An underwater photograph of a vibrant coral reef. The scene is dominated by a variety of marine life, including branching corals in shades of yellow, orange, and red, alongside large, textured sponges in green, purple, and blue. The background is a deep, dark blue, suggesting a clear, deep-sea environment. The lighting highlights the intricate structures and colors of the reef organisms.

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**CHANGES IN A MEDITERRANEAN CORALLIGENOUS
SPONGE ASSEMBLAGE AT DECENNIAL AND
PLURI-MILLENNIAL TEMPORAL SCALE**



UNIVERSITÀ DEGLI STUDI DI GENOVA

**Changes in a Mediterranean coralligenous
sponge assemblage at decennial and
pluri-millennial temporal scale**

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Summary

Coralligenous, an invaluable source of marine diversity (animal and algae), is considered together with the *Posidonia oceanica* meadows, the main biodiversity hot spot of the entire Mediterranean basin. Being built through the stratification over time of coralline algal (limestone), sediments and animal skeletons, coralligenous is defined as a bio-construction. These structures began to develop about 8,000 years ago, when the sea level was 13-16 m lower than today. About 2,000 years ago, their development seems to have stalled substantially in various parts of the Mediterranean, for causes not yet fully clarified. For these reasons and for its key ecological role for both sessile and mobile animals, it is protected (but without legal constraints) by the Barcelona Convention action plan (UNEP-MAP-RAC / SPA, 2008, 2017), by the EU Habitats Directive and in the Bern Convention. Despite these measures, coralligenous bio-constructions of the Mediterranean Sea are threatened by the changes, more and more sudden, of the chemical / physical conditions of the marine waters due to climate change. Studying biodiversity related to coralligenous concretions, can be useful for understanding the spatial and temporal dynamics of this important habitat in recent times. Also to define its diversity in the past is undoubtedly an important element to understand the structural and biodiversity temporal trends

suffered during its formation processes (also related to the climatic changes that have occurred over time). At this juncture, its major animal component the Porifera (>300 species) play a fundamental role in the ecological and growth dynamics of the coralligenous. This taxon (especially those with siliceous spicules) with representatives living on and within the coralligenous concretions is particularly suitable to focus on present and past diversity, precisely because the siliceous spicules remain intact over time if sedimented within the biogenic constructions. The purpose of my PhD work was precisely to characterize the coralligenous concretions by using the populations/species of living sponges today vs those existing in the past (up to ~8,000 years ago) by a comparative analyses and also evaluating the dynamic variation of the specific wealth, linked to the climatic changes that have taken place over the millennia, of this community during the entire evolutionary history of bio-constructions. The samplings were carried out by SCUBA diving in four sites, Bogliasco (Liguria - Ligurian Sea), Tavolara Marine Protected Area (Sardinia - Tyrrhenian Sea), Porto Cesareo (Puglia - Ionian Sea) and Tricase Porto (Puglia - Ionian Sea, Otranto Canal). As for Liguria, 5 samples were taken by underwater corer, while for Sardinia and the two Apulian sites, 2 pinnacles per site (~20 l in volume), were

collected with a hammer and chisel trying to obtain the most basal part and therefore as old as possible. As for the pinnacles, the sponges settled on the surface of the coralligenous were initially taken and identified at the species level. Subsequently the blocks have been divided into slices, one of which is parallel to the growth direction of the block and other perpendicular (in variable number) to it. Endolithic sponges have been collected from perpendicular slices by binocular analysis and identified at species level. From the slice parallel to the growth, a "virtual" carrot was obtained, divided into blocks of ~4 cm each side and each block was dated with the ^{14}C in order to have the most linear data possible. From the blocks the sediments cemented over time and containing the siliceous spicules of the sponges are extracted and through the taxonomic study it was possible to study the different species richness values of the spongofauna during the entire evolutionary history of these bioconstructions. The various studies conducted have shown an effective temporal stability of the Porifera community, in fact most of the ancient spicules observed belong to genera still present in and on bioconstructions. An important exception is represented by the genus *Alveospongia* (Axinellida), once widespread in all the presently studied communities and today totally absent from the entire Mediterranean basin. Other genera like *Didiscus* Dendy, 1922, *Annulastrella*

Maldonado, 2002, *Forcepia* Carter, 1974, *Nethea* Sollas, 1888 and *Thrombus* Sollas, 1886, once variously represented, today can only be found in deep faunas such as those related to white corals. Despite this stability, the wealth of the sponge community shows evident variations over the millennia that seem to be in agreement with the climatic variations known for the northern hemisphere.

Riassunto

Fonte inestimabile di diversità marina (animale e vegetale), il coralligeno, è considerato insieme alle praterie di *Posidonia oceanica*, il principale *hot spot* di biodiversità di tutto il bacino del Mar Mediterraneo. Essendo “costruito” tramite la stratificazione nel tempo di talli algali (calcarei), sedimenti e scheletri animali, il coralligeno è definito una bio-costruzione. Tali strutture hanno cominciato a svilupparsi circa 8000 anni fa, quando il livello del mare era 13-16 m inferiore rispetto ad oggi. Circa 2000 anni fa, il loro sviluppo sembra essersi sostanzialmente bloccato in diversi punti del Mediterraneo, per cause non ancora completamente chiarite. Per questi motivi e per il suo ruolo ecologico estremamente importante sia per animali sessili bentonici che mobili, è salvaguardato (ma senza vincoli legali) dal piano d’azione della Convenzione di Barcellona (UNEP-MAP-RAC/SPA, 2008, 2017), dalla Direttiva *Habitat* dell’UE e nella Convenzione di Berna. Nonostante queste misure, le bio-costruzioni mediterranee sono minacciate dai mutamenti, sempre più spesso repentini, delle condizioni chimico/fisiche delle acque marine dovuti ai cambiamenti climatici. Studiare la biodiversità marina e in questo caso quella legata alle concrezioni coralligene, può essere utile per capire le dinamiche di funzionamento e crescita/decrecita di questo importante *habitat* nei tempi recenti; inoltre avere

un’idea della diversità che lo caratterizzava nel passato è senza dubbio un importante elemento per capire i mutamenti strutturali e di biodiversità (anche collegati ai cambiamenti climatici succedutisi nel tempo) subiti nel corso della durata della sua formazione. In questo frangente, i Poriferi, che giocano un ruolo fondamentale nella dinamica ecologica e di crescita del coralligeno e ne rappresentano la maggiore componente animale con oltre 300 specie presenti, sono particolarmente adatti per studi di diversità sia collegati al presente che al passato grazie allo studio delle spicole silicee. Lo scopo del lavoro del mio dottorato è stato proprio quello di caratterizzare i popolamenti di spugne viventi oggi, sul e nel del coralligeno, e quelli esistenti nel passato (fino a circa 8000 anni fa) mettendoli a confronto tra loro e valutando inoltre la variazione dinamica della ricchezza specifica, legata ai cambiamenti climatici susseguitisi nell’arco dei millenni, di questa comunità durante l’intera storia evolutiva delle bio-costruzioni. I campionamenti sono stati effettuati tramite immersioni subacquee in quattro siti, Bogliasco (Liguria - Mar Ligure), Area Marina Protetta di Tavolara (Sardegna - Mar Tirreno), Porto Cesareo (Puglia - Mar Ionio) e Tricase Porto (Puglia - Mar Ionio Canale d’Otranto). Per quanto riguarda Bogliasco, 5 campioni sono stati prelevati tramite carotatore subacqueo, mentre per gli altri tre

siti, 2 pinnacoli per sito (di circa 20 l di volume), sono stati raccolti con mazzetta e scalpello cercando di ottenere la parte più basale e quindi più antica possibile. Per quanto riguarda i blocchi, inizialmente le spugne che vivono sulla superficie del coralligeno sono state prelevate e classificate a livello di specie. In seguito i blocchi vengono divisi in fette, di cui una parallela alla direzione di crescita del blocco e tot perpendicolarmente a essa; da queste ultime, tramite analisi al binoculare vengono raccolte le spugne endolitiche e classificate a livello di specie. Dalla fetta parallela alla crescita, è stata ottenuta una carota “virtuale”, divisa in blocchetti di circa 4 cm di lato e ognuno di questi è stato datato con il ^{14}C in modo da avere un dato più lineare possibile. Dai blocchetti sono estratti i sedimenti cementati nel tempo e contenenti le spicole silicee delle spugne che vivevano nello stesso periodo e tramite lo studio tassonomico si è potuto studiare la differente ricchezza specifica della spongofauna durante l’intera storia evolutiva delle bio-costruzioni. I vari studi condotti hanno mostrato una effettiva stabilità temporale della comunità dei Poriferi, infatti la maggior parte delle spicole antiche osservate fanno parte di generi ancor oggi presenti nelle e sulle biocostruzioni. Un’importante eccezione è rappresentata da *Alveospongia*, un tempo diffusa in tutte le comunità studiate e oggi totalmente assente dall’intero bacino del Mediterraneo. Altri

generi, come *Didiscus* Dendy, 1922, *Annulastrella* Maldonado, 2002, *Forcepia* Carter, 1974, *Nethea* Sollas, 1888 e *Thrombus* Sollas, 1886, un tempo variamente rappresentati, oggi sono riscontrabili solo in faune profonde come quelle legate ai coralli bianchi. Nonostante questa stabilità, la ricchezza della comunità a poriferi, mostra evidenti variazioni nel corso dei millenni che sembrano in accordo con le variazioni climatiche note per l’emisfero settentrionale.

1. Coralligenous general characteristics

In Mediterranean Sea, coralligenous formations constitute typical and diversified habitats which create structural complexity and sources of important ecosystem services, these structures are considered one of the most important hot spots of Mediterranean biodiversity together with *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows (Boudouresque, 2004). The term “coralligenous” refers to a secondary hard substrate, formed by carbonate layers overlap mainly due to the activity of several encrusting calcareous algae (*Lithophyllum*, *Mesophyllum* *Lithothamnion*, and *Peyssonnelia* genera) and animal skeletons. These calcareous algae can be considered major builders, in the Holocene epoch, together with a suite of other invertebrates with a calcareous skeleton (Ballesteros et al, 2006). Thanks to the presence of its own bio-constructors and bioeroders the structure of these biogenic concretions is constantly evolving. The holes and crevices that characterizes the coralligenous structure, support a complex community dominated by filter organisms like sponges, hydrozoans, serpulids, polychates, molluscs, bryozoans and tunicates (Ballesteros et al, 2006).

Coralligenous assemblages represent the climax biocenosis of the circalittoral zone

(Pérès and Picard, 1964), where live endangered or commercially important fish species (Salomidi et al, 2012). These bioconstructions are considered of high conservation interest for their biogeographic uniqueness, their complex physical structure, their high species biodiversity, their occurrence stratified throughout the different benthic marine zones and their very slow growth (Ballesteros, 2006; Agnesi et al, 2008; Salomidi et al, 2012).

2. Coralligenous structural and habitat's organization

In the Mediterranean Sea, coralligenous represents the most monumental bioconstruction along the shelf, where it forms large structures that may be up to 4 m high and greater than 50 m in lateral continuity (Bosence, 1983; 1985). Architecture and morphology are primarily controlled by biological carbonate productivity that responds to climate, oceanography, physiography, changes in accommodation space and terrigenous supply (Schlager, 1991; 1993; Betzler et al, 1997). Historically, in coralligenous assemblages two main geomorphologies have been

described by Pérès and Picard, 1964 (Ballesteros, 2006):

Banks (Fig. 1), which can fall into the “coralligène de plateau” definition and consist of frameworks definable like "pinnacles" with a variable high (0.5 to 4 m) built on horizontal substrates;



Fig. 1 Typical coralligenous of Tavolara banks. Photo by Dott. Marco Bertolino.

Cliffs (Fig. 2), which can fall into the “coralligène de l’horizon inférieur de la roche littorale” definition and consist of structures developed along vertical cliffs with a thickness range of 0.2 to 2 m.



Fig. 2 Typical cliffs coralligenous (Portofino). Photo by Prof. Carlo Cerrano.

Despite this division, some problems arise in the attempt to classify the coralligenous formations in these two categories due to the high variability of bioconstructions in terms of geometry, size, areal distribution and stabilized substrate (Bracchi et al, 2016). The coralligenous geomorphology can vary according to many environmental factors and therefore to the geographical and vertical origin, the extension, the slope and the shape of the geomorphologies. For these reasons Laborel (1961) identified four different geomorphotypes: cliffs (paleo cliff and sheer cliffs), banks and waterfalls.

Furthermore, coralligenous atolls, whose origin is still unresolved, have been discovered between 100 and 130m depth off the northern coasts of Corse (Bonacorsi et al, 2012).

3. Geographical and bathymetric distribution

Coralligenous habitats, defined as highly heterogeneous systems, where the environmental variables together with distribution and abundances of taxa can differ greatly on both a geographical and a local (tens of metres) scale (Ferdeghini et al, 2000; Balata et al, 2005; Virgilio et al, 2006). Although some efforts have been made to increase information on the distribution of this sensitive habitat (Martin et al, 2014), knowledge of the geographical and depth distribution of coralligenous assemblages as

well as their biodiversity and its relation to their functioning is still needed for their conservation and sustainable use (UNEP-MAP-RAC/SPA 2009).

Habitat mapping is crucial in order to obtain reliable estimates of the total area occupied by each habitat, so as to reach the required conservation targets and to implement appropriate management measures (UNEP-MAP-RAC/SPA 2009). A bibliographic database plays a major role in the study of habitat distribution and its changes over time. Acoustic technologies are increasingly being used for monitoring benthic habitats (Zapata-Ramirez et al, 2013), and those used for mapping coralligenous communities normally include side-scan sonars and multibeam sonars that allows us to infer seafloor topography (Bonacorsi et al, 2012; Gordini et al, 2012). Martin et al, 2014 did thorough review of existing spatial datasets showing the distribution of coralligenous habitats across the Mediterranean Sea was undertaken, highlighting current gaps in knowledge.

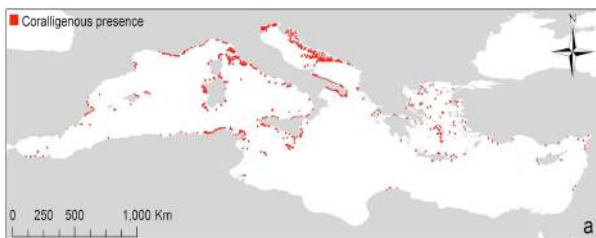


Fig. 3 Occurrences of coralligenous outcrops along the Mediterranean Sea (Martin et al., 2014)

Predictive modelling was then carried out, based on environmental predictors, to produce

the first continuous maps of this habitat across the entire basin (Fig. 3). In situ depth of occurrences collected from the publications (Fig. 4) revealed that records were located between 10 and 140 m, peaking in the shallower sector of this range. Based on this, modelling was restricted to the 0–200 m depth zone. Published information was found to be insufficient for deriving a value of sampling effort across depth bins (Martin et al, 2014).

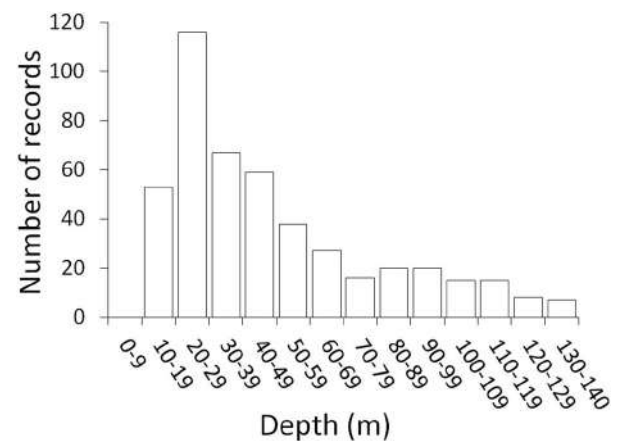


Fig. 4 Depth distribution of coralligenous habitats across the Mediterranean basin (Martin et al., 2014)

Despite this data and the common presence of the bioconstruction in Mediterranean Sea, complete cartographic data on their distribution are a major knowledge gap (Ingrosso et al, 2018). These authors reported the distribution of coralligenous along the Italian Seas studied through various documents (peer-reviewed articles; international, national and regional reports; grey literature) reporting spatial information (e.g. maps or detailed acoustic mapping) and create a map (Fig. 5).

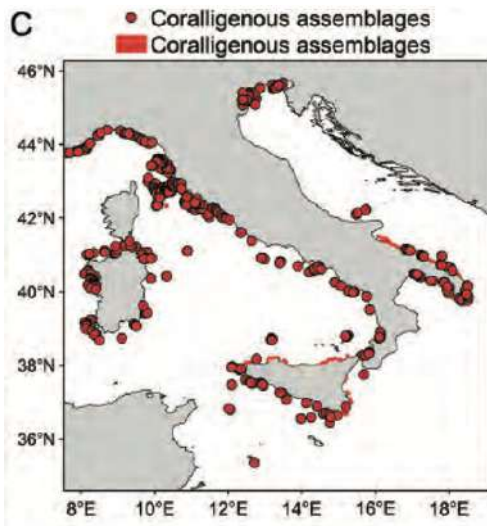


Fig. 5 Spatial distribution of coralligenous formations along the Italian seas (Ingrosso et al., 2018)

4. Coralligenous biodiversity

Coralligenous has been identified as Mediterranean priority habitats by the EU Habitats Directive (92/43/CE) and represent some of the richest assemblages found in Mediterranean, harboring approximately 10% of marine Mediterranean species (Pérès and Picard, 1964; Laubier, 1965; Ros et al, 1985; Bouduresque, 2004; Ballesteros, 2006). The species that characterize such assemblages belong to various taxonomic groups like encrusting calcareous algae, sponges, cnidarians, polychaetes, bryozoans and tunicates (Garrabou et al, 2002; Ballesteros, 2006). Most of these species are long-lived and vulnerable to various types of threats (Garrabou et al, 1998; Teixidó et al, 2011). In fact, many coralligenous outcrops have already been

affected by various stressors such as nutrient enrichment, overexploitation, invasive species, increase in sedimentation, mechanical impacts as well as climate change, resulting in dramatic consequences for many species and even for the structure and biodiversity of the whole assemblages (Balata et al, 2007; Garrabou et al, 2009; Piazzini et al, 2012; Cebrián et al, 2012; Teixidó et al, 2013; Cecchi et al, 2014).

The holes and crevices of the coralligenous support a complex community dominated by suspension feeders (sponges, hydrozoans, serpulid polychaetes, molluscs, bryozoans and tunicates). Laubier (1966) first emphasized the high biodiversity of the coralligenous and listed 544 invertebrate species from this assemblage in Banyuls. Later, Hong (1980), in an exhaustive survey of the coralligenous of Marseille, listed a total of 682 species, while other authors (Ros et al, 1984) reported 497 species of invertebrates from the algal concretions of the Medes Islands. Recently, Romdhane (2003) reported 35 algal species and 93 animal species from a coralligenous formation along a vertical cliff in the gulf of Tunis. However, the number of species living in the coralligenous assemblages is still undefined, because of the richness of the fauna (Laubier, 1966), the habitat

complexity (Péres and Picard, 1964; Ros et al, 1985), the wide depth range of the conglomerates (Ballesteros, 2006), the sporadic presence of cryptic species and the scarcity of reference studies. A rapid, non-destructive protocol for biodiversity assessment and monitoring of coralligenous, based on photographic sampling, was recently proposed by Kipson et al (2011). Because of the coralligenous bioconstruction's complex spatial structure, characterized by holes and cavities supporting different microhabitats (Pica et al, 2014), a rich and diversified fauna (both sessile and vagile, excavating, and buried in the soft sediments accumulated inside holes) can be hosted and maintained in them (Ballesteros, 2006). As a consequence of this peculiar heterogeneity, the coralligenous habitat harbours a biodiversity higher than any other Mediterranean habitat but the estimates of this biodiversity are far from being updated and exhaustive (Ballesteros, 2006; Bertolino et al, 2013). Ballesteros (2006) made a census of 1241 invertebrates in the coralligenous habitat, and these data, as underlined by the author, are conservative.

5. Manufacturing process

Coralligenous age

Building and bio-eroding process must be positively balanced to allow the growth of these bioconstructions (Garrabou and Ballesteros, 2000). As already mentioned, the greatest contribution to coralligenous bioconstructions is due to coralline macroalgae of the genera *Mesophyllum*, *Lithophyllum* and *Neogoniolithon* (Ballesteros, 2006). However, this process is also due to animal organisms such as foraminiferan, cnidarians, bryozoans molluscs and serpulid polychaetes; as far as erosion is concerned, the greatest bio-eroders are cyanobacteria, boring sponges, boring mollusc, sipunculids and grazing sea urchins (Ballesteros, 2006; Sartoretto, 1998; Sartoretto and Francour, 1997).

Regarding the age of this bioconstruction, Bertolino et al 2017 dating two pinnacles from the Ionian Sea found that the oldest part dates back to 6207 years with an average growth rate of approximately 0.15 mm per year.

6. Porifera diversity

Taxonomic revisions of literature data shown to record 291 sponge species associated with coralligenous formations of Mediterranean Sea in particular Italian Seas (Labate 1967; Sarà 1968, 1969, 1973, Annicchiarico 1980; Corriero et al, 2004; Baldaconi and Corriero 2009; Kipson et al, 2011; Bertolino et al, 2013, 2014; Calcinai et al, 2015). Longo et al 2017, increased the number of sponge species associated with the Mediterranean to 306 and Costa et al 2019 to 310. Longo et al (2017) results showed substantial and significant differences between the deep and shallow sponge assemblages. About 30% (46 species) of the total sponges found were exclusive to the deep sites, and 32% (49 species) to shallow sites. Therefore, depth seems to be the most important descriptor of the differences in community structure, in terms of environmental factors varying with it (mainly light, temperature and nutrients). Usually, the amount of available nutrients is considered the variable that best explains the distribution of coralligenous communities in the Mediterranean models (Martin et al, 2014).

