraordinary high density of this assemblage is due to the northward current from the Strait of Messina (Bo et al., 2009). In the Gulf of St. Eufemia, where currents slow down and sedimentation is high, arborescent sea fans (e.g. *Callogorgia verticillata* (Pallas, 1766), *Paramuricea macrospina* (Koch, 1882), *P. clavata*, *Villogorgia bebyroides* (Koch, 1887), *Leptogorgia sarmentosa* (Esper, 1789), *C. rubrum* and *Bebyrce mollis* Philippi, 1842) and antipatharians (e.g. *A. subpinnata*, *Parantipathes larix* (Esper, 1788) and *Antipathes dichotoma* Pallas, 1766), as well as a rich sponge assemblage settle on coralligenous shoals arising from a muddy bottom. These habitats are small oases of hard substrata interspersed in a muddy bottom (Bo et al., 2011, 2012a).

Coralligenous banks were recently described in the Sicily channel as outcrops of dome like pinnacles arising from a rocky plateau at about 100 m depth. Dense patches of the precious coral *C. rubrum* and of the sea fan *E. cavolini* characterize the macrobenthic assemblage of these coralligenous pillars. The lack of overlap between the two species suggests that they have different ecological requirements. In this area the illegal fishing of *C. rubrum* with trawling devices produces an intense impact on this peculiar assemblage (Cattaneo Vietti et al., 2017).

Finally, flourishing coralligenous assemblages dominated by filter feeding structuring species and a kelp canopy have been described also in offshore locations such as the Vercelli and Palinuro seamounts in the Tyrrhenian Sea between 60 and 120 m depth (Bo et al., 2011; Würtz and Rovere, 2015).

2.2.4 *Cladocora caespitosa* Formations/Reefs

Morri et al. (2000a) listed eight coral species as potential bio constructors in the Mediterranean Sea. Five of them, *Dendrophyllia ramea* (Linnaeus, 1758), *Dendrophyllia cornigera* (Lamarck, 1816), *Madrepora oculata* Linnaeus, 1758, *Desmophyllum dianthus* (Esper, 1794) and *Lophelia pertusa* (Linnaeus, 1758), live in deep waters and will be treated later. Three species, *Madracis pharensis* (Heller, 1868), *Oculina patagonica* de Angelis, 1908,

and *Cladocora caespitosa* (Linnaeus, 1767), live in shallow water and are obligatorily or facultative zooxanthellate, i.e., they may harbour microalgal endosymbionts that are known to enhance coral calcification (Schuhmacher, 1984 and references therein).

The bioconstructions of *C. caespitosa* are the best known (Fig. 3B). This species, endemic to the Mediterranean Sea, exhibits growth rates that may exceed 5 mm year^{-1} (Peirano et al., 1999) and calcification rates that average $1.1\text{--}1.7 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Rodolfo Metalpa et al., 1999), which is comparable to values of many tropical reef corals (Peirano et al., 2001). The colonies of *C. caespitosa*, obligatorily zooxanthellate, are common throughout the Mediterranean on rocks and pebbles about 3–30 m depth, often in turbid water (Bianchi, 2009). When abundant, *C. caespitosa* may typically occur in two distinct formations: beds and banks (Morri et al., 2000b). Beds are composed by numerous small (10–30 cm in diameter) subspherical colonies in dense populations. Banks are made up of large colonies, reaching several decimetres in height and covering areas of several square metres. Banks originate from beds under conditions of undisturbed accretion by means of three mechanisms: (i) fusion of adjacent colonies; (ii) “pouring” of the build up due to gravity; and (iii) inclusion of satellite colonies (Peirano et al., 1998). Mixed distributions of beds and banks can also be found, while a third formation has been recently described: free living coral nodules or coralliths (Keresting et al., 2017a,b).

Banks are the most important bioconstructions of *C. caespitosa* and may deserve to be called reefs. They harbour a rich associated biota comprising several phyla (Antoniadou and Chintiroglou, 2010; Koukouras et al., 1998; Lumare, 1966), but no species seems exclusive to this habitat (Bianchi, 2009). In the Gulf of Trieste (North Adriatic Sea), Pitacco et al. (2014) estimated 89 infauna taxa associated with *C. caespitosa* and the most abundant were molluscs (50%), followed by polychaetes (20%) and crustaceans (7%). Along the Italian coast (Fig. 3D), banks have been described in the Gulf of Manfredonia (Colantoni and Gallignani, 1975), the Ionian Sea (Lumare, 1966), the Ligurian Sea (Morri et al., 1994b) and the Gulf of Trieste (Pitacco et al., 2014; Zunino et al., 2018).

2.2.5 Vermetid Reefs

Vermetids are sessile and gregarious prosobranch gastropods of the family Vermetidae, widely distributed in the warm southern waters of the Mediterranean Sea (Keen, 1961), where their reefs or platforms are built up by a complex of four cryptic species, all previously named *Dendropoma petraeum* (Monterosato, 1884) (Fig. 4A). Templado et al. (2016) split the old taxon

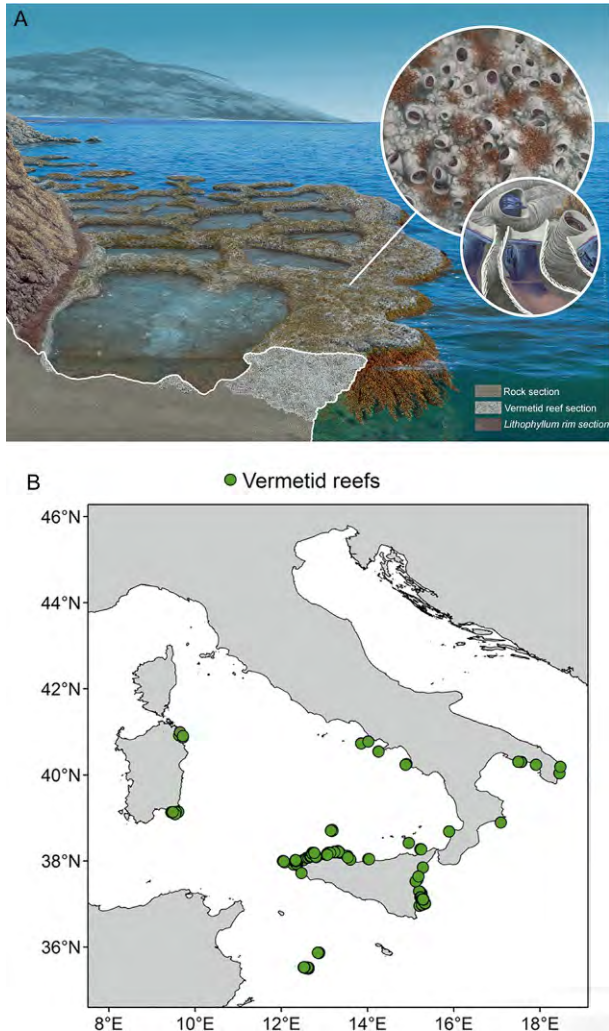


Fig. 4 (A) A vermetid reef platform and its hypothetical section. The circle represents a close up of the rugged tubular shells of *D. cristatum* adults, sometimes cemented by the coralline alga *N. brassica-florida*. The shell openings of *Dendropoma* are sealed by a chitinous operculum. (B) The distribution of vermetid reefs along the Italian coast. Points represent data with no associated surface area. Boundaries of points of data are enhanced for illustrative purposes and do not reflect the real habitat extent. Panel (A): Alberto Gennari.

D. petraeum into four species, two of which are widespread along the Italian coasts: *Dendropoma cristatum* (Biondi, 1859) in the Tyrrhenian Sea, and *Dendropoma* sp., a still unnamed species, in the Ionian Sea and the Salento Peninsula (Templado et al., 2016).

The vermetid reef or “trottoir à vermetes” (according to Molinier and Picard, 1953) is a biogenic formation bordering the rocky shores at the tide level. They have very different morphologies (Antonioli et al., 1999), but on the most developed vermetid reef platforms an outer and an inner margin can be identified. The outer margin is the most biologically active portion of the platform expanding seaward and it is composed of a rich layer of *Dendropoma* shells and *Neogoniolithon brassica-florida* (Harvey) Setchell & L.R. Mason encrusting thalli. The inner margin, instead, is less dense of *Dendropoma* individuals and it is subjected to emersion during low tide. Between the two margins, shallow depressions—the cuvettes (Molinier and Picard, 1953; Pérès and Picard, 1952)—can be found, which usually hold water during low tide and calm sea and are covered by perennial canopy forming brown algae and encrusting organisms. Below the outer margin, the vermetid reef is usually fringed by a characteristic upper subtidal belt made by the canopy forming alga *Cystoseira amentacea* var. *stricta* Montagne. *Dendropoma* snails and *N. brassica-florida* encrustations can be supported in the process of bioconstruction by other intertidal organisms, namely, the foraminiferan *Miniacina miniacina* (Pallas, 1766), the coralline algae *Lithophyllum incrustans* Philippi, *L. byssoides* and *Neogoniolithon mamillosum* (Hauck) Setchell & L.R. Mason, by some encrusting bryozoans, and the solitary vermetid *Vermetus triquetrus* Bivona Bernardi, 1832 (Safriel, 1975). The bioconstruction is also subjected to strong bioerosion from a rich group of boring organisms such as sponges, bivalves and sipunculid worms (Bressan et al., 2001).

In Italy (Fig. 4B), most of the vermetid reefs are in northern Sicily, between Milazzo Cape and the Egadi Islands (Chemello, 2009; Milazzo et al., 2017). Some concretions are also reported in southeastern Sicily between Catania and Syracuse, and on the Pelagian, Aeolian and Ustica Islands (Chemello, 2009). To date, information on vermetid bioconcretions in the rest of Italy is scarce: small vermetid ledges are reported at Ischia Island, in the Gulf of Naples (Scuderi et al., 1998; Soppelsa et al., 2007) and on the NE coast of Sardinia (Schiaparelli et al., 2003), likely representing the northernmost records of this vermetid formation. In the south, some records also exist for the Apulia and Calabria coasts (see Chemello and Silenzi, 2011), while in the Campania region, reef formations are only present along a portion of the coast around the Licosa islet and also on some close submerged old walls (Donnarumma et al., 2018).

2.2.6 Sabellariid Reefs

Two polychaete species, *Sabellaria alveolata* (Linnaeus, 1767) and *Sabellaria spinulosa* (Leuckart, 1849), family Sabellariidae are reported for the Mediterranean

Sea. The first one is a bioengineer that builds relevant biogenic structures, while the second one is mostly solitary, but can construct small clumps.

Sabellariid reefs are compact bioconstructions resulting from the aggregation of tubes made up of sand grains and bioclasts, cemented with mucus, which develop on both solid and soft bottoms (Fig. 5A). The worms construct these tubes around themselves, in close proximity to one another,

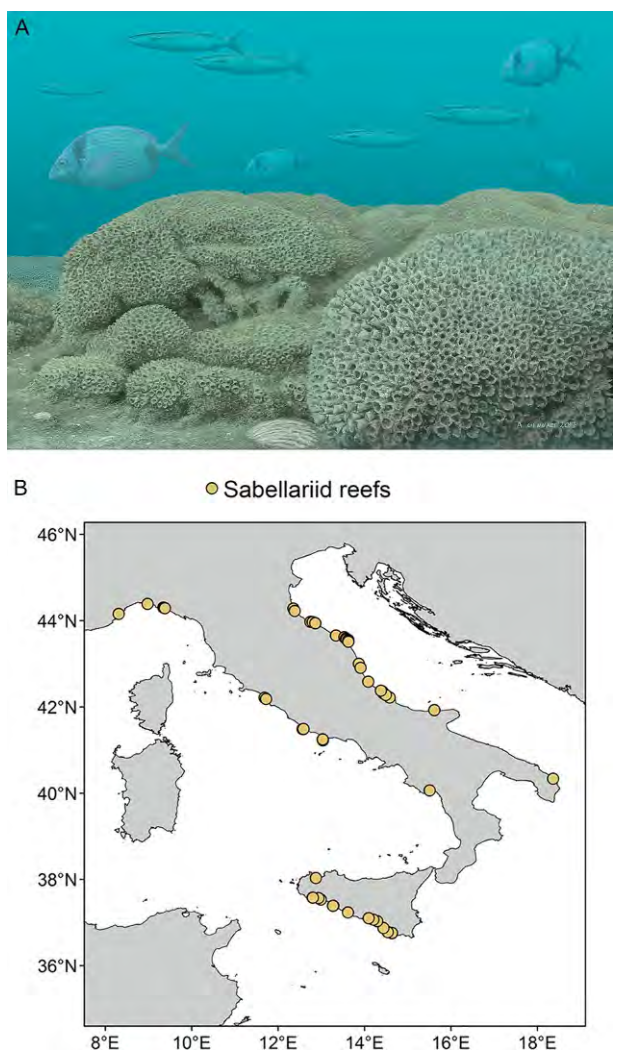


Fig. 5 (A) Sabellariid reefs on soft bottoms. (B) Distribution of sabellariid reefs along Italian coast. *Points* represent data with no associated surface area. Boundaries of points of data layers are enhanced for illustrative purposes and do not reflect the real habitat extent. *Panel (A): Alberto Gennari.*

creating a honeycomb like structure, hence the name “honeycomb worms” for these polychaetes. The larvae settle mainly on existing *Sabellaria* reefs or on their dead remains, and in marine shallow areas where suitable sedimentological and hydrodynamic conditions occur. These bioconstructions require a good supply of sand grains and a strong water movement and can develop as thin crusts, mounds and hummocks, to tubular or barrier like aggregations (Delbono et al., 2003).

