

Cold-Water Carbonate Bioconstructions

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Abstract Cold-water carbonate bioconstructions are the product of complex interactions between calcifying organisms and the surrounding environment, and deeply contribute in affecting the evolution of the submarine landscape in space and time. Important variables contributing to their development, growth and/or demise include sedimentary dynamics, food supply, physical and chemical characteristics of water masses and local hydrodynamic regimes. Geomorphological studies of bioconstructions are therefore critical in deciphering the physical and biological processes contributing to their development. The aim of this chapter is to summarise the state of the art of geomorphic studies on temperate coralligenous bioconstructions and cold-water coral reefs/mound systems, both representing the two most important and largest carbonate bioconstructions in temperate and deep-sea waters. The importance of these biogenic constructions covers several aspects. They can represent important carbonate factories of the deep sea, archives of past climate and oceanographic conditions and they support increased species diversity and complex biotic interactions with respect to the surrounding seafloor. Because of their remote location (from hundreds to thousands of meters below sea level), only since the last tens of years, technological advances are allowing fine-scale physical and ecological investigations of these bioconstructions, containing ecosystem engineers able to strongly modify the landscape heterogeneity. An increased

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awareness of their potential extension and significance as natural resource, is now steering scientific efforts towards the need to overcome the gaps in knowledge and contribute to prevent their vulnerability to an increasing human pressure.

1 Introduction

Many marine organisms can contribute to the creation, development and maintenance of complex biogenic three dimensional structures, commonly named bioconstructions, which develop through the accretion or accumulation of organogenic deposits, and are able to affect the evolution of the submarine seascape in space and time. From a semantic point of view, “bioconstruction” is a term having a landform connotation as well as a process meaning. Bioconstruction, bioerosion and bio-protection represent biologically mediated components of earth surface processes and constitute the main subjects of bio-geomorphological studies (Naylor 2005). Within the marine realm, bioconstructions are produced all over the submerged environment, from coastal areas to the deep-sea, by different organisms belonging to extremely diverse taxa (bacteria, algae, numerous species of metazoans). Bioconstructions can form through biologically-induced or biologically-controlled calcification, or may result from material bind from other sources (e.g. using organic cement or sediment baffling) or develop from a combination of the two processes (Lowenstam 1981; Riding 2002; Naylor 2005). Plants and animals generally having a calcareous composition create a new hard substrate by skeletal deposition followed by superposition and overgrowing, or adhere to pre-existent hard substrates, and persist as solid elements after their death. Within time, the accumulation of these limy remains may lead to the development of solid and complex constructions which may give rise to relevant landforms, with living communities generating new frameworks over a build-up of cemented skeletal remains of dead organisms (Wood 1999; Riding 2002). The growing dynamics and ecological functioning of building organisms clearly affect the morphological variability of bioconstructions. Sedimentary dynamics, physical and chemical characteristics of water masses and local hydrodynamic regimes (waves and currents) are in most cases critical variables exerting a major control on growth and demise of bioconstructions in space and time. The study of the origin, configuration and evolution of landforms created by bioconstructors requires therefore a strongly multidisciplinary approach to comprehensively understand the links between biotic and physical processes involved in their formation. Furthermore, geomorphological studies are revealing to be critical in deciphering the physical and biological processes that contributed to the development and distribution of bioconstructions. A rich and diverse terminology has been adopted to describe the calcareous biogenic landforms created by sessile organisms. Some of the most adopted terminology does not specifically refer to the natural processes involved in their formation, neither to their composition or structure. This is the case of the terms “concretion” or “build-up” (see Riding 2002 for a deeper analysis and a comprehensive list of references). Others debated definitions are aimed to address the sedimentological, geomorphological and ecological characteristics contributing to

the formation of bioconstructions. This is the case of the term reef. Riding (2002) presented a comprehensive review of the composition and structure of biogenic reefs, occurring at a large variety of scales and depths, drawing the attention to the high diversity and variable sedimentary composition of the reef-forming deposits. Despite classical common definitions of reefs generally being based on the dominant constituent organisms (e.g.: microbial, algal, archaeocyath, stromatoporoid, coral, rudist, etc.—see Table 1 in Cocito 2004), these generally lack a focus on their geomorphic aspect. The term reef refers here to a persistent bioconstructed morphologic framework (generally formed by several interacting organisms) with a clear three dimensional expression, which influences the local sedimentary dynamics and oceanography and supports living benthic communities. Other terms which refer to biogenic-mediated geomorphic features with a distinct shape are banks, originally indicating biogenetic accumulations resulting from baffling and binding processes of benthic organisms (Lowenstam 1950; Klement 1967; Riding 2002), but now largely adopted to generically indicate sub-horizontal biogenic frameworks surrounded by marked breaks of slope, and mounds (Toomey and Finks 1969; Wilson 1975; James and Bourque 1992; Bosence and Bridges 1995; Riding 2002; Roberts et al. 2006; Foubert and Henriet 2009; Rodríguez-Martínez 2011), indicating positive reliefs, from few to hundreds of meters tall, and generally displaying rounded, semicircular, ellipsoid or elongated shapes. Mounds can be composed of a variety of dominant organisms capable of trapping or baffling fine sediments (e.g. cold water corals, bryozoans, polychaetes) and therefore occurring in a variably-composed sedimentary matrix. Mound structures have been recognized in several geological records (Hebbeln and Samankassou 2015), with the oldest features being of early Palaeozoic age (Monty 1995). A rigorous nomenclature explaining the different origin, composition and structure of banks and mounds is in any case still missing, as confirmed by the rich sequence of adopted adjectives (mud-mounds, detrital mounds, carbonate mounds, carbonate mud mound, lime mud mound, microbial mounds, mud-banks, reef mounds, stromatactis mounds, etc.) (see Table 4.2 in Roberts et al. 2009).

Bioconstructions of coastal and shelf seas have been the subject of comprehensive studies since more than a century. Tropical coral reefs, for example, are the most studied bioconstructions on a global scale, mainly owing to the ecological relevance of these large ecosystems, considered among the most important hotspots of marine biodiversity. Tropical corals are able to create entire bio-constructed coastal landforms, several hundreds of kilometres long and hundreds of meters across, whose extension is easily visible in satellite images. These reefs are widely addressed in all basic texts on marine biology, coastal geomorphology and stratigraphy (Wood 1999; Montaggioni and Braithwaite 2009; Woodroff and Webster 2015). Other widely studied coastal and shallow water bioconstructions are found in temperate seas (James and Clarke 1997; Pedley and Carannante 2006). These concretions create complex structures in moderate to strong hydrodynamic regimes, from the coastal intertidal environment to the infralittoral setting, whose deepest limit is marked by a strong decrease of light, insufficient to support the photosynthetic rate of photophilous plants. The dominant coastal temperate bio-constructors are coralline algae such as *Lithophyllum byssoides* (Lamarck) Foslie, vermetid gastropods, other species of coralline algae and several bryozoans,

polychaetes and oysters, able to develop solid and few meters thick calcareous rims, sub-horizontal benches and sporadic reefs along the coastline (Laborel 1987; Relini 2009; Kružić 2013).

The extension and the geomorphological characteristics of important submerged bioconstructions, able to form large reefs and mound structures in partially unexplored deeper environments, have been revealed only over the last 30 years thanks to the availability of seafloor acoustic mapping techniques and the development of scientific Remotely Operated Vehicles (ROV). This is the case for the coralligenous formations and cold-water coral reefs and mounds, the latter developing in a wide depth range, from tens up to a few thousands of meters. The importance of these biogenic constructions covers several aspects. They can represent important carbonate factories of the deep sea (Titschack et al. 2008), and archives of past climate and oceanographic conditions (Frantz et al. 2005; Montagna et al. 2006; Ries 2006; Kamenos et al. 2012; Thierens et al. 2013). They support increased species diversity and complex biotic interactions with respect to the surrounding seafloor.