7. Cryptic Porifera

All around the world, the most diversified marine habitats are related to biobuilders, such as hard corals in tropical areas and crustose coralline algae in temperate waters.

The high biodiversity hosted by bioconstructions is likely related to the three-dimensional structure of the substratum (rich in holes and microhabitats) facilitating the coexistence of several species with different ecological requirements and offering an ideal habitat to escape from predation and from substrate competition, moreover, in the coralligenous habitat, the presence of pockets of soft-sediments allows the contemporary presence of both hard- and soft-bottom species (Ballesteros, 2006) and the peculiar structure leads to the entrapment of sediments that can represent a sort of black box, telling the story of the ancient assemblages (Bertolino et al, 2014). In past Hong (1982) showed that the species of the cryptofauna in the coralligenous framework could represent about 7% of the total amount in terms of animal species. Pica et al (2014) calculated, applying X-ray microtomography techniques, an average micro-porosity of about 40% in the coralligenous habitat and about 25% of area occupied by sponges out of the total surface of

crevices. At this scale, it was not possible to analyse the micro-patterns of boring sponges (Calcinai et al, 2003) but siliceous spicules were well evident. Just like the coral reefs, also for coralligenous accretions, it is possible to hypothesise that cryptic fauna may play a crucial functional role. The holes and crevices of this biogenic structure support a complex community dominated by suspension feeders, with sponges representing the most abundant taxon (Ballesteros, 2006; Bertolino et al, 2013). Bertolino et al (2013), sectioning big coralligenous blocks into slices identified the presence of 27 exclusively endolithic species giving an idea of the richness of this group inside the coralligenous substrata. Moreover, it was stated that the diversity of coralligenous sponges has remained stable over a millennial span of time, and this extended stability may be related to the environmental stability of the inner habitat of the conglomerates (Bertolino et al, 2014). A study of Calcinai et al 2015, about a comparison between the sponge fauna living outside and inside the coralligenous bioconstructions at two different depths (15 m and 30 m) in the Ligurian Sea, pointed out that the number and biomass of the cryptic sponges, living inside the coralligenous substrata, were significantly higher than those of the epibenthic layer. These data, even if

relative to a single benthic taxon, clearly demonstrated the great importance that the cryptic fauna plays in the coralligenous habitat. The same sponge species can be found in very different environmental conditions, with different shapes and habitus, they could be either creeping or encrusting or massive (Sarà et al, 1998).

8. Ancient Porifera communities

Growth dynamics of coralligenous formations allow to detect the sponge fauna successions: when sponges die their siliceous spicules, highly resistant to disintegration, remain trapped inside the concretions and are accumulated and compacted with sediments. This high resistance to spicules dissolution lets to describe the quantitative and qualitative variations of the sponge fauna along the whole Holocene (Bertolino et al, 2014). To date, few radiocarbon dating of coralligenous accretions are available, but is generally accepted that these builds-up had their maximum growth rate in a timespan between 8000 and 5000 yrs BP. After this period, just the shallower concretion's grow rates were recorded (from 10 to 35 m depth), while deeper concretion growth rates are negligible (deeper than 50 m). Wiedenmayer (1994) conducted an accurate review about Porifera communities of the geological

past, in the post-Paleozoic era, treating the Australian sponge fauna.

Lukowiak (2016) studied Australian porifera too, but about the late Holocene epoch. The work, thanks to the taxonomic study of the “paleospicules” of the SW Australia, could define the environmental features basing on the species found. Moreover Lukowiak and Pisera (2017) studied the evolutionary history, thanks to the ancient sediment spicules, of Australian sponge communities present during the late Eocene epoch (about 34 millions yrs BP), in particular focusing on Pachastrellidae family, pointing out many differences respect to the current ones; in this way they could describe the evolution of that taxonomic group. As mentioned, siliceous sponge spicules appear a good proxy to evaluate the different assemblages that have occurred on and inside these build-ups over a multi-millennial span of time. Recent studies and references regarding this topic, the subject of this doctoral thesis, are reported in full in the next chapters.

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The dynamics of a Mediterranean coralligenous sponge assemblage at decennial and millennial temporal scales

Abstract

This paper concerns the changes occurred over both decennial and millennial spans of time in a sponge assemblage present in coralligenous biogenic build-ups growing at 15 m depth in the Ligurian Sea (Western Mediterranean). The comparison of the sponge diversity after a time interval of about 40 years (1973–2014) showed a significant reduction in species richness (about 45%). This decrease affected mainly the massive/erect sponges, and in particular the subclass Keratosa, with a species loss of 67%, while the encrusting and cavity dwelling sponges lost the 36% and 50%, respectively. The boring sponges lost only one species (25%). This changing pattern suggested that the inner habitat of the bioconstructions was less affected by the variations of the environmental conditions or by the human pressures which, on the contrary, strongly affected the species living on the surface of the biogenic build-ups. Five cores extracted from the bioherms, dating back to 3500 YBP, allowed to analyse the siliceous spicules remained trapped in them in order to obtain taxonomic information. Changes at generic level in diversity and abundance were observed at 500/250-years intervals, ranging between 19 and 33 genera. The number of genera showed a sharp decrease since 3500–3000 to 3000–2500 YBP. After this period, the genera regularly increased until 1500–1250 YBP, from when they progressively decreased until 1000–500 YBP. Tentatively, these changes could be related to the different climatic periods that followed one another in the Mediterranean area within the considered time span. The recent depletion in sponge richness recorded in the Ligurian coralligenous can be considered relevant. In fact, the analysis of the spicules indicated that the sponges living in these coralligenous habitats remained enough stable during 3000 years, but could have lost a significant part of their biodiversity in the last decades, coinciding with a series of warming episodes.

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Additional Resources

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1. Introduction

The Mediterranean littoral hard bottoms are often characterized by coralligenous communities that develop, with different growth patterns, depending on sedimentation rates, water transparency, substrate mineralogy and morphology [1, 2]. Coralligenous substrata are biogenic build-ups, mainly due to the carbonate deposition of several encrusting coralline algae (*Lithophyllum*, *Lithothamnion*, *Mesophyllum* and *Peyssonnelia*) growing in dim light conditions [3, 4, 5] and, in lesser extent, to the calcareous skeletons of some benthic animals [6, 7, 8].

These bioconstructions form a complex mosaic of micro-habitats, with crevices and cavities, produced by the irregular growth of algal talli and by the destructive action of some boring organisms, such as sponges and bivalves [2]. The age of these build-ups, estimated by ¹⁴C, can also go back to 8000 YBP [5, 9, 10, 11], when the Mediterranean Sea level was lower than now, although, after 6000 YBP, the deepest build-ups stopped developing and the carbonate deposition appeared negligible [5].

These build-ups may develop both on vertical cliffs, where they produce a series of overhanging ridges with the growth axis perpendicular to the rocky wall [2], but also on flat rocky bottoms, often forming columnar structures diffused in shallow waters, between 10 and 30 m depth [8, 12].

These structures are younger than the coralligenous settled on the vertical cliffs because they started to grow when the sea level increased.

They show a slow growth rate (0.2–4 mm/year), reach a thickness comprised between 0.5 and 3.4 m, and are often characterized by cavernous structures [8, 13]. Sponges are the most representative animal group of these habitats, with more than 300 recorded species, living in different zones of the bioconstructions and showing different growth patterns. Massive/erect species live on the surface of the build-ups, others encrust their surface or fill crevices and holes and, finally, boring species actively excavate the carbonate structure [14]. The different sponge categories contribute, according to their different habitus, to the strengthening, stabilization or erosion of the bio-carbonate structures [15].

Recently, Bertolino *et al.* [11] pointed out a method, based on the study of free spicules embedded in the sediment filling the inner holes of coralligenous accretions, to identify species living in the past on and inside these structures. The spicule analysis, coupled with the age estimation of the coralligenous containing the spicular remains, allowed the reconstruction of the sponge fauna of the bioconstructions along their entire life span.

The present study was dedicated to the description of the sponge fauna living on the coralligenous build-ups (Fig 1) arising from a

flatted bottom 15 m depth, off the Bogliasco marina (Ligurian Sea, Western Mediterranean Sea), at two different temporal scales. At a decennial span of time, we have compared the actual sponge fauna (2014) with the records obtained from the same habitat 40 years before by Pansini and Pronzato [16]. During this span of time, in the '70 and '80s years of the past century, the outcrops were subject to the destructive date-mussel fishery, at last forbidden by the Italian law in 1998. Moreover, thanks to the study of five cores of the bioherms going back 3500 YBP, the dynamics of the sponge fauna along the last part of the Holocene were investigated, analysing the siliceous spicules remained trapped inside the bioconstruction, when the sponge dies.

2. Materials and methods

The studied sponge fauna was present in the coralligenous build-ups, arising on a flat bottom 15 m deep, on a belt 70–90 m wide, 300 m off the Bogliasco marina (Ligurian Sea, Western Mediterranean) (44,374418° N, 9,06734° E) (Fig 1). Sampling on the build-ups was performed by SCUBA diving, during summer 2014. Fifteen standard areas of 400 cm² (20 x 20 cm) were completely scraped using hammer and chisel to a depth of 3 cm in the aim of collecting also the sponges growing inside the bioherms. The collected sponges were sorted and identified at species level in laboratory. The sponge abundance

was estimated as the per cent presence of each species on the total scraped areas. The obtained data were compared with those recorded during a survey conducted in 1973 with the same methods and in the same area [16].

Moreover, to study the structure of the sponge assemblage during the entire life of the build-ups, five core samples were obtained by a pneumatic corer operated by professional divers from five different build-ups (Fig 1). All the samples were conducted from top to bottom of the accretions, in order to reach the basal rock. The core samples had a length ranging from 9 cm to 45 cm.

According to the method proposed by Bertolino *et al.* [11] and improved in this work, the core samples were divided in 3 cm thick portions by a stone-saw. Each portion was placed in hydrogen peroxide (240 vol) that was changed three times at intervals of 24h. This method released all the sediment entrapped in the cavities of the bioherm. The pieces of biocarbonates were removed and dried, while the obtained sediment was treated with boiling nitric acid to eliminate the carbonate fraction, rinsed twice in distilled water and twice in alcohol 95%, and dried. For each sample of the sediment, three replicates of 10 mg each were mounted on a microscope slide. Microscopic analysis of the spicules contained in the sediment was done to investigate the sponge species living in ancient times. Whenever possible, the

embedded spicules were attributed to a genus. Finally, each spicule type was counted.

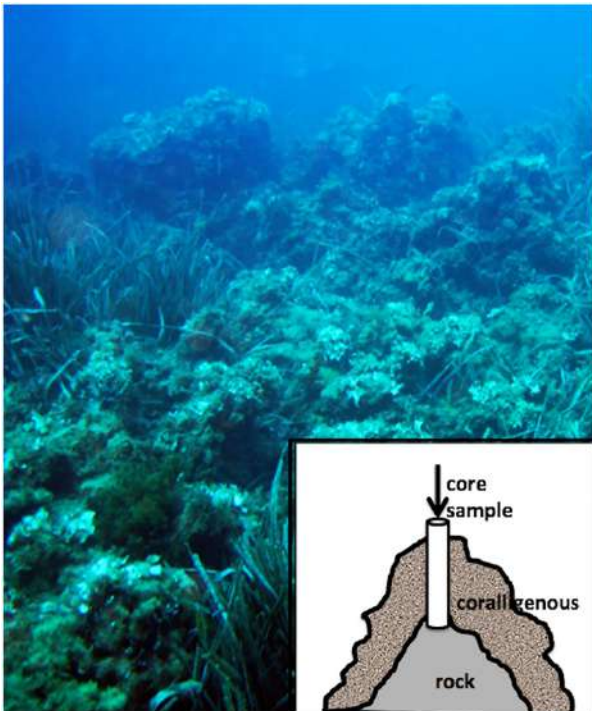


Fig 1. A view of the studied coralligenous of Bogliasco (Ligurian Sea) mixed with patches of the seagrass *Posidonia oceanica*. The drawing shows a core sample conducted on a build-up and reaching the basal rock.

After the sediment extraction, each portion of the bioherm was ^{14}C dated by Accelerator Mass Spectrometry (AMS) at the Center of Dating and Diagnostic (CEDAD) of the University of Salento [17] (Table 1).

Samples were converted to carbon dioxide by acid hydrolysis (H_3PO_4) and the extracted CO_2 was converted to graphite after cryogenic purification [18]. Conventional radiocarbon age was then calculated from the $^{14}\text{C}/^{12}\text{C}$ isotopic ratios measured with the AMS system after correcting for isotopic fractionation and chemical processing and machine background. Conventional radiocarbon ages were then calibrated in

calendar years by using the MARINE13 [19] curve and a $\Delta R = 58 \pm 15$ as average value for the Mediterranean Sea [20]. Calibrated radiocarbon ages were expressed as years cal BP and used in the following chronological discussion and interpretations.

Since the age determination of each portion of bioherm appeared inconsistent with a temporal growth in all the build-ups, we have considered each portion independently, assuming that the spicules present may have approximately the same age as the surrounding bio-deposed carbonates. This assumption is coherent with the fact that spicules of boring and cavity dwelling sponges remain *in situ* when they die. On the other hand, we hypothesise that a large part of the spicular remains of massive/erected or encrusting species fall down and accumulate in the coralligenous crevices, although their incorporation could be partially biased by local hydrodynamic conditions. By this way, we have obtained the trend of sponge diversity, evaluated as number of recorded genera, and the trend of the amount of the spicules entrapped in the build-ups along a span of time ranging from 3500 to 600 YBP and subdivided in intervals of 250/500 years each.

Distance from the basal rock	Core samples				
	B1	B2	B3	B4	B5
cm	Years Before Present (YBP)				
0–3	1024 ± 65	1019 ± 65	2833 ± 65	1367 ± 60	1974 ± 65
3–6	2082 ± 75	1483 ± 65	2806 ± 55	517 ± 38	3442 ± 55
6–9	1422 ± 60	1884 ± 60	3423 ± 60	948 ± 55	2422 ± 80
9–12	1298 ± 45	1492 ± 65		1757 ± 65	871 ± 55
12–15	1826 ± 65	2240 ± 65		1877 ± 60	3104 ± 75
15–18	1356 ± 55	1671 ± 70		1698 ± 70	
18–21	1970 ± 65	1040 ± 65		1408 ± 65	
21–24	560 ± 45	1318 ± 45		1311 ± 45	
24–27		1247 ± 45		620 ± 55	
27–30		801 ± 60			
30–33		1214 ± 50			
33–36		1363 ± 60			
36–39		957 ± 55			
39–42		1374 ± 60			
42–45		1010 ± 60			

Table 1. Calibrated radiocarbon ages of the different layers of each core sample. Uncertainty refers to one standard deviation confidence level. Present assumed as 1950AD.

3. Results

The studied coralligenous build-ups, present off the Bogliasco coast on a rocky bottom at 15 m depth, were irregular in shape, about 40–70 cm high, rich in crevices and holes. They were covered by a dense community of photophylous algae (mainly *Padina pavonica*, *Acetabularia acetabulum*, *Codium* spp., *Dictyota dichotoma*, *Dyctiopteris* spp.) while patches of the sea grass *Posidonia oceanica* and sandy pouches were dispersed among the coralligenous accretions (Fig 1).

The sponge fauna settled on these bioherms sampled in 2014 was composed by 51 species (Table 2, S1 Table), with variable abundances among different accretions. The average number of species per scraped area was 8.6 ± 0.97 with maximal of 15 and minimal of 4 species. Considering the complex of the recorded species some differences were observed according to the different kinds of growth pattern (massive/erect, encrusting,

cavity dwelling, and boring) (Figs 2 and 3).

The most numerous species belonged to the category of the encrusting sponges (24 species), followed by massive/erect (13 species), cavity dwelling (10 species) and boring (4 species). The cavity dwelling *Jaspis johnstonii* and *Dercitus (Stoeba) plicatus*, together with the encrusting *Crambe crambe*, were the most frequent, present in almost 60% of the samples. Other common species, present in more than 40% of the samples, were *Phorbastenia tenacior* (encrusting), *Chondrosia reniformis* (massive) and *Jaspis incrustans* (cavity dwelling).

Pansini and Pronzato [16], studying the same sponge assemblage in the same locality (Fig 2), recorded 81 species (Table 2). At that time, according to the growth patterns, the massive/erect (31 species) and the encrusting (28 species) were the most representative (Fig 3). The most abundant sponges were *Eurypon vescicularis* and *Bubaris vermiculata* present

at least in 60% of the samples. *Spongia* (*Spongia*) *virgultosa*, *Jaspis johnstonii*, *Triptolemma simplex* and *Timea stellata* were recorded in more than 40% of the examined samples. Comparing the results of the two surveys separated by a 40 years time span, a strong loss of sponge diversity was observed. On a total of 97 recorded species in both the study periods, only 35 species (36%) were in common, while 16 species were recorded as new entries in 2014 and 46 species, observed in 1973, were lost (Fig 2). This decrease was not homogenously distributed among the sponge growth patterns: the massive/erect species experienced the major loss (21 lost species, 68%), while the encrusting and cavity dwelling sponges lost 14 (50%) and 9 species (52%) respectively, while the boring ones lost only 1 species (25%) (Fig 3). A similar pattern was observed also at generic level with a loss of 20% of the genera recorded in 1973. The only boring genus (*Cliona*) was shared by both surveys; the number of cavity dwelling and encrusting genera was very similar, while the massive/erected genera lost 40%. From a taxonomic point of view, the most impressive reduction involved the subclass Keratosa that dropped from 14 species in 1973 to only 4 species in 2014. Also the species belonging to the sub-order Astrophorina were strongly reduced, shifting from 9 to 5. Other species, very abundant in 1973, were absent in 2014: for example, *Triptolemma simplex* and *Timea stellata* were

not more recorded, as well as the other two species of the genus *Timea* (*T. fasciata* and *T. irregularis*). The most frequently recorded species in 1973, *Eurypon vesicularis* and *Bubaris vermiculata*, although still present in 2014, showed a reduction in their abundance. On the contrary, the genus *Hymedesmia*, not found in 1973, was now recorded with at least three species.

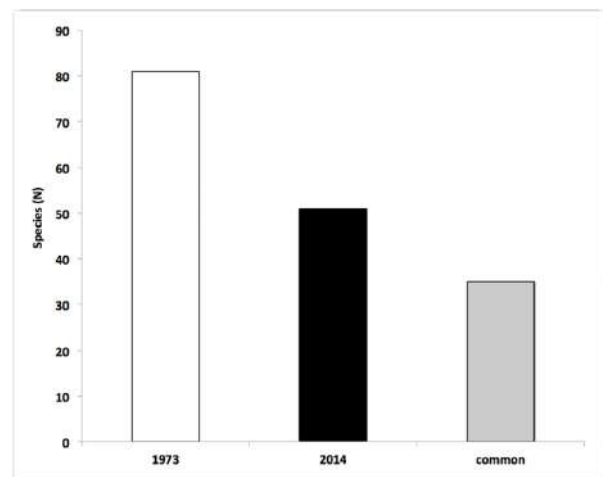


Fig 2. Sponge species number recorded in the Bogliasco coralligenous assemblage during the samplings of 1973 and 2014. The grey bar indicates the species number shared by the two surveys.

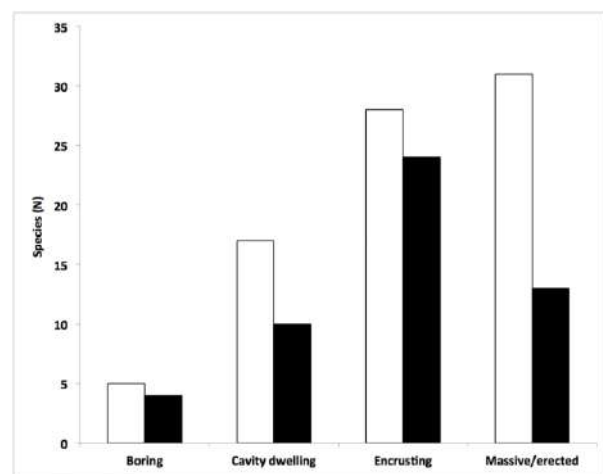


Fig 3. Sponge species number recorded in the Bogliasco coralligenous assemblage during the samplings of 1973 (white bars) and 2014 (black bars), according to the sponge different growth patterns. The main reduction was recorded within the massive/erect sponges.