Sabellaria bioconstructions occur along the midlittoral–upper infralittoral zone, from the lower shore into the sublittoral, arising from the sandy sea floor or they can form banks adhering to hard bottoms. They often reach the sea surface and remain exposed at low tide. The Mediterranean *S. spinulosa* reef does not host a distinctive associated fauna (Gravina et al., 2018), while the faunal characterization of Italian *S. alveolata* reefs revealed the preferential and stable association with the phyllodocid polychaete *Eulalia ornata* Saint Joseph, 1888 along their range (Bertocci et al., 2017; Schimmenti et al., 2016). In general, the sabellariid reef provides an array of microhabitats suitable for the settlement of many hard and sandy bottom species, thus characterizing it as an important hot spot of biodiversity (Cole and Chapman, 2007; Dubois et al., 2002, 2006).

Along the Italian coasts, *Sabellaria* reefs have been reported from the coasts of Liguria (Delbono et al., 2003), Latium (Giordani Soika, 1956; La Porta and Nicoletti, 2009; Taramelli Rivosecchi, 1961), Southern Sicily (Bertocci et al., 2017; Molinier and Picard, 1953; Schimmenti et al., 2016), Apulia (Gravina et al., 2018; Lisco et al., 2017), Abruzzo (Gadaleta et al., 2015) and Marche and Emilia Romagna (unpublished data) (Fig. 5B). The reefs occurring in the Tyrrhenian Sea and in the Sicily Strait are built by the species *S. alveolata* or by aggregations of tubes of both the sabellariid species, with *S. alveolata* resulting the dominant bioconstructor (Bertocci et al., 2017), while for the first time in the Mediterranean Sea, real reef structures constructed by *S. spinulosa* have been reported along the Apulian coasts (Gravina et al., 2018; Lisco et al., 2017). Recently, *S. spinulosa* reefs have been reported in the Southern Adriatic near San Foca (Lecce), seemingly outcompeting and overgrowing *P. oceanica* meadow at its upper limit, 1.5 m depth (S. Piraino, unpublished observations).

2.2.7 Cold-Water Coral Frameworks

Among the cold water corals (CWCs), *M. oculata* and *L. pertusa* are certainly the most charismatic building deep marine bioconstructions in the Mediterranean Sea (Fig. 6A). These colonial species, together with the solitary

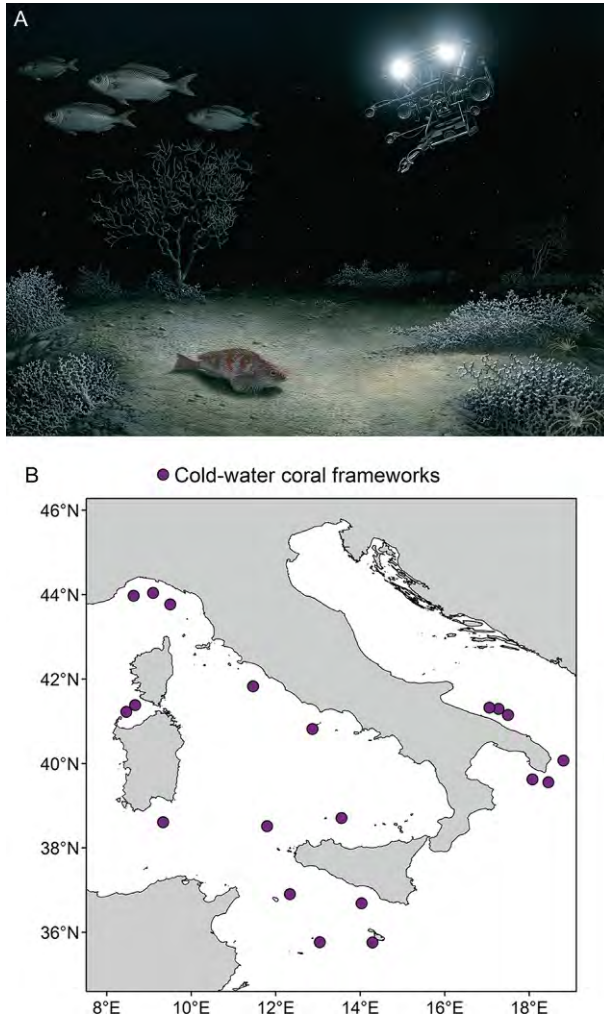


Fig. 6 (A) Cold-water corals (*L. pertusa* and *M. oculata*) in the deep sea. (B) distribution of living cold-water corals along Italian coast. Points represent data with no associated surface area. Boundaries of points of data layers are enhanced for illustrative purposes and do not reflect the real habitat extent. Panel (A): Alberto Gennari.

pseudo reef forming coral *D. dianthus*, are also known as “white corals” (Pérès and Picard, 1964; Roberts et al., 2006). CWCs can live in large (monospecific or mixed) aggregations that change the structural heterogeneity of the environment, hence acting as habitat formers from 200 to 1000m depth (Chimienti et al., 2018b; Freiwald et al., 2009; Lo Iacono et al., 2018; Mastrototaro et al., 2010). The great biodiversity associated with CWCs

can be separated into functional groups based on the ways in which the fauna uses the coral habitat and its complex substrata (Henry and Roberts, 2017). It comprises microscopic fauna associated with the coral biofilm, macro benthic grazers, deposit feeders and small benthic predators that find refuge among reef polyps, coral branches and other microhabitats, as well as larger sessile suspension and filter feeding epifauna. Many benthopelagic and benthic demersal fish communities also visit the CWC frameworks to forage, find refuge and breed. Mediterranean CWCs reefs account so far for over 500 associated species (Rueda et al., 2018).

CWCs were once considered as being present in the Mediterranean Sea only as dead skeletal remains from the Pleistocene, the postglacial conditions having arrested their development (Delibrias and Taviani, 1985). Their supposed extinction was disproved with the advent of the deep sea exploration technologies, first by occasional findings of living colonies (e.g. Fredj and Laubier, 1985; Mastrototaro et al., 2002; Tunesi and Diviacco, 1997), soon followed by the discovery of lush CWC sites, with highly developed bio constructions (Chimienti et al., 2018a,b). At least 20 living white coral occurrences are known so far for Italian and Maltese waters and, at four of these sites, the substantial coral growth and high colony density define true CWC provinces (Taviani et al., 2011, 2016, 2017). These are located in the Northern Ionian Sea (Santa Maria di Leuca), in the Southwestern Adriatic Sea (Bari Canyon), in the Strait of Sicily (South Malta) and in the Sardinia Sea (Nora Canyon: Taviani et al., 2017; Tavolara and Coda Cavallo Canyons: Chimienti et al., 2018b; D. Moccia et al., personal communication) (Fig. 6B). Only two more coral provinces have been currently recognized within the Mediterranean basin: in the Gulf of Lion and in the eastern Alboran Sea (Taviani et al., 2016). So far, the Italian seas play a crucial role in the presence and distribution of CWC bioconstructions. Several abiotic factors such as suitable substrate, water temperature, oxygen concentration and water flow regimes influence their occurrence, distribution and abundance in the deep sea (Gori et al., 2013; Roberts et al., 2009b). In particular, appropriate currents are needed for an adequate trophic supply and for preventing coral smothering by sediments; these are one of the main drivers in CWC distribution (Carlier et al., 2009; Roberts et al., 2009a). The Levantine Intermediate Water (LIW), formed in the northern portion of the eastern Mediterranean and flowing westward, together with the cascading of cold water from the Northern Adriatic cold engine towards the Ionian Sea, has a profound influence on CWC growth and distribution (Freiwald et al., 2009; Taviani et al., 2016).

2.2.8 Serpulid Reefs, Including Biostalactites

Serpulidae are a large family of polychaetes that produce a calcareous tube in which they live (Bianchi, 1981). Tubes typically encrust any hard substrate and may be considered “secondary framework builders”, filling crevices and cementing rubble in coralligenous reefs and other marine bioconstructions (Bianchi et al., 1995). The scissiparous species *Salmacina dysteri* (Huxley, 1855) may form large “pseudocolonies”, which are nevertheless very fragile and do not exhibit any significant constructional capacity (Bianchi and Morri, 2000). In contrast, some gregarious species can grow erect attached to each other, thus acting as “primary frame builders” and forming huge aggregates (Aliani et al., 1996). The individual tubes are small (rarely longer than 10 cm or wider than 1 cm), but their aggregations can form reef like structures more than 1 m thick that may cover tens of square metres (Bianchi et al., 1995). Serpulid reefs are well known in the geological past (Fagerstrom, 1987), and mass occurrences of recent serpulid species have been reported from many sites (Ten Hove, 1979). In Italy, major serpulid reefs, formed by *Ficopomatus enigmaticus* (Fauvel, 1923) or *Hydroides dianthus* (Verrill, 1873), have been described from brackish lagoons (Bianchi and Morri, 1996, 2001), but these will not be further discussed here.

In fully marine waters, serpulids may develop conspicuous assemblages in submarine caves, even encrusting preexisting speleothemes, as first described for the Mediterranean by Ten Hove and Van Den Hurk (1993) and in Italy by Bianchi and Morri (1994) and Antonioli et al. (2001). Particular serpulid structures in submarine caves are the so called biostalactites. They develop in completely dark parts based on single (e.g. Cape of Otranto) or few (e.g. Plemmirio Islands) (Fig. 7C) serpulid species, whose aggregations become substrate for smaller invertebrates and bacteria (Belmonte et al., 2009; Guido et al., 2012). Biostalactites grow far from the entrance on rocky walls where generally Serpulidae dominate (Bussotti et al., 2006) and where other benthic species are less competitive. Biostalactites can protrude a few cm from the basal substrate (Plemmirio) but also up to 2 m (Cape of Otranto, Fig. 7A) and they can be also oblique or horizontal. Freshwater inflows (even intermittent) seem to favour their formation. The engineering species always have been referred to the genus *Protula*, but recent genetic analyses of the Otranto species showed the existence of a still unnamed species. The growth of Otranto biostalactites started about 6000 years ago, corresponding with the sea level during its postglacial rise (Belmonte et al., 2009, 2016). The outer surfaces of the biostalactites are encrusted by living and dead fauna of several invertebrate