The aim of this chapter is to summarise the state of the art on geomorphology, distribution and main composition of the temperate coralligenous bioconstructions and cold-water coral reefs/mound systems, representing the two most important and largest carbonate bioconstructions in the deep ocean.

2 Coralligenous Bioconstructions

Coralligenous (C) bioconstructions represent calcareous build-ups of biogenic origin (i.e.: organic frame-reefs; Riding 2002), formed since the Holocene transgression in the Mediterranean, through the multi-stratified accretion in dim light condition of encrusting coralline algae and invertebrate associations (Sartoretto et al. 1996; Ballesteros 2006). They are generally distributed from a few meters (Sarà 1971) down to about 120–150 m water depth, the deepest C occurrence corresponding to the oligotrophic, transparent waters of the Eastern Mediterranean basin (Laubier 1966; Hong 1982; Ballesteros 2006). C produces distinct biogenic reef-like frameworks from few to tens of meters large and up to 4–6 m thick on sub-horizontal seafloors across different depths, or covering hard and complex surfaces along the lower limit of submerged rocky-coast and circalittoral slopes, displaying variable lateral continuity and thickness. C thrives with low to moderate level of nutrient inputs, temperatures from 10 to 23 °C and low to moderate hydrodynamics (Relini 2009), promoting the development of the biogenic framework and limiting the deposition of terrigenous sediments (Morganti et al. 2001; Balata et al. 2006). Low light conditions represent the key parameter that controls the growth of coralline algae in C (Relini 2009). The depth-range of C is therefore variable through the photic zone, since a number of environmental parameters and physical settings determine the total illumination reaching the seafloor. Submarine topography for instance has a significant effect on modulating the seafloor

illumination, since seafloor irregularities (escarpments, overhanging walls, caves, etc.) can create a number of favourable low-light conditions even at shallow depths.

The term Coralligenous (or Coralligène, the original French name) refers to a complex of biocoenoses (C complex) and to the habitat it represents (Laborel 1961). The main dominating communities correspond to calcareous algae (shallower sectors of the bioconstruction), suspension feeders (deeper sectors, cavities and overhangs), borers (inner sectors) and even soft-bottom fauna (within sediments deposited in cavities, depressions and holes) (Fig. 1). The volumetrically most important framework builders in C are calcareous red algae Corallinophycidae (CCA), bryozoans, polychaetes and cnidarians (Laubier 1966; Di Geronimo et al. 2002; Novosel et al. 2004; Cocito 2004; Basso et al. 2007; Ballesteros 2006; Giaccone et al. 2009; Rosso and Sanfilippo 2009). The interplay of biotic and abiotic factors (mainly: light penetration, availability of trophic resources, substrate exposition, sedimentation rate, freshwater influence, biotic interactions) produces several C facies, unevenly distributed along geographical and depth gradients (Pérès 1982; Bellan-Santini et al. 1994, Sartoretto 1994; Canals and Ballesteros 1997; Casellato and Stefanon 2008; Bonacorsi et al. 2012). Ballesteros (2006) provided a first quantification of the number of species (about 1670) forming the coralligenous communities and identified an algal-dominated assemblage in the relatively shallow C, contrasting with an animal-dominated C in the deep. An overview of the environmental factors influencing their development and distribution, illustrating most of the complex biotic relationships and ecological processes that create and destroy the calcareous frameworks was also provided (Ballesteros 2006).

Significant literature has been also produced on the physical/geological characterization of the reef-like structures formed by the coralligenous biocoenoses, including their fossil counterparts (Bosence and Pedley 1982; Carannante and Simone 1996; Rasser 2000; Nelson et al. 2001; Rasser and Piller 2004; Nalin et al. 2006; Bracchi et al. 2016).

First pioneer studies carried out by Johannes Walther (1860–1937, see Ginsburg et al. 1994) and Abel (1961) interestingly outlined a number of similarities between Mediterranean C and Red Sea coral reefs, in terms of structural complexity. As for coral-reefs (and most of bioconstructions), C are indeed complex features in terms of their physical structure, associated biota and the ecological processes they generate (Laubier 1966). Their morphology can reach a high degree of complexity, with rugged surfaces and many cavities and overhangs due to irregular growth of the benthic calcifiers, erosional processes, boring organisms, or a combination of these factors. In these dark crevices and under overhangs the shade-loving assemblages develop, including sponges and, in some cases, the precious red coral *Corallium rubrum*, whose occurrence suggested the name Coralligène (= generating the coral, Marion 1883; Basso et al. 2007; Virgilio et al. 2006; Relini 2009). Space competition among encrusting calcifiers, differential growth rates, cementation, episodes of sedimentation and partial erosion generates through time a significant

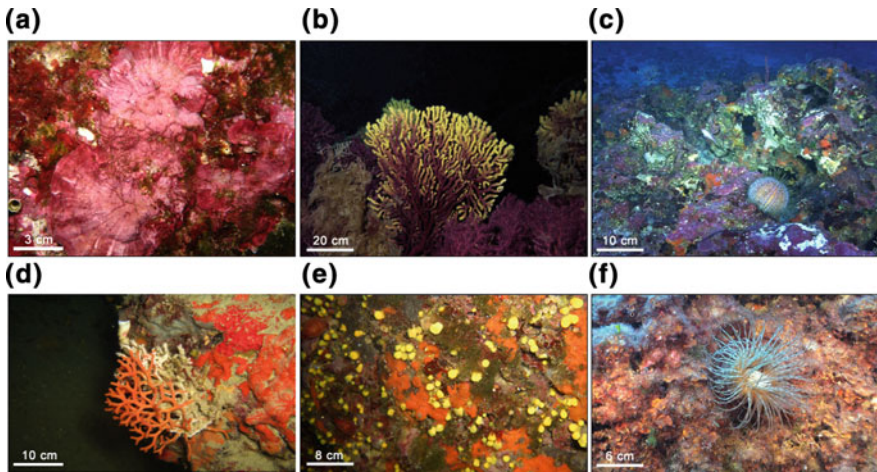


Fig. 1 Characteristic organisms of coralligenous formations. **a** Pink layered/foliose encrusting calcareous red algae growing at the surface of a biogenic substrate (coralligenous). Serpulid tubes also occur; **b** Fan-shaped red to yellow branching colonies of Octocorallia (*Paramuricea clavata*) growing at the top of a coralligenous build-up. The colonies are typically oriented on a plane that is normal to the direction of the main current; **c** Sub-horizontal coralligenous substrate encrusted by various species of purple coralline algae and orange sponges. Note the small branching colonies of the Octocorallia *Eunicella* sp. and the large sea urchin *Echinus melo* feeding on algae; **d** Branching colony of the bryozoan *Pentapora fascialiss* growing on the flank of a coralligenous build-up, where several species of encrusting sponges also occur. One *Halocynthia papillosa* ascidian (sea-squirt) is attached below the *Pentapora* colony and tiny tube-dwelling serpulids grow at its base; **e** *Cerianthus membranaceus* (Anthozoa) on coralligenous substrate covered by coralline red algae and *Peyssonnelia* spp.; **f** Overhanging surface of coralligenous substrate bordering a submarine cave, encrusted by numerous solitary corals (the yellow Scleractinia *Leptopsammia pruvoti*), the ascidians *H. papillosa*, sponges and algae. Photos courtesy of F. Mastrorotaro

structural complexity and environmental heterogeneity (Jones et al. 1994), which in turn controls the distribution and abundance of coexisting species, and increasing the C habitat biodiversity.