Species	Growth pattern	Pansini & Pronzato (1973)	Present paper
Agelas oroides (Schmidt, 1864)	ME	0–10	20
<i>Hymenhabdia oxytrunca</i> Topsent, 1904	Ec	21–40	0
Axinella damicornis (Esper, 1794)	ME	0–10	13,3
<i>Axinella polyoides</i> Schmidt, 1862	ME	P	0
<i>Axinella</i> sp.	ME	0–10	0
Eurypon cinctum Sarà, 1960	Ec	P	6,6
<i>Eurypon clavatum</i> (Bowerbank, 1866)	Ec	0–10	0
<i>Eurypon</i> cf. <i>clavatum</i> (Bowerbank, 1866)	Ec	0	6,6
Eurypon major Sarà & Siribelli, 1960	Ec	P	13,3
Eurypon vesciculare Sarà & Siribelli, 1960	Ec	60–80	13,3
<i>Eurypon viride</i> (Topsent, 1889)	Ec	11–20	0
Eurypon sp.	Ec	0–10	6,6
<i>Raspaciona aculeata</i> (Johnston, 1842)	Ec	21–40	0
Bubaris vermiculata (Bowerbank, 1866)	Ec	60–80	6,67
<i>Desmanthus incrustans</i> (Topsent, 1889)	Ec	0–10	0
Acanthella acuta Schmidt, 1862	ME	P	20
Dictyonella incisa (Schmidt, 1880)	ME	P	13,3
<i>Dictyonella pelligera</i> (Schmidt, 1862)	Ec	0–10	0
Cliona celata Grant, 1826	Br	0–10	6,66
Cliona janitrix Topsent, 1932	Br	21–40	6,66
<i>Cliona lobata</i> Hancock, 1849	Br	0–10	0
<i>Cliona schmidtii</i> (Ridley, 1881)	Br	0	13,3
Cliona viridis Schmidt, 1862	Br	21–40	26,6
<i>Cliona</i> sp.	Br	0–10	0
Spirastrella cunctatrix Schmidt, 1868	Ec	11–20	13,3
<i>Diplastrella bistellata</i> (Schmidt, 1862)	Ec	21–40	0
<i>Haliclona (Gellius) angulata</i> (Bowerbank, 1866)	Cd	11–20	0
<i>Haliclona (Gellius) dubia</i> (Babic, 1922)	Ec	P	0
<i>Haliclona (Gellius) lacazei</i> (Topsent, 1893)	Ec	0	13,3
Haliclona (Gellius) sp.	Ec	0–10	6,6
Haliclona (Halichoclona) fulva (Topsent, 1893)	Ec	0–10	6,6
<i>Haliclona (Reniera) cf. mediterranea</i> Griessinger, 1971	Ec	0	13,3
<i>Haliclona (Reniera) cinerea</i> (Grant, 1826)	Ec	21–40	0
<i>Haliclona (Reniera) cratera</i> (Schmidt, 1862)	ME	0–10	0
Haliclona (Reniera) sp.	Ec	11–20	20
Haliclona (Soestella) valliculata (Griessinger, 1971)	Ec	11–20	13,3
Petrosia (Petrosia) ficiformis (Poiret, 1789)	ME	P	26,6
<i>Oceanapia</i> sp.	ME	0	6,6
<i>Acamus tortilis</i> Topsent, 1892	Cd	0–10	0
<i>Batzella inops</i> (Topsent, 1891)	Ec	0	6,67
Crambe crambe (Schmidt, 1862)	Ec	21–40	73
<i>Hymedesmia (Hymedesmia) baculifera</i> (Topsent, 1901)	Ec	0	6,6
<i>Hymedesmia (Hymedesmia) cf. gracilisigma</i> Topsent, 1928	Ec	0	6,6
<i>Hymedesmia (Hymedesmia) sp.</i>	Ec	0	6,6
<i>Phorbas fictitius</i> Bowerbank, 1866	Ec	0	13,3
Phorbas tenacior (Topsent, 1925)	Ec	11–20	40
Mycale (Mycale) massa (Schmidt, 1862)	ME	0–10	13,3
<i>Myxilla (Myxilla) rosacea</i> (Lieberkühn, 1859)	Ec	0	6,6
Polymastia inflata Cabiocch, 1968	ME	11–20	6,6
Halichondria (Halichondria) bowerbanki Burton, 1930	ME	21–40	6,6
<i>Halichondria (Halichondria) contorta</i> (Sarà, 1961)	Cd	21–40	0
Halichondria (Halichondria) genitrix (Schmidt, 1870)	Cd	11–20	20
<i>Halichondria (Halichondria) semitubulosa</i> Lieberkühn, 1859	ME	P	0
Halichondria sp.	Cd	P	20
<i>Hymeniacion perlevis</i> (Montagu, 1818)	Ec	0	6,6
Aptos aptos (Schmidt, 1864)	Cd	21–40	27
<i>Protosuberites epiphytum</i> (Lamarck, 1815)	Ec	0–10	0
<i>Suberites carnosus</i> (Johnston, 1842)	ME	0–10	0

<i>Terpios gelatinosa</i> (Bowerbank, 1866)	Ec	11–20	6,6
<i>Tethya aurantium</i> (Pallas, 1766)	ME	0–10	0
<i>Tethya citrina</i> Sarà & Melone, 1965	ME	21–40	0
<i>Timea fasciata</i> Topsent, 1934	Ec	21–40	0
<i>Timea irregularis</i> Sarà & Siribelli, 1960	Ec	0–10	0
<i>Timea stellata</i> (Bowerbank, 1866)	Cd	41–60	0
<i>Dercitus (Stoebea) plicatus</i> (Schmidt, 1868)	Cd	21–40	73,3
<i>Jaspis incrustans</i> (Topsent, 1890)	Cd	0	33,3
<i>Jaspis johnstonii</i> (Schmidt, 1862)	Cd	41–60	66,6
<i>Stelletta dorsigera</i> Schmidt, 1864	ME	0–10	0
<i>Stelletta lactea</i> Carter, 1871	Cd	0	6,6
<i>Erylus discophorus</i> (Schmidt, 1862)	Cd	21–40	20
<i>Erylus euastrum</i> (Schmidt, 1868)	Cd	21–40	0
<i>Geodia cydonium</i> Schmidt, 1862	Cd	0–10	0
<i>Penares helleri</i> (Schmidt, 1864)	Cd	21–40	0
<i>Caminella intuta</i> (Topsent, 1892)	ME	P	0
<i>Pachastrella monilifera</i> Schmidt, 1868	Cd	0–10	0
<i>Triptolemma simplex</i> (Sarà, 1959)	Cd	41–60	0
<i>Trachycladus minax</i> (Topsent, 1888)	ME	0–10	0
<i>Spongionella pulchella</i> (Sowerby, 1804)	ME	11–20	0
<i>Dysidea fragilis</i> (Montagu, 1818)	ME	0–10	0
<i>Dysidea</i> sp.	ME	11–20	0
<i>Pleraplysilla spinifera</i> (Schulze, 1879)	Ec	0–10	0
<i>Ircinia dendroides</i> (Schmidt, 1862)	ME	0–10	0
<i>Ircinia variabilis</i> (Schmidt, 1862)	ME	0	6,6
<i>Sarcotragus fasciculatus</i> (Pallas, 1766)	ME	P	0
<i>Sarcotragus spinosulus</i> Schmidt, 1862	ME	P	13,3
<i>Spongia (Spongia) nitens</i> (Schmidt, 1862)	ME	P	0
<i>Spongia (Spongia) officinalis</i> Linnaeus, 1759	ME	0–10	0
<i>Spongia (Spongia) virgultosa</i> (Schmidt, 1868)	Cd	41–60	20
<i>Spongia (Spongia) zimocca</i> Schmidt, 1862	ME	0–10	0
<i>Cacospongia mollior</i> Schmidt, 1862	ME	P	0
<i>Fasciospongia cavernosa</i> (Schmidt, 1862)	Cd	P	6,6
<i>Scalarispongia scalaris</i> (Schmidt, 1862)	ME	0–10	0
<i>Chondrosia reniformis</i> Nardo, 1847	ME	0–10	33,3
<i>Corticium candelabrum</i> Schmidt, 1862	ME	0–10	0
<i>Plakina dilopha</i> Schulze, 1880	Ec	P	0
<i>Plakina trilopha</i> Schulze, 1880	Ec	P	13,3
<i>Oscarella</i> sp.	ME	0	13,3
Boring species (Br)		5	4
Cavity dwelling species (Cd)		17	10
Encrusting species (Ec)		28	24
Massive/erect species (ME)		31	13
Total recorded species		81	51
Total species in common: 35			

Table 2. Percent abundance and growth pattern of the sponge species recorded during the two surveys. The species in bold were shared by the two surveys.

The study of the core samples indicated that the bioherms were always based on portions of rock emerging from the substratum. The thickness of these build-ups ranged, in the five considered core samples, from 9 to 45 cm, and their ages, estimated by ¹⁴C analysis, covered a span of time comprised between 600 and 3500 YBP (Table 1).

The age determination of all the examined cores indicated a non coherent sequence of the age of the layers with a linear temporal growth, showing older layers overlapping the younger ones. A gross reconstruction of the Bogliasco coralligenous sponge assemblages over a span of time of about 3000 years was possible thanks to the taxonomic analysis of

the siliceous spicules embedded in the sediment contained into the cavities of these bioherms (Fig 4). Forty genera in total were recognisable in the assemblage: 4 of them were of boring sponges, 14 genera of cavity dwelling and encrusting species, and 8 genera of massive/erect sponges (Table 3, S2, S3, S4, S5 and S6 Tables). Twenty-four genera recorded in the ancient-assemblages (60%) were observed again in the recent surveys (1973, 2014). However, among the four recorded genera of boring sponges, only *Cliona* was still present in the recent surveys, while *Spiroxya*, *Dotona* and *Alectona* were no more detected. Seventy-one, 58 and 57% of cavity dwelling, encrusting and massive/erected species respectively were in common with the recent sponge fauna of the build-ups. In particular, among the massive/erect genera, we have recorded the genus *Alveospongia* (fam. Heteroxyidae), determined on the basis of spiny microrhabdose microscleres (Fig 5). This genus, recently described in shallow-waters off Canavieiras (Bahia, Brazil) [21] was, until now, unknown in the Mediterranean Sea. The sponge diversity at generic level, evaluated at 500/250-year intervals, ranged between 19 and 33 genera, with a trend characterised by a sharp decreases from 3500–3000 to 3000–2500 YBP. After this period, the number of recorded genera regularly increased until 1500–1250 YBP and then progressively decreased until 1000–500 YBP (Fig 6).

From a quantitative point of view, it was observed that the total number of recorded spicules slightly decreased from 3500–3000 to 3000–2500 YBP and remained about constant until to 2000–1500 YBP. After this period, the value strongly increased in the period 1250–1000 YBP to decrease again in the most recent period (Fig 7).

The dominant spicules inside the bioherms were always the micrasters, belonging to some genera of the sub-order Astrophorina (probably *Jaspis*, *Geodia*, *Stelletta* and others). This quantity ranged from 75 to 87% of all the recorded spicules in all the considered periods.

4. Discussion

The sponge fauna of the Bogliasco coralligenous build-ups was analysed over both a decennial and millennial span of time. As already stated in similar habitats [22], the sponge assemblage showed a patchy distribution with significant differences in species richness among the considered build-ups. The comparison of the sponge diversity, recorded during the present survey, as well as that studied by Pansini and Pronzato [16] indicated a significant reduction of species richness (about 45%) in 40 years. The same analysis, conducted at generic level, indicated a loss of 20% of the genera present in the survey of 1973. This evidence is in agreement with the already known simplification of the superficial benthic communities of the

Mediterranean Sea occurred mainly as a consequence of a number of mass mortality events that took place also in the Ligurian Sea since 1986, when sponges were the principal casualties [15, 23, 24, 25, 26, 27].

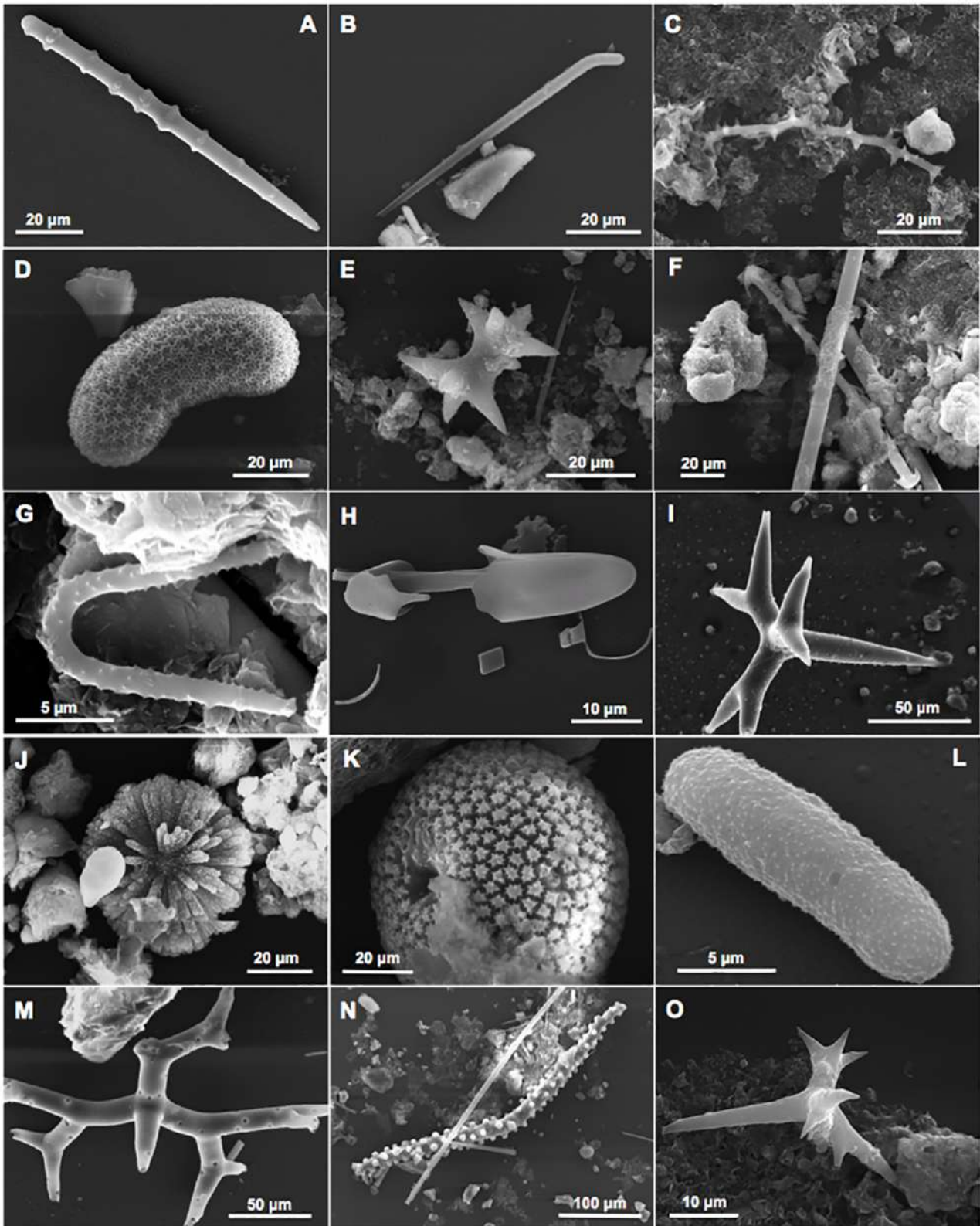


Fig 4. Examples of spicules embedded in the sediment inside the coralligenous crevices. A, achantostyle of *Agelas*; B, rhabdostyle of *Rhabderemia*; C, spiraster of *Cliona*; D, selenaster of *Placospongia*; E, diploster of *Diplastrella*; F, cladotylole of *Acarnus*; G, forcept of *Forcepia*; H, anisochela of *Mycale*; I, dichotriene of *Dercitus*; J, sterraster of *Erylus*; K, sterraster of *Geodia*; L, microstrongyle of *Pachastrella*; M, dichomesotriene of *Triptolemma*; N, tubercolate oxea of *Alectona*; O, dilophose calthrop of *Plakina*.

Recorded genera	Growth pattern	Considered spans of time (YBP)						
		500–1000	1000–1250	1250–1500	1500–2000	2000–2500	2500–3000	3000–3500
Agelas	Ms		X	X				
<i>Alveospongia</i>	Ms	X	X	X	X	X		X
Eurypon	Ec	X	X	X	X	X	X	X
<i>Rhabderemia</i>	Ms	X	X	X	X	X	X	X
Bubaris	Ec				X			
Acanthella	Ms	X	X	X	X	X	X	
Cliona	Br	X	X	X	X	X	X	X
<i>Dotona</i>	Br	X	X	X	X	X	X	X
<i>Spiroxya</i>	Br	X	X	X	X	X	X	X
<i>Placospongia</i>	Ec	X		X	X		X	X
Diplastrella	Ec	X	X	X	X	X	X	X
<i>Dendroxea</i>	Cd		X	X				
Petrosia	Ms	X	X	X	X	X		
Acarnus	Cd	X	X	X	X	X	X	X
Batzella	Ec		X		X			
<i>Forcepia</i>	Ec	X	X	X				
<i>Crella</i>	Ec	X	X	X	X	X		X
<i>Clathria</i>	Ec				X	X		
<i>Antho</i>	Ec	X	X	X	X	X	X	X
Mycale	Ec	X						
Myxilla	Ec					X		
Aaptos	Cd	X	X	X	X	X	X	X
Protosuberites	Ec	X	X	X	X	X	X	X
Tethya	Ms	X	X	X	X	X		X
Timea	Cd	X	X	X	X	X	X	X
Dercitus	Cd	X	X	X	X	X	X	X
Jaspis	Cd	X	X	X	X	X	X	X
Stelletta	Cd	X	X	X	X	X		X
Erylus	Cd	X	X	X	X	X	X	X
Geodia	Cd	X	X	X	X	X	X	X
Penares	Cd	X	X	X	X			
Pachastrella	Cd		X	X				
Triptolemma	Cd			X	X			
<i>Alectona</i>	Br			X				X
<i>Thoosa</i>	Cd	X		X	X	X	X	X
<i>Samus</i>	Cd	X	X	X	X	X		X
<i>Chondrilla</i>	Ms	X	X	X	X			X
Corticium	Ms		X					
Plakina	Ec	X	X	X	X	X	X	X
<i>Plakortis</i>	Ec		X			X		
Boring genera (Br)		3	3	4	3	3	3	4
Cavity dwelling genera (Cd)		11	12	14	12	10	8	10
Encrusting genera (Ec)		8	7	7	9	7	5	6
Massive/erect genera (ME)		6	8	7	6	5	2	4
Total recorded genera		29	32	33	31	27	19	25

Table 3. List of the genera identified on the basis of spicular remains recorded in the layers belonging to the considered spans of time. Genera in bold were also recorded in the recent surveys.

However, analysing the drop of the sponge diversity in this area, we cannot even rule out the impact of the date-mussels fishing

conducted on the coralligenous build-ups until 1998, when this destructive activity was banned along the Italian coasts [28].

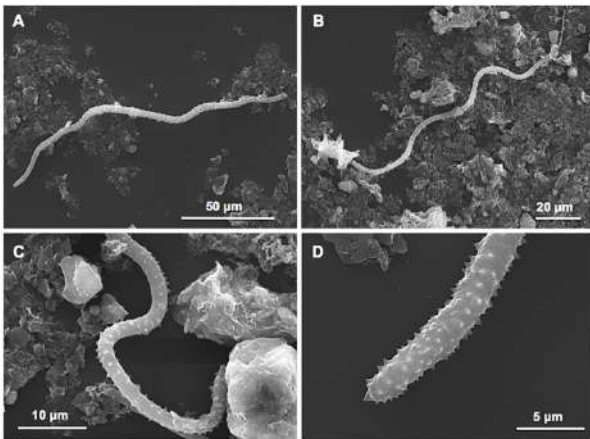


Fig 5. *Alveospongia* sp. A, B two different examples of sinuous acanthomicrostrongyles typical of the genus; C, detail of the microspiny surface of acanthomicrostrongyles; D, magnification of the acanthomicrostrongyles tip.

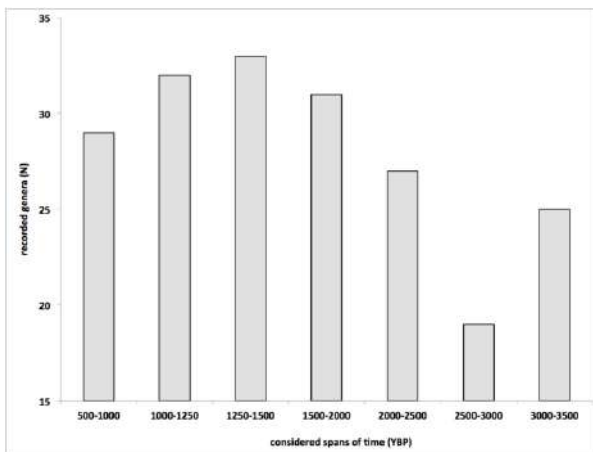


Fig 6. Number of sponge genera recorded in the considered periods. Note the sharp decreases corresponding to the temperature collapse at the end of the Bronze Age (3000–2500 YBP). After this period, the sponge diversity progressively increased during the Little Climatic Optimum (2500–1500 YBP) to decrease again during the Dark Age Cold Period (1500–1000 YBP).

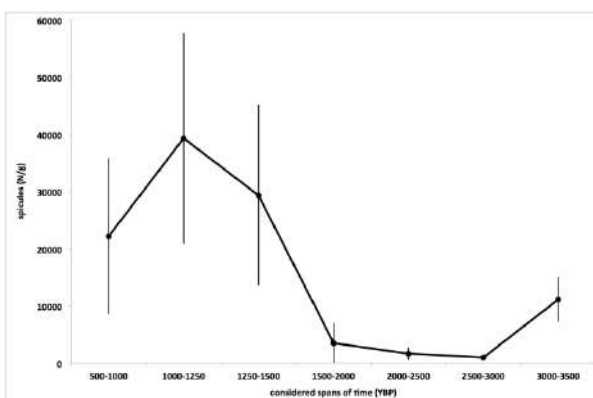


Fig 7. Average total spicule amount per sediment g (\pm SE) in each considered period.

It was already stated the long time necessary for the recovering of the benthic communities deeply stressed by this fishing [29].

Both at specific and generic level, the massive/erect sponges, and in particular the Keratosa, were the most prone to change in the last decades, suggesting that the species living in the inner habitat of the bioherms were less affected by the variations of the environmental conditions or by the human pressures than those present on the substratum surface.

Nevertheless also some cavity dwelling species as *Triptolemma simplex* and *Timea* spp., that 40 years ago were frequent, disappeared in the Bogliasco area. These species were recently recorded, although at major depth, along the Portofino Promontory that is close to the studied site [11, 14]. This depth change is in agreement with the effects of the global warming which drove some littoral species to disappear from shallow waters and eventually to move down deeper, within their bathymetric range of distribution, a phenomenon already recorded for other shallow water taxonomic groups [30, 31, 32].

Through the study of millennial variations of the sponge assemblage, we have presently recorded 24 genera of the ancient-assemblages (60%), suggesting a remarkable stability across a 3500 yrs span of time. However, in terms of growth patterns the sponge diversity did not remain homogeneous during this long span of time. It showed a

strong reduction of massive/erect species, while the cavity dwelling and boring ones decreased less (Fig 8). This evidence confirms, also on millennial span of time, the higher stability of the inner coralligenous habitat and underlines the strong attractiveness to sponge colonisation of this peculiar habitat both in terms of species diversity and biomass [11, 33].