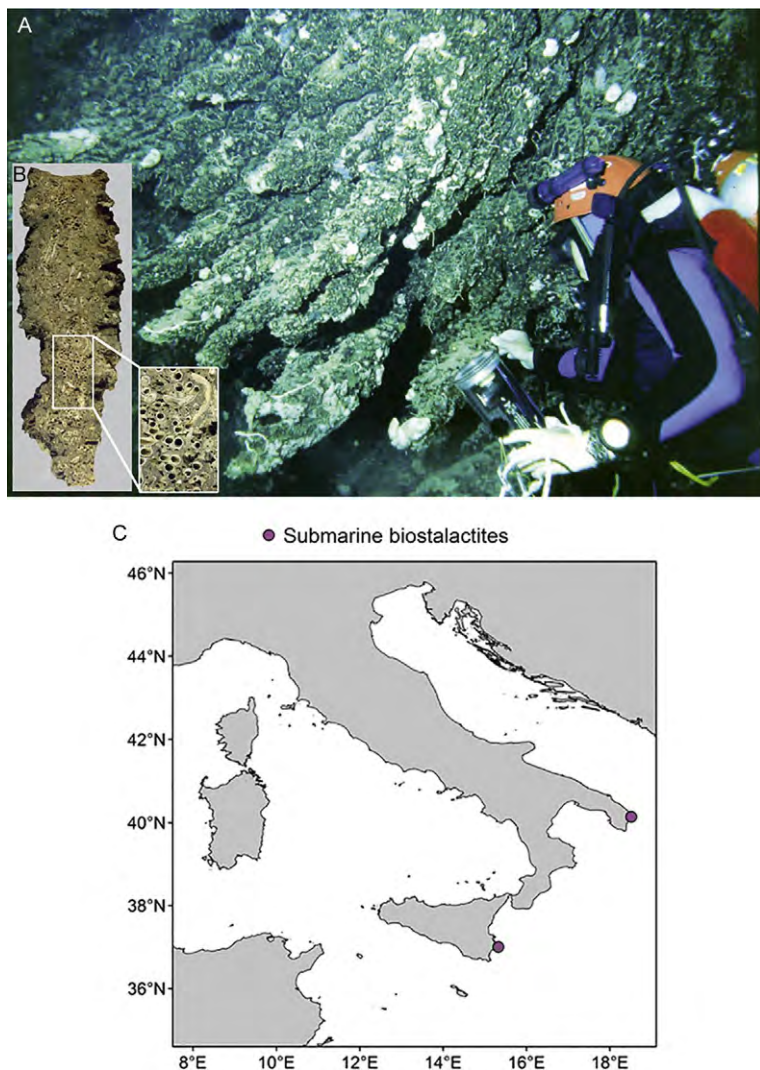


Fig. 7 (A) Biostalactites in a submarine cave at the Cape of Otranto (Onorato et al., 2003). (B) View of a longitudinal section. The *magnified image* shows the serpulid tubes that form the core of the bioconstruction, in a carbonate matrix of bacterial origin. (C) Biostalactite distribution along the Italian coast. *Points* represent data with no associated surface area. Boundaries of points of data layers are enhanced for illustrative purposes and do not reflect the real habitat extent.

groups (Onorato et al., 2003; Sanfilippo et al., 2015). Serpulidae and Bryozoa are the dominant taxonomic groups, followed by Porifera and Foraminifera. Other invertebrates, such as Bivalvia, Brachiopoda, Hydrozoa, Anthozoa, Cirripedia and Polychaeta Terebellidae, are relatively rare.

3. PROCESSES

3.1 Building/Bioeroding Processes and the Age of Bioconstructions

The growth of these bioconstructions depends on a positive balance between building and bioeroding processes (e.g. Garrabou and Ballesteros, 2000). Coralline macroalgae of the genera *Mesophyllum*, *Lithophyllum* and *Neogoniolithon* provide the greatest contribution to coralligenous bioconstructions (Ballesteros, 2006). Several species of the genus *Peyssonnelia*, mostly *Peyssonnelia heteromorpha* (Zanardini) Athanasiadis and *Peyssonnelia rosa-marina* Boudouresque & Denizot, also participate in the building process as do as many calcified nonphotosynthetic organisms, such as the foraminiferan *M. miniacea*, cnidarians and bryozoans. Molluscs and serpulid polychaetes can play a minor constructive role.

Cyanobacteria (e.g. *Hyella caespitosa* Bornet & Flahault, 1888; *Mastigocoleus testarum* Lagerheim ex Bornet & Flahault, 1886; *Leptolyngbya terebrans* (Bornet & Flahault ex Gomont) Anagnostidis & Komárek, 1988), perforating sponges (e.g. *Cliona celata* Grant, 1826 and *Cliona viridis* (Schmidt, 1862)), boring molluscs (e.g. *Hiattella arctica* (Linnaeus, 1767), *Rocellaria dubia* (Pennant, 1777) and *Lithophaga* (Linnaeus, 1758)), sipunculids (e.g. *Aspidosiphon muelleri* Diesing, 1851) and grazing sea urchins (e.g. *Sphaerechinus granularis* (Lamarck, 1816)) often erode or dissolve coralligenous bioconstructions (Ballesteros, 2006; Sartoretto, 1998; Sartoretto and Francour, 1997).

The bioconstruction process in CWC reefs is mainly due to the branched stony corals *M. oculata* and *L. pertusa*. When solitary corals such as *D. dianthus* settle on these colonies, they can contribute also. Moreover, a symbiotic interaction with the polychaete *Eunice norvegica* (Linnaeus, 1767) seems to significantly help the bioconstruction process (Mueller et al., 2013). This species forms parchment like tubes within living coral branches that are later calcified by the coral (Buhl Mortensen, 2001). In particular, *E. norvegica* is mainly involved in strengthening the reef structure by thickening and connecting coral branches (Roberts, 2005; Tursi et al., 2004). In addition, massive sponges such as *Pachastrella monilifera* Schmidt, 1868 and *Poecillastra compressa* (Bowerbank, 1866) can form mixed grounds with CWCs, as it happens in Santa Maria di Leuca and in the Bari Canyon (Bo et al., 2012b; Longo et al., 2005).

A suite of endolithic assemblages of microborers (i.e. bacteria, fungi and foraminiferans) and macroborers (i.e. sponges) bioerode CWC bioconstructions. The main macroboring sponges belong to the genera *Cliona* and *Spiroxya* (Longo et al., 2005). The bioerosion process seems to be

represented by a bioerosion succession, generally beginning with the infestation of bacteria and fungi, followed by other species. Bioerosion predominantly affects the dead parts of the coral skeleton (Beuck and Freiwald, 2005), but in stressed corals the infestation can increase and also affect living areas.

Some Mediterranean bioconstructions can be ephemeral and rapidly degrade once the bioconstructors die, such as *Sabellaria* reefs, whereas others remain stable for millennia, such as coralligenous formations. The rims of *L. byssoides* are fairly persistent: in conditions of stable sea level they can grow for centuries, up to 900–1000 years (Faivre et al., 2013; Verlaque, 2010). Many large rims currently present in the Mediterranean Sea were formed during two periods of global cooling in which the sea level was stable (Dark Age Cold Period, AD 450–950, and during the Little Ice Age, AD 1400–1850, Faivre et al., 2013). The bioconstruction activity of *L. byssoides* produces a very hard calcareous rock that is only eroded slowly, and which maintains the integrity of the rim for a long time, so that its ecosystem engineering function persists even when the living alga is no longer present. Unfortunately, in the last decades, reports of deteriorated *L. byssoides* rims have become increasingly frequent (Faivre et al., 2013; Laborel et al., 1993; Verlaque, 2010) and a careful monitoring of these structures is now urgently needed.

Coralligenous pinnacles dating back 6207 years from the Ionian Sea (Bertolino et al., 2017b) showed a core partially made up by serpulid (*Protula* sp.) remains, a feature in common with other bioherms studied in the Southern Ionian Sea (Di Geronimo et al., 2002) and with pseudo stalactites found in several marine caves from the Aegean and Ionian Seas (Guido et al., 2013; Sanfilippo et al., 2017). Moreover, the sediments trapped in the crevices of these bioherms can host a high number of embedded siliceous spicules that have been considered to be a good proxy for evaluating changes of sponge biodiversity on a millennial timescale (Bertolino et al., 2013, 2017a,b).

The age of the deepest coralligenous bioherms can be traced back also to 8000 years ago (Ballesteros, 2006), whereas coralligenous platforms from shallower waters were dated to around 6000 years ago (Bertolino et al., 2017a). Generally speaking, these biostructures began to grow along the Mediterranean coast when the effects of ice cap melting were still very relevant, due to glacio–hydro–isostatic processes and tectonic uplifts (Pirazzoli, 2005) and the sea level was from 13.5 to 16.5m lower than at present (Sivan et al., 2001). Under these conditions, the calcification rate was facilitated,

leading to a quick growth of these bioherms. However, the accumulation rates appeared low ($0.006\text{--}0.83\text{ mm year}^{-1}$), oscillating greatly with different depths and time periods (Ballesteros, 2006; Garrabou and Ballesteros, 2000; Sartoretto et al., 1996; Teixidó et al., 2011). The highest rates ($0.20\text{--}0.83\text{ mm year}^{-1}$) were recorded between 8000 and 5000 years BP. In more recent times, appreciable radiocarbon accumulation rates of $0.11\text{--}0.42\text{ mm year}^{-1}$ have been recorded only for bioherms growing in relatively shallow waters (10–35 m depth) (Bertolino et al., 2013), while an average growth rate of about 0.15 mm year^{-1} was measured on coralligenous pillars from the Ionian Sea (Bertolino et al., 2017b), a rate comparable with that recorded by Di Geronimo et al. (2002) for similar pillars (0.27 mm year^{-1}) in the southern Ionian Sea. Radiocarbon dating in bioherms from different localities of the Ligurian Sea indicated average growth rates ranging from of 0.03 to 0.05 mm year^{-1} over 3000 years (Bertolino et al., 2013). In some cases, the growth of the bioherms showed an incoherent and chaotic temporal growth pattern (Bertolino et al., 2017a), with older layers overlapping younger ones. This phenomenon could be related to favourable periods for carbonate deposition, alternating with partial destruction phases due, for example, to intense mud deposition after episodes of intense floods (Fig. 8).

In the northern Adriatic continental shelf, biogenic frameworks are generally superimposed on hard bottoms of still debated origin. Marine sediments may be consolidated by methane related calcium carbonate cementation, thanks to seepage of CH_4 rich fluids, observable near many offshore reefs (Gordini et al., 2012). Meandering shaped morphologies and the distributions of many reefs, especially those off Chioggia, suggest the importance of Pleistocenic rivers, Holocene tidal channels and beach bars which are initial substrate for current coralligenous build ups. The lithification of these sandy palaeochannels is estimated to have started from 7000 years BP, likely due to the interaction between marine and less saline fluids related to onshore freshwater discharge at sea through a sealed water table (Tosi et al., 2017).

Sabellaria bioconstructions, which are formed from tubes made by sand grains, are mostly ephemeral. They strictly depend on the balance between bottom sediment features and water movement, supplying sand and particles for tube building and growth. *Sabellaria* larvae show preferential settlement either onto living bioconstructions or onto their ruins, so ensuring reef persistence and recovery. Hence, the age of these bioconstruction greatly exceeds the age of the living worms, since the reef may repeatedly follow a cyclical progression of settlement, growth and destruction phases

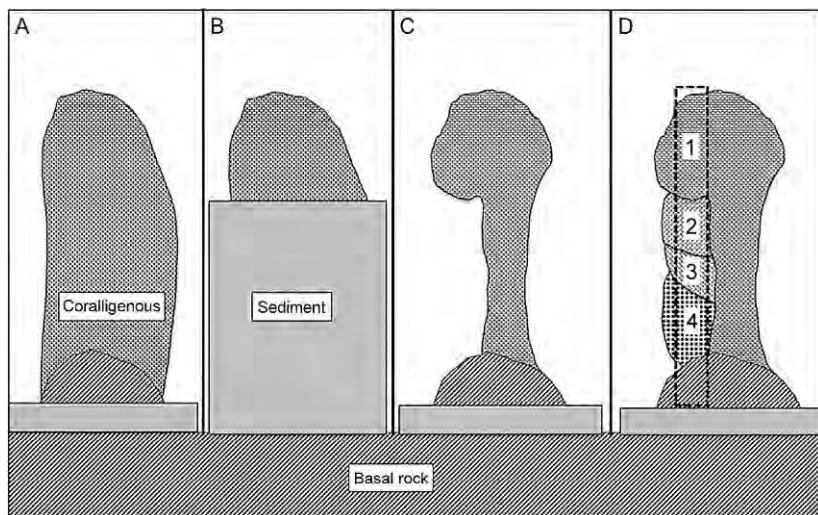


Fig. 8 Hypothetical evolutionary scenario of the coralligenous accretions of Bogliasco. (A) In a first phase the algal growth results in pillar-like bioherm. (B) Bottom sediments increase during periods of heavy floods, partially or totally burying the pillars and killing the algal cover. (C) During the burying or after the removal of the sediments, part of the structure becomes prone to erosive processes, giving rise to mushroom-like structures. (D) In following phases, the coralline algae grow again in sciaphilous microhabitats, determining the irregular temporal layering of the structure (the numbers 1–4 indicate different sheets of deposition from the oldest to the youngest). In this situation, in a core sample (dotted rectangle), younger sheets can overlap with older ones.