2.1 Geomorphology of Coralligenous Bioconstructions

The extent to which the C biota can modify the submarine environment, affecting the evolution of submerged landforms is extremely variable. C can cover and drape quite homogeneously the pre-existing hard substrate enhancing its topographic complexity, or produce new distinct geomorphic features on the seafloor, of variable shapes and dimensions, that characterize the seascape in wide areas of the continental shelf. A precise description of their 3D morphological development and extension is however often overlooked. In literature C formations are generally indicated as reefs, concretions, frameworks, build-ups, pillars, outcrops, but they

still lack a detailed systematic classification of morphotypes and associated processes, since the drivers that control their differentiation have been poorly investigated (Bracchi et al. 2015, 2016; Doxa et al. 2016).

A first attempt of showing the relevance of C in marine geomorphological research has been provided by Laborel (1961), with the description of five coralligenous types: cave and overhang concretions, wall concretions, concretions at the base of submarine walls, concretions over flat rocky surfaces and platform coralligenous assemblages. These types were distinguished according to their position and exposure to light penetration along an almost steep coastal belt and submerged shelf and the type of substrate on which they grow. Pérès and Picard (1951, 1964) introduced the term “coralligène de plateau” to describe C settled on a coarse bioclastic sub-horizontal bottom and originated from the coalescence of algal concretions (rhodoliths; Bosellini and Ginsburg 1971; Nalin et al. 2006), distinguishing this type of C from the one growing on sloping and complex rocky surfaces. Following Pérès and Picard (1964), most authors indicate C as *banks* when they develop on flat bottoms (e.g.: coralligène de plateau), whereas the term *rim* is used to refer to those lips and rims growing on sub-vertical substrates (e.g.: cliffs or slopes in the circalittoral), and also occurring at the opening of submarine caves (Laborel 1987; Ballesteros 2006). These authors thus introduced a first “geomorphological” classification, trying to merge two different criteria to distinguish C: the “morphology” and the “genesis”, this latter related to the type of substrate on which C develops. However, in several cases the genesis of banks is not related to the coralligène de plateau, and on the other hand, a vertical C structure could develop with no need of an underlying cliff (Basso et al. 2007; Bracchi et al. 2015).

Both coralligenous rims and coralligenous banks vary considerably in their 3D morphological development, showing a wide range of morphotypes (Fig. 2). Rims may be poorly developed or grow to extreme sizes reaching widths of more than 3 m (Laborel 1987; Ballesteros 2006). They can be single or multiple features and may set up at regular or irregular intervals. Rocky vertical or sub-vertical walls, which can be found along the open shelf or in submerged caves, represent the typical settings for the development of coralligenous rims (Laborel 1987).

When forming banks, C generally occurs in groups rather than as isolated structures. A rich descriptive terminology (e.g.: heads, blocks, vertical pillars, columns, ridges etc.) has been used to refer to the variety of morphotypes they can develop and since the availability of advanced hydro-acoustic mapping systems (such as MB swath bathymetry) calibrated by visual systems such as ROV and drop cameras, research on the geomorphology of submerged bioconstructions has advanced (Figs. 1 and 2). Bracchi et al. (2015) described the morphological diversity across and between individual C structures, mainly featured in columns and ridges and covering more than 436 km² of the whole Apulian continental shelf, in the southern-central Mediterranean (Campiani et al. 2014). The proposed classification can be considered descriptive, since it is based on the C morphological aspects, whereas the interpretation of genetic relationships and processes between C and substrata are on purpose not explored. According to Bracchi et al. (2015) ridges

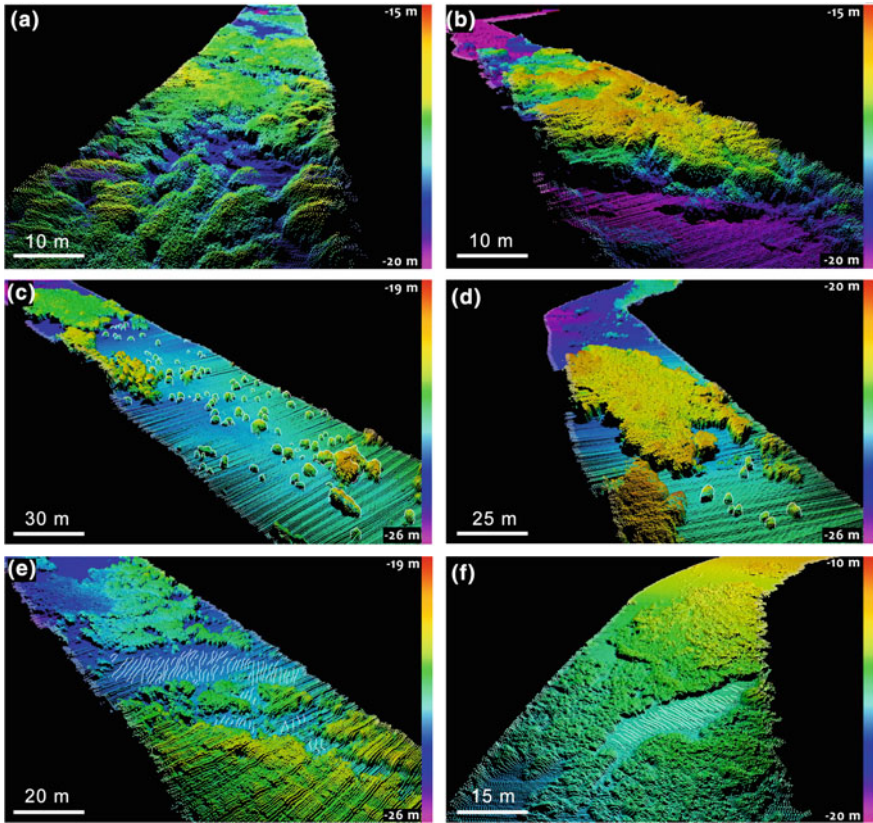


Fig. 2 Multibeam point data acquired along different continental shelf regions of the Mediterranean. **a** Large continuous coralligenous bioconstructions showing an almost flat top with a typical bumpy aspect; **b** Edge of a large coralligenous bioconstruction, rising almost 5 m from a flat seafloor, with a rugged and pitted surface and vertical to stepped, irregular boundaries; **c** Single isolated coralligenous bioconstructions (smaller are roughly 1 m large and no more than 1 m high), distributed along a flat seafloor. Larger coralligenous bioconstructions with distinct boundaries are visible at the end of the multibeam line; **d** Large (ca. 40 m wide) coralligenous bioconstructions rising from 1 to 2 m from the seafloor, with a flat surface and distinct vertical boundaries. Minor isolated coralligenous bioconstructions (ca. 1 m large and no more than 1 m high) are also visible on the *right*; **e** Large coralligenous bioconstructions (more than 40 m wide and from 1 to 2 m high) with indistinct boundaries and separated by a channel. Note the subaqueous dunes documenting the action of unidirectional bottom currents; **f** Coralligenous bioconstructions with internal sediment patches where subaqueous dunes are visible

can reach lateral extensions of tens of meters with heights ranging between 2 and 5 m. Columns represent more distinct features on the seafloor, which may occur in clusters or be isolated, often in association with *Posidonia oceanica* meadows, or with coarse detritic sediments. In most cases, the action of bottom currents and low sedimentation rates seem to represent favourable conditions, which promote

coralligenous development instead of the deposition of terrigenous sediments. Bedforms documenting the action of unidirectional bottom currents are often mapped along the edges of bioconstructions and between them, where sediments and detritic sediment accumulate within the more depressed areas (Fig. 2). Coralligenous atolls, with a radius ranging from 20 to 30 m, have been recently mapped offshore northern Cap Corse (Bonacorsi et al. 2012), northern Mediterranean, between 106 and 112 m water depth. These features form a circular crown structure (made up of coralligenous bioconstructions combined with praline rhodoliths and many invertebrates) with a central core formed by a rounded C formation up to 3 m wide and 0.5 m high (Bonacorsi et al. 2012) surrounded by soft sediments. Similar morphologies have never been observed in other locations, likely owing to the lack of extensive high-resolution acoustic mapping of the (Mediterranean) seafloor, specifically below 50 m of water depth. The shape of these unique and peculiar features has been related to external inherited processes responsible for the initial creation of hard substrates (i.e. gas venting associated to pockmark formation—see Chapter “Cold Seep Systems”).