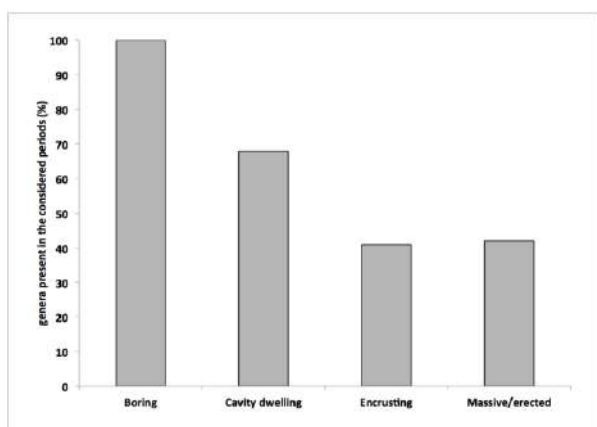


Fig 8. Percent of sponge genera recorded in all the considered periods according to the different growth patterns.

We have also to consider that in 3500 years the Mediterranean Sea witnessed at least five different climatic periods: the Late Bronze Age Collapse, a sharp temperature decrease occurred about 3000–2500 yrs BP, the Little Climate Optimum, a gradual drying and warm period between the Greek Classical Period (5th century BC) and the Late Roman Period (4th century AD), the Dark Ages Cold Period, a second short and cooler period between 4th and 9th century, the Medieval Warm Period (MWP), which characterised the Europe between 10th and 14th century, and finally

the Little Ice Age (LIA) that last from the 16th to the 19th centuries [34, 35, 36, 37, 38]. For example, the Medieval Warm Period favoured glacial melting which, ultimately, resulted in a salinity decrease and in a drop of 1–4°C in surface sea-water temperature [39], while the carbonate deposition seems to have had a halt. In fact, reduced air temperatures in spring and winter, or stochastic phenomena as floods, could have determined changes in seawater temperatures, salinity, turbidity and sediment regimes which, in turn, could have had relevant impact on the development of these bio-structures. This kind of phenomena can be at the base of the incoherent age determination of the coralligenous bioconstructions of Bogliasco. This puzzling situation, with older layers overlapping younger ones, could be related to favourable phases for carbonate deposition, alternate with partial destruction phases imputable, for example, to intense mud deposition after episodes of important floods. Fig 9 shows a hypothetical evolutionary scenario characterised by a first phase of algal growth on the rocky substrata resulting in pillar-like bioherm (Fig 9A), similar to those recorded from several regions of the Southern Mediterranean [8]. Periods of heavy floods could have increased the bottom sediments, partially or totally burying the pillars and killing the algal coverage (Fig 9B). During the burying or after the removal of the sediments, a part of the structure could be

prone to erosive processes, giving rise to mushroom-like structures (Fig 9C).

In following phases, the coralline algae could grow again in sciaphilous micro habitats, determining the irregular temporal layering of the structure (Fig 9D). In this situation, in a core sample, younger sheets can be overlapped by older ones. The temperature variations at millennial scale seemed to affect also the sponge richness: in fact, the number of genera observed in the bioherms decreased contemporaneously to the Late Bronze Age Collapse, to progressively increase during the Little Climate Optimum and to decrease again in the Dark Ages Cold Period. This datum is in good agreement with the sponge abundance (evaluated as average number of spicules) (Fig 10), suggesting that the warmer periods favoured the proliferation of the sponge assemblages. Also recent studies have put in evidence different responses in facing the global warming. In the Aegean Isle of Kos, for example, an increase, by one order of magnitude, of the overall abundance of the horny sponge *Ircinia retidermata* was estimated [40]. On the contrary, in a pre-coralligenous assemblage of the Portofino Marine Protected Area, sponges remained almost constant in terms of total coverage over a span of time of 25 years; red encrusting sponges (mainly *Crambe crambe* and *Spirastrella cunctatrix*) were always the most

abundant, but the massive/erect ones suffered the major losses [11, 41].

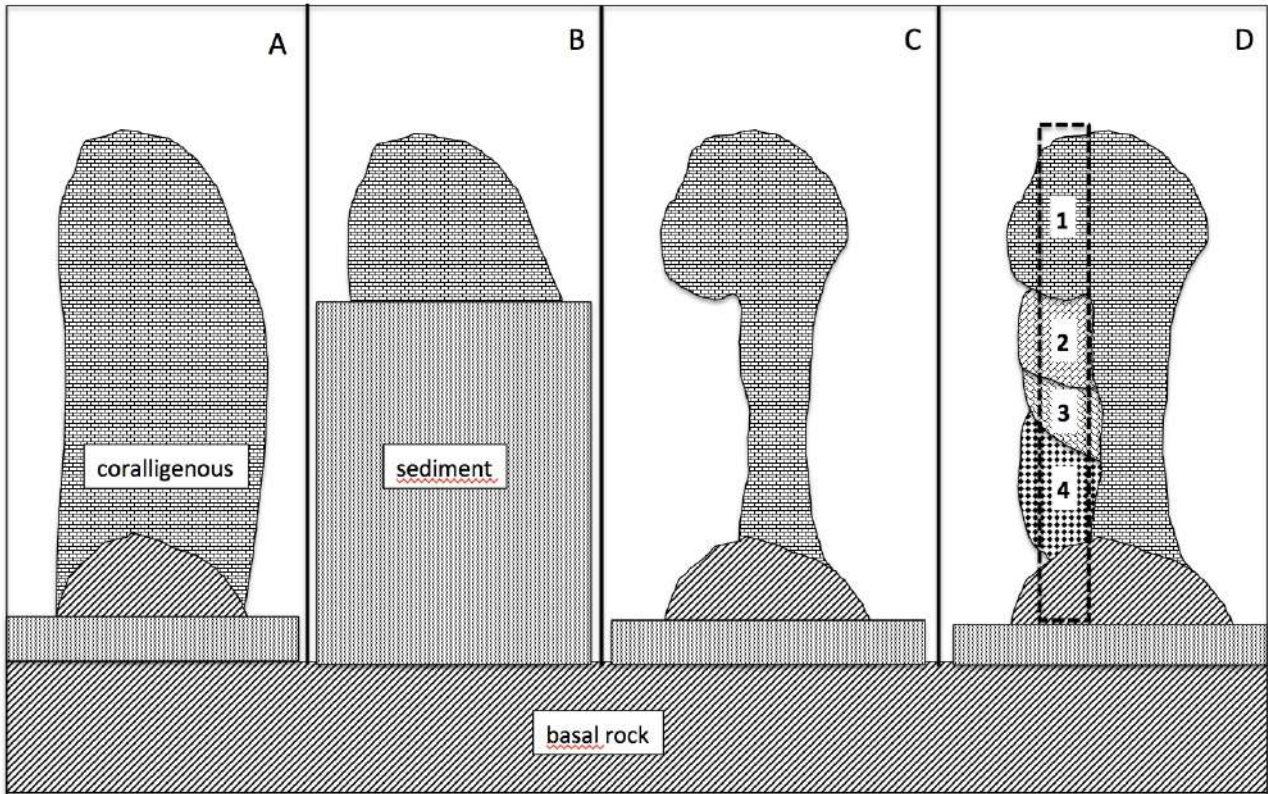


Fig 9. Hypothetical evolutionary scenario of the coralligenous accretions of Bogliasco. A) In a first phase the algal growth resulted in pillar-like bioherm. B) Periods of heavy floods could have increased the bottom sediments, partially or totally burying the pillars and killing the algal coverage. C) During the burying or after the removal of the sediments, a part of the structure could be prone to erosive processes, giving rise to mushroom-like structures. D) In following phases, the coralline algae could grow again in sciaphilous microhabitats, determining the irregular temporal layering of the structure (the number from 1 to 4 indicated different sheets of deposition from the oldest to the youngest). In this situation, in a core sample (dotted rectangle), younger sheets can be overlapped by older ones.

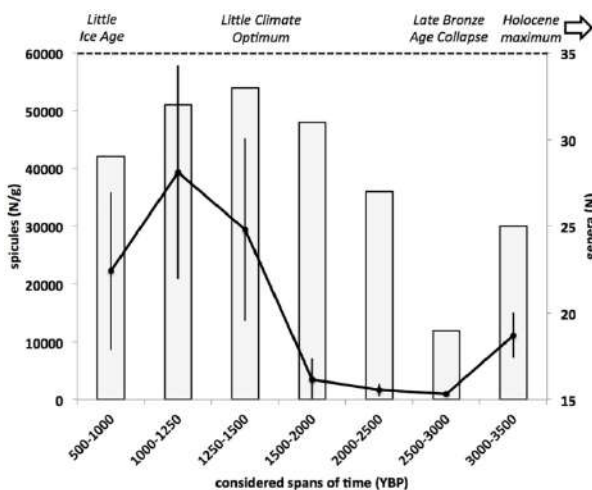


Fig 10. Trend of sponge diversity evaluated as number of genera present in each period (grey bars) compared with the trend of sponge abundance evaluated as average amount of spicules per sediment g present in the same periods.

It is remarkable that the comparison of the genera recorded in ancient assemblages and modern ones showed that the amounts of genera with cavity dwelling and encrusting habits remained quite constant, maintaining a comparable diversity along the entire development of the bioherms. On the contrary, the boring genera shifted from four in ancient assemblages, to only one. This evidence is in agreement with the shift of ancient boring communities dominated by the genera *Alectona*, *Thoosa*, *Dotona* to modern communities mainly characterised by species belonging to the genus *Cliona*, as already

recorded in coral reefs [42]. More caution is necessary in the evaluation of the increasing of massive/erect sponge genera in recent communities. In fact, a number of these sponges have no siliceous spicules and it is reasonable to expect that the spicules of massive species living on the build-up surface have less probability to be trapped into it.

The coralligenous communities are habitats of European Community interest (Flora Fauna Habitat Directive 92/43/EC, 1170–1114 Code: reefs) due to their high species richness and their important role in the balance of the carbonates at sea [2, 43, 44]. Moreover, they are potential indicators in monitoring the environmental quality of coastal waters according to the Marine Strategy Framework Directive (2008/56/EC). Unfortunately, these habitats are very vulnerable and their structures and biodiversity threatened not only by the changing climate conditions and temperature anomalies [45], but also by pollution, excessive sedimentation, turbidity, biological invasions, fishing and diving

activities, and by the synergistic effects of all these stressors [26, 46, 47]. Therefore these marine ecosystems have a high conservation value and it is required to maintain and restore their proper functioning to enable their preservation for future generations. The concerns raised in recent years towards the depletion of these habitats seem to be confirmed by the results of this study. In fact, the sponge fauna of the upper coralligenous, one of the most representative taxa of these habitats [14], has suffered in recent years a strong decrease in quali- and quantitative terms, showing, in the Ligurian Sea, a depletion which appears to have never been recorded before. The taxonomic analysis of siliceous sponge spicules, a powerful tool for a tentative reconstruction of ancient sponge assemblages [48, 49, 50], indicated that the sponge genera present in the coralligenous habitats remained enough stable in the last 3500 years [11].

Supporting information on Online version (See DOI)

S1 Table. Modern sponge species recorded in the 15 scraped standard areas and relative percent presence.

(DOCX)

S2 Table. Presence of spicules referred to different genera or supergeneric taxa in core sample 1.

(DOCX)

S3 Table. Presence of spicules referred to different genera or supergeneric taxa in core sample 2.

(DOCX)

S4 Table. Presence of spicules referred to different genera or supergeneric taxa in core sample 3.

(DOCX)

S5 Table. Presence of spicules referred to different genera or supergeneric taxa in core sample 4.

(DOCX)

S6 Table. Presence of spicules referred to different genera or supergeneric taxa in core sample 5.

(DOCX)

Acknowledgments

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Have climate changes driven the diversity of a Mediterranean coralligenous sponge assemblage on a millennial timescale?

Abstract

Changes occurring over a pluri-millennial span of time (6207–1767 yr B.P.) within the sponge assemblages present in two coralligenous pillars, about 60 cm high, collected at 20 m depth, inside the Marine Protected Area of Porto Cesareo (Ionian Sea, Mediterranean Sea) have been studied. The sponge diversity has been analyzed at generic level, using as a proxy the siliceous spicules trapped into the sediment present into the crevices of these bioherms. In total, 41 genera of ancient demosponges were identified. The modern sponge fauna of these coralligenous pillars totals 31 genera, 15 of them shared with the ancient assemblages. The sponge biodiversity during the considered span of time showed critical changes, with remarkably similar trends in both the considered pillars. Tentatively, these changes were attributed to different climatic events that affected the Mediterranean area during the studied time span. The number of genera, 6000 yr B.P., was low and increased between 5500 and 4000 yr B.P. During the Late Bronze Age (4000–3000 yr B.P.), a new decrease was recorded, followed by a further increase around 2000 yr B.P. Afterwards, the bioherms stopped growing and no more siliceous spicules were trapped. From a biogeographic point of view, the wide presence of spiny microrhabdose microscleres belonging to the genus *Alveospongia* (Heteroxyidae), recently described from the tropical Atlantic and still unknown in the Mediterranean Sea, has to be underlined. In addition, the trends recorded over time in the Ionian Sea match with those already observed in the Ligurian Sea. The comparison between the past periods and the modern one shows evident changes in biodiversity in both areas. The sharp variations of the seawater temperature occurred in both the Mediterranean regions could have driven the changes in genus richness. Using sponges to interpret the effects of climate changes can be a profitable strategy to unravel long term changes in biodiversity, supporting future predictions.

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1. Introduction

Climate changes have been proven to largely affect biodiversity of Mediterranean coastal habitats (Gatti et al., 2015; Bertolino et al., 2016; Betti et al., 2017; Longobardi et al., 2017). During the last decades, Mediterranean marine communities have shown significant changes in taxa composition and distribution. Simplifications of the superficial benthic communities have been also observed, often due to a sharp reduction in habitat formers (e.g. macroalgal and animal forests) (Gatti et al., 2015), caused by several mass mortality events of different invertebrates occurred from 1999 CE to 2006 CE (Cerrano et al., 2000; Garrabou et al., 2009). Understanding if these changes represent the signal of a directional trend driven by the global warming is one of present challenges of marine ecology. The possibility to reconstruct the dynamics of the benthic communities over a millennial span of time, crossing relevant climatic variations, can be critical for the interpretation of these modifications. The coralligenous communities characterize the Mediterranean rocky subtidal from 15 to 120 m depth. These carbonatic structures are mainly due to the activity of several encrusting calcareous algae (*Lithophyllum*, *Lithothamnion*, *Mesophyllum* and *Peyssonnelia*) that, in

the Holocene period, can be considered major builders together with a suite of other invertebrates with a calcareous skeleton. The shape of the build-ups is different according to local sedimentation rates, light intensity, water transparency, substrate slope and erosion effects (Laborel, 1961; Sartoretto et al., 1996; Garrabou and Ballesteros, 2000; Cerrano et al., 2001; Ballesteros, 2006; Teixidó et al., 2011; Boudouresque et al., 2016).

The carbonatic build-ups in shallow water often form columnar structures whose height is in relation to depth and sea level rise (Sarà and Pulitzer-Finali, 1970; Di Geronimo et al., 2002). They have begun to grow around 8000 yr B.P., when sea level was from 13.5 to 16.5 m lower than now (Sivan et al., 2001), due to glacio-hydro-isostatic effects and tectonic uplifts (Pirazzoli, 2005). About 2000 yr B.P. the deposition of the algal carbonate seemed to slow down or stop as balanced by the demolition processes of an array of adverse boring species (mainly sponges and bivalves) (Ballesteros, 2006).

Sponges, with more than 300 recorded species (Bertolino et al., 2013; Longo et al., 2017), are the most diversified group of macro-benthic organisms living on coralligenous formations. Several massive/ erect and encrusting species live on the conglomerate surface, but the greatest diversity is recorded inside the

concretions where sponges act both as borers and fillers of cavities and excavations (Bertolino et al., 2013; Calcinai et al., 2015).

The Mediterranean coralligenous bioconcretions represent an excellent opportunity to evaluate changes occurring in the fauna of hard substrates in the last part of the Holocene. Using sponge assemblages present in two coralligenous build-ups inside the Marine Protected Area (MPA) of Porto Cesareo (Ionian Sea), we were able to reconstruct changes in species composition and abundance occurred over a pluri-millennial span of time (6207–1767 yr B.P.) in this area. We anticipate that this study will provide critical insights on the possibility to use siliceous remains (Łukowiak et al., 2013; Łukowiak, 2016) trapped into sediments accumulated in these bio-constructions (Bertolino et al., 2014; in press) to address the challenge of understanding the effects of different climatic conditions on the invertebrates in the Mediterranean Sea.

2. Materials and methods

The two studied coralligenous columnar structures were collected in the MPA of Porto Cesareo, Ionian Sea (Fig. 1A–B), where numerous coralligenous pinnacles arise from the rocky bottom covered by a layer of sand about 30 cm thick (Fig. 1C). Sampling was performed by SCUBA

diving, during summer 2015, at 20 m depth.

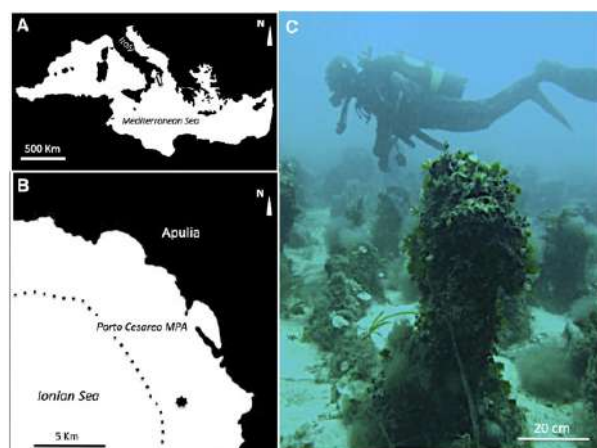


Fig. 1. A) General view of the Mediterranean Sea. The arrow indicates the position of the MPA of Porto Cesareo in the Ionian Sea. B) Map of the MPA. The asterisk indicates the sampling site. The dotted line shows the bathymetric line of 30 m depth. C) The underwater habitat of the MPA of Porto Cesareo at 20m depth with the coralligenous pillars.

All the living sponges present on the surface of the freshly collected bioherms were photographed and sampled. To collect sponges living inside the carbonate formation, as boring and cavity-dwelling species, the pinnacles were cut into slices about 4 cm thick by a stone saw and the presence of living specimens was ascertained by a stereo-microscope. Finally, from the central vertical slice of each pinnacle, small cubes with a side of about 4 cm (Fig. 2) were cut in order to obtain a sort of sliced core of the bioherm. Each cube was soaked for three days in hydrogen peroxide (240 vol), changing the solution daily, in order to release all the sediment entrapped into the cavities of the conglomerate.

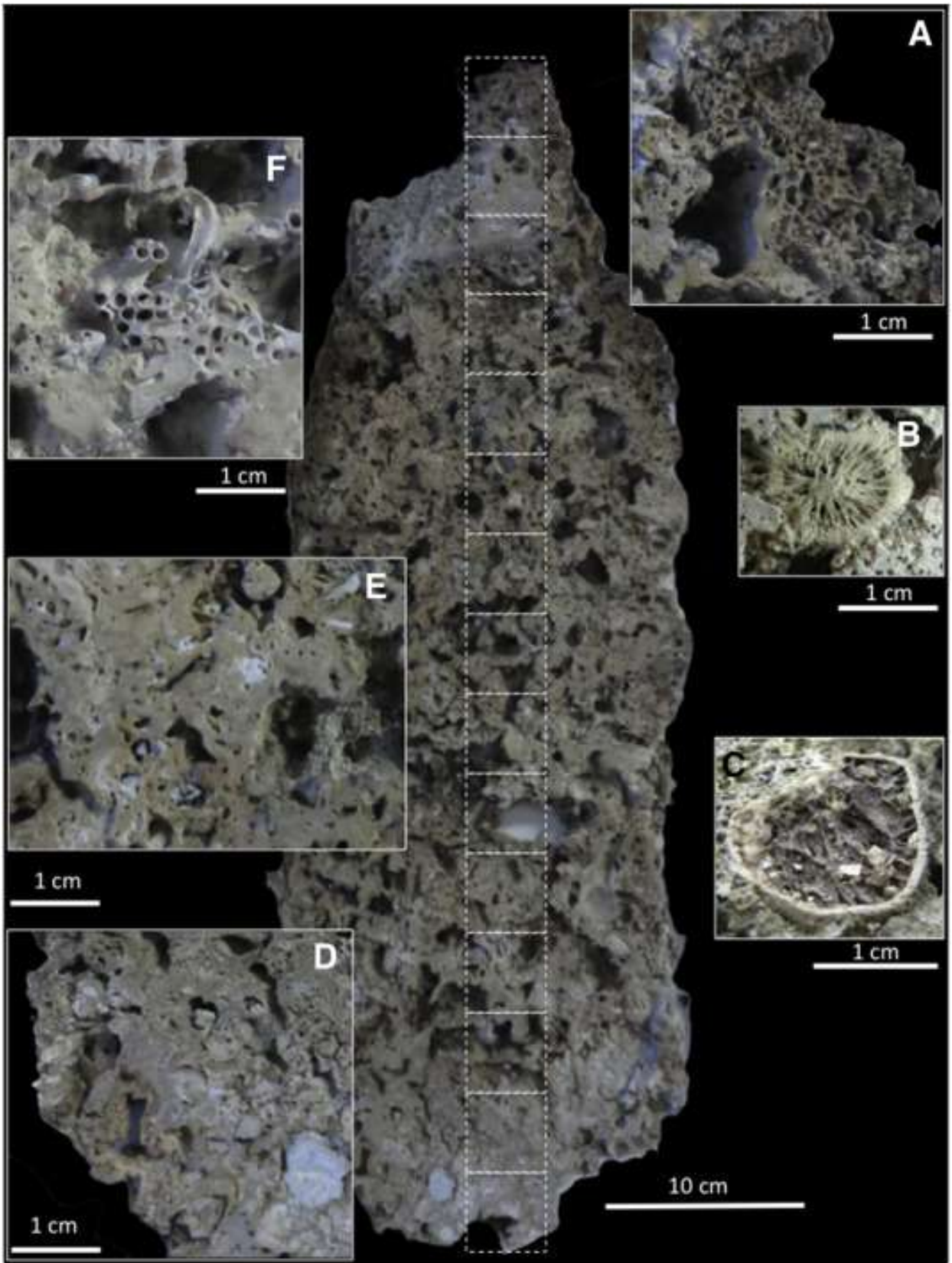


Fig. 2. Vertical section of a coralligenous pinnacle showing the complex three-dimensional inner structure characterised by layers of coralline algae, clusters of serpulid tubes and cavities. The central broken line represents the transect of cubes used for the study of the spicule assemblages over time. Immediately under the surface, groups of chambers, due to the action of boring sponges, are visible (A). In some larger crevices close to the surface, some living sponges as *Stelletta stellata* (B) and *Geodia cydonium* (C) are recognisable. A compact detritus filled the spaces and crevices among the calcified algae (D, E). The tubes of serpulids are the main animal component in the bioherm (F).