(Gruet, 1971–1972). Tube growth rates range from 4.4 to 6 mm day⁻¹ (Hendrick and Foster Smith, 2006) and the complete cycle requires from several months to more than 10 years (Gruet, 1986). The *S. spinulosa* reef recorded along the Apulian coasts showed cyclical fluctuations over a period of 1 year (Gravina et al., 2018). Little is known about the duration of fluctuations taken by older biogenic structures in palaeontological timescales (Schäfer, 1972). More recently, historical data from the North Sea have documented the persistence of *Sabellaria* reefs over a period of approximately 1 century (Firth et al., 2015). A documented age of 60 years was revealed for some Italian *S. alveolata* reefs. Indeed, previous studies dating back to the 1950s (Giordani Soika, 1956; Molinier and Picard, 1953; Taramelli Rivosecchi, 1961) report extensive bioconstructions from the Latium and Sicily coasts, with detailed descriptions consistent with the present observations from the same sites (M.F. Gravina, personal observations; Schimmenti et al., 2016). Along the Adriatic coasts, at Torre del Cerrano, structural changes of *S. spinulosa* bioconstructions showed a *Sabellaria*–*Mytilus* succession spreading

over a period of 15 years (Gadaleta et al., 2015). However, no historical data are available on the age of the *S. spinulosa* reef off Apulian coast, only recently discovered to be an actual “reef” (Gravina et al., 2018).

M. oculata and *L. pertusa* are able to build huge bioconstructions that can exceed 1 m in height and width per colony (e.g. Angeletti et al., 2014; Taviani et al., 2017), which remain after the death of the coral, providing an exploitable hard substrate for many associated species (Mastrototaro et al., 2010; Vertino et al., 2010). On a geological timescale, such highly structured bioconstructions can produce true carbonate mounds that some times endure for many hundred thousand to millions of years of discontinuous coral succession (Taviani et al., 2011).

Biostalactite building is mainly due to serpulid tubes that do not lie on the substrate but which elevate the worm crowns by several centimetres. This living stage, however, is still far from the final aspect of the biostalactite, as worm tubes become embedded in a thick calcareous coat of bacterial origin. Guido et al. (2014) described a commensal symbiotic link between worms and bacteria: these use organic matter coming from the worms that, in their turn, build their tubes with mineral pelites of bacterial origin. The tubes are made of biotic carbonate, and those in the Otranto biostalactites have ages that have been dated by the ^{14}C method (Belmonte et al., 2009, 2016). The elongation/growth of three 50 cm biostalactites required thousands of years, starting during the last postglacial period when the sea level rose to the present level and submerged the cave (about 6000 years ago). The measured slow growth (50 cm in 6000 years) however, when compared with the growth of each serpulid tube (some centimetres in few years), still awaits an explanation.

3.2 Connectivity

Connectivity affects marine population dynamics (Moritz et al., 2013) and community responses to pressures (Wasserman et al., 2012) and is important for conservation decisions in both reserve network design (Boero et al., 2016; Cerdeira et al., 2010) and restoration actions (Raeymaekers et al., 2008). Knowledge on the connectivity of different bioconstructions is limited, though a variety of techniques have been developed to fill this gap such as genetic analyses, dispersal simulation models and β diversity studies.

3.2.1 Genetic Connectivity

Bioconstructors have a low dispersal capability compared to actively motile organisms, such as fish and marine mammals and reptiles, so might be expected to have a lower population connectivity. In fact, dispersal in bioconstructors

relies exclusively on larvae and propagules, whose duration is often limited in time. However, this hypothesis requires testing, since the relationship between pelagic larval duration (PLD) and genetic structure is far from linear, and the larval/propagule biology of bioconstructors is itself often poorly known. For animals, several recent reviews showed a poor correlation between PLD and population genetic structure, suggesting that patterns of connectivity in the marine realm are difficult to predict based on life history features alone (Costantini et al., 2018; Riginos et al., 2011; Weersing and Toonen, 2009). Usually, small scale genetic structuring is consistent with short PLD, often contrasting with species with long living larvae (Pascual et al., 2017). Moreover, at larger spatial scales, other biotic (e.g. presettlement processes) and/or abiotic (e.g. hydrodynamics, geomorphology) variables may shape the genetic structuring of populations.

So far, genetic connectivity of animal bioconstructors and benthic organisms inhabiting Mediterranean bioconstructions is poorly known. The few available studies have focused mainly on Porifera, Cnidaria, Echinodermata and Tunicata, using mitochondrial and microsatellite genetic markers (Costantini et al., 2017). An analysis of a wider array of invertebrates living in bioconstructions is highly desirable, but is currently limited by the lack of knowledge on life histories and distributions, and by the availability of species specific genetic markers (Adjeroud et al., 2014; Casado Amezua et al., 2011, 2012; Costantini et al., 2017).

The 2b RAD Genotyping by Sequencing technique (Wang et al., 2012) is useful for genotyping a high number of SNP markers across the entire genome in nonmodel organisms (Paterno et al., 2017). Its application to several hundred individuals of five of the most abundant species in Mediterranean coralligenous reefs (*Leptopsammia pruvoti* Lacaze Duthiers, 1897, *C. caespitosa*, *Myriapora truncata* (Pallas, 1766), *Parazoanthus axinellae* (Schmidt, 1862) and *P. clavata*) collected in all Italian seas revealed a strong and highly significant genetic structuring among populations for all species (Costantini et al., 2018; L. Zane and E. Boscarì, unpublished observations). Each species showed geographical differentiation, with a high percentage of genetic variation explained by population subdivision, indicating strong isolation between samples. Genetic data for the five species indicated that the strongest barriers to gene flow were between the western (Tyrrhenian and Ligurian Seas) and the eastern (Adriatic and Ionian Seas) samples. This result suggests that genetic data, besides showing isolation between sites, keep a trace of historical processes and contemporary factors leading to and maintaining the separation of the two basins. However, strong differences

were also evident within each geographic area, since all the pairwise comparisons were highly significant, including those involving the closest sampling sites (about 70 km for *C. caespitosa*, *M. truncata* and *P. davata*, and about 5 km for *L. pruvoti*). Similarly, previous studies on coralligenous cnidarians, based on microsatellites (*C. rubrum*, *E. singularis* and *P. davata*) (Cannas et al., 2015, 2016; Costantini et al., 2016a,b, 2017; Mokhtar Jamaï et al., 2011; Pilczynska et al., 2016), showed populations structuring at different spatial scales (from local to Mediterranean) and a strong differentiation among patches separated by distances ranging from tens of kilometres to metres. Thus, both the 2b RAD approach and previous microsatellite results support the hypothesis of negligible dispersal, even at the very local scale, which may be caused by the very short duration of the free swimming larval stage. These results indicate a much higher structuring in bioconstructors than is shown in fish and other invertebrates over comparable areas (Boissin et al., 2016; Paterno et al., 2017).

Information concerning genetic connectivity in algal bioconstructors is limited. In general, molecular data for Mediterranean macroalgae are still scarce (and have been produced mainly in studies with a taxonomic focus). Coralline algae of the genera *Lithophyllum*, *Mesophyllum*, *Lithothamnion* and *Neogoniolithon* produce the largest algal bioconstructions in the Mediterranean Sea, and these sessile algae disperse by means of nonflagellate spores (bisporos, carpospores, tetraspores). Red algal spores are small cells with limited active movement and are devoid of storage substances: they settle only on hard substrata and remain viable for only a few days (Norton, 1992; Santelices, 1990). Although their dispersal is substantially affected by the velocity of waves and water currents, these propagules do not disperse more than a few kilometres, with most of them settling much closer to the parental source (Gaylord et al., 2002). Furthermore, the calcareous nature of the thallus prevents long distance dispersal by floating, a mechanism known to be important for other morphological types of seaweeds (Norton, 1992). A strong genetic structuring can be expected for Mediterranean coralline bioconstructors, and this hypothesis is supported by data available for the only species investigated in detail, *L. byssoides*. Pezzolesi et al. (2017) sequenced 2 organellar markers in populations of this species from 15 sites in the Central Mediterranean, for which they found high haplotype diversity. The observed patterns did not show a clear correspondence with the main biogeographic boundaries recognized in this area (Patarnello et al., 2007); they were interpreted as a result of both past climatic events in the hydrogeological history of the Mediterranean and by poor propagule dispersal. *L. byssoides* spores are able to settle and germinate only

in the intertidal; it can therefore be presumed that populations separated by stretches of sea or sandy shore extending for tens of kilometres have very limited genetic connectivity. Data from subtidal Corallinales are presently not available.

The role of both physical (hydrodynamics, currents, waves, tide, winds) and biological factors (PLD, larval growth and lifespan, larval behaviour, spawning time) is crucial to explain connectivity among *Sabellaria* bio constructions in the intertidal zone, where they occur as irregular patchy banks. Larval dispersal and potential connectivity have been modelled for *Sabellaria* reefs in the English Channel, which are the largest known reefs in Europe, and this work has revealed the crucial role played by hydrodynamic and meteorological conditions on larval dispersion along coastal areas (Ayata et al., 2009). To face deficiency of information about potential and realized connectivity among *Sabellaria* populations in the Italian seas, the reefs occurring along the Tyrrhenian coasts (Latum) are presently being studied in terms of genetic connectivity and using a biophysical modelling approach which simulates larval dispersal under hydrodynamic and meteorological factors at very local spatial scales (Bonifazi, 2018).

Deep sea connectivity among species and habitats is still poorly known (Hilário et al., 2015). The LIW and the cascading of Northern Adriatic waters into the Ionian Sea are the main conveyor belts sustaining active CWC growth in the Mediterranean Sea. These water masses can be possible vectors for larval dispersal, connecting the different coral sites and provinces of the basin (Chimienti et al., 2018b). Genetic connectivity among the different sites in the Mediterranean Sea and with the Atlantic Ocean has yet to be comprehensively studied.

Connectivity among biostalactites in different caves is unknown. These structures have been only recently described in detail and the currently available information from different geographic sites most probably does not refer to the same engineer species. Further, the *Protula* species responsible for the Otranto biostalactites is new to science (Causio et al., 2015) and is still poorly known. No other populations of this species are known at the present, but even the connections among close caves in the same area (the Cape of Otranto) are unstudied and information on the production and dispersal of larvae or propagules of any type is lacking.

3.2.2 Connectivity Models

Since wide scale spatial and temporal sampling with a high degree of resolution is often impossible, researchers tend to turn to models in order to

investigate marine connectivity (Kool et al., 2012). Dispersal models represent a valid methodological approach to identify patterns of potential connectivity among marine bioconstructions. Recently, a dispersal model driven by satellite mapping of ocean currents was developed to evaluate the potential connectivity between coralligenous assemblages of the central Mediterranean Sea (Ingrosso et al., 2017a; Fig. 9). The model was parametrized using the distribution of coralligenous formations in different marine subregions (Fig. 9A) along with information on the dispersal capacity of the Mediterranean scleractinian coral *C. caespitosa*, as a typical coralligenous bioconstructor species. The model proved to be efficient in summarizing some important features of the coralligenous network: high internal connectivity was detected in the Eastern Central Tyrrhenian, South Adriatic and Sardinia Sea, whereas, considering the amount of propagule exchanged among marine zones, the Strait of Sicily and the Northern Tyrrhenian Sea were the main sink and source sites, respectively. The South Eastern Tyrrhenian Sea emerged as a critical stepping stone area within the general connectivity network (Fig. 9C), on the contrary the North Adriatic Sea was the most isolated and poorly connected. These preliminary results were just indicative and must be confirmed by in situ genetic data.

3.2.3 β -Diversity of Bioconstructions

β Diversity, the spatial turnover of species composition across latitudinal and environmental gradients, was first introduced to formally link local (α) to regional (γ) species richness (Whittaker, 1960). β Diversity can be seen as the contribution to regional species richness that comes from spatial heterogeneity within the same habitat or from species accumulation across habitats. This concept is receiving increasing interest because it captures fundamental processes that maintain biodiversity at multiple scales. For example, at local scales, β diversity may be promoted by habitat specialization and strong biotic interactions, whereas, at larger scales, such as along environmental and latitudinal gradients, β diversity may reflect habitat filtering and dispersal limitation (Anderson et al., 2011; Gaston et al., 2007a,b; Kraft et al., 2011; Myers et al., 2013; Tuomisto et al., 2003).