Despite the lack of a comprehensive investigation on the role of Quaternary geomorphic processes on the C distribution and growing processes, the inherited geomorphic landscape of the seafloor likely plays a fundamental role affecting the morphological diversity of C. A quite good documentation exists on the relevance of some major environmental parameters such as slope, current exposure, water transparency, temperature and sedimentation in controlling the differentiation in coralligenous biocoenoses. Nevertheless, most research lacks the investigation of the relationships between the variability of the framework morphologies and changes in the associated biological community and parameters. Some authors documented how the observed differentiation in shape and dimension of C is often inherited from the morphology of the hard substrates that allowed the settlement and growth of coralline algae. Most of them are represented by continental shelf rocky outcrops (Bracchi et al. 2015, 2016) and/or modified relic morphologies originated during previous low-stand or transgressive stages of the sea level (e.g. beach-rocks, sediment bars, etc. Navone et al. 1992) and located in areas subject to low sedimentation rate. After the initial settlement of coralline algae and during the time of coralligenous development, rising in sea-level caused changes in hydrodynamic regime, sediment input and light penetration. The interplay of these ecological controls influenced different growth rates of benthic calcifiers and the development dynamics of C, in turn affecting its 3D morphology (Pèrès and Picard 1951, 1964; Sartoretto et al. 1996; Di Geronimo et al. 2005; Nalin et al. 2006; Bracchi et al. 2016).

C formations were thus affected by Mediterranean sea-level oscillations during the Quaternary. Since the present-day C depth distribution coarsely corresponds to that portion of seafloor that was emerged during the last glacial maximum, the build-up of C must have occurred during the last transgression. Investigations in the north-western Mediterranean provided evidence that circalittoral C formed mostly in the early Holocene (from about 8.5 kyrs BP) at a paleodepth not greater than 10–15 m and with a maximum accumulation rate (about 0.83 mm y^{-1}) between 5 and 8

kyrs BP (Sartoretto et al. 1996). After that period a decrease in accumulation rate (about 0.006 mm y^{-1} or nil) has been documented for C deeper than 50 m of water depth, suggesting that significant accumulation rates presently occur only at shallow water depth (Sartoretto 1994; Sartoretto et al. 1996; Ballesteros 2006).

2.2 *Coralligenous Distribution*

C is common in the whole Mediterranean Sea, although the bioconstructions seem to be more abundant in the Adriatic, Aegean and Tyrrhenian Seas and in the Algero-Provençal Basin. A much lower number of occurrences have been reported for the Levantine Sea and Tunisian Plateau/Gulf of Sidra (Martin et al. 2014), although lack of reports of C at any particular site does not necessarily imply their absence, especially for the deep circalittoral, which has not been fully investigated by acoustic mapping and ground truthing (i.e.: video inspections). For the same reason, most of the C occurrences reported in literature are located between 10 and 50 water depth, while less information exists for the deeper sites (50–150 m). Several efforts have been promoted in order to fill these gaps (Campiani et al. 2014), although insufficient data are still available on the regional distribution of C across the whole Mediterranean Sea. The only available quantitative information on C extension actually corresponds to the Apulian continental shelf, where a total surface of 436 km^2 of seafloor is covered by coralligenous habitats (Campiani et al. 2014).

A tentative large-scale assessment of the predicted distribution of C on a basin scale has been modelled on the basis of existing records of a total 2763.4 km^2 of Mediterranean C (Martin et al. 2014). Bathymetry, slope of the seafloor and nutrient input were the three main contributors to the model (combined contribution of 84.1%), whilst the remaining three predictors (euphotic depth, phosphate concentration and geostrophic velocity of sea surface current) had a minor contribution. Unfortunately, the resulting model has a weak support by direct observations and published data. Considering the available polygon data and their associated surface areas, it is estimated that as much as 95% of coralligenous habitat may still need to be mapped across the Mediterranean basin, especially in deeper areas (Martin et al. 2014).

3 Cold-Water Coral Reefs and Carbonate Mounds

3.1 *Cold Water Corals and Physical Habitats*

Corals are marine animals belonging to the phylum Cnidaria, a large and complex taxonomic group. According to Cairns (2007) the generic term “coral” includes all cnidarians belonging to the classes Anthozoa and Hydrozoa that produce calcium

carbonate secretions. This definition encompasses over 5000 colonial and solitary species, ranging from stony corals (or true corals), provided with continuous carbonate exo- or endoskeletons (e.g. Scleractinia, Stylasteridae, Coralliidae), to soft corals (most Alcyonacea) formed by organic tissues and secondarily by microscopic biomineralised sclerites. Among the stony corals, able to build a hard carbonatic skeleton, there are some species known as “framework building” corals, owing to their ability to form complex three-dimensional carbonate structures, providing shelter and resources for a wide range of organisms. Most framework-building corals belong to the order Scleractinia and produce aragonite skeletons. Over 95% of them (around 765 species) consists of zooxanthellate species (Roberts et al. 2009) that live in warm, shallow and oligotrophic waters and contribute to the formation of colourful and diverse tropical reefs through photosynthetic processes of symbiotic algae. Very few species of framework building corals are azooxanthellate (18), i.e. they lack symbiotic dinoflagellates, 17 of them thriving in cold and generally deep waters. The latter are generally defined as stony “cold-water corals” (CWC) and, unlike tropical corals, they do not require the occurrence of light neither of warm and shallow waters. They cover a wide range of depths (39–3000 m) and latitudes (70°N–60°S) and feed on organic particles and organisms advected by water masses. CWC bioconstructions therefore develop where oceanography plays an important role in food transport processes (Mienis et al. 2014). Recent studies suggest a coupling between the CWC reef fauna and the surface productivity in relation to the local hydrography and sedimentary dynamics (Mienis et al. 2014; Mohn et al. 2014; Moreno Navas et al. 2014).

The most common framework building cold water corals are *Lophelia pertusa* and *Madrepora oculata*, observed worldwide, with larger occurrence in the North Atlantic and Mediterranean waters (Roberts et al. 2009). *L. pertusa* and *M. oculata* are most commonly observed in waters between 7 and 10 °C although they are able to tolerate a wider temperature range, between 4 and 15 °C (Brooke et al. 2013; Naumann et al. 2014) (Fig. 3). These species have been found on a depth range from tens of meters up to 1500/2000 m (Zibrowius 1980), and along different physiographic and geomorphologic settings. Other CWC species able to create bioconstructions are *Solenosmilia variabilis*, *Enallopsammia profunda*, *Oculina varicosa* and *Goniocorella dumosa* (Roberts et al. 2006; Hebbeln et al. 2016).