The pieces of conglomerate were removed and dried, while the obtained sediment was treated with boiling nitric acid to eliminate the carbonate fraction, rinsed twice in distilled water and twice in alcohol 95%, and dried. For each sample of sediment, three replicates of 10 mg each were mounted on a microscope slide. Microscopic analysis of the spicules contained in the sediment was performed to investigate the sponge species living in ancient times. Whenever possible, the embedded spicules were attributed to a sponge genus. After the sediment extraction, each portion of the conglomerate was ¹⁴C dated by Accelerator Mass Spectrometry (AMS) at the Center of Dating and Diagnostic (CEDAD) of the University of Salento (Calcagnile et al., 2005). Samples were converted to carbon dioxide by acid hydrolysis (H₃PO₄) and the extracted CO₂ was converted to graphite after cryogenic purification (D'Elia et al., 2004). Conventional radiocarbon ages were then calculated from the ¹⁴C/¹²C isotopic ratios measured with the AMS system after correcting for isotopic fractionation and chemical processing and machine background. Conventional radiocarbon ages were then calibrated in calendar years by using the MARINE13 (Reimer et al., 2013) curve and a $\Delta R=58\pm 15$ as average value for the Mediterranean Sea (Reimer and McCormac, 2002). Calibrated radiocarbon ages were expressed as cal yr B.P. and used in

the following chronological discussion and interpretations (Table 1).

Distance from the basal rock	Core samples	
	Pillar 1	Pillar 2
cm	Years before present (yr B.P.)	
0-4	6207 ± 60	6145 ± 50
4-8	6069 ± 45	5840 ± 50
8-12	6037 ± 45	5792 ± 45
12-16	5307 ± 45	5249 ± 45
16-20	4332 ± 45	4967 ± 45
20-24	4629 ± 45	5291 ± 45
24-28	4587 ± 45	4868 ± 45
28-32	3873 ± 45	4524 ± 45
32-36	3395 ± 45	3618 ± 45
36-40	3009 ± 45	4260 ± 45
40-44	2571 ± 45	3305 ± 45
44-48	2576 ± 45	3348 ± 45
48-52	2633 ± 45	3343 ± 45
52-56	2421 ± 45	2611 ± 45
56-60		1767 ± 45

Uncertainty refers to one standard deviation confidence level.
Present assumed as 1950 CE.

Table 1 Calibrated radiocarbon ages of the different layers of each core sample.

The diversity of the sponge assemblage during the entire duration of the coralligenous bioherms was estimated as presence/absence of the recorded genera. The persistence of the single genus on millennial scale was evaluated as percent presence of the spicules referred to that genus within all the samples of both pillars falling inside the considered millennium. On the whole, the contribution of each order to the sponge diversity was evaluated as percent abundance of the spicules referred to species of that order.

3. Results

The coralligenous bioherms present in the Porto Cesareo MPA are pillars with a diameter ranging from 20 to 35 cm and a height varying from 40 to 150 cm (Fig. 1). Longitudinal sections revealed that the pillars were made by coralline algae laid

perpendicularly to the growth axis. Abundant tubes of the serpulid *Protula* sp. were evident among the coralline algae and contributed to the building of the bio-structure. The inner crevices of the conglomerate were filled by compact fine sediments (Fig. 2). The ^{14}C measures along the main axis of the two considered pillars established their ages varying from 6207 to 2421 yr B.P. for pillar 1 and from 5145 to 1767 yr B.P. for pillar 2 (Table 1). These measurements indicated a coherent sequence of the layers with a linear temporal growth: the bioherms evolved quite regularly, showing growth rates of about 0,15 mm per year, very similar in both the pillars (Fig. 3).

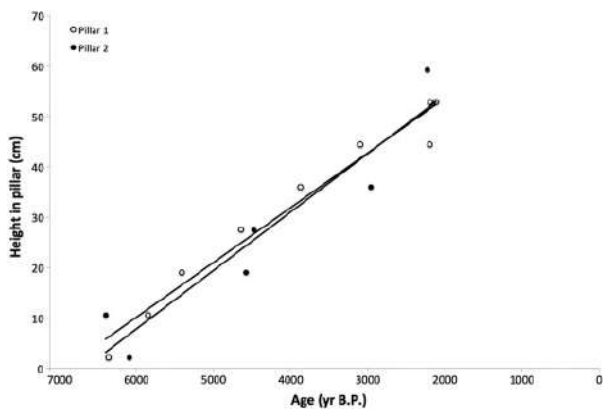


Fig. 3. Growth rate of the two examined pillars. The spots (black, Pillar 1; white, Pillar 2) are the carbon age determinations. In both the pillars, the rate of about 1.5 mm per decade seems constant.

In situ, the pillars were covered by a dense community of photophyllous macroalgae such as *Flabellia petiolata*, *Padina pavonica*, *Codium* sp. and *Halimeda tuna*, while sponges represented the dominant invertebrate group.

The living sponge fauna of these coralligenous build-ups comprised 49 species belonging to 31 genera (30 in pillar 1; 33 in pillar 2; 14 in common). Most of them (47) were demosponges, whose 45 with a skeleton made of siliceous spicules. Moreover, one species belonged to *Calcarea* and one to *Homosclerophorida*. About one third of these sponges showed an encrusting growth form, whereas massive/erect species were the 24% of the total. The boring species were the 16% and those that developed in all sort of cavities, conventionally called cavity dwelling species were the 26% (Table 2). The diversity of the paleo-sponge assemblage has been studied at generic level, analysing the siliceous spicules embedded in the sediment trapped into the crevices of these bioherms. In total, 41 genera were recognized in the two pillars (39 in pillar 1 and 21 in pillar 2, 19 in common). 15 of these genera were present also in the modern sponge fauna recorded on the two pillars (Table 3). The temporal study of the sponge richness variation showed very similar trends in the two pillars (Fig. 4). The sponge richness had an initial sharp increase that stopped about 6000 yr B.P. and remained stable until about 4000 yr B.P. Afterwards, species richness dropped again, reaching minimum values around 3500–3300 yr B.P. In the following millennium a slow recovery, which no more attained the maximum values recorded in the previous period, was finally observed.

Order	Species	Growth pattern	Pillar 1	Pillar 2	
Leucosolenida	<i>Sycon</i> cf. <i>humboldti</i> Risso, 1827	ME		X	
	<i>Eurypon gracilis</i> Bertolino, Pansini & Calcinai, 2013	Ec	X		
Axinellida	<i>Eurypon major</i> Sarà & Siribelli, 1960	Ec	X	X	
	<i>Eurypon viride</i> (Topsent, 1889)	Ec	X	X	
	<i>Eurypon</i> sp.	Ec	X		
	<i>Axinella damicornis</i> (Esper, 1794)	ME	X		
	<i>Axinella verrucosa</i> (Esper, 1794)	ME		X	
	<i>Acanthella acuta</i> Schmidt, 1862	ME	X	X	
	<i>Dictyonella marsilii</i> (Topsent, 1893)	Ec	X	X	
Bubarida	<i>Bubaris carcisis</i> Vacelet, 1969	Ec		X	
Clionaida	<i>Cliona celata</i> Grant, 1826	Br	X		
	<i>Cliona</i> cf. <i>celata</i> Grant, 1826	Br		X	
	<i>Cliona janitrix</i> Topsent, 1932	Br	X		
	<i>Cliona schmidtii</i> (Ridley, 1881)	Br	X	X	
	<i>Cliona viridis</i> (Schmidt, 1862)	Br		X	
	<i>Cliona</i> sp.	Br	X	X	
	<i>Pione vastifica</i> (Hancock, 1849)	Br	X		
	<i>Diplastrella bistellata</i> (Schmidt, 1862)	Ec	X		
	<i>Diplastrella ornata</i> Rützler & Sarà, 1962	Ec	X	X	
	<i>Spirastrella cunctatrix</i> Schmidt, 1868	Ec	X	X	
	Haplosclerida	<i>Haliclona</i> sp.	Ec		X
		<i>Petrosia</i> (<i>Petrosia</i>) <i>ficiformis</i> (Poiret, 1798)	ME	X	X
<i>Siphonodictyon insidiosum</i> (Johnson, 1889)		Br		X	
<i>Lissodendoryx</i> (<i>Anomodoryx</i>) <i>cavernosa</i> (Topsent, 1892)		Fl		X	
Poecilosclerida	<i>Crambe crambe</i> (Schmidt, 1862)	Ec		X	
	<i>Phorbas dives</i> (Topsent, 1891)	Ec	X	X	
	<i>Phorbas tenacior</i> (Topsent, 1925)	Ec	X		
	<i>Mycale</i> (<i>Aegogropila</i>) <i>tunicata</i> (Schmidt, 1862)	Ec		X	
	<i>Mycale</i> (<i>Mycale</i>) <i>lingua</i> (Bowerbank, 1866)	Ec	X		
	<i>Myxilla</i> (<i>Myxilla</i>) <i>rosacea</i> (Lieberkühn, 1859)	Ec		X	
Polymastiida	<i>Polymastia</i> sp.	ME		X	
	<i>Halichondria</i> (<i>Halichondria</i>) cf. <i>bowerbanki</i> Burton, 1930	ME	X		
Suberitida	<i>Halichondria</i> (<i>Halichondria</i>) <i>genitrix</i> (Schmidt, 1870)	Fl		X	
	<i>Aaptos aaptos</i> (Schmidt, 1864)	Fl	X	X	
	<i>Suberites</i> sp.	ME	X		
Tethyida	<i>Tethya aurantium</i> (Pallas, 1766)	ME	X		

	<i>Timea stellata</i> Topsent, 1934	<i>Fl</i>	X	X
Tetractinellida	<i>Dercitus (Stoeba) plicatus</i> (Schmidt, 1868)	<i>Fl</i>	X	X
	<i>Jaspis incrustans</i> (Topsent, 1890)	<i>Fl</i>	X	X
	<i>Jaspis johnstoni</i> (Schmidt, 1862)	<i>Fl</i>		X
	<i>Stelletta stellata</i> Topsent, 1893	<i>Fl</i>		X
	<i>Stelletta grubii</i> Schmidt, 1862	<i>Fl</i>		X
	<i>Calthropella (Corticellopsis) recondita</i> Pulitzer-Finali, 1983	<i>Fl</i>		X
	<i>Geodia conchilega</i> Schmidt, 1862	<i>Fl</i>	X	
	<i>Geodia cydonium</i> (Linnaeus, 1767)	<i>Fl</i>		X
	<i>Penares helleri</i> (Schmidt, 1864)	<i>Fl</i>		X
Dictyoceratida	<i>Spongia (Spongia) officinalis</i> Linnaeus, 1759	<i>ME</i>	X	
	<i>Spongia (Spongia) virgultosa</i> (Schmidt, 1868)	<i>ME</i>	X	
Homosclerophorida	<i>Oscarella</i> sp.	<i>ME</i>	X	

ME, massive/erect species; Ec, encrusting species; CD, cavity dwelling species; Br, boring species.

Table 2 List of the present sponge species recorded in the two pillars.

	Growth pattern	Pillar 1	Pillar 2	Considered periods (YBP)				
				7000-6000	6000-5000	5000-4000	4000-3000	3000-2000
<i>Agelas</i>	ME	X	X	X	X	X	X	X
<i>Hymerabdia</i>	Ec		X			X		
<i>Alveospongia</i>	ME		X	X	X	X	X	X
<i>Didiscus</i>	Ec		X			X		
<i>Eurypon</i>	Ec	X	X	X	X	X	X	X
<i>Rhabderemia</i>	ME	X	X	X	X	X	X	X
<i>Bubaris</i>	Ec		X		X	X	X	
<i>Monocrepidium</i>	Ec		X			X	X	
<i>Acanthella</i>	ME	X	X	X	X	X	X	
<i>Cliona</i>	Br	X	X	X	X	X	X	X
<i>Dotona</i>	Br		X		X	X	X	X
<i>Spiroxya</i>	Br	X	X	X	X	X	X	X
<i>Placospongia</i>	Ec		X		X	X	X	X
<i>Diplastrella</i>	Ec		X	X	X	X	X	X
<i>Spirastrella</i>	Ec		X	X	X	X	X	X
<i>Haliclona (Gellius)</i>	Ec		X		X			
<i>Petrosia</i>	ME	X	X	X	X	X	X	X
<i>Acarnus</i>	Fl	X	X	X	X	X	X	X
<i>Batzella</i>	Ec		X		X	X	X	X
<i>Crella</i>	Ec		X			X	X	
<i>Clathria</i>	Ec		X				X	X
<i>Antho</i>	Ec		X		X			
<i>Myxilla</i>	Ec	X		X				
<i>Aaptos</i>	Fl	X	X	X		X		
<i>Protosuberites</i>	Ec		X		X	X	X	X
<i>Tethya</i>	ME	X	X	X	X	X	X	X
<i>Timea</i>	Fl		X		X	X	X	X
<i>Dercitus (Stoeba)</i>	Fl	X	X	X	X	X	X	X
<i>Stelletta</i>	Fl	X	X	X	X	X	X	X
<i>Erylus</i>	Fl	X	X	X	X	X	X	X
<i>Penares</i>	Fl		X	X	X	X	X	
<i>Geodia</i>	Fl		X	X	X	X	X	X
<i>Pachastrella</i>	Fl	X		X	X	X		
<i>Triptolemma</i>	Fl	X	X	X	X	X	X	X
<i>Alectona</i>	Br	X	X	X	X	X	X	X
<i>Delectona</i>	Br	X	X		X	X	X	X

<i>Thoosa</i>	Br	X	X	X	X	X	X	X
<i>Samus</i>	Fl	X	X	X	X	X	X	
<i>Chondrilla</i>	ME		X	X	X	X	X	X
<i>Corticium</i>	ME		X		X		X	
<i>Plakina</i>	Ec	X	X	X	X	X	X	X
TOTAL		21	39	26	34	36	34	27

In bold, the genera found also in the present pillar assemblage. ME, massive/erect species; EC, encrusting species; CD, cavity dwelling species; Br, boring species.

Table 3 List of genera recorded in the past considered periods in both the pillars.

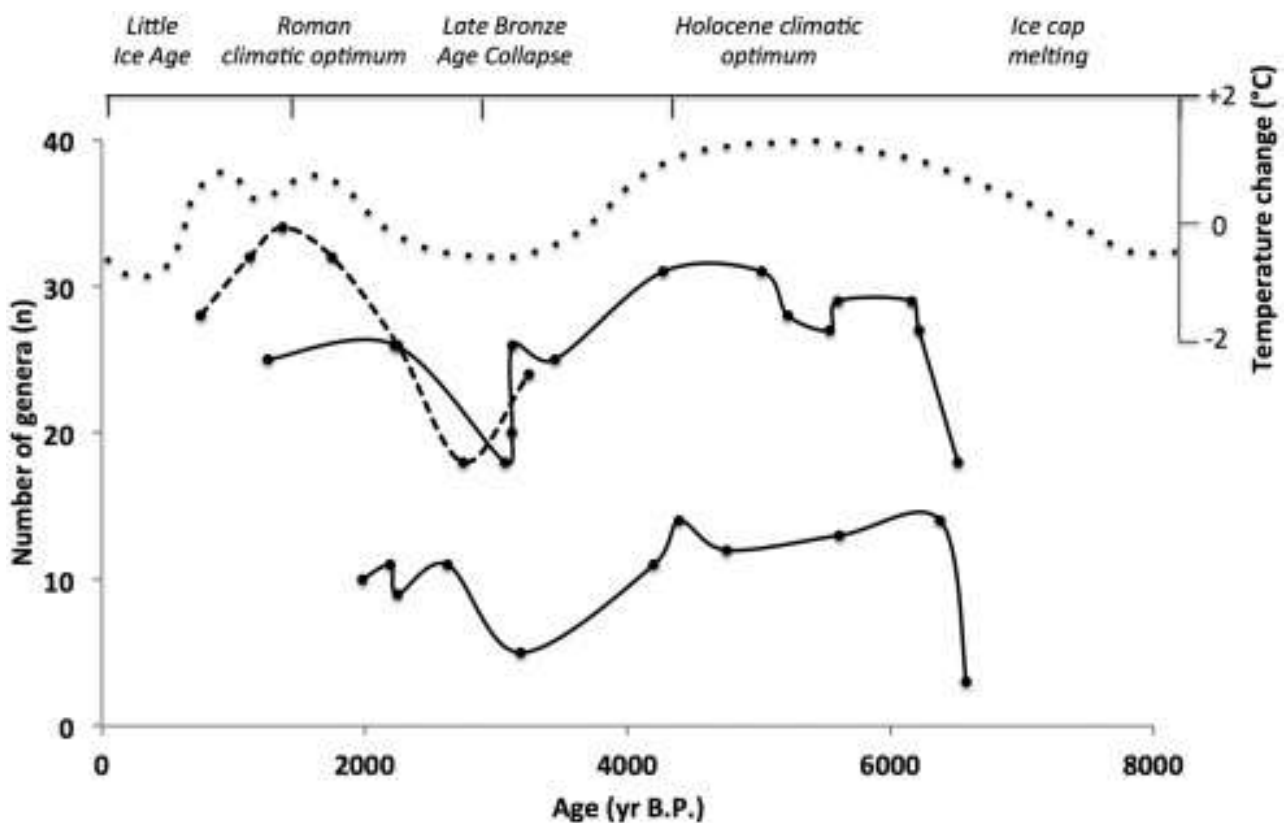


Fig. 4. Trends of the number of sponge genera recorded in each layer of both the pillars (continuous lines a and b). The dashed line represents the trend of the genus number recorded in coralligenous outcrops from Bogliasco, Ligurian Sea (Bertolino et al., 2017). The trend is in agreement with the estimated temperature variations in the Northern Hemisphere during the same span of time (Folland et al., 1990). Note the low values recorded in both the pillars about 6500 yr B.P. at the end of the *melting ice cap*, the high values recorded for about two millennia during the *Holocene maximum*, the drastic decrease recorded about 3300 yr B.P. in coincidence with the *Bronze Age temperature collapse*, followed by a new increase during the *Roman Climatic Optimum* and finally by a new decrease in the *Little Ice Age*.

At the level of single genera (Fig. 5), the analysis revealed that some genera among the massive/erect sponges, as *Petrosia*, *Tethya*, *Agelas* and *Rhabderemia*, were quite constantly present in all the studied periods, while others, as *Alveospongia*, *Chondrilla*, *Achantella* and *Corticium*, were almost or exclusively present from 6000 to 3000 yr B.P., with strong reductions or disappearance at the two temporal extremes of the studied period. The latter pattern was typical of a great part of the encrusting genera. Only one third of them (*Myxilla*, *Spirastrella*, *Diplastrella*, *Plakina*, *Eurypon*) were already present, although with a low persistence, in the oldest considered period. Numerous other genera appeared in the intermediate millennia to reduce again in the more recent one. The sponges living inside the coralligenous bioherms (cavity dwelling and boring) appeared more persistent. Nevertheless out of the 6 boring genera recorded, only *Cliona* (mainly due to *C. janitrix*) is present in the living sponge assemblage.

Particularly significant was the record of sinuous acanthomicrostrongyles referable to the genus *Alveospongia*, recently described from Brazil (Santos et al., 2016) which were present in pillar 2 although with variable abundance (Fig. 5).

The quantitative contribution of different kinds of spicules was estimated at level of order. In both the pillars, the spicules belonging to the order Clionaida were the

most abundant (32% and 42% in pillar 1 and pillar 2, respectively), followed by those belonging to Tetractinellida (25% and 10%), Haplosclerida (25% and 6%), Heteroscleromorpha (12% and 1%), Tethyida (3% and 4%). In pillar 2 a high percent of spicules of Bubarida (25%), almost negligible in pillar 1, was recorded (Fig. 6).

4. Discussion

Both the carbonate pillars have shown a regular, continuous growth during their life. Since about 6000 yr B.P. they continued to develop until around 2000yr B.P. when they stopped growing, sharing a common trend with all the Mediterranean coralligenous formations (Ballesteros, 2006). Their growth rate (0.15 mm per year) was comparable with that recorded by Di Geronimo et al. (2001) for similar pillars (0.27 mm/year) found in the southern Ionian Sea. The stop of growth was explained by the stable, but rather unfavourable, environmental conditions resulting from the decrease in irradiance caused by the sea level variation occurred in the last millennia (Ballesteros, 2006). The structure of the studied pillars showed a high contribution of carbonate tubes of large serpulids, differently from what observed in the Ligurian Sea (Bertolino et al., 2014, 2017), where the algal component was largely dominant. The importance of serpulids was already detected in the bioherms of Southern Ionian Sea (Di Geronimo et al., 2001).