β Diversity also offers insights into how species assemblages respond to anthropogenic influences (Socolar et al., 2016). Habitat fragmentation, species introductions and the establishment of protected areas may increase or decrease β diversity depending on the prevalence of processes that enhance or reduce variation in species composition among sites. For example, human interventions that increase species connectivity, such as the provision of

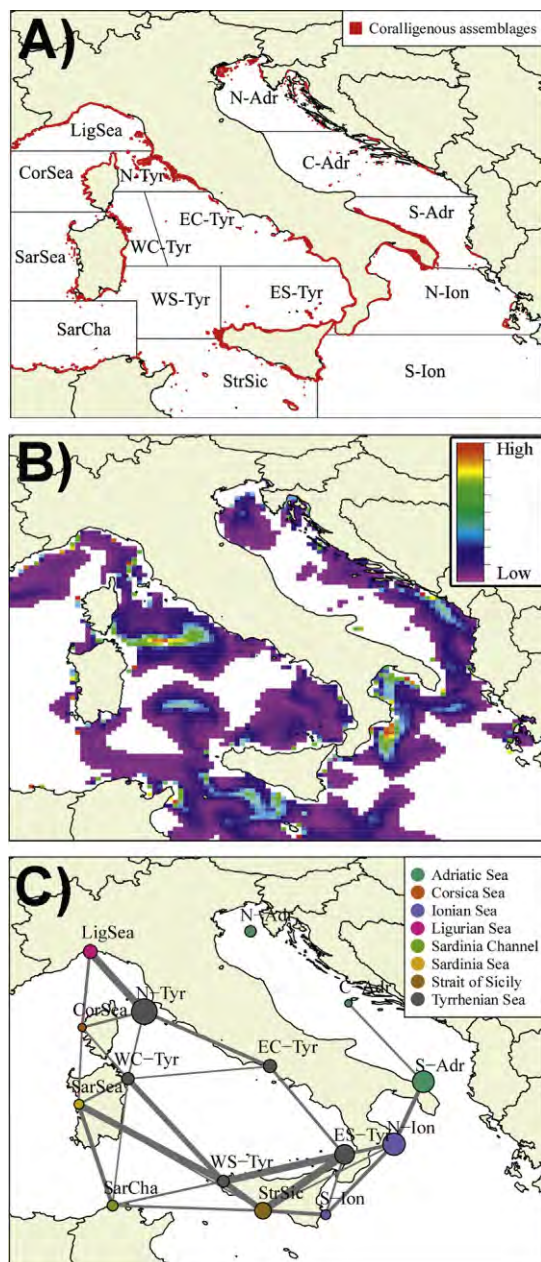


Fig. 9 Connectivity model of coralligenous habitat in the Central Mediterranean Sea. (A) Spatial distribution of coralligenous areas used in the connectivity analysis and boundaries of Mediterranean subregions according to Bianchi (2004) and Relini (2008). *(Continued)*

corridors, will increase dispersal and this effect should result in reduced spatial turnover in species composition, enhancing the homogeneity of species assemblages. Thus, β diversity may be used as an indirect measure of species connectivity (Thrush et al., 2010). Low values of β diversity (i.e. high similarity of species composition) among sites featured by common environmental conditions can be a consequence of a high connectivity among them through propagule dispersal. However, high values of β diversity (corresponding to low similarity in species composition) can provide evidence of isolation only after the exclusion of the influence of postsettlement processes. In fact, dissimilar assemblages could actually be well connected through larval and propagule dispersal and the low similarity could be the result of postsettlement mortality events, which may be different across sites. Instead, if the differences are really due to low connectivity, compositional differences should be evident at the initial steps of settlement and/or recruitment in experimentally manipulated plots. Thus, β diversity is suitable for identifying connections between populations and communities, although a high species turnover does not necessarily imply a lack of connectivity. All this implies the need to combine and integrate β diversity analyses with other tools and approaches.

β Diversity has received little attention in biogenic assemblages. Balata et al. (2007) showed that increased sedimentation reduced β diversity on western Mediterranean biogenic reefs, muffling natural differences in species composition between vertical and horizontal substrata. This result supports the importance of β diversity as a measure that can readily capture changes in biogenic assemblages. The analysis of β diversity may reveal the processes that shape assemblages on bioconstructions, especially in low subtidal environments (30–50 m depth, as in coralligenous formations). These formations thrive in environments that are generally less variable than shallower

Fig. 9—Cont'd (B) Visualization of a 30-day larval dispersal based on AVISO current data. (C) Potential coralligenous connectivity in the different subregions. The node dimension is proportional to the coralligenous area and the line width reflects the intensity of connections. Acronyms: Central Adriatic (C-Adr), Corsica Sea (CorSea), Eastern-Central Tyrrhenian (EC-Tyr), Eastern-Southern Tyrrhenian (ES-Tyr), Ligurian Sea (LigSea), Northern Adriatic (N-Adr), Northern Ionian (N-Ion), Northern Tyrrhenian (N-Tyr), Sardinia Channel (SarCha), Sardinia Sea (SarSea), Southern Adriatic (S-Adr), Southern Ionian (S-Ion), Strait of Sicily (StrSic), Western-Central Tyrrhenian (WC-Tyr), Western–Southern Tyrrhenian (WS-Tyr). *Panel (A): From Martin, C.S., Giannoulaki, M., De Leo, F., Scardi, M., Salomidi, M., Knittweis, L., et al., 2014. Coralligenous and maërl habitats: predictive modelling to identify their spatial distributions across the Mediterranean Sea. Sci. Rep. 4, 5073. <https://doi.org/10.1038/srep05073>.*

habitats, where gradients due to hydrodynamic forcing and light variation are much stronger. This idea of reduced abiotic variation with depth leads to the hypothesis that β diversity should also decrease from shallower to deeper habitats because of the reduced importance of habitat filtering, a key mechanism maintaining β diversity. Unfortunately, this hypothesis has not been tested yet, but the outcome would be particularly interesting, in whatever direction. Support for the hypothesis would indicate that habitat filtering is reduced in low subtidal environments and, possibly, that connectivity is an important assembling process. Rejection of the hypothesis would also be appealing, suggesting that dispersal limitation and species interactions become stronger with increasing depth to compensate for the weakening of habitat filtering.

Harsh abiotic conditions in shallow waters, in terms of intense light intensity, temperature and water movement, especially in the intertidal, can favour assemblages that tolerate such extreme situations, so forming low diversity communities where individual species are prominent. As depth increases, especially on hard substrates, clonal species become dominant and biotic interactions, especially competition for space, become the main drivers of the composition of assemblages where clonal species are dominant (Jackson, 1977).

Understanding the relative contribution of these processes will be increasingly important, since abiotic variation is expected to increase with climate change, as we have already seen with recent heat waves reaching low subtidal environments (Garrahou et al., 2009). These extreme events can alter the mechanisms that maintain biodiversity on bioconstructions, and β diversity seems particularly suited to detect these changes.

4. MEASURES

4.1 Major Threats to Mediterranean Bioconstructions

The intensive human exploitation of the Mediterranean Sea has many profound negative effects on marine biota. Industrial, urban and agricultural pollution, coastal development, climate change, increases in sedimentation, trawling, anchoring and introduction of alien species represent the main threats for Mediterranean marine benthic communities (Ballesteros, 2006; Coll et al., 2010; Piazzi et al., 2012). Although with variable spatial and temporal extent, and variable intensity, almost all coastal biodiversity of the Mediterranean is affected by these threats (UNEP MAP RAC/SPA, 2003). Below is a synthesis of the main threats affecting bioconstructions.

4.1.1 Pollution

Chemicals introduced in the marine environment from land based (agricultural runoff, industrial and urban waste) and sea based (oil spills, shipping) sources of pollution could result in severe impacts on bioconstructions by impeding growth and reproduction of building organisms, and causing diseases or mortality in sensitive species. Several studies have correlated gradients of increasing pollution to increasing impacts on bioconstructions, in particular for those in the intertidal or superficial waters, such as *L. byssoides* and vermetid reefs, which are primarily exposed to coastal sources of pollution. Such species are highly sensitive to chemical pollution (Blanfuné et al., 2016; Verlaque, 2010), and large concretions are present only in condition of high environmental quality (Ballesteros et al., 2007; Chemello, 2009; Di Franco et al., 2011).

Bioconstructors inhabiting the shallow subtidal may be strongly affected as well. For instance, the presence of coastal industries has been associated with an increased spatial heterogeneity and decreased diversity of coralligenous assemblages (Bevilacqua et al., 2012, 2018). The decline of *C. caespitosa* reefs has been observed in relation to industrial discharge (El Kateb et al., 2016), and chemicals are likely to have detrimental effects also on *A. calycularis* as on other corals (Wear and Thurber, 2015). Toxic substances may induce metabolic changes, decrease rates of growth and reproduction or reduce viability of corals (Pastorok and Bilyard, 1985). Domestic detergents may cause high coral mortality and reduced tissue growth (Shafir et al., 2014), whereas inorganic pollutants have harmful effects on fertilization and embryo development (Humphrey et al., 2008) and on early life history stages of coral species (Humanes et al., 2017). Products such as sunscreen UV filters containing benzophenone 2 induce deformity in coral planulae (Downs et al., 2014) and, by promoting viral infection, potentially play an important role in coral bleaching (Danovaro et al., 2008). Pharmaceuticals have negative ecological consequences on aquatic invertebrates even at very low concentration (Brodin et al., 2014) by affecting spawning, larval release, locomotion and fecundity (Fong and Ford, 2014).

Plastic litter is increasingly recognized as a potential threat to bioconstructions, even for deep water corals (Fig. 10D). In a recent study, Savini et al. (2014) documented plastic bags and debris to be the most represented type of marine litter in CWC banks in the northern Ionian Sea. In this case, the major effects are due to the entanglement of debris on colonies, causing impediments for normal polyp activities (e.g. feeding). Moreover,

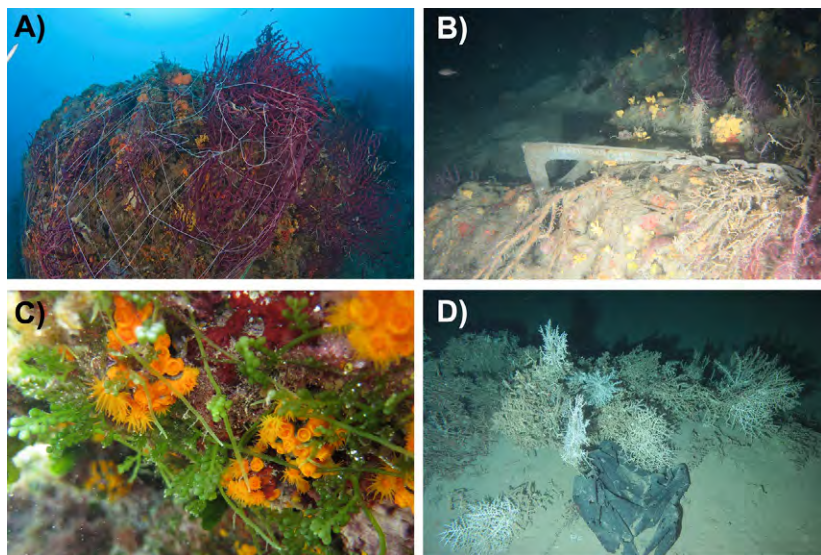


Fig. 10 Threats to bioconstructions: (A) the negative impact of gothic nets and (B) anchoring on the coralligenous habitat. (C) The nonindigenous species *C. cylindracea* overgrows on colonies of *A. calycularis*. (D) Plastic litter on *M. oculata* coral frame. Panel (A): Photo: Paolo Fossati. Panel (B): Photo: University of Genova. Panel (C): Photo: Fabio Badalamenti. Panel (D): Photo: University of Cagliari/ISPRA.

degradation of plastic debris generates huge amounts of microplastic fragments that can be ingested by polyps (Hall et al., 2015) with detrimental consequences for the colonies. Marine debris of anthropogenic origin were also documented in the coralligenous outcrops using ROVs. Their occurrence was massive and widespread (Angiolillo et al., 2015; Cau et al., 2015a, 2017a). Gorgonians were the most commonly affected organisms, followed by red coral, antipatharians, sponges and other invertebrates. The lowest abundance of marine debris was recorded in Sardinia, representing a minor potential source of litter in comparison to more populated regions, such as Campania and Sicily (Angiolillo et al., 2015).