The occurrence of hard substrates on which coral colonies can start to settle is probably the most relevant pre-requisite for CWC bioconstructions to grow. However, oceanographic forcing and food input also represent key environmental variables for their survival (Duineveld et al. 2004, 2007; Van Oevelen et al. 2009). Suitable environments for cold-water coral settlement are regions where the interaction between large scale seafloor morphology and water mass dynamics (bottom currents, internal waves controlled by tides or density interfaces) create moderate to strong hydrodynamics and turbulent mixing, coupled with reduced terrigenous input and a constant delivery of organic matter. These settings generally coincide with outer shelf/upper slope regions (Thiem et al. 2006; Dullo et al. 2008), fjords (Freiwald et al. 2004; Försterra et al. 2005), seamounts (De Vogelaere et al., 2005; Tracey et al., 2011), landslides (De Mol et al. 2009; Lo Iacono et al. 2014a;

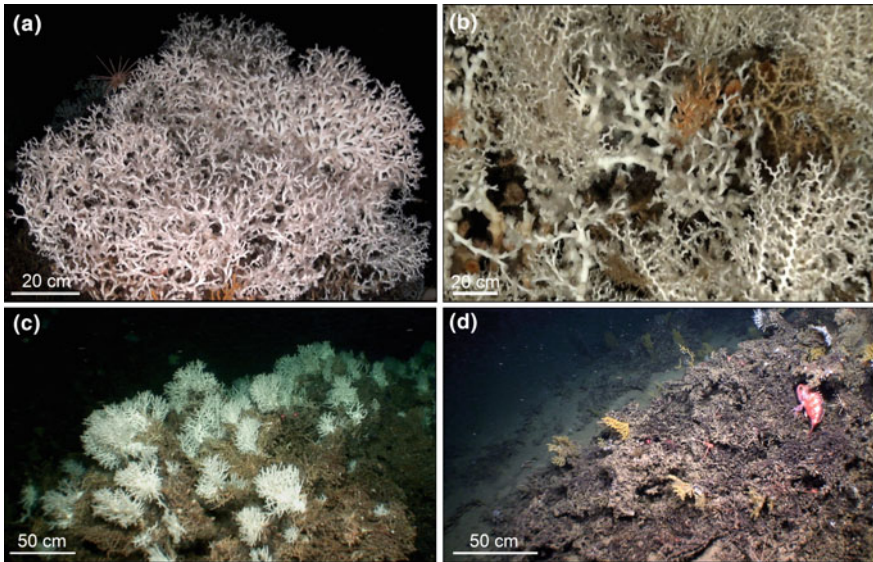


Fig. 3 Dominant species of a CWC reef. **a** A colony of *Lophelia pertusa*; **b** *L. pertusa*, white and pink *M. oculata*; **c** CWC reef with living colonies of *Madrepora oculata*; **d** CWC reef with dead frameworks of *L. pertusa* and living colonies of the gorgonian *Acanthogorgia hirsuta*. Photos in (a) and (b): © Oceana

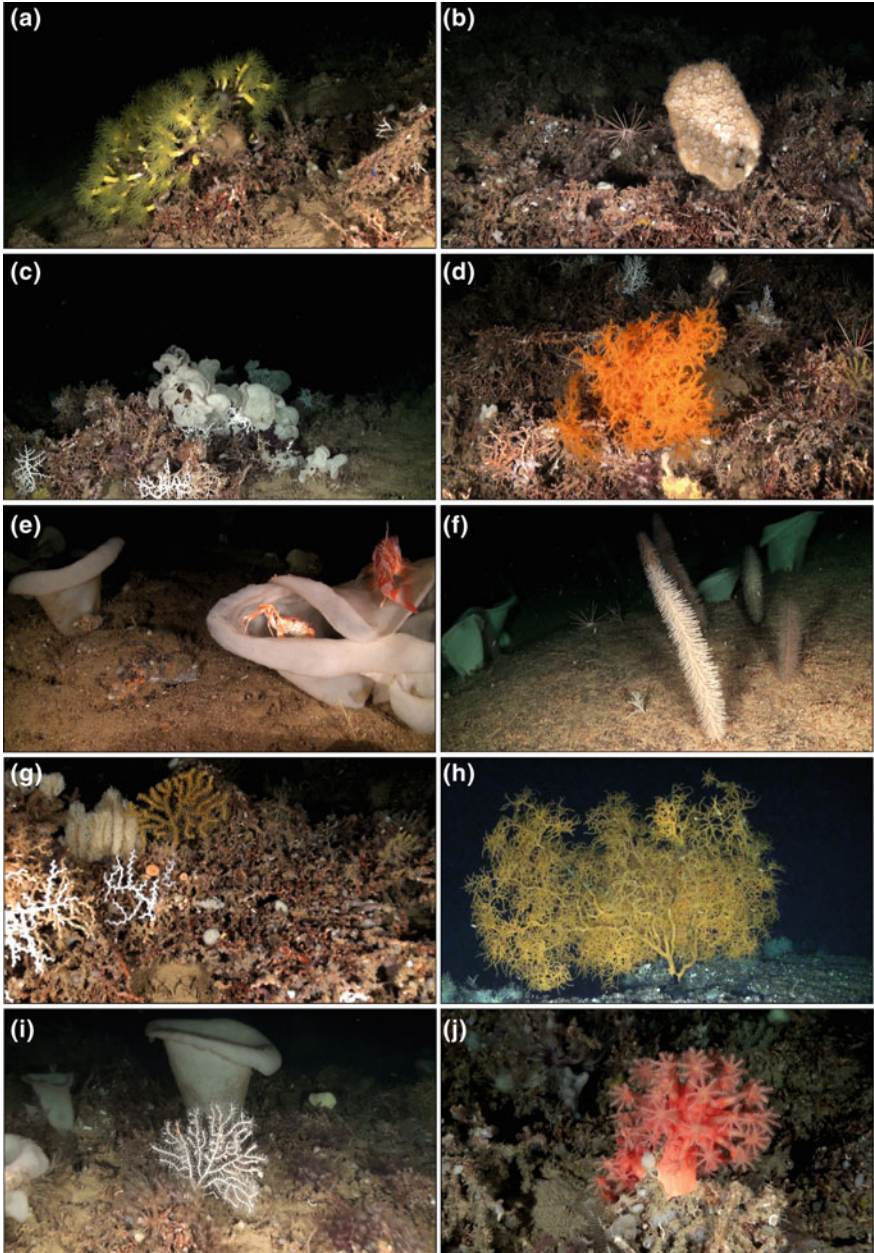
Savini et al. 2016), canyons (Orejas et al. 2009; Huvenne et al. 2011; Gori et al. 2013) and ocean gateways (Lo Iacono et al. 2014b; Lo Iacono et al. 2016). CWC are often observed along outer shelves and fjords of sub-polar and high latitude regions, settling on iceberg plough-marks and other erosive features produced during the last glacial cycle (Freiwald et al. 1999, 2002; Lindberg et al. 2007). Along the open slope, substrates providing suitable habitats for CWC settlement generally coincide with abrupt geomorphologies inherited from previous geologic events, such as landslides or fault scarps (Fosså et al. 2002; Colman et al. 2005; De Mol et al. 2009; Lo Iacono et al. 2014a; Savini et al. 2016). Following a feedback mechanism, the complex terrain of these settings enhances moderate to strong hydrodynamics, in turn maintaining exposed morphologies and low sedimentation rates along the CWC reefs. Steep or vertical walls of submarine canyons flushing organic-rich sediments to the deep-sea are also suitable habitats for CWC. The abrupt morphology and complex terrains of canyons naturally protect benthic ecosystems from the impact of destructive trawl fishing, taking a strategic role in designing new strategies for the conservation of natural resources (Orejas et al. 2009; Huvenne et al. 2011). Finally, seamounts and volcanic banks are prominent topographic highs, able to increase the upwelling of nutrient-rich waters resulting in a remarkable diversity and richness of fish and benthic fauna, including CWC (Genin et al. 1986; Duineveld et al. 2004; Rogers et al. 2007).

3.2 Cold Water Coral Reefs

If suitable environmental conditions (temperature, salinity, dissolved oxygen and pH values, turbulent current regimes and food availability) persist in time, framework building CWC are able to form extensive and complex carbonate reefs. CWC reefs develop in a delicate interplay between coral growth and bioerosion processes, giving rise to a complex ecosystem consisting of live coral colonies trapping and baffling suspended fine sediments, interspersed with dead reef framework, coral rubble and bioturbated sandy muds (Freiwald et al. 2004; Roberts et al. 2009), where other organisms (gorgonians, anthipatarians, sponges, polychaetes, molluscs, crustaceans, bryozoans, echinoderms, cirripeds and brachiopods) also contribute to the carbonate build-up (Fig. 4).