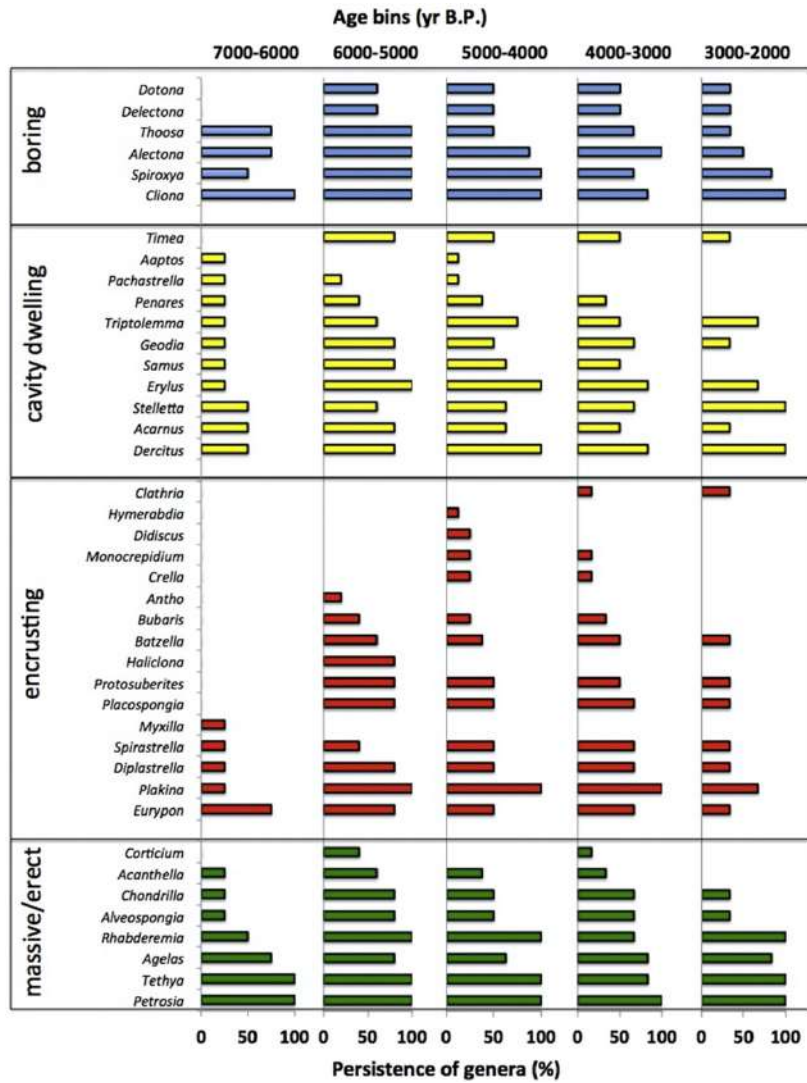


Fig. 5. Persistence of the sponge genera characterised by the different growth patterns in the layers obtained by both the pillars grouped in periods of 1000 years. Abundance is calculated as percent presence of a single genus in all the layers of a specific millennium.

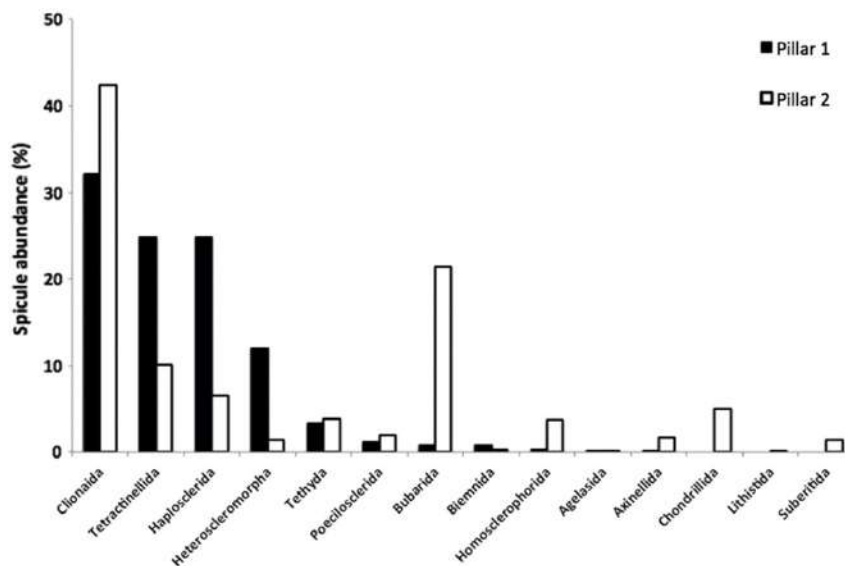


Fig. 6. Percent composition of the spicules - grouped at level of orders - in the two pillars. Black bars, Pillar 1; white bars, Pillar 2.

Moreover, serpulids were able to build pseudo-stalactites as those found in the caves of the Otranto Cape, close to Porto Cesareo. The latter bioherms have had a growth rate comparable to our pillars in the first phase of their development (15.6 mm/100 yr) that progressively decreased during time, reaching a final value of 3.8 mm/100 yr (Belmonte et al., 2009). The wide presence of serpulid aggregations inside the bioherms can probably be a specific feature of the pillar-like coralligenous formations typical of southern Mediterranean coasts. The modern sponge fauna of the build-ups off the Apulia coasts was studied by Sarà (1966, 1969), but a more comprehensive list of sponge species was provided by Corriero et al. (2004) and Longo et al. (2017) who focussing on the area of Porto Cesareo (Ionian Sea), recorded in total 66 species, 40 of which from coralligenous pillars. During our survey we found 49 sponge species, 18 of which were shared with the list of Corriero et al. (2004). These data indicate that the sponge fauna of this habitat is extremely rich and far from a complete knowledge. The richness of the ancient sponge assemblages showed significant changes in the considered time span, but remarkably similar trends were observed in both the considered pillars. Moreover the trend of sponge diversity is in agreement with the change of temperatures estimated for the Northern Hemisphere in the same span of time (Folland et al., 1990). The considered

bio-constructions have probably begun to grow 8000 yr B.P. in very shallow water, following the melting of the former Northern Hemisphere ice cap and Alp glaciers: in these conditions, the sponge assemblage was poor. In fact, according to many authors (Antonioli and Oliverio, 1996; Antonioli et al., 2001, 2002; Lambeck et al., 2004; Taricco et al., 2009) the Mediterranean sea level rose from -10 to -4 m about 6500 yr B.P., a time very close to the measured birth date of the Otranto pseudo-stalactites, at present sampled at a depth of -8 m (Belmonte et al., 2009). Afterwards, between 6500 and 4000 yr B.P., during the Holocene Climatic Optimum, the sea level increased gradually and the sponge assemblage became more complex, reaching a generic richness never again achieved in the following periods. During the temperature decreases of the Late Bronze Age Collapse (4000–3000 yr B.P.) (Drake, 2012), a new reduction was recorded, followed by a subsequent increase around 2000 yr B.P., in relation with the Roman Climatic Optimum. Afterwards, the bioconcretions stopped growing, probably because the reduction of light intensity caused by the sea level rise, reduced the algal growth that was balanced by the boring sponge activity (Ballesteros, 2006). In these conditions, no more siliceous spicules were trapped (Fig. 4). As a whole the Porto Cesareo sponge community, from a quantitative point of view, was dominated by boring sponges, particularly Clionids,

accounting for more than one third of the totally recorded spicules. It is intriguing that *Cliona* was constantly recorded during the entire life of the bioconcretions whereas other sponge boring genera, like *Spiroxya*, *Dotona*, *Delectona*, *Thoosa* and *Alectona*, were not more recorded in the living assemblage. A similar situation was also recently observed in the coralligenous formations from the Ligurian Sea (Bertolino et al., 2017), recalling the observations of Wiedenmayer (1994) from tropical coral reefs.

From a biogeographic point of view, it is worth stressing the wide presence of sinuous acanthomicrostrongyles belonging to *Alveospongia*, a genus of Heteroxyidae recently described by Santos et al. (2016) from the tropical Atlantic and also found in the paleo-assemblages of the coralligenous build-ups of the Ligurian Sea (Bertolino et al., 2017).

It is also remarkable that the trends recorded in the Ionian Sea match with those observed in the Ligurian Sea (Bertolino et al., 2017). In particular, by comparing past and modern periods, a significant change in biodiversity was evident in both the areas, whereas the loss in genus richness could be related to sharp decreases of seawater temperature (Fig. 4). In the light of these results, we can confirm that a better interaction between the paleoecological and geophysical studies in the Mediterranean area might contribute to improve our knowledge on the evolution of

the littoral benthic communities in the last millennia as underlined by Pirazzoli (2005).

5. Conclusions

Sponges represent the main taxon characterizing the Mediterranean coralligenous bioconcretions and their siliceous spicules appear a good proxy to evaluate the different assemblages that have occurred on and inside these build-ups over a multi-millennial span of time. The regular, continuous growth during the last 6000 yr of the two considered carbonated pillars, about 60 cm high, collected at 20 m depth within the Porto Cesareo MPA (Ionian Sea), allowed to evaluate the sponge richness over a considerable span of time. In total, 41 genera were identified among the ancient demosponges, and 31 genera in the living assemblage, showing remarkable changes in the number of recorded taxa. Only 15 living genera are shared with the ancient assemblages. From a quantitative point of view, the Porto Cesareo sponge community was dominated by boring sponges, particularly Clionids, accounting for more than one third of the totally recorded spicules. Tentatively, the diversity changes were attributed to the different climatic events that affected the Mediterranean area during the studied time span. Probably the considered pillars started to grow 8000 yr B.P. when the effects of ice cap melting were still very significant with low water temperature and

high salinity: with these ecological conditions the sponge assemblage was poor. Afterwards the sponge richness appeared to increase during warmer periods and decrease during the cooler ones: this phenomenon is still observed in other Mediterranean regions as the Ligurian Sea. In synthesis, the sharp variations of sea water temperature that occurred in both the Mediterranean regions could have driven the changes in genus richness. Using sponges to interpret the

effects of climate change can be a profitable strategy to unravel long-term changes in biodiversity, supporting future predictions on the environmental evolution.

These considerations are in agreement with recent evidences of a good persistence, and in some case of an abundance increasing of the Mediterranean sponge communities subject to recent water warming episodes (Betti et al., 2017; Bianchi et al., 2014).

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Ancient and recent sponge assemblages from the Tyrrhenian coralligenous over millennia (Mediterranean Sea)

Abstract

The demosponge siliceous spicules, entrapped in the Mediterranean coralligenous bioherms, are a good tool for reconstructing the sponge ancient communities across time, also allowing a comparison with the current biodiversity. The aim of this paper has been the description of the ancient sponge assemblages of the coralligenous bioherms grown up in the Tavolara Capo Coda Cavallo Marine Protected Area (northeastern Sardinia, Tyrrhenian Sea) between 5800 and 3700 YBP and its comparison with the living sponge community. On the base of radiocarbon age determinations, it was possible to estimate that these bioherms cover a span of time ranging from the Holocene Climatic Optimum until the Bronze Age Crisis. Their growth rates, 0.21–0.24 mm year⁻¹, were of the same order of estimations conducted around the Mediterranean. The Tavolara ancient sponge diversity was compared with those found in ancient accretions from Ligurian Sea and Ionian Sea. Our results supported the already described general trend, supporting the hypothesis that the genus richness in the coralligenous bioherms was driven by climatic vicissitudes. Nevertheless, our data strongly indicated that the sponge diversity is also related to the conditions of the coralligenous structures: in the accretions characterized by an active growth of coralline algae the number of sponge genera is similar to those recorded in the ancient assemblages while in coralligenous where the accretion is stopped the number of sponge genera strongly decreases probably due to the competition with frondose macroalgae.

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1. Introduction

The Mediterranean rocky subtidal zone is often characterized by carbonate bioherms, generally called coralligenous, present from 15 to 120 m depth (Ingrosso et al. 2018), according to water transparency and dynamics. The thickness of these structures varies from a few centimeters to more than 2 m (Ballesteros 2006), with different and complex geomorphotypes (Bracchi et al. 2017). These build-ups are mainly due to the millenarian deposition of some encrusting calcareous red algae (*Lithophyllum*, *Lithothamnion*, *Mesophyllum*, *Neogoniolithon*) whose remains were cemented by microbial carbonates (Laborel 1961, 1987; Laubier 1966; Sartoretto et al. 1996; Garrabou and Ballesteros 2000; Riding 2000; Giaccone 2007; Teixidó et al. 2011; Guido et al. 2013; Pergent-Martini et al. 2014). They began growing along the Mediterranean coast when the effect of ice cap melting was still significant (Pirazzoli 2005) and the sea level was from 13.5 to 16.5 m lower than now (Sivan et al. 2001), reaching their major development during the Flandrian transgression. In fact, the oldest bioherms go back to 7700 YBP (Sartoretto et al. 1996; Ballesteros 2006), while those present in shallower waters, were dated around 6000 YBP (Bertolino et al. 2017a, b). The animal contribution to these structures was generally considered negligible (Hong 1980; Ros et al. 1985), although columnar

bioherms, including a large amount of serpulid tubes, are known mainly in the Ionian Sea (Di Geronimo et al. 2002; Belmonte et al. 2009; Bertolino et al. 2017b). In addition, it is well known that some endolithic sponges (*Cliona* and allied species) (Cerrano et al. 2001), polychaetes (*Polydora* and allied species) (Dagli et al. 2011), bivalves (*Rocellaria*, *Lithophaga*) (Schiaparelli et al. 2005) and sea-urchins (*Sphaerechinus granularis*) (Sartoretto and Francour 1997) with their different activities favor the carbonate crumbling. The coralligenous bioherms have hosted and host rich assemblages of demosponges, generally characterized by a skeleton composed by siliceous spicules. Actually, more than 300 species were found in these bioherms, showing different growth forms: erect and massive, encrusting, filling as well as boring (Bertolino et al. 2013, 2014; Longo et al. 2017).

The demosponges linked to coralligenous habitats left their spicules entrapped into the cavities of these bio-concretions over 6000–8000 years, where they were gradually obliterated by a thin silt. The study of these remains through dated core samples has allowed to evaluate the changes of sponge biodiversity in the coralligenous on a millennial timescale, evidencing that sponge diversity changes were driven mainly by water temperature (Bertolino et al. 2017a, b). In particular, between 6000 and 4500 YBP,

during the Holocene Climatic Optimum, the sponge assemblage of the bioherms became very complex, reaching a generic richness never again achieved in the following ages (Bertolino et al. 2017b).

The first aim of this paper has been the study of the variations of the composition, at millennial scale, of the sponge assemblage within the coralligenous bioherms present in the Tavolara Capo Coda Cavallo Marine Protected Area (northeast Sardinia, Tyrrhenian Sea) (Fig. 1a, b), and its comparison with the living community. Moreover, the data and trends recorded in the Tavolara Island coralligenous were compared with those obtained from other accretions present in other Mediterranean localities (Bertolino et al. 2017a, b) at different depths and with different growth dynamics and fates.

2. Materials and methods

Ancient and present sponge assemblages were studied in two coralligenous bioherms (outcrops 1 and 2, with a volume of about 40 dm³ respectively) (Fig. 1c, e, f) collected at 42 m depth within the Tavolara Capo Coda Cavallo Marine Protected Area (northeast Sardinia, Tyrrhenian Sea). Samplings of coralligenous conglomerates were performed by SCUBA diving during summer 2016. After collection, the build-ups were divided into vertical slices about 4 cm thick by a stone saw. All the living sponges present on the surface of the conglomerates and those boring

or filling the cavities—detected by a visual analysis of the slice—were collected and identified.

Finally, from the central slice of each build-up, a longitudinal transect (40 cm height, block 1 and 48 cm height, block 2), oriented from the apex to the bottom, was conducted and divided in serial sub-samples (8 and 10, respectively) about 5 cm thick (Fig. 1d). The thin sediments filling the crevices among algal strata were released by soaking each piece in hydrogen peroxide (60 wt%), changed three times at 24h intervals. The sponge spicules present in the released sediments were concentrated by dissolving the carbonate fraction with boiling nitric acid. For each sample of sediment, three replicates of 10 mg each were mounted on a microscope slide. Microscopic analysis of the spicules extracted from the sediment was performed to investigate the sponge communities up to the lower possible taxonomic level. After the sediment extraction, each portion of the conglomerate was ¹⁴C dated by accelerator mass spectrometry (AMS) at the Center of Dating and Diagnostic (CEDAD) of the University of Salento (Calcagnile et al. 2005). Calibrated radiocarbon ages were expressed as calBP and used in the chronological discussion and interpretation. The diversity between the current sponge assemblage and those observed in the past (5800–4700 YBP) was estimated as presence/absence of the recorded species (Table 1).

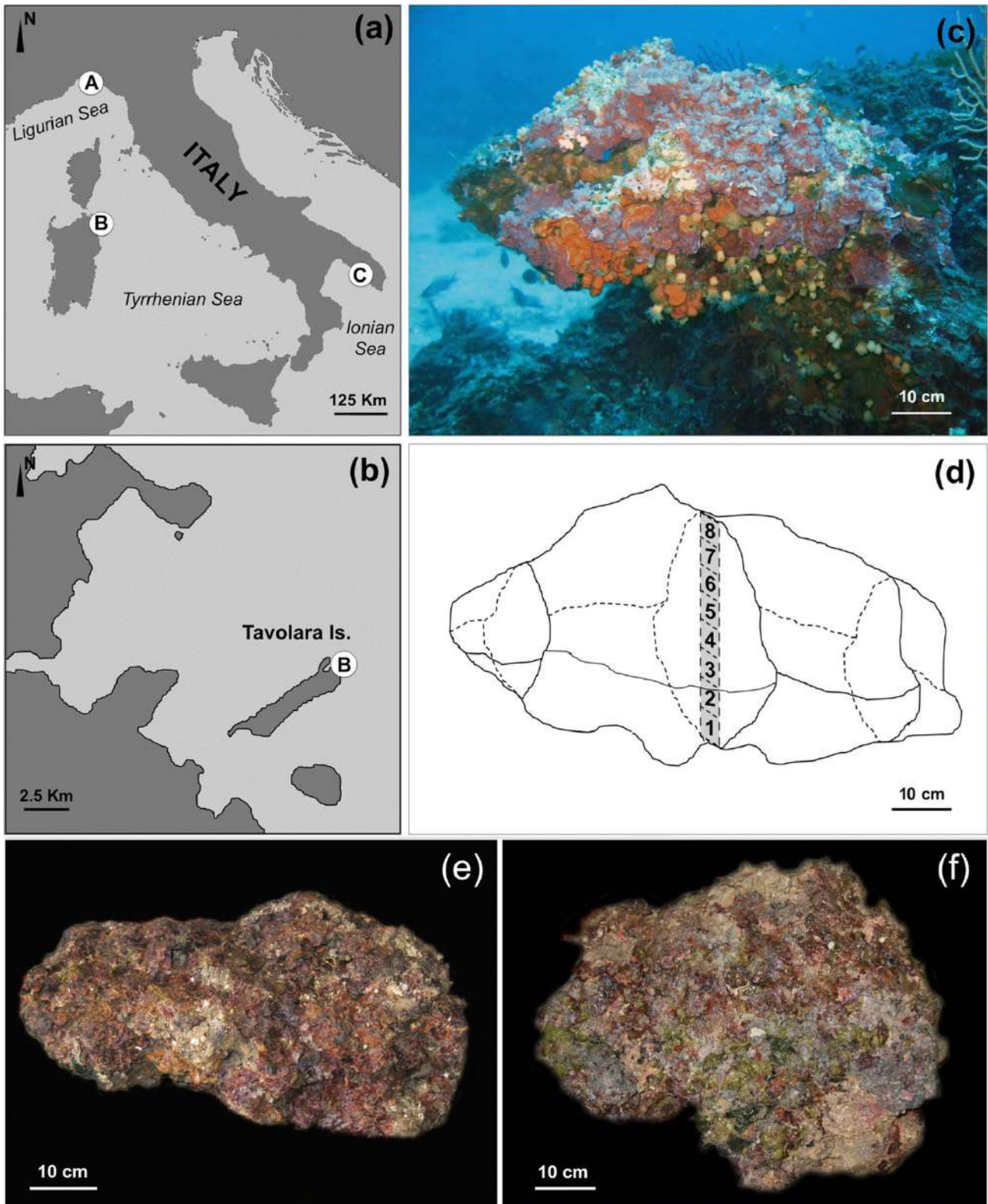


Fig. 1 a Location of the Italian sites where the paleo-sponge communities within the coralligenous outcrops were studied. a, Bogliasco; b, Tavolara Is.; c, Porto Cesareo. b Map of the Tavolara-Capo Coda Cavallo MPA with the sampling site (Punta del Papa: 40°54'48"N, 09°44'35"E). c Underwater view of coralligenous outcrop 2 within the Tavolara MPA. d Schematic drawing of the same outcrop showing the position of the studied subsamples. e View of the upper side of the collected outcrop 1. f View of the upper side of the collected outcrop 2

The species found in the living assemblage but devoid of siliceous spicules, were not considered in the analysis, because it was impossible to detect their presence in the ancient assemblages.

Finally, a multi-dimensional scaling (MDS) ordination permitted to investigate differences and similarities, only at generic level, in time and space among three ancient and current sponge communities coming from Tavolara Island (Tyrrhenian Sea), Porto Cesareo (Ionian Sea), and Bogliasco (Ligurian Sea) (Table 2).