4.1.2 Organic Enrichment

Eutrophication (i.e. excessive nutrient load), mostly related to wastewater discharge, is a widespread problem in coastal waters (Howarth et al., 2000), enhancing algal blooms followed by algal death, decomposition and oxygen depletion leading to mass mortalities (Stachowitsch et al., 2007). Generally, eutrophication can impact ecosystems directly, causing

changes in species composition, as addition of limiting nutrients can cause shifts in competitive hierarchies (Emery et al., 2001) and promote alien species invasions (Williams and Smith, 2007). Sessile habitat forming species characterizing bioconcretions are the most heavily impacted by these threats (Altieri and Witman, 2006). Wastewaters profoundly affect the structure of coralligenous communities by inhibiting coralline algae growth, increasing bioerosion rates, decreasing species richness and densities of the largest individuals of the epifauna, eliminating some taxonomic groups and increasing the abundance of highly tolerant species (Ballesteros, 2006; Cormaci et al., 1985; Hong, 1980, 1982).

Water eutrophication particularly affects *Sabellaria* reefs. Despite *Sabellaria*'s tolerance to poor water quality, increasing inputs of nutrients along the shore are responsible for the indirect impact to the reef, causing massive green algae blooms, which significantly lower the rate of *Sabellaria* larval recruitment (Dubois et al., 2006). Evidence for such damage has been recorded along the Sicily coasts (F. Badalamenti, personal communication).

Although there are a general lack of studies on the impact of aquaculture facilities situated over or near to bioconcretions such as coralligenous outcrops or maërl beds, their effects should match those produced by wastewater dumping. For instance, in the Adriatic Sea, Kružić and Požar Domac (2007) documented the impact of tuna farming on the banks of *C. caespitosa*.

4.1.3 Climate Change

Climate change is the threat to marine ecosystems that is causing most concern worldwide. Regarding bioconstructions, the rise of both sea level and water temperature, ocean acidification and the increasing intensity and frequency of extreme weather events may act from local to large scale, altering coastal and offshore environments, with severe consequences to both shallow and deep sea habitats (Hoegh Guldberg et al., 2014; Pörtner et al., 2014; Wong et al., 2014).

In the long term, the rise of sea level will cause profound changes of midlittoral habitats, affecting bioconstructions in superficial waters, such as those of *L. byssoides* that thrive only in the midlittoral zone. This species cannot survive conditions of constant submersion, as it is rapidly covered and overgrown by sublittoral algae (mainly soft red algae and articulated coral lines). The formation of large rims of *L. byssoides* is therefore possible only if the sea level remains stable (or rises very slowly) over long periods (Faivre et al., 2013). Recent observations in other areas of the central Mediterranean

(Verlaque, 2010) suggest that, if the sea level rise is sufficiently gradual, this species can move upwards on the shore and grows in height. If the rate of sea level rise is too fast, however, the rims will not be able to cope with it and the living alga will disappear and the growth of these structures will no longer be possible.

More proximate effects of climatic changes have resulted in intensifying atmospheric events, sea water warming and summer hot waves (Rivetti et al., 2014). The increasing power of extreme sea storms expected under the climate change scenario in the Mediterranean Sea will likely have a deep physical impact on *L. byssoides* and *Sabellaria* reefs, given their prevalent shallow distribution (Firth et al., 2015; Nissen et al., 2014), but also on deeper bioconstructions such as coralligenous outcrops (Cocito et al., 1998; Teixido et al., 2013). Multiple climate driven effects, such as thermal anomalies and floods, can affect coralligenous outcrops (Bavestrello et al., 1994; Cerrano et al., 2000), often interacting with local human impacts in altering the composition and structure of coralligenous communities (Roghi et al., 2010). Seawater warming and summer hot waves may induce mass mortality episodes in gorgonians and other coralligenous organisms (Cerrano et al., 2000), causing depth shifts of the communities (Gatti et al., 2017; Ponti et al., 2014, 2018). These phenomena have caused repeated episodes of bleaching and mortality in *C. caespitosa* reefs colonies in recent years (Jiménez et al., 2016; Kersting et al., 2013; Kružić et al., 2012, 2014; Rodolfo Metalpa et al., 2000, 2005). Recovery of *C. caespitosa* from impacts of various kinds may be relatively rapid (Casado et al., 2015; Kersting et al., 2014b), but this species is believed to be living close to its thermal limit during the summer period, so that a long term increase of sea water temperature could be lethal for this coral (Rodolfo Metalpa et al., 2006a,b). Deep mass mortalities have been recently reported for red coral populations thriving on deep coralligenous concretions of the Gulf of Salerno at a depth range between 80 and 100 m and attributed possibly to local downwelling currents inducing an unusual drop of the thermocline, sudden warm water emissions or local landslides generating turbidity currents (Bavestrello et al., 2014).

Climate change may have a positive effect on the thermophilic stenotherm coral *A. calycularis*, whose distribution could extend northwards due to warming of the superficial waters (Bianchi, 2007). However, this species seems particularly sensitive to high summer temperatures, suggesting that different climatic processes could combine in modifying the distribution of bioconstructors (Prada et al., 2017). The interplay between sea water warming and ocean acidification is particularly concerning. For instance,

sensitivity to high summer temperatures may increase tissue mortality in *A. calycularis*, which in turn makes the corals more susceptible to ocean acidification affecting net calcification.

Today's surface ocean is saturated with respect to calcium carbonate, but increasing atmospheric carbon dioxide concentrations are reducing ocean pH and carbonate ion concentrations, thus reducing the level of calcium carbonate saturation (Gattuso et al., 2015). If these trends will continue, key marine bioconstructors, such as corals, shellfish and calcified algae, will be threatened. Direct physiological effects of decreased pH on bioconstructors typically include changes in survival, calcification, growth, development, reproduction and abundance (Kroeker et al., 2013). A recent work revealed that pH reduction impairs the recruitment success of the reef building gastropod *D. cristatum* (as *D. petraeum*), likely causing shell dissolution of the recruits and altering their shell mineralogy (Milazzo et al., 2014).

The coralline algae are vulnerable to ocean acidification (Fabricius et al., 2015; McCoy and Kamenos, 2015) due to their high Mg calcite skeletons that are more soluble than other forms of calcium carbonate (Andersson et al., 2008); hence, ocean acidification will impact the coralline algae (Cornwall et al., 2017). Martin and Gattuso (2009) concluded that, on the long term, a combination of increased $p\text{CO}_2$ and elevated temperatures may lead to dissolution exceeding calcification in *Lithophyllum cabiochiae* (Boudouresque & Verlaque) Athanasiadis, one of the main bioconstructor coralline algae in the coralligenous. These authors, however, reported that the intensity of this effect is seasonally variable. Differences in sensitivity to acidification can also be expected in relation to habitat and depth; for instance, slow flow habitats (such as deep coralligenous habitats) might become refugia from ocean acidification for calcifying organisms (Hurd, 2015). However, the areas of dense water formation are preferential sites for atmospheric carbon dioxide absorption and through them the ocean acidification process can quickly propagate into the deep layers. In the Gulf of Lions and in the Adriatic Sea, the two most active deep convection area of the Mediterranean Sea (Boero, 2015), the ocean acidification of the deep layer can be particularly strong (Ingrosso et al., 2017b; Touratier et al., 2016) and this may negatively affect CWCs in the near future (Gori et al., 2016).

Scaling up the direct effects of ocean acidification from single species to ecosystem level parameters, such as habitat complexity or density of bio constructions, is difficult (Sunday et al., 2017). However, an overall reduction of structural complexity has been detected in the biogenic habitat that rely on calcification for their structure (Kroeker et al., 2013), which in turn may

negatively affect the associated biodiversity. Since most bioconstructions are the result of calcification processes, ocean acidification has the potential to change seascapes dramatically.

4.1.4 Fisheries

Fishing activities have several direct and indirect effects on bioconstructions, particularly in subtidal habitats, affecting single species (Terrón Sigler, 2016; Terrón Sigler et al., 2016b) or whole bioconstructions (Cerrano et al., 2001). A major mechanism of disturbance consists of direct mechanical damage caused by fishing gears (Piazzi et al., 2012), whereas indirect effects involve increase in sediment load due the physical disturbance on the sea bottom and sediment resuspension, or damage from ghost nets (Fig. 10A). Along North European coasts, physical damage has been reported to seriously impact *Sabellaria* reefs, caused mainly by trawling for shrimps and dredging for oysters and mussels (Dubois et al., 2002, 2006; Riesen and Riese, 1982).

Both artisanal and recreational fisheries affect coralligenous bio constructions, damaging their three dimensional structure (e.g. both removing pieces of the biogenic structure and the living tissue of the arborescent organisms, such as gorgonians) as suggested by the widespread occurrence of lost fishing lines and ghost nets in these environments (Bavestrello et al., 1997; Cau et al., 2015a, 2017a; Di Camillo et al., 2018). Artisanal and recreational fishing (e.g. long lines) are also the main fishing practices affecting continental coralligenous animal forests and CWC bioconstructions, as these fisheries target commercial species gravitating within or around these ecosystems (Angiolillo et al., 2015; Bo et al., 2014, 2015; D'Onghia et al., 2012; Gori et al., 2017). Bottom trawling, in contrast, only marginally affects these bioconstructions, due to the protection offered by hard substrates and coral mounds (Enrichetti et al., 2018; Mastrototaro et al., 2013), which can seriously damage the fishing gear, thereby making such areas less accessible to trawl fishing activities and providing a natural refuge for the associated fauna (D'Onghia et al., 2011). Under particular conditions, however, trawling can cause severe damage, as in the northern Adriatic, where mesophotic biogenic habitats, due to their flat shape, shallow depth, low relief and high friability, are threatened by this fishing activity, especially when carried out by methods such as Rapido gear (Pranovi et al., 2000).

4.1.5 Coastal Development

The functioning of coastal marine habitats depends also on a dynamic balance between sediment input and export; human activities influence these

systems by either increasing or decreasing sediment delivery. Most anthropogenic alterations of the shoreline (e.g. urbanization, construction of ports and coastal defences) could have some impact on bioconcretions through the significant alterations of sedimentary regimes. The increase in sedimentation rates is a major problem in coastal waters worldwide. Sedimentation disproportionately impacts nearshore ecosystems such as coastal estuaries, where increasing sediment loads lead to both burial of benthic communities and increasing water turbidity, reducing light penetration and leading to numerous associated negative effects (Thrush et al., 2004). Increasing sedimentation is a major problem for rocky reefs (Airoldi, 2003), coral reefs (Rogers, 1990), sea grass systems (Orth et al., 2006) and soft sediment communities (Thrush et al., 2004). Coralligenous communities and *Sabellaria* reefs are also very vulnerable to changes in hydrological and sedimentary regimes resulting from coastal engineering works (Balata et al., 2007; Gatti et al., 2012, 2015a; Roghi et al., 2010; Vorberg, 2000). Coastal urbanization and the artificial sheltering of intertidal communities by the construction of jetties and marinas are a great impact on vermetid reefs (Di Franco et al., 2011). Human induced changes to land cover, including urbanization, loss of forests and intensification of agricultural practices in vulnerable areas (e.g. mountainous coastal regions), may dramatically increase soil erosion and sediment deliveries to coastal waters at regional levels, increasing turbidity and sedimentation and therefore threatening intertidal and subtidal bioconstructions (Mateos Molina et al., 2015).

4.1.6 Direct Physical Disturbance

Several activities, mostly related to human visitation and recreation, can lead to impacts on bioconstructions through direct physical disturbance of the building species (e.g. Milazzo et al., 2002). For instance, boat anchoring (Fig. 10B) has a high destructive potential in coralligenous formations (Ballesteros, 2006). Generally, bioconstructors characterizing this habitat are very fragile and can be easily detached or broken by anchors and chains, and they show a low recovery potential. Thus, in areas subjected to intense anchoring, it is unlikely that this community will fully recover from damage. Sometimes, due to lack of management, boat anchoring is a huge problem even within protected areas. This kind of impact often overlaps with recreational SCUBA diving (Chimienti et al., 2017). Due to their spectacular appearance, coralligenous formations are the most popular habitat for recreational diving in the Mediterranean Sea. Uncontrolled or too many

visits by divers in coralligenous communities produce important effects over certain large or fragile suspension feeders that inhabit coralligenous assemblages (Ballesteros, 2006; Casoli et al., 2016; Coma et al., 2004; Garrabou et al., 1998; Guarnieri et al., 2012; Linares et al., 2005; Sala et al., 1996). The proportion of damage varies significantly with the frequency of SCUBA diving and sometimes results in damage of bioconstructors like red algae, bryozoan and coral colonies. Mechanical impacts by divers and snorkelers cause serious damages to *A. calycularis* colonies (Di Franco et al., 2009; Milazzo et al., 2002). In areas where its dense reefs attract tourists, damages to colonies were frequently caused by accidental contacts with nonexpert divers (Terrón Sigler et al., 2016a).