When unidirectional bottom currents prevail, the most pronounced geomorphic features along reefs generally correspond to ridge-like elongated reliefs, or “cigar shaped” reefs, few to hundreds of meters long, whose orientation is generally controlled by the main current patterns and where different sectors generally correspond to distinct habitats (Freiwald et al. 2002; Buhl-Mortensen and Lepland 2007; Buhl-Mortensen et al. 2016a). The specific dominance of living coral communities decreases from the head to the tail of the reef along the current direction, in parallel with an increase of dead framework and coral rubble supporting higher biodiversity (Fig. 6 in Buhl-Mortensen and Lepland 2007 and Fig. 8 in Freiwald et al. 2004). The generally asymmetric geomorphology of the reef and the orientation of the living colonies facing the bottom currents along its front may indicate a migration of the reef against the direction of local currents, which generally range between 5 and 20 cm s⁻¹ (Buhl-Mortensen et al. 2016a), suggesting these features as dynamic geomorphic elements developing under an interacting mechanism between coral growth rates and hydrodynamic regimes.

The most thriving reefs mapped until the present are located along the western Norwegian (Sula and Røst reefs) and Scottish margins (Mingulay reef) within a depth range of 30–450 m, and are mainly dominated by *Lophelia pertusa* communities (Freiwald et al. 2002; Roberts et al. 2005, 2009). More than 370 species associated to CWC bioconstructions are reported from the Mingulay reef and more than 1100 from the Norwegian reefs (Freiwald et al. 2002). The Norwegian Røst Reef, the world’s largest known cold-water coral reef, has a length of about 35 km, a width of up to 2.8 km and is around 35 m thick (Fosså et al. 2005), probably developed through merging processes of several single reefs. Uranium/Thorium dating indicates that many of the Norwegian reefs started to develop around 9 kyr BP, during the sea level rise of the last glacioeustatic cycle (Rokoengen and Østmo 1985; Buhl-Mortensen 2000). Morphometric analyses suggest a linear relationship between reef height and width, with their width being two to five times larger than their height (Buhl-Mortensen et al. 2001). Despite possible hiatuses and demise stages, vertical reef accretion rates for the Norwegian margin are estimated to be around 1.2 mm y⁻¹ (Buhl-Mortensen 2000).



◀**Fig. 4** Examples of accompanying species in habitat forming CWC reefs. **a** *Dendrophyllia cornigera*. **b** Sea urchin *Cidaris cidras* and an unidentified sponge, **c** Sponge *Pachastrella molinifera* and living colonies of *M. oculata*. **d** The black coral *Leiopathes glaberrima* and the gorgonian *Acanthogorgia hirsuta* (along the *right side*). **e** The sponge *Asconema setubalense*, the fish *Helicolenus dactylopterus*, the crab *Bathynectes* sp. **f** The black coral *Parantipathes larix* and the sponges *Asconema setubalense*. **g** The gorgonian *Acanthogorgia hirsuta*, an unidentified sponge and living colonies of *Madrepora oculata*. **h** The black coral *Leiopathes glaberrima*. **i** The gorgonian *Villogorgia bebrycoides* and the sponge *Asconema setubalense*. **j** The cnidarian *Anthomastus grandiflorus*. *Photos* © Oceana

3.3 Development of Cold Water Coral Reefs and Mounds

A key characteristic for reef development both in space and time is the cyclic alternation between reef growth, bioerosion and sediment accumulation. Corals can gradually form coalescing thickets (Squires 1964) starting from small isolated colonies, owing to their *capability to form* extensive skeletal carbonate structures. Subsequently, passing through the stage of coral coppice (Squires 1964), they may give rise to CWC reefs, displaying a complex 3D structure and reaching dimension of up to hundreds of meters. Wilson (1979) presented a pioneering work on the spatial development of a reef. According to this model, different stages of coral growth give rise to a progressive outwards expansion of the bioconstruction, where colonies are spatially organized in concentric rings, named “Wilson rings” (Fig. 3 in Wilson 1979). This process of reef generation starts when small and adjacent coral patches nucleate around an initial coral colony (“ticket stage” of the reef development). During the following coral coppice stage, an increased production of coral rubble through bioerosion processes provides new available substrate for the growth of young colonies along the external border and within the innermost regions of the bioconstruction, which gradually become a complex 3D reef structure, where the amount of dead corals and coral debris by far exceeds the number of living colonies (Wilson 1979; Roberts et al. 2009). Actual models consider the cyclic alternation of distinct environmental stages as the most important factor for reef development in time. Changing environmental conditions induce crucial shifts in the dominating processes along the reef including oceanographic and sedimentary regimes, physical/chemical processes, biodiversity and species composition (Roberts et al. 2009; Douarin et al. 2009). After an initial settlement of colonies on hard substrates, a following expansion of coral frameworks coincides with suitable environmental conditions persisting in time, during which sediments trapped and baffled by thriving corals constitute an important structural component of the reef (Dorschel et al. 2007; Frank et al. 2009; Douarin et al. 2009). A general demise stage of living reefs occurs during the transition towards less suitable environmental conditions (e.g.: changing temperature, decreased food supply and productivity), bringing the start of coral collapse and increased production of coral debris and associated fauna. A consequent decrease of the reef seafloor complexity reduces the hydrodynamic regimes at the bottom and may increase the hemipelagic sediment accumulation (Douarin et al. 2009).

Within tens to hundreds of thousands of years, the alternation of suitable and unsuitable environmental conditions along reefs generally corresponds to cyclic interchanges between dominance of coral growth (thriving stages of the reefs) and fine sediment accumulation (demise stages). These long scale variations, generally related to the Quaternary glacioeustatic oscillations and associated changes in oceanographic conditions (Dorschel et al. 2005; Roberts et al. 2006, 2009), can give origin to pronounced morphologies defined as Cold-Water Coral mounds, forming through several cycles of reef development and representing sensitive carbonatic archives of past climatic and oceanographic changes (Kano et al. 2007; Raddatz et al. 2011; Fink et al. 2013; Thierens et al. 2013). CWC mounds correspond to positive reliefs generally occurring in clusters or as isolated features, distributed across a depth range of 70–1200 m and whose geomorphology corresponds to semi-circular, conical, tear-drop or linear ridge-like shapes (Kenyon et al. 2003; Masson et al. 2003; Van Rooij et al. 2003; van Weering et al. 2003; Huvenne et al. 2009; Lo Iacono et al. 2014a, b) (Fig. 5).