3. Results

The studied coralligenous bioherms arose from a flat bottom, forming cushion-like structures at 42-m depth within the Tavolara Capo Coda Cavallo Marine Protected Area (northeast Sardinia, Tyrrhenian Sea) (Fig. 1c). The biological coverage of the coralligenous bioherms of Tavolara was due to different living coralline algae (*Lithophyllum*, *Lithothamnion*, *Neogoniolithon*) and several carbonate skeleton animals, mainly the scleractinian *Leptopsammia pruvoti*, and the bryozoans *Myriapora truncata*, *Pentapora fascialis*, *Reteporella* sp. Among sponges, *Agelas oroides*, *Aplysina cavernicola*, *Cliona* sp., *Dysidea fragilis*, *Oscarella* sp., *Petrosia ficiformis*, *Phorbastenacior*, *Pleraplysilla spinifera*, *Spirastrella cunctatrix*, were the most abundant.

The estimated age of the two studied bioherms was similar. The basal layer of the first block resulted 5800 years old and the apical one 3700 years old, with a total growth period of 2100 years. In the second block, the age varied from 5300 years at the base to 4150 years at the top, with a period of growth of about 1150 years. The estimated growth rates were very similar in both the blocks, being 0.21 and 0.24 mm year⁻¹, respectively (Fig. 2).

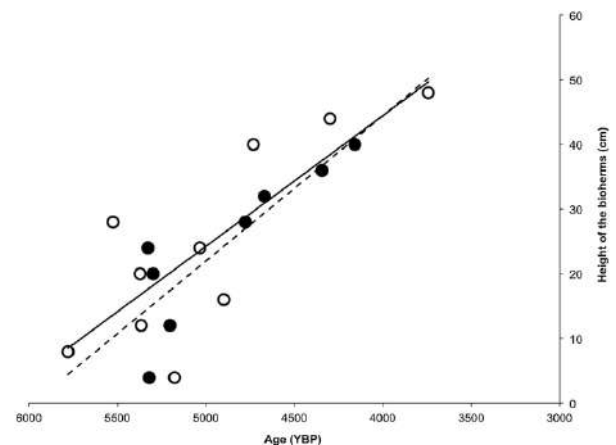


Fig. 2 Growth rates of the two examined coralligenous outcrops. The spots (black, outcrop 1 and white, outcrop 2) are the carbon age determinations. Regression lines: outcrop 1 continuous line, $R = 0.86$; outcrop 2 dashed line, $R = 0.80$

The analysis of the sponge richness of ancient vs. recent assemblages in the two considered bioherms allowed the identification of 87 species of demosponges. Thirty-eight of them were present only in the ancient assemblages, 37 only in the recent ones and 12 species were in common. Some of the species that are not present anymore in the Tavolara coralligenous are particularly remarkable. *Alveospongia* sp. was an important component of the ancient

community and was already found in other coralligenous ancient communities of the Mediterranean Sea (Bertolino et al. 2017a, b). At present, however, it was recorded only outside the Mediterranean Sea, in Brazilian waters (Santos et al. 2016). A group of species recorded in the Tavolara ancient assemblage, encompassing *Annulastrella verrucolosa*, *Forcepia* sp., *Nethea amygdaloides* and *Thrombus abyssis*, are now typical of deep water, in particular associated with the deep cold-water coral reefs (CWC) (Longo et al. 2005; Mastrototaro et al. 2010; Calcinai et al. 2013; Sitjà and Maldonado 2014; D’Onghia et al. 2015).

At generic level, 60 taxa were recorded, 47 of them were present in the ancient assemblages, 42 in the recent ones, and 29 were in common. Eighteen out of the genera present in the ancient assemblages were not found in the current one, whereas 13 genera are to be considered as new entries in the living assemblage (Table 2, Fig. 3).

The analysis of similarity among the ancient and recent assemblages of Tavolara Island with those studied by Bertolino et al. (2017a, b) in Bogliasco (Ligurian Sea) and Porto Cesareo (Ionian Sea) (Fig. 4), showed higher levels of similarity among the three considered ancient assemblages with respect to those recorded among the recent ones. However, it is remarkable that the recent assemblage from Tavolara Island appeared

more similar to the three ancient communities than to the other living ones (Fig. 4).

In addition, according to the growth habit, the composition of the ancient assemblages appears quite similar to that of the living ones. The most abundant sponges were always the encrusting (Ec), followed by the filling (Fl), massive/erect (ME), and boring ones (Br) (Fig. 5).

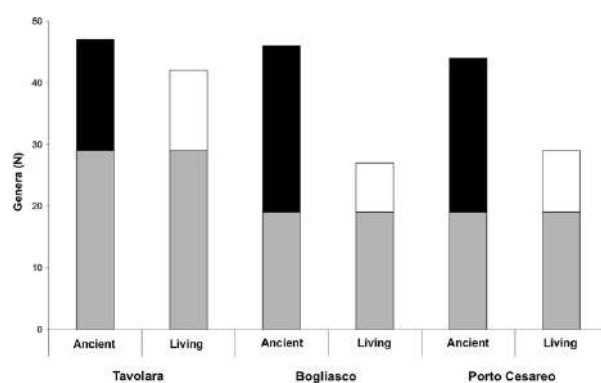


Fig. 3 Number of lost genera (black bar), new entries (white bar) and genera in common (grey bar) among the ancient and living sponge assemblages in the coralligenous from the considered sites. The sponge genera with skeleton devoid of siliceous spicules were not considered here. (Tavolara Island, this paper; Bogliasco, from Bertolino et al. 2017a; Porto Cesareo, from Bertolino et al. 2017b)

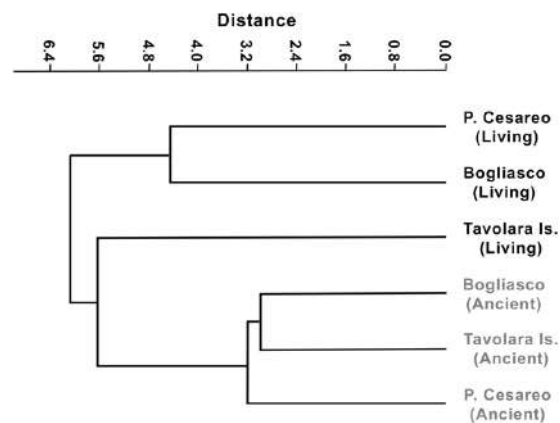


Fig. 4 Multi-dimensional scaling (MDS) ordination among the ancient sponge communities (grey) and the living ones (black) in Tavolara Island (present paper), Bogliasco (from Bertolino et al. 2017a) and Porto Cesareo (from Bertolino et al. 2017b)

Species	Ancient assemblage	Living assemblage
<i>Aaptos aaptos</i> (Schmidt, 1864)	+	+
<i>Acanthella acuta</i> (Schmidt, 1962)	---	+
<i>Acanthella</i> sp.	+	---
<i>Acarus</i> sp.	+	---
<i>Agelas oroides</i> (Schmidt, 1864)	+	+
<i>Alectona millari</i> Carter, 1879	+	---
<i>Alveospongia</i> sp.	+	---
<i>Annulastrella verrucolosa</i> (Pulitzer-Finali, 1983)	+	---
<i>Antho</i> sp.	+	---
<i>Axinella damicomis</i> (Esper, 1794)	---	+
<i>Axinella</i> cf. <i>polypoides</i> Schmidt, 1862	---	+
<i>Axinella verrucosa</i> (Esper, 1794)	---	+
<i>Batzella inops</i> (Topsent, 1891)	+	---
<i>Bubaris vermiculata</i> (Bowerbank, 1866)	---	+
<i>Bubaris</i> sp.	+	---
<i>Chondrilla nucula</i> Schmidt, 1862	+	---
<i>Cliona janitrix</i> Topsent, 1932	+	+
<i>Cliona</i> sp.	+	+
<i>Cliona viridis</i> (Schmidt, 1862)	---	+
<i>Corticium candelabrum</i> Schmidt, 1862	+	---
<i>Crambe crambe</i> (Schmidt, 1862)	---	+
<i>Crella</i> (<i>Grayella</i>) <i>pulvinar</i> (Schmidt, 1868)	---	+
<i>Crella</i> sp.	+	---
<i>Delectona</i> sp.	+	---
<i>Dercitus</i> (<i>Stoæba</i>) <i>plicatus</i> (Schmidt, 1868)	+	+
<i>Dictyonella incisa</i> (Schmidt, 1880)	---	+
<i>Dictyonella marsilii</i> (Topsent, 1893)	---	+
<i>Diplastrella bistellata</i> (Schmidt, 1862)	+	+
<i>Dotona pulchella mediterranea</i> Carter, 1880	+	+
<i>Dysidea fragilis</i> (Montagu, 1814)*	---	+
<i>Erylus discophorus</i> (Schmidt, 1862)	+	---
<i>Erylus euastrum</i> (Schmidt, 1868)	---	+
<i>Erylus</i> sp.	+	---
<i>Eurypon cinctum</i> Sarà, 1960	---	+
<i>Eurypon clavatum</i> (Bowerbank, 1866)	---	+
<i>Eurypon coronula</i> (Bowerbank, 1874)	+	---
<i>Eurypon denisae</i> Vacelet, 1969	---	+
<i>Eurypon major</i> (Sarà & Siribelli, 1960)	---	+
<i>Eurypon viride</i> (Topsent, 1889)	+	+
<i>Eurypon</i> sp.	+	+
<i>Forcepia</i> sp.	+	---
<i>Geodia cydonium</i> (Jameson, 1811)	---	+
<i>Geodia</i> sp.	+	---
<i>Halichondria</i> (<i>Halichondria</i>) <i>genitrix</i> (Schmidt, 1870)	---	+
<i>Halichondria</i> sp.	---	+
<i>Haliclona</i> (<i>Gellius</i>) sp.	+	---
<i>Haliclona</i> (<i>Halichoclona</i>) <i>fulva</i> (Topsent, 1893)	---	+
<i>Haliclona</i> (<i>Soestella</i>) sp.1	---	+
<i>Haliclona</i> (<i>Soestella</i>) sp.2	---	+
<i>Haliclona</i> sp.	---	+
<i>Hymenabdia</i> sp.	+	---
<i>Jaspis incrustans</i> (Topsent, 1890)	---	+
<i>Jaspis johnstonii</i> (Schmidt, 1862)	---	+
<i>Jaspis</i> sp.	+	---
<i>Mertia normani</i> Kirkpatrick, 1908	---	+
<i>Mertia</i> sp.	+	---

Species	Ancient assemblage	Living assemblage
<i>Monocrepidium vermiculatum</i> Topsent, 1898	+	---
<i>Mycale</i> sp.	+	---
<i>Nethea amygdaloides</i> (Carter, 1876)	+	+
<i>Pachastrella monillifera</i> Schmidt, 1868	---	+
<i>Penares euastrum</i> (Schmidt, 1868)	+	---
<i>Penares</i> sp.	+	---
<i>Petrosia</i> (<i>Petrosia</i>) <i>ficiformis</i> (Poirer, 1789)	+	+
<i>Placospongia decorticans</i> (Hanitsch, 1895)	+	---
<i>Plakina trilopha</i> Schulze, 1880	+	---
<i>Plakina</i> sp.	+	---
<i>Plakortis simplex</i> Schulze, 1880	---	+
<i>Protosuberites epiphytum</i> (Lamarck, 1815)	+	---
<i>Pseudotrachya hystrix</i> (Topsent, 1890)	---	+
<i>Rhabderemia</i> sp.	+	---
<i>Samus anonymus</i> Gray, 1867	+	---
<i>Spirastrella cunctatrix</i> Schmidt, 1868	+	---
<i>Spiroxya heteroclita</i> Topsent, 1896	---	+
<i>Spiroxya sarai</i> (Melone, 1965)	---	+
<i>Spiroxya</i> sp.	+	---
<i>Spongia virgultosa</i> (Schmidt, 1868)*	---	+
<i>Stelletta lactea</i> Carter, 1871	---	+
<i>Stelletta stellata</i> (Topsent, 1893)	---	+
<i>Stelletta</i> sp.	+	---
<i>Tethya</i> sp.	+	---
<i>Thoosa</i> sp.	+	---
<i>Thrombus abyssii</i> (Carter, 1873)	+	---
<i>Timea stellata</i> (Bowerbank, 1866)	---	+
<i>Timea unistellata</i> (Topsent, 1892)	---	+
<i>Timea</i> sp.	+	---
<i>Trachycladus minax</i> (Topsent, 1888)	---	+
<i>Triptolemma simplex</i> (Sarà, 1959)	+	+

* Indicates the species that have not a spicular skeleton

Table 1 List of the species recorded in ancient (grey column) and present (white column) sponge assemblages from Tavolara Island

Site		Tavolara Is. Tyrrhenian Sea		Porto Cesareo Ionian Sea		Bogliasco Ligurian Sea	
Depth (m)		42		20		15	
Age (YBP)		5,800-3,700		6,200-1,700		3,500-600	
Growth rate (mm/y)		0.21-0.24		0.15		0.15	
Main components		Coralline algae		Coralline algae and serpulids		Coralline algae	
Shape		cushions		pillars		cushions	
<i>Aptos</i>	Fl	+	+	+	+	+	+
<i>Acanthella</i>	ME	+	+	+	+	+	+
<i>Acarus</i>	Fl	+	+	+	---	+	---
<i>Agelas</i>	ME	+	+	+	---	+	+
<i>Aka</i>	Br	---	+	---	---	---	---
<i>Alectona</i>	Br	+	---	+	---	+	---
<i>Alveospongia</i>	ME	+	---	+	---	+	---
<i>Annulastrella</i>	Fl	+	---	---	---	---	---
<i>Antho</i>	Ec	+	---	+	---	+	---
<i>Axinella</i>	ME	+	+	+	+	+	+
<i>Batzella</i>	Ec	+	---	+	---	+	+
<i>Bubaris</i>	Ec	+	+	+	+	+	+
<i>Calthropella</i>	ME	---	---	---	+	---	---
<i>Chondrilla</i>	ME	+	---	+	---	+	---
<i>Clathria</i>	Ec	---	---	+	---	+	---
<i>Cliona</i>	Br	+	+	+	+	+	+
<i>Corticium</i>	ME	+	---	+	---	+	---
<i>Crambe</i>	Ec	---	---	---	+	---	+
<i>Crella</i>	Ec	+	+	+	---	+	---
<i>Delectona</i>	Br	+	+	+	---	---	---
<i>Dendroxea</i>	Fl	---	+	---	---	+	---
<i>Dercitus</i>	Fl	+	+	+	+	+	+
<i>Dictyonella</i>	Ec	+	+	+	+	+	+
<i>Didiscus</i>	Ec	---	---	+	---	---	---
<i>Diplastrella</i>	Ec	+	+	+	+	+	---
<i>Dotona</i>	Br	+	+	+	---	+	---
<i>Erylus</i>	Fl	+	+	+	---	+	+
<i>Eurypon</i>	Ec	+	+	+	+	+	+
<i>Forcepia</i>	Ec	+	---	---	---	+	---
<i>Geodia</i>	Fl	+	+	+	+	+	---
<i>Halichondria</i>	ME	+	+	+	+	+	+
<i>Haliclona</i>	Ec	+	+	+	+	+	+
<i>Hymedesmia</i>	Ec	---	+	---	---	---	+
<i>Hymeniacidon</i>	Ec	---	---	---	---	---	+
<i>Hymenhabdia</i>	Ec	+	---	+	---	---	---
<i>Jaspis</i>	Fl	+	+	---	+	+	+
<i>Lissodendoryx</i>	ME	---	+	---	+	---	---
<i>Merlia</i>	Ec	+	+	---	---	+	---
<i>Monocrepidium</i>	Ec	+	---	+	---	---	---
<i>Mycale</i>	Ec	+	+	---	+	+	+
<i>Myxilla</i>	Ec	---	---	---	+	---	+
<i>Nethea</i>	Fl	+	---	+	---	+	---
<i>Oceanapia</i>	ME	---	---	---	---	---	+
<i>Pachastrella</i>	Fl	---	+	+	---	+	---
<i>Pachastrissa</i>	Ec	---	+	---	---	---	---
<i>Paratimea</i>	Ec	---	+	---	---	---	---
<i>Penares</i>	Fl	+	---	+	+	+	---

Site		Tavolara Is. Tyrrhenian Sea		Porto Cesareo Ionian Sea		Bogliasco Ligurian Sea	
Depth (m)		42		20		15	
Age (YBP)		5,800-3,700		6,200-1,700		3,500-600	
Growth rate (mm/ly)		0.21-0.24		0.15		0.15	
Main components		Coralline algae		Coralline algae and serpulids		Coralline algae	
Shape		cushions		pillars		cushions	
<i>Petrosia</i>	ME	+	+	+	+	+	+
<i>Phorbacia</i>	Ec	---	---	---	+	---	+
<i>Pione</i>	Br	---	---	---	+	---	---
<i>Placospongia</i>	Ec	+	---	+	---	+	---
<i>Plakina</i>	Ec	+	+	+	---	+	+
<i>Plakinastrella</i>	ME	---	+	---	---	---	+
<i>Plakortis</i>	Ec	---	+	---	---	+	---
<i>Plocamionida</i>	Ec	---	+	---	---	---	---
<i>Poecillastra</i>	Fl	---	+	---	---	---	---
<i>Polymastia</i>	ME	---	---	---	+	---	---
<i>Prosuberites</i>	Ec	+	+	+	---	+	---
<i>Pseudotrachya</i>	ME	---	+	---	---	---	---
<i>Rhabderemia</i>	ME	+	---	+	---	+	---
<i>Samus</i>	Fl	+	+	+	---	+	---
<i>Siphonodictyon</i>	Br	---	---	---	+	---	---
<i>Spirastrella</i>	Ec	+	---	+	+	+	+
<i>Spiroxya</i>	Br	+	+	+	---	+	---
<i>Stelletta</i>	Fl	+	+	+	+	+	+
<i>Suberites</i>	ME	---	---	+	+	---	---
<i>Terpios</i>	Ec	---	---	---	---	---	+
<i>Tethya</i>	ME	+	---	+	+	+	---
<i>Thoosa</i>	Br	+	---	+	---	+	---
<i>Thrombus</i>	Ec	+	---	---	---	---	---
<i>Timea</i>	Fl	+	+	+	+	+	---
<i>Trachycladus</i>	ME	---	+	---	---	---	---
<i>Triptolemma</i>	Fl	+	+	+	---	+	---
TOTAL GENERA		47	42	42	29	40	26
Spicule-less sponges							
<i>Chondrosia</i>	ME	---	---	---	---	---	+
<i>Dysidea</i>	ME	---	+	---	---	---	---
<i>Fasciospongia</i>	ME	---	---	---	---	---	+
<i>Ircinia</i>	ME	---	---	---	---	---	+
<i>Oscarella</i>	ME	---	---	---	+	---	+
<i>Sarcotragus</i>	ME	---	---	---	---	---	+
<i>Spongia</i>	ME	---	+	---	+	---	+

Tavolara Island., this paper; Porto Cesareo (from Bertolino et al. 2017b); Bogliasco (from Bertolino et al. 2017a)

Table 2 Main features of the considered coralligenous bioherms and list of genera (with growth habit—ME, Massive Erect; Br, Boring; Fl, Filling; Ec, Encrusting) recorded in the ancient (grey column) and present (white column) sponge assemblages from three different localities of the Mediterranean Sea

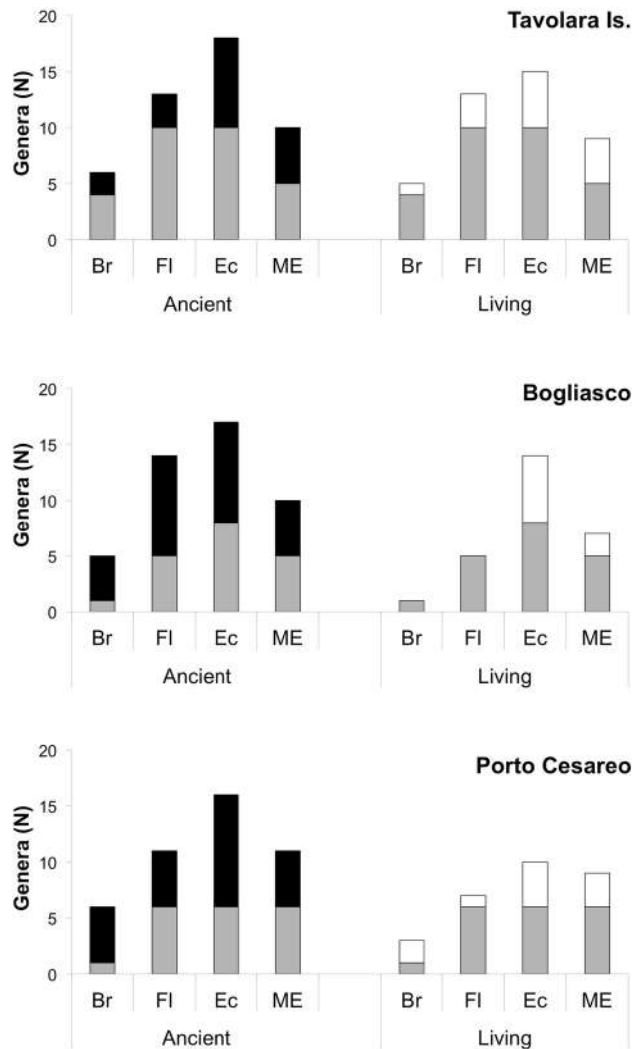


Fig. 5 Number of lost (black bar), new entries (white bar) and genera in common (grey bar) among the ancient and living sponge assemblages according to the different growth habits in three different sites (Tavolara Island, this paper; Bogliasco, from Bertolino et al. 2017a; Porto Cesareo, from Bertolino et al. 2017b). *Br* boring; *FI* filling; *Ec* encrusting; *ME* massive-erect

4. Discussion

The vicissitudes that the Mediterranean coralligenous assemblages underwent during the entire Holocene (rising of sea level, changes in water temperature, salinity, light irradiance, water transparency, sedimentation rates, trophic supply, etc.) influenced the entire structure of these bioherms as well as their biodiversity. Their accumulation rates varied across time and depth: the highest values (0.53–0.83 mm year⁻¹) were recorded between 8000 and 6000 YBP, but afterwards

the only appreciable growth rates (0.11–0.42 mm year⁻¹) were recorded at 10–35 m depth, since the growth rates of deeper (> 50 m) coralligenous formations were lower or null (Sartoretto et al. 1996). The comparison among the coralligenous growth observed in Tavolara Island and those previously measured in other bioherms present at lower depth, as those of Porto Cesareo and Bogliasco (Bertolino et al. 2017a, b), suggested some similarities and inequalities. All the considered bioherms developed on a

flat bottom with a perpendicular orientation and their growth speed appeared comparable, ranging between 0.15 and 0.24 mm year⁻¹ (Table 2). On the contrary, the time span of the growing phases was different. The coralligenous formations from Tavolara and Porto Cesareo started to grow about 6000 YBP, while the first base of the Bogliasco bioherms dated 3500 YBP. In Tavolara Island the coralligenous seems to have stopped to grow about 3700 YBP, while in the other localities the slowdown occurred about 2000–1000 YBP (Bertolino et al. 2017a, b). The sponge diversity of the considered ancient assemblages was remarkably similar in term of genus number (47, 46, and 44 for Tavolara Island, Bogliasco and Porto Cesareo, respectively), having in common the 69.8% of the recorded genera. On the contrary, the generic richness changed significantly among the living communities. Albeit the number remained similar (42 genera) in Tavolara Island, strong reductions (27 and 29 genera, respectively) were recorded in Bogliasco and Porto Cesareo, due to a loss of taxa, not balanced by new entries in the recent ones (Fig. 3). Today these living communities appeared much more diversified, having only 24.6% of the genera in common, and as evidenced also by the similarity analysis (Fig. 4). Therefore, starting from the bulk of common genera in the three ancient communities, a process of differentiation occurred over time (Fig. 6). The same trend

was evident also considering the genera divided according to their growth habit (Fig. 6), which, however, maintained remarkably similar percent ratios both in ancient and recent assemblages: the richest groups were always those of the encrusting sponges followed by filling genera, while boring and massive/erect ones showed a lower number of taxa (Fig. 3).