Also for *Sabellaria* reefs, the main anthropogenic impacts related to the physical disturbance are linked to frequency of human visitation. Along Italian coasts, one of the main threats to these biogenic reefs is linked to trampling (Plicanti et al., 2016). Often, the impact is further exacerbated by the direct removal of *Sabellaria* worms, which are used as bait for recreational fisheries. The vermetid reef building species *D. cristatum* is similarly sensitive to trampling, which often causes the death of individuals and the detachment of settled larvae. Thus, given their very low dispersal ability (Calvo et al., 1998), they are unlikely to recover from local depletion and habitat degradation (Galil, 2013). Moreover, the increase of water movements linked to maritime traffic also impacts on vermetid reefs (Graziano et al., 2007).

4.1.7 Biological Threats

The rates of invasion of nonindigenous species (NIS) have increased in the last 2 centuries, and particularly in the last 50 years (Ruiz et al., 2000), as a consequence of globalization and industrialization. Coastal marine habitats are particularly exposed to the impact related to this threat (Williams and Grosholz, 2008) due to the concentration of activities that promote invasion (e.g. shipping, aquaculture, fisheries and aquarium trade). Invasive species can displace native species and alter food web dynamics, changing habitat structure by altering species diversity (Ruiz et al., 1999). Knowledge on the effects of NIS on Mediterranean coralligenous communities is scant. To date, three algal species are threatening these communities: *Womersleyella setacea* (Hollenberg) R.E. Norris, *Caulerpa cylindracea* Sonder and *Caulerpa taxifolia* (M. Vahl) C. Agardh. They colonize only relatively shallow water coralligenous reefs (to 60 m) (Ballesteros, 2006), where they cover the basal layer of encrusting corallines and increase sedimentation rates, impairing

both coralligenous growth and survival. The invasion of the red alga *W. setacea*, currently distributed along most of the Mediterranean basin (Athanasiadis, 1997), leads to lower species richness than that is observed at noncolonized sites (Piazzi et al., 2012). Similar effects have been documented for the other two algae (Cebrian et al., 2012; Gatti et al., 2015b). In some areas, especially *C. cylindracea* has totally invaded the coralligenous community, raising concerns for the conservation of this habitat (Meinesz and Hesse, 1991; Piazzi et al., 2005). However, healthy gorgonian forests made by *P. clavata* seem able to reduce the invasiveness of *C. cylindracea* in coralligenous habitats (Ponti et al., 2018).

At shallow depth, *C. cylindracea* may overgrow the anthozoan *C. caespitosa* (Gatti et al., 2015b; Kersting et al., 2014a; Kružić et al., 2008). In the National Park Mljet in Veliko Jezero (between 8 and 14m depth) approximately 150m of coastline characterized by coral bank of *C. caespitosa* was partially affected by this invasive alga (Kružić et al., 2008). Similarly, *C. cylindracea* has occasionally been observed to overgrow colonies of *A. calycularis* in Sicily (Fig. 10C).

Marine diseases, which often combine with climate change, represent another biological threat driven by human activities. Globally, examples of recent disease outbreaks with major impacts in marine ecosystems include the Caribbean urchin die off (Hughes, 1994), various coral diseases (e.g. Aronson and Precht, 2001), lobster declines in the north Atlantic (Glenn and Pugh, 2006) and marine mammal diseases (Kim et al., 2005). It is presumed, even if not yet assessed, that diseases could represent a threat for bioconstructions in general. Similar to the spread of NIS, disease outbreaks can be driven by human activities such as aquaculture with its artificially dense populations, and shipping and ballast water transport, facilitating the transport of disease vectors. Various synergistic stressors can weaken populations' disease resistance (Harvell et al., 2004), and other environmental changes can enhance disease effects (e.g. Bruno et al., 2007). Marine diseases are probably increasing in the ocean due to human activities (Harvell et al., 1999), but documenting the human influence on disease outbreaks is difficult due to lack of historical baselines.

Mucilages are another biological threat: algal aggregates and exudates can cause severe damage to erect suspension feeders (mainly gorgonians) especially on coralligenous formations (Schiaparelli et al., 2007). These blooms are still not well understood, but they are apparently caused by eutrophication. For instance, the benthic assemblages of the northern Adriatic biogenic reefs were strongly affected by recurring anoxic crises and accumulation of mucilaginous aggregates (Precali et al., 2005).

4.2 Current Conservation Measures

Although not legally binding, the Barcelona Convention's Action plan adopted in 2008 for the conservation of coralligenous outcrops and other calcareous bioconcretions in the Mediterranean Sea prescribes that “coralligenous/maërl assemblages should be granted legal protection at the same level as *P. oceanica* meadows” (UNEP MAP RAC/SPA, 2008, 2017). Coralligenous outcrops also appear in the EU Habitats Directive (under habitat type 1170 “Reefs”), and in the Bern Convention. Two maërl forming Mediterranean species, *Lithothamnion corallioides* (P. Crouan & H. Crouan) P. Crouan & H. Crouan and *Phymatolithon calcareum* (Pallas) W.H. Adey & D.L. McKibbin ex Woelkerling & L.M. Irvine, are included in Annex V of the Habitats Directive. Finally, under European law, destructive fishing is prohibited over Mediterranean coralligenous and maërl bottoms. The substantial lack of relevant geospatial data on these habitats, however, significantly hinders the effective implementation of these policies.

Bioconstructions are a potential proxy for monitoring the marine environmental quality according to the EU Marine Strategy Framework Directive (MSFD) 2008/56/EC (European Community, 2008), which requires the maintenance and restoration of marine biodiversity and ecosystem functioning. Bioconstructions host species of Community interest, such as the red coral *C. rubrum*, listed in Annex V of the EU Habitats Directive and other species, including commercial sponges, such as *Spongia officinalis* Linnaeus, 1759 and *Spongia lamella* (Schulze, 1879), gorgonians *P. clavata*, the gold coral *Savalia savaglia* (Bertoloni, 1819) and, deeper, the black corals *A. subpinnata*, *A. dichotoma*, *P. larix* and *Leiopathes glaberrima* (Esper, 1788). Black corals have been included in Annex II (List of Endangered or Threatened Species) of the Barcelona Convention; their trade is regulated by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) and have been listed as “least concern” in accordance with the IUCN Italian Committee, with the exception of *L. glaberrima*, commonly associated to deep white coral reefs, listed as “endangered” with special reference to its exceptional millennial longevity, hence high vulnerability (Bo et al., 2015).

A total of 211 sessile megabenthic species have been recorded on the coralligenous reefs of Liguria, sponges being the richest group. Twelve biological communities were identified: eight of them correspond to habitats described in the classification of the European Nature Information System (EUNIS) (Tunesi et al., 2006): (1) association with *C. zosterooides* (EUNIS equivalent: A4.261); (2) association with *Mesophyllum lichenoides* (J. Ellis) Me. Lemoine (A4.266); (3) facies with *E. cavolini* (A4.269); (4) facies with

E. singularis (A4.26A); (5) facies with *P. clavata* (A4.26B); (6) facies with *P. axinellae* (A4.26C); (7) facies with *L. sarmentosa* (A4.322); and (8) facies with *C. rubrum* (A4.713). The remaining four have no EUNIS equivalent and would require further investigation: (1) facies with *Eunicella verrucosa* (Pallas, 1766); (2) facies with *L. pruvoti*; (3) facies with massive/erect sponges; and (4) facies with *P. fascialis*. The distribution of these 12 habitats correlates with light intensity, geomorphology, sediment load and hydrodynamics (Cocito et al., 1997). The high spatial, morphological and biological heterogeneity of the coralligenous assemblages in Liguria is worth being protected. In total, the Ligurian coralligenous assemblages cover a surface area of 130.9 ha, but only 48.3 ha (37%) is within regional or national MPAs (Cánovas Molina et al., 2016).

C. caespitosa banks were abundant during the Pliocene (Peirano et al., 2009), but are presently rare and localized (Kersting and Linares, 2012; Kružić and Benković, 2008). Their decline led to the inclusion of *C. caespitosa* in the IUCN Red List as an “endangered” species (Casado Amezu’a et al., 2015). Following the Natura 2000 Interpretation Manual (European Commission, 2013), *A. calycularis* bioconstructions are listed as biogenic reefs; they are in the list of strictly protected species of the Bern Convention (Annex II), in the list of Endangered or Threatened species of the Barcelona Convention (Annex II), but the CITES classified this species as being of “least concern” in accordance with the IUCN Italian Committee.

Dendropoma cristatum (= *D. petraeum*) is a threatened species and it is included in the Annex II of the Bern Convention and in Annex II of Barcelona Convention. Moreover, it is included in the EU Habitat Directive and in the Spanish Catalogue of Threatened Species (Templado et al., 2004). In Italy, the presence of this species led to the national designation of MPAs along Sicilian coasts (MPA “Egadi Islands” and MPA “Capo Gallo—Isola delle Femmine”) and Campanian coasts (MPA “Santa Maria di Castellabate”). However, only a part of the vermetid reefs (53.3% in frequency and 15.6% in length) are really protected on Northwestern Sicilian coasts (Chemello, 2009; Chemello et al., 2014), and no vermetid reefs are protected along the Ionian coasts and the Salento Peninsula.

Regarding *Sabellaria* reefs no protection measures are provided for the great majority of them, the only protected reef being placed at the Torre del Cerrano MPA along the Central Adriatic coast. The deep water coral *L. pertusa* and *M. oculata* are included in the CITES list (Appendix II) and, according to Natura 2000 Interpretation Manual of the European Commission (2013), in the category “Reefs” (habitat type 1170) of the

EU Habitat Directive. However, the available information regarding the current status of these deep water communities at Mediterranean scale indicates a 40%–50% decline over the last 50–60 years, mostly due to bottom trawling (Orejas et al., 2009). As a result, more incisive protection measures and good management strategies are urgently needed (Otero et al., 2017).

Finally, *L. byssoides*, coralligenous, *C. caespitosa* banks, vermetid, sabellariid and sepulid reefs are also included in the European Red List of Habitats (Gubbay et al., 2016).

5. GUIDELINES AND RECOMMENDATIONS: A HOLISTIC APPROACH TO SUPPORT MANAGEMENT AND CONSERVATION STRATEGIES

The two main marine protection tactics enforced in Italy comprise nationally designated MPAs and Sites of Community Importance (SCIs) as part of the Natura 2000 network. On the one hand, the Ministry of the Environment and Protection of Land and Sea designates Italian MPAs, as the marine counterpart of Italian National Parks. Typically, they all have a management plan, a president, a director, a staff and a budget. On the other hand, Italian Regions, based on the EU Habitats Directive, designate the SCIs that, in most cases, have neither a management plan and budget nor a staff of any kind. The protection of the marine environment is further enforced through an entangled multitude of initiatives, usually termed as OECMs (Other Effective Area based Conservation Measures) (IUCN WCPA, 2018). Currently, the harmonization of protection tactics into a single strategy involves the extension of MPAs so as to comprise most SCIs. This will allow for a consistent management. The enforcement of protection, indeed, distinguishes “real” MPAs, where protection is enforced, from “paper parks” (Guidetti et al., 2008), where measures are simply on paper. The Italian situation is rapidly changing and it is not useful now to provide precise data that will soon be outdated. In general, many Italian MPAs have been designated where seascapes are particularly attractive for scuba divers and “beauty” has been the main reason for their proposal (Boero, 2017b). Since bioconstructions, and especially coralligenous ones, are particularly spectacular, many MPAs include bioconstructions. Italian Regions, instead, focused the designation of SCIs almost only on *Posidonia* meadows, but their attention is now turning towards bioconstructions as part of the “reef” category of the EU Habitats Directive (Fraschetti et al., 2009).