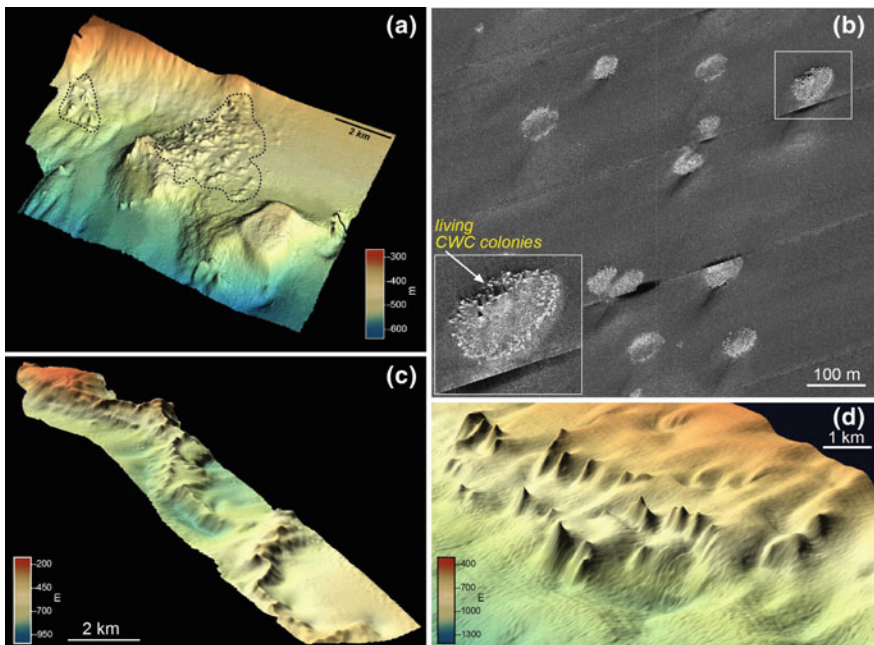
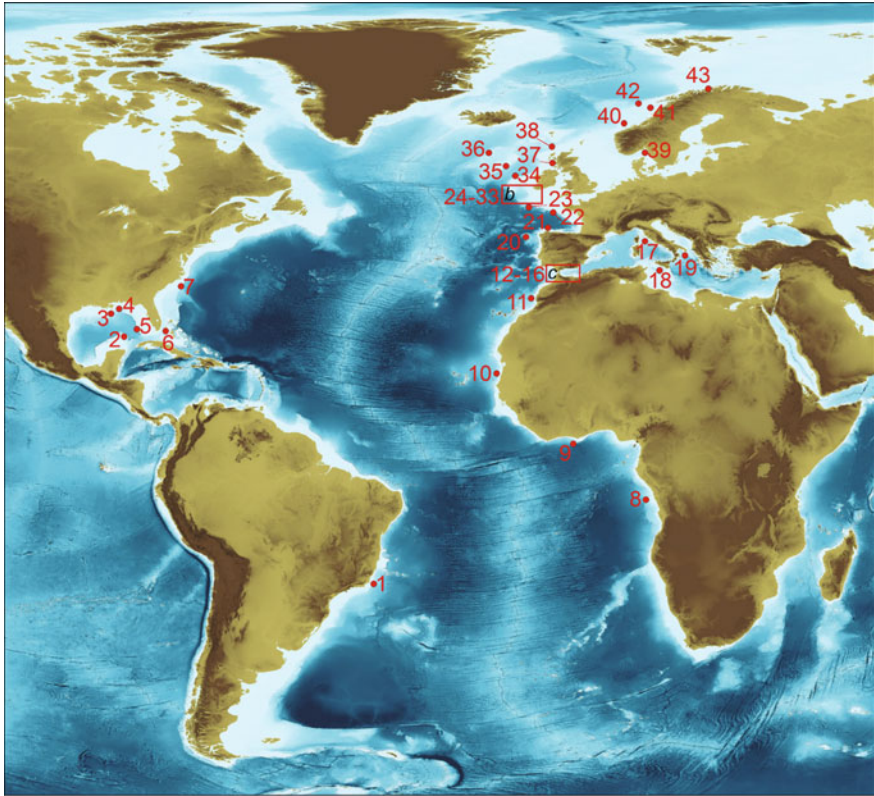


Fig. 5 **a** MB 3D model showing the two clusters of the West Melilla CWC mounds (max 45 m tall), Alboran Sea, Western Mediterranean. The larger cluster developed on a buried submarine landslide, as suggested by its lobular shape (see Lo Iacono et al. 2014a); **b** side-scan snar mosaic showing the elliptical Darwin CWC mounds (Eastern Atlantic). The *inset* highlights the sharp and contrasting acoustic facies associated to living CWC colonies (see Huvenne et al. 2009; Victorero-Gonzalez et al. 2016); **c** MB 3D model showing the linear CWC Cabliers mound system, Alboran Sea, Western Mediterranean, developed on a volcanic substrate. Note the deep incised erosive moat along the base of the mound (see also Lo Iacono et al. 2014b); **d** MB 3D model showing the circular Magellan mounds, eastern Atlantic (data from GSI—INFOMAR Project)

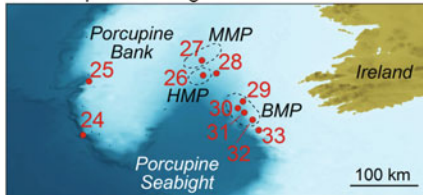
The height of cold-water coral mounds can vary from a few meters to up to hundreds of meters whereas the width of their base can reach hundreds of meters for sub-circular shapes to up to few tens of kilometres for linear features. Geo-acoustic mapping of such important geomorphic features has unveiled hundreds of CWC mound fields, mainly spread along the NE and NW Atlantic margins and the central-western Mediterranean (Fig. 6), where they deeply affect the present-day seascape configuration. The largest mounds, observed along the North East region of the Atlantic Sea (Irish Margin, Porcupine Seabight and Rockall Trough) are also defined as Giant Mounds. These features can reach dimensions of up to 350 m high and few kilometres wide (Kenyon et al. 2003; Mienis et al. 2007) and correspond to carbonate factories reaching back to Pliocene times (2.6 Ma; Kano et al. 2007). However, recent studies revealing the existence of new large mound fields along the western African margin reinforce the need for further mapping expedition along less known areas. Interestingly, the large-scale distribution patterns of mounds coincide in most cases with the boundaries between prominent water masses in the Atlantic and developed close to prominent density interfaces, once more suggesting the primary role of the oceanography in the development and maintenance processes of CWC ecosystems.

Living reefs and coral assemblages are generally observed along and around the top of the mounds, coinciding with increased rugosity values of the seafloor (Guinan et al. 2009). The flanks of the mounds, that can reach steep slope gradients, are smoother and commonly characterized by dead coral framework, coral rubble and fine sediments, sometimes transported to deeper depths through the action of gravitational processes, reflected in small down flank organogenic sedimentary trails and lobes (Roberts et al. 2005). The elevated morphology of mounds, protruding into the water column, creates topographic obstacles, which steer the intensity and direction of bottom currents, in turn contributing in maintaining and enhancing their shapes. Fine grained deposits can be observed along the lee sides of mounds, sheltered from dominant bottom currents and extending from few to hundreds of meters, whereas large sediment wave fields composed of coarse coral debris can be found along the inter-mound areas, more exposed to the action of vigorous hydrodynamics (Kenyon et al. 2003; Huvenne et al. 2009). However, these processes are still poorly understood at small spatial scales (meters to tens of meters), mainly owing to the paucity of high resolution morpho-sedimentary models and oceanographic records, allowing to observe these interactions at the spatial scales they occur.

Elongated mounds extending for up to tens of kilometres have often been observed above tectonic trusts or linear volcanic ridges (Lo Iacono et al. 2014b) and related to the action of unidirectional bottom currents (Messing et al. 1990; Correa et al. 2012; Hebbeln et al. 2014). Unidirectional currents flowing along linear geomorphic features (tectonic ridges, shelf margins) probably contribute in merging adjacent sub-circular isolated mounds in longer linear coalescent systems (Eisele et al. 2014; Buhl-Mortensen et al. 2016b). Supporting this observation, a global pyramidal distribution of mound dimensions shows several small mounds compared to few larger features (Huvenne et al. 2003; Roberts et al. 2009).



b: Porcupine Seabight



c: Alboran Sea



The erosive action of strong bottom currents, enhanced by the morphology of the mound itself, can generate tens of meters deep and hundreds of meters wide linear scoured depressions along the bases of mounds, defined as “moats” Esentia et al. (2018). These erosive features are generally associated with “contourite drifts”, corresponding to elongated sedimentary deposits with variable size and thickness developing under moderate to strong persistent current regimes (Van Rooij et al. 2003; Hebbeln et al. 2016; Esentia et al. 2018). The side by side development of contouritic systems and CWC mounds suggests a complex interaction between transport of organic and clastic sediments under moderate to strong hydrodynamic regimes and the development of these prominent bioconstructions. As for the CWC