These measures, however, protect the sites where important habitats, usually benthic, are located, focusing just on the patterns of biodiversity distribution. The EU MSFD, with the definition of Good Environmental Status, calls for a more holistic approach that considers not only patterns of biodiversity distribution but also the ecosystem processes that allow for their presence and well being. The instruments to achieve this goal are many (e.g. Maritime Spatial Planning, Integrated Coastal Zone Management, the Ecosystem Approach, the Networks of MPAs, identification of multi parametric indexes evaluating biodiversity and seafloor integrity) and are often developed with no coordination, thus leading to a vision that is still fragmented.

Boero et al. (2016) provide guidelines to design networks of MPAs in the Mediterranean and the Black Seas, proposing the consideration of ecological space as a suite of Cells of Ecosystem Functioning as being compact units of management and conservation, where biodiversity patterns and ecosystem processes are spatially linked by high levels of connectivity. Bioconstructions, in this vision, are part of larger ecosystems and must be managed as such. A precondition for effective management, however, requires that biodiversity patterns are known, along with accurate habitat mapping. Then, each habitat must be managed and protected via two approaches: a proximate one, aiming at removing direct human impacts (i.e. MPAs), and an ultimate one embracing ecosystem processes that have an influence on the managed systems through connectivity (Networks of MPAs).

Coralligenous formations of any kind are considered as the major example of the “reefs” category of the EU Habitats Directive and, as such, should become SCIs, if they are not already included in nationally designated MPAs. The long time required for their building (millennia) does not give hope for their quick recovery if they are destroyed; hence any form of impact on them should be avoided, with effective regulations of human activities of any kind. The northern Adriatic mesophotic biogenic habitats, because of their extent, biodiversity and implications for fisheries and carbon regulation, have been the status of “Zona di Tutela Biologica” (ZTB) (Zone of Biological Protection, indeed a regulated no take zone) with a Decree of the Italian Ministry of Agricultural, Food and Forestry Policies (G.U. n. 193 of 19 8 2002). The increasing awareness of the vulnerability of these habitats has led to some efforts to protect these habitats with the institution of SCIs, part of the Natura 2000 network (SCI IT3250047; IT3250048; IT3330009). However, as these biogenic habitats occur as a patchy network of biodiversity hot spots, conservation efforts should not be addressed to protect single reefs, but should preserve a system of connected sink–source sites.

For the near future, effective protection must be based on the complete mapping of these habitats, including their geomorphology (area, shape, height), and on detailed information on their species composition. A further task will require understanding of the ecosystem processes that allow for their persistence.

Reefs of *A. calycularis* occur along Mediterranean rocky shores, particularly in the western and central areas of the basin. The beauty of these sites often attracts tourists but, especially at shallow sites, inexperienced SCUBA divers can cause mechanical damage to the reefs. These shallow sites are generally not larger than a few hundred square metres, or even less, but they are important sources of sexual propagules (Musco et al., 2016). Besides MPAs, where management should prevent damage, the creation of microprotected areas with some specific restrictions could be the best practice to achieve the conservation of this natural Mediterranean monument, contributing to increase awareness by people through specific communication projects. Some small coves and cliffs in the Gulf of Castellammare in Sicily, and also many sites in the Gulf of Naples, appear to be good candidates to test and implement focused protection schemes. The larval biology of *A. calycularis* is still poorly known: Pellón and Badalamenti (2016) showed that planulae are released through the tentacles, but their ecology is far from being known. Mechanically damaged colonies of *A. calycularis* might possibly be restored with transplantation techniques. Musco et al. (2017), in fact, demonstrated that fragments of dislodged colonies can be reimplanted.

More accurate information on the vermetid reef building species biology and population connectivity is essential to optimize vermetid reef protection (Milazzo et al., 2017). Pending the availability of this information, these bio constructions should be actively protected, based on the precautionary principle, and should become SCIs. It is very important not only to monitor the state of the endangered species *Dendropoma* spp. but also to enhance the knowledge of the highly diverse associated communities for a better understanding of this peculiar ecosystem. Its actual protection should be guaranteed by the establishment and proper management of MPAs or SCIs, according to Natura 2000 procedures of the European Union. An additional major problem is represented by the ongoing and projected levels of ocean acidification affecting the ecophysiological performance of this and many other reef building organisms, likely leading to a further reduction of the species abundance and diversity they support (Doney et al., 2009; Donnarumma et al., 2014; Milazzo et al., 2014; Sunday et al., 2017).

Sabellaria bioconstructions, due to their key functional role as habitat formers for large biodiversity and to their importance for coastal protection

from erosion, require effective protection, for instance using SCIs. Protective measures must prevent gleaning, trampling and organic pollution, since *Sabellaria* reefs are sensitive to these stressors. More information is required about the distribution of these reefs, their characteristics, spatial distribution and temporal short term variability. Long term persistence and resilience must also be evaluated, so as to distinguish temporary from persistent reefs. The life cycle of *S. alveolata* and the occurrence of larvae in the plankton should also be studied, so as to understand recruitment and larval dispersal, leading to the evaluation of connectivity among reefs.

The distribution of CWCs in the Mediterranean Sea is increasingly becoming better known with the advancement of oceanographic technologies. The unique deep sea bioconstructions of CWCs are true hot spots of biodiversity worthy of proper governance and protection, and they represent a Vulnerable Marine Ecosystem (Fabri et al., 2014). CWCs provinces have been recognized as essential fish habitat for several species of commercial or conservation interest (D'Onghia et al., 2010, 2012). For this reason, the General Fisheries Commission for the Mediterranean (GFCM) created the legal category of "Deep sea Fisheries Restricted Area" where the use of towed gears and dredges is forbidden, as has happened in Santa Maria di Leuca coral province (Mastrototaro et al., 2010). The institution of deep sea ecosystems protection strategies needs to be implemented further, considering new findings of a wide range of vulnerable and valuable deep sea habitats.

Recent decades have represented an extraordinary turning point for the investigation of the deep ecosystems in the Mediterranean Sea. ROVs have contributed to giving a visual identity to the habitats and assemblages that were partially known from the first zonation efforts (Pérès and Picard, 1964). Despite the great amount of work carried out, however, much is still to be done. Future perspectives in the study of CWC distribution concern the identification and exploration of other possible coral sites along the main path of the LIW (Chimienti et al., 2018b). These scleractinians occur in areas where the interaction between currents and topography can generate high speed flow (Orejas et al., 2009). New investigations along precipitous topographies (e.g. canyons, ridges and seamounts) will greatly enhance our knowledge of coral sites and provinces. This would help to refine habitat models that predict the location of new coral bioconstructions based on habitat topography and hydrodynamic conditions. Apart from new areas, it will be crucial to explore the margins of the presently known sites and provinces, possibly deeper than 1000 m depth. Some of these sites are likely to represent parts of a discontinuous deep sea belt of CWC bioconstructions. Explorative efforts could lead to the discovery of other large white coral belts, as

has been the case for the Apulian margin, where an almost continuous belt of patchy white coral bioconstructions connects the south western Adriatic populations with those inhabiting the Ionian margin (Angeletti et al., 2014; D'Onghia et al., 2015).

Biostalactites, deriving from a new and presumably endemic species with a particularly restricted geographic range (Cape of Otranto), require urgent protection interventions following the precautionary principle: we cannot expect to know more about these structures before protection is enforced!

Altogether, all bioconstructions can be assigned to the “reefs” category of the EU Habitats Directive and, as such, be designated as SCIs. As with the better known *P. oceanica* meadows (Fig. 1), bioconstructions are present in most Italian waters (Fig. 11), even if there are still some gaps in their knowledge, especially for the coast of Calabria, both on the Tyrrhenian and on the

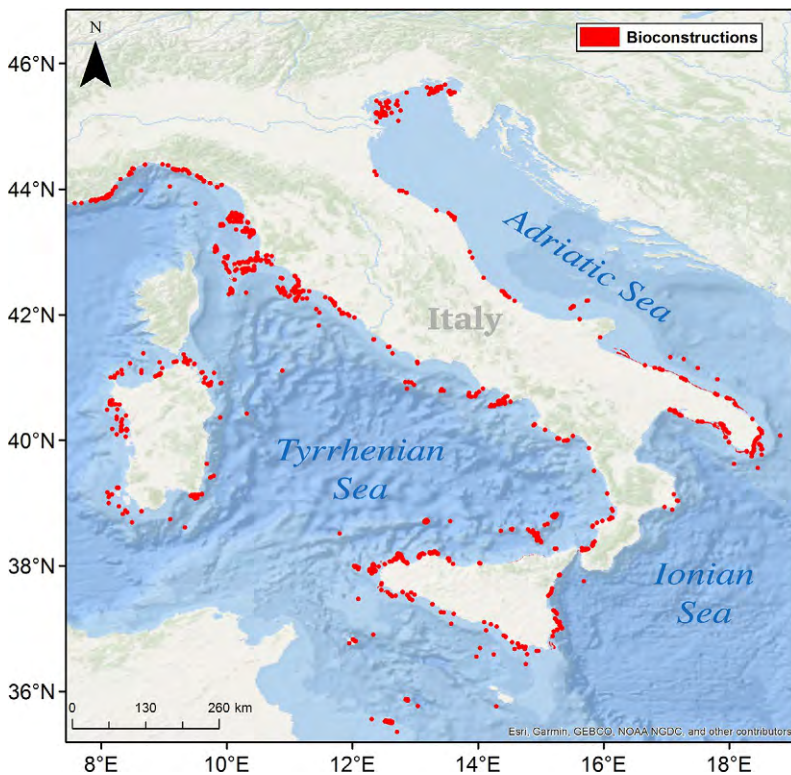


Fig. 11 Distribution pattern of marine bioconstructions along the Italian coast. Boundaries of point and polygon features of the data layers have artificially been enhanced for illustrative purposes, so they do not reflect the real habitat extent.

Ionian Seas. The few explorations of this long stretch of coast have revealed very rich communities (e.g. Bo et al., 2011, 2012a,b). The south Adriatic coast of Italy is very rich in bioconstructions and *Posidonia*, whereas these are almost absent in the Central Adriatic, characterized by long stretches of sandy coasts and bottoms where mainly *Sabellaria* reefs are present.

Fraschetti et al. (2008) remarked that bioconstructions are original and vulnerable habitats that deserve absolute priority in conservation measures. Bioconstructors, in fact, replace the original geological habitat and become themselves a habitat that, even if they die, remains in place for some time, but loses its most peculiar feature: life. Both the European and the Italian authorities recognize this importance, since both nationally designated MPAs and SCIs designated in Italian waters almost invariably comprise either bioconstructions or *Posidonia* meadows or both.

The importance of some bioconstructions, especially coralligenous ones, is more elusive than that of both tropical and cold water coral formations, where the corals are both the habitat and its benthic component. If corals die, the perception of life disappears. Coralligenous formations, on the contrary, are the habitat for a wealth of spectacular living sponges, cnidarians, bryozoans and ascidians that are not the primary “makers” of the substrate, this role being played by coralline algae and bacterial mats. The “beauty” of coral formations is seen in the corals, whereas the “beauty” of coralligenous formations is seen in what covers the bioconstruction.

The distribution patterns of Italian coastal bioconstructions are quite well known, but many gaps are still to be filled for the deep sea and for some stretches of coast. The state of these formations must be continuously monitored so as to assess their condition and, in case of deterioration, to develop specifically tailored management options, even though they will be probably insufficient if a full understanding of the processes that allow for their persistence is not available. The knowledge of patterns, then, should be upgraded with an improving knowledge of processes, as shown here with connectivity models as a preliminary example.

6. CONCLUSIONS

The basic principle of guidelines to preserve bioconstructions, then, is very simple: impacts affecting them must be identified and removed. This can be straightforward for direct impacts, but global impacts such as climate warming are more difficult to manage. Extensive mass mortalities of important species that grow on coralligenous formations, such as sponges and sea

fans, occurred during periods of deepening of the mixed layer (Rivetti et al., 2014), but the impact on the bioconstructing algae is still poorly known. The avoidance of direct stress on biogenic structures as a result of protection policies leads to healthier habitats that, hopefully, will better respond to global stressors such as warming and acidification.

In the case of impacts that alter the conditions of a given habitat, Jones et al. (2018) suggest two restoration options: passive restoration, i.e., the reestablishment of natural conditions with no further intervention, and removal of impacts; and active restoration that might be attempted if passive restoration does not occur, even if it is difficult to conceive a human driven reestablishment of communities such as coralligenous ones, whose construction requires millennia. For some bioconstructions, however, restoration through transplants (e.g. of colonies of *A. calycularis*) might be a noticeable exception.

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