◀**Fig. 6** Distribution map of the largest CWC mounds and living reefs along the Atlantic margins and the Mediterranean Sea. 1 Campos Basin Mounds—Lopes and Hajdu (2014), 2 Campeche Mounds—Hebbeln et al. (2014), 3 Gulf of Mexico Mounds—Georgian et al. (2016), 4 Visca Knoll Mounds—Brooke and Schroeder (2007), 5 West Florida Mounds—Neumann et al. (1977), 6 Florida Mounds—Grasmueck et al. (2006), 7 Cape Lookout Mounds—Mienis et al. (2014), 8 Angola Mini Mounds—Le Guilloux et al. (2009), 9 Ghana Mounds—Buhl-Mortensen et al. (2016b), 10 Banda Mounds—Eisele et al. (2014), 11 Eugen Seibold Mounds—Glogowski et al. (2015), 12 Pen Duick Mounds—Van Roij et al. (2011), 13 West Melilla Mounds—Lo Iacono et al. (2014a), 14 East Melilla Mounds—Fink et al. (2013), 15 Cabliers Mound—Lo Iacono et al. (2014b), 16 Chella Mound—Lo Iacono et al. (2018), 17 Tuscan Archipelago Mounds—Remia and Taviani (2005), 18 Pantelleria Mounds—Martorelli et al. (2011), 19 Santa Maria di Leuca Mounds—Savini et al. (2014), 20 Breoghan Mounds—Somoza et al. (2014), 21 Ferrol and Coruña Canyon mini Mounds—unpublished, 22 Penmarc'h and Guilvinec mini Mounds—De Mol et al. (2011), 23 Explorer and Dangeard mini Mounds—Stewart et al. (2014), 24 Arc Mounds—Mohn et al. (2014), 25 Porcupine Bank Canyon Mounds—Mazzini et al. (2012), 26 Hovland Mounds—Hovland et al. (1994), 27 Magellan Mounds—Hovland et al. (1994), 28 Viking Mounds—Foubert et al. (2011), 29 Galway Mounds—Dorschel et al. (2007), 30 Therese Mounds—De Mol et al. (2007), 31 Challenger Mound—Kano et al. (2007), 32 Macnas Mounds—Wilson et al. (2007), 33 Enya Mounds—Van Rooij et al. (2009), 34 Pelagia Mounds—Kenyon et al. (2003), 35 Logachev Mounds—Kenyon et al. (2003), 36 Francken Mounds—Wienberg et al. (2008), 37 Mingulay Mounds—Roberts et al. (2005), 38 Darwin Mounds—Masson et al. (2003), 39 Tisler Reef—Wild et al. (2009), 40 Sula Reef—Freiwald et al. (2002), 41 Traena Reef/Mounds—Lindberg (2004), 42 Røst Reef—Freiwald et al. (2004), 43 Stjærnsund Reef/Mounds—Freiwald et al. (1997). *MMP* Magellan Mound Province (Hovland et al. 1994); *HMP* Hovland Mound Province (Hovland et al. 1994); *BMP* Belgica Mound Province (Henriet et al. 1998)

mounds, the sedimentary records of contouritic drifts are controlled by regional changes of sedimentary regimes controlled by past glacioeustatic changes (Hernández-Molina et al. 2014).

4 Biodiversity of Deep-Sea Bioconstructions: Environmental Issues, Management Strategies and Future Perspectives

CWC reefs and mounds and coralligenous bioconstructions are considered hotspots of biodiversity in the deep marine realm, contributing to regulate the dynamics of natural resources in the ocean, including fish stocks of economic importance (Guidetti et al. 2002, Salomidi et al. 2012, Paoli et al. 2016, Tribot et al. 2016 Roberts et al. 2009 and references therein). They have been declared as sensitive and vulnerable marine ecosystems by national and international legislations and are actually included in the list of endangered habitats by governmental organizations and conservation agencies (OSPAR 2008) (red list habitats).

CWC reefs for instance, serve as important spawning, nursery, feeding and refuge areas for a multitude of fishes and invertebrates (Fosså et al. 2002; Husebø et al. 2002; Colman et al. 2005; Stone 2006; Ross and Quattrini 2007; Baillon et al. 2012; Henry et al. 2013). Diversity within these reefs has been found to be orders of

magnitude higher than the surrounding seafloor, in some case rivalling shallow-water reefs (Rogers 1999; Henry and Roberts 2007). Their rough morphology, made up of crevices cavities and small build-ups, provides habitats for several other species. Norwegian authorities and EU have introduced regulations to ban destructive bottom trawling activities along such vulnerable ecosystems (Fosså and Skjoldal 2010), assigning to Norway the largest European deep-sea area protected from the threat of industrial activities.

Despite their relevant role in marine ecosystems and ocean biodiversity, the existence and conservation of these benthic communities is being seriously compromised by human-related activities. The physico-chemical perturbations caused by the increasing emissions of CO₂, such as the increasing temperature and the decreasing pH (i.e. ocean acidification), have a negative impact on the calcification of the skeleton of calcareous algae and invertebrates (Rodolfo-Metalpa et al. 2010; Basso 2012). It is expected that ocean acidification will enhance both bioerosion and chemical dissolution of carbonates in the future, with undersaturation expected to affect especially the deep, cold-water carbonates (Guinotte et al. 2006; Tribollet et al. 2009; Lunden et al. 2013; Murray et al. 2016; Wisshak et al. 2014). The presence of commercial fisheries in these habitats induced destructive bottom trawling which strongly threatened the habitat complexity and biodiversity of deep-sea bioconstructions. Trawling over deep coral areas can be compared to land deforestation for the relevant loss of biodiversity that both processes involve (Watling and Norse 1997). Conservation groups are making scientific and political communities aware of the vulnerability of deep coral habitats to such massive exploitation in several Exclusive Economic Zones around the world. In an effort to protect these unique resources, researchers are refining acoustic mapping techniques and statistical models that are able to perform solid prediction of their distribution (Tittensor et al. 2009; Ross and Howell 2012; Robert et al. 2015, 2016). The Barcelona Convention's Action plan adopted in 2008 for the conservation of coralligenous outcrops and other calcareous bio-concretions declared the need of legal measures for their protection. Deep-sea bioconstructions are also considered with particular attention in the EU's Habitats Directive (under 1170 "Reefs"), and in the Bern Convention. More recently, the Marine Strategy Framework Directive (MSFD; European Parliament and Council of the European Union 2008; European Commission 2010), aimed at achieving the "Good Environmental Status" (GES) of all marine waters by 2020, required each Member State to develop a strategy of knowledge-based sustainable management for its marine waters. On the basis of the Barcelona Convention and other international initiatives for the environmental protection of deep-sea ecosystems (UNEP-MAPRAC/SPA 2008, 2010; UNEP-MAP 2011), a group of habitat types, among which C ad CWC, has been identified as of special scientific or biodiversity interest (MSFD, Annex III, Table 1). The implementation of appropriate monitoring measures is indeed instrumental to guarantee a sustainable management of C and CWC., Although an extensive array of increasing high quality data on CWCs exists for the northeast Atlantic margin, there are still several gaps in understanding the functioning and evolution of these complex habitats, even regarding any potential relationship

between their ecological dynamics and the resulting geomorphic expression. Furthermore, the lack of full coverage high-resolution seafloor maps in the deep-sea may introduce a bias in the recorded extension of these relevant geomorphic features. For instance, recent oceanographic expedition along the western African and South American margins are revealing the existence of new CWC mound fields, where living reefs are supporting a high biodiversity (Le Guilloux et al. 2009; Eisele et al. 2014; Lopes and Hajdu 2014; Glogowski et al., 2015; Buhl-Mortensen et al. 2016b).

New data on less explored areas may be of great significance, both regionally and globally, for:

- (1) refining the assessment of biodiversity at a global scale
- (2) better define the resilience of deep-sea habitats to human induced climatic forcing
- (3) better estimating the contribution to the ocean carbon budget of cool-water carbonatic systems
- (4) better constraining on a basin scale the main paleoceanographic events in recent time, including high-resolution focus on late Pleistocene and Holocene rapid climate events.

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