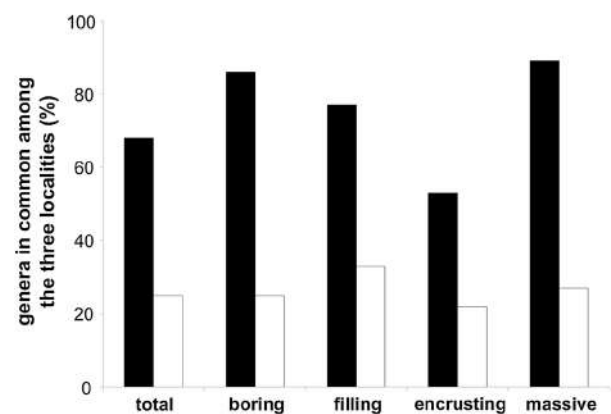


Fig. 6 Percent of sponge genera in common among all the three sites according to the different habits. Black bars, ancient assemblages; white bars, recent assemblages

Also, the abundances of each genus seemed to have had different fates over time. All the genera present in the current communities were always present in the past. On the contrary, eight genera, widely diffused in the past, were no more recorded (Table 3). This evidence suggests that, on the whole, the sponge coralligenous community resulted impoverished over time. Moreover, the Tavolara Island recent assemblage appeared more similar to the three ancient communities than to the recent ones. It is possible to hypothesize that some of these differences

have been due to the different fates of the considered coralligenous formations.

Taxon	Growing habit	Lost
<i>Alectona</i>	Boring	↓
<i>Thoosa</i>	Boring	↓
<i>Antho</i>	Encrusting	↓
<i>Placospongia</i>	Encrusting	↓
<i>Alveospongia</i>	Massive/erect	↓
<i>Chondrilla</i>	Massive/erect	↓
<i>Corticium</i>	Massive/erect	↓
<i>Rhabdermia</i>	Massive/erect	↓
		Persistent
<i>Cliona</i>	Boring	=
<i>Aaptos</i>	Filling	=
<i>Dercitus</i>	Filling	=
<i>Stelletta</i>	Filling	=
<i>Bubaris</i>	Encrusting	=
<i>Dictyonella</i>	Encrusting	=
<i>Eurypon</i>	Encrusting	=
<i>Haliclona</i>	Encrusting	=
<i>Axinella</i>	Massive/erect	=
<i>Acanthella</i>	Massive/erect	=
<i>Halichondria</i>	Massive/erect	=
<i>Petrosia</i>	Massive/erect	=

Table 3 Persistent and lost sponge genera in the ancient vs. recent assemblages

At Tavolara, at 42-m depth, the carbonate deposition by corallinaceans is still active and probably balanced by demolition processes. On the contrary, at Porto Cesareo and Bogliasco, the bioherms were completely covered by frondose macroalgae, being the encrusting algae apparently dead and the carbonate deposition null or negligible. These different conditions probably affected the structure of the sponge communities. In fact, the macroalgal coverage, determining a sort of algal whiplash (Kiirikki 1996), shaped a habitat more and more unfavorable for sponges with a consequent loss of taxa and a low acquisition of new entries. On the contrary, when the coralline algae deposition

remained significant, the living sponge assemblages continued to host a number of taxa comparable to that of the ancient communities, determining a rather stable generic richness, over the considered period of time.

The Mediterranean coralligenous sponge community appeared not so stable across the time: the number of genera was low about 6000 YBP and increased between 5500 and 4000 YBP during the Holocene Climatic Optimum. In the Late Bronze Age (4000–3000 YBP), a new decrease was recorded, followed by a further increase during the Little Climate Optimum (around 2000 YBP) (Bertolino et al. 2017a, b). Afterwards, the bio-concretions stopped growing and no more siliceous spicules were trapped. The data from the Tavolara bioherms fits with this general trend (Fig. 7) and confirm that the study of the siliceous spicules trapped into the crevices of the bioherms represents an ideal instrument not only for evaluating the sponge richness over a considerable span of time, but also for interpreting the effects of climate change, supporting future predictions on the environmental evolution.

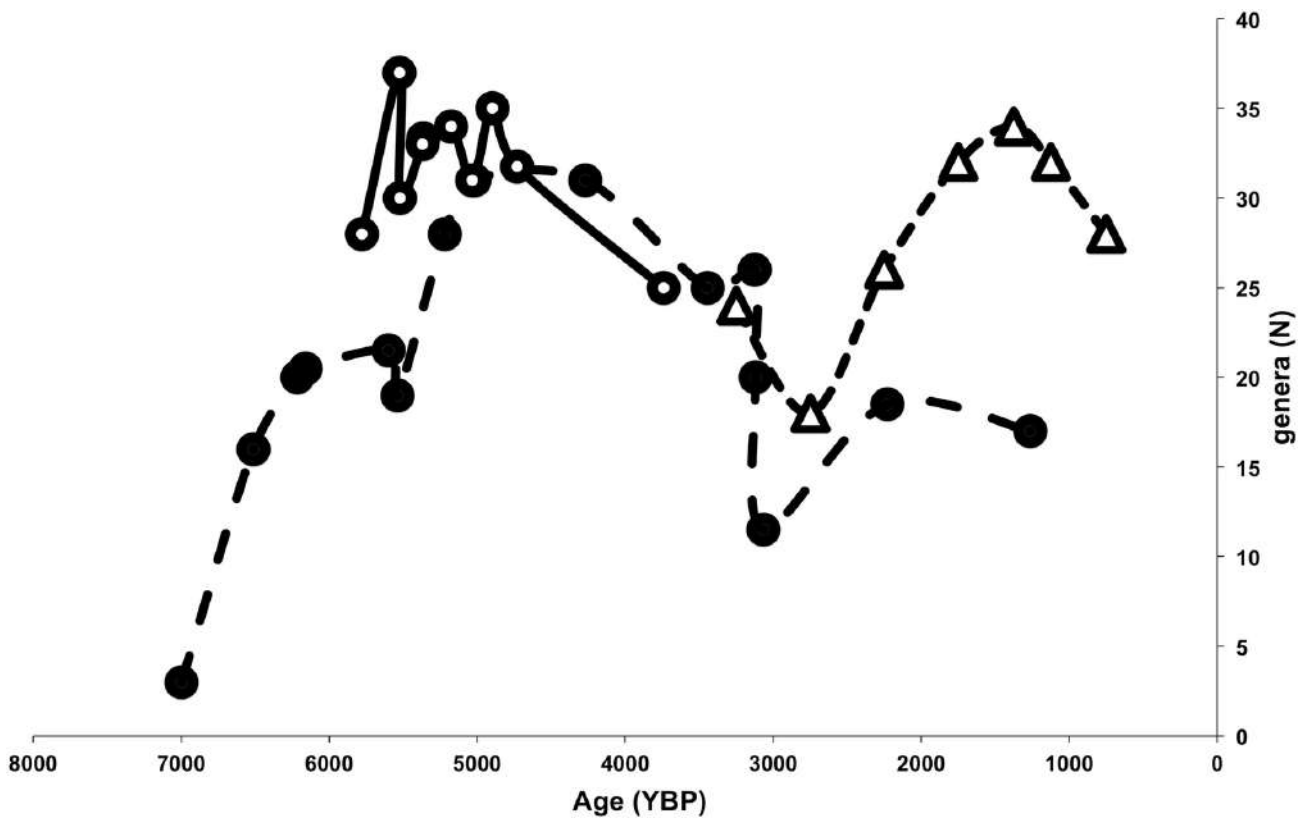


Fig. 7 Trends of the number of sponge genera recorded between 7000 and 750 YBP within different coralligenous bioherms. The high richness between 6000 and 4500 YBP, during the Holocene Climatic Optimum, is evident in each studied ancient community. White circles, Tavolara Is. (Tyrrhenian Sea); Black circles, Porto Cesareo (Ionian Sea); white triangles, Bogliasco (Ligurian Sea)

Acknowledgements

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Sponge community variation along the Apulian coasts (Otranto Strait) over a pluri-decennial time span. Does water warming drive a sponge diversity increasing in the Mediterranean Sea?

Abstract

Climate change and heavy anthropic pressures are giving rise to important modifications in the rocky benthic communities of the Mediterranean Sea. In particular, sponge assemblages have been deeply affected due to the susceptibility of some species to dramatic phenomena such as mass mortalities or widespread variations in the abundance of other species. For this reason, long-term biodiversity monitoring of the sponge assemblages is important for understanding the direction of changes over time. We studied the sponge fauna living off Tricase Porto (Otranto Strait) and compared its composition with the results of a study conducted in the same area 50 years ago. The comparison indicated that the sponge diversity of this area has strongly increased in the last 50 years and a large number of the sponges recorded in the old survey are still present in the recent community. This evidence matches with other results obtained from different localities of the Mediterranean Sea indicating an increase of sponge diversity, possibly due to the present water warming. The description of two new Demosponge species, *Diplastrella boeroi* sp. nov. and *Spirastrella angulata* sp. nov., is also provided.

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Additional Resources

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1. Introduction

The Mediterranean Sea is considered a hotspot of biodiversity with a high rate of endemism (Bianchi & Morri, 2000; Coll et al., 2010). In recent decades climate change and heavy anthropic pressures are giving rise to important modifications in the rocky benthic biocoenoses of this semi-closed basin (Cerrano et al., 2000; Lejeusne et al., 2010; Bianchi et al., 2012; Di Camillo & Cerrano, 2015; Montefalcone et al., 2018). With almost 720 species (Pansini et al., 2011; van Soest et al., 2018), sponges are one of the most diversified group of hard bottom organisms. The effects of global changes on the Mediterranean sponge fauna were approached in several papers evidencing different trajectories of changes. In some studies sponges, mainly keratasas, were among the groups most affected by the mass mortality events observed in the Mediterranean Sea during the last decades (Gaino & Pronzato, 1991; Gaino et al., 1992; Rizzello et al., 1997; Pronzato, 1999; Cerrano et al., 2000; Pronzato & Manconi, 2008; Garrabou et al., 2009; Pronzato et al., 2012). Other studies demonstrated that some species enhanced their covering during the present episode of global warming. In the Ligurian Sea it was stated that the encrusting red sponge *Crambe crambe* (Schmidt, 1862) strongly increased covering in correspondence to the disease affecting the common anthozoan *Parazoanthus axinellae* (Schmidt, 1862)

(Cerrano et al., 2006). In the same area a survey on a coralligenous vertical cliff, 25 years after a previous one, indicated that some species, such as *Axinella* spp. and the red encrusting sponges (*C. crambe* – *Spirastrella cunctatrix* Schmidt, 1868), strongly increased their abundance while massive species such as *Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789) and *Chondrosia reniformis* Nardo, 1847 reduced their covering (Bertolino et al., 2016). More recently an increase in sponge diversity was recorded in two Ligurian marine semi-submerged caves surveyed again 50 years after the first study (Costa et al., 2018). It thus is important to collect data about the trajectory of the change of different sponge communities from other regions of the Mediterranean Sea. The coast of the Salento Peninsula (Apulia, south-east Italy) is characterized by karst cliffs rich in semi-submerged marine caves of environmental importance as emphasized by Sarà (1974) and more recently by Belmonte et al. (1999) and Bussotti et al. (2002, 2006). A large area of coralligenous outcrops characterizes the continental shelf in front of this stretch of coast (Bracchi et al., 2015, 2017). This region, that accounts for more than 4% of the total Mediterranean sponge fauna (Sarà, 1960, 1969; Pulitzer-Finali, 1983; Corriero et al., 2004; Longo et al., 2015, 2017) was thoroughly surveyed in the period 1967–70 by Pulitzer-Finali (1983), particularly in the area of Tricase Porto (Otranto Strait). The rich

Pulitzer-Finali reference collection (preserved at DiSTAV) of sponges offers a unique possibility to compare the present sponge fauna with that present in the same zone about 50 years ago, presumably before the onset of global warming. The aim of this work is therefore the characterization of the sponge fauna living off Tricase Porto (Otranto Strait) and the comparison of the actual sponge fauna (2017) with that studied in the same area about 50 years ago. Special attention has been dedicated to the description of two new species recorded during the present survey.

2. Materials and methods

The study area is located off Tricase Porto, just south of the narrowest point of the Otranto Strait (Figure 1). The samples were collected between June and August 2017. The sampling methods were similar to those used by Pulitzer-Finali (1983) in his faunistic collections conducted between 1967 and 1970. The focus was on coralligenous, semi-submerged caves, rocky substrate down to 40 m depth by scuba diving and deep waters to 60 m depth by trammel net and a dredge to collect coralligenous fragments. For sampling we used the same techniques as Pulitzer-Finali (scuba diving and trammel), moreover we collected blocks of coralligenous formation by diving using hammer and chisel and we analysed them in the lab through the method described by Bertolino et al. (2014). Sponge samples were dried or preserved in

95% ethanol and processed by standard methods (Rützler, 1978). Taxonomic decisions are in agreement with the Systema Porifera (Hooper & van Soest, 2002), the Demosponge revision of Morrow & Cárdenas (2015) and the World Porifera Database (WPD) (van Soest et al., 2018). For the two new species length and width of at least 30 spicules per type were measured. Minimum, mean (in parentheses) and maximum values of spicule dimensions are reported. Dissociated spicules and dried tissues were transferred onto stubs, sputter coated with gold and observed by a scanning electron microscope (SEM). The type material of new species was deposited in the Museo Civico di Storia Naturale ‘G. Doria’ of Genova (MSNG). The type material of re-described species was deposited in the Department for Earth, Environment and Life Sciences (DiSTAV-University of Genoa). The identified species were grouped according to their prevailing growth pattern, i.e. Massive/Erected (ME), Encrusting (En), Cavity dwelling (Cd) and Boring (Br).

3. Results

During the 2017 survey, a total of 110 sponge species (including two new species (Figures 2–3)) were recorded belonging to three classes: Calcarea (2), Homoscleromorpha (7) and Demospongiae (101) (Table 1). Twenty-five species are new findings for the Ionian Sea (Table 1; Table S1).

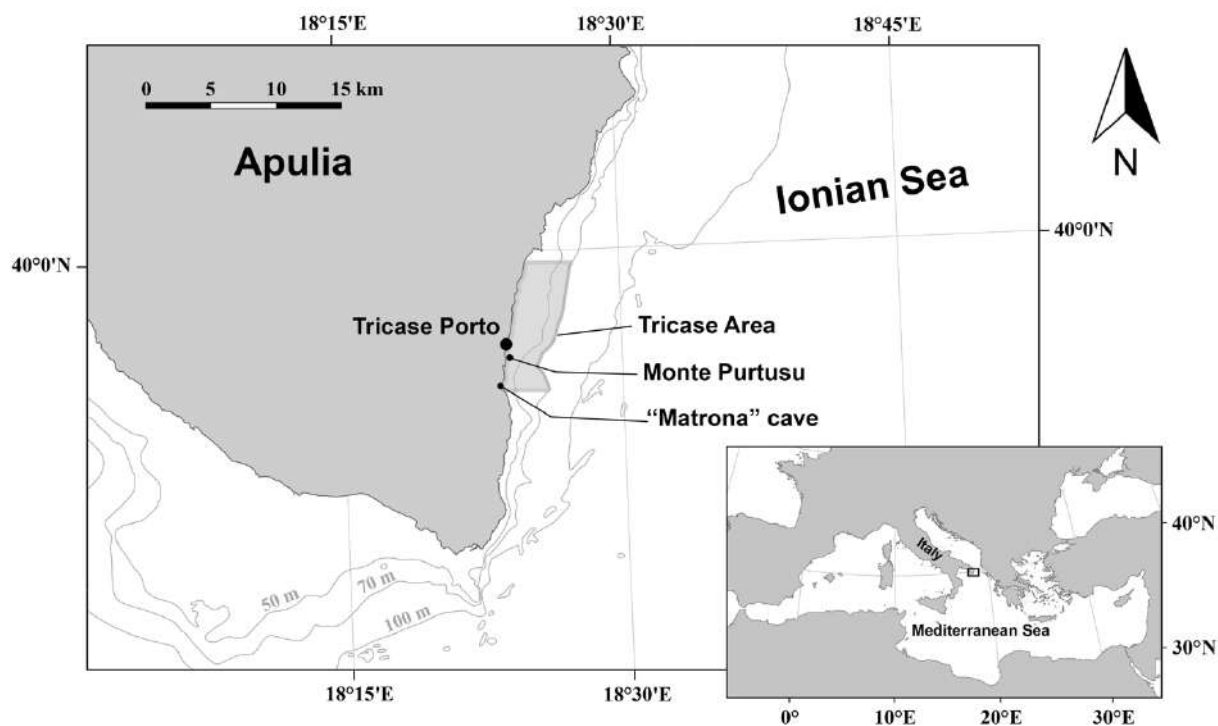


Fig. 1. Studied area in front of Tricase Porto (Otranto Canal – Ionian Sea).

Species	Growth Habit	Coralligenous		Semisubmerged Caves		Rocky substrate up to 40 m depth		Deep waters till 60 m depth	
		1967/1970	2017	1967/1970	2017	1967/1970	2017	1967/1970	2017
<i>Clathrina clathrus</i> (Schmidt, 1864)	ME						+		
<i>Sycon raphanus</i> Schmidt, 1862	ME								+
<i>Agelas oroides</i> (Schmidt, 1864)	ME	+	+			+	+		
<i>Hymerhabdia oxytrunca</i> Topsent, 1904 *	Ec		+						
<i>Prosuberites longispinus</i> Topsent, 1893	Ec	+	+						
<i>Axinella cannabina</i> (Esper, 1794)	ME							+	+
<i>Axinella damicornis</i> (Esper, 1794)	ME	+	+			+	+		
<i>Axinella rugosa</i> (Bowerbank, 1866)	ME	+							
<i>Axinella verrucosa</i> (Esper,	ME	+	+			+	+		

1794)									
<i>Axinella polypoides</i> Schmidt, 1862	ME								
<i>Didiscus stylifer</i> Tsumamal, 1969	Ec	+	+						
<i>Eurypon cinctum</i> Sarà, 1960 *	Ec		+						
<i>Eurypon clavatum</i> (Bowerbank, 1866)	Ec		+						
<i>Eurypon coronula</i> (Bowerbank, 1874) *	Ec		+						
<i>Eurypon gracilis</i> Bertolino, Pansini & Calcinai, 2013	Ec		+						
<i>Eurypon major</i> Sarà & Siribelli, 1960	Ec		+						
<i>Eurypon obtusum</i> Vacelet, 1969 *	Ec		+						
<i>Eurypon topsenti</i> Pulitzer- Finali, 1983	Ec					+			
<i>Eurypon viride</i> (Topsent, 1889)	Ec		+						
<i>Raspaciona aculeata</i> (Johnston, 1842)	Ec	+	+						
<i>Raspailia (Raspailia)</i> <i>viminalis</i> Schmidt, 1862 *	ME								+
<i>Halicnemia geniculata</i> Sarà, 1958 *	ME		+						
<i>Rhabderemia gallica</i> van Soest & Hooper, 1993 *	Ec		+						
<i>Rhabderemia minutula</i> (Carter, 1876)	CD		+						
<i>Bubaris carcisis</i> Vacelet, 1969	Ec		+						
<i>Bubaris vermiculata</i> (Bowerbank, 1866)	Ec	+	+						
<i>Monocrepidium</i> <i>vermiculatum</i> Topsent, 1898 *	Ec		+						
<i>Rhabdobaris implicata</i>	ME		+						

Pulitzer-Finali, 1983 *									
<i>Desmanthus incrustans</i> (Topsent, 1889)	Ec		+						
<i>Acanthella acuta</i> Schmidt, 1862	ME	+				+	+		
<i>Dictyonella incisa</i> (Schmidt, 1880)	ME	+	+			+	+		
<i>Dictyonella obtusa</i> (Schmidt, 1862)	ME						+		
<i>Dictyonella</i> sp.	ME		+						
<i>Cliona amplicavata</i> Rützler, 1974 *	Br		+						
<i>Cliona burtoni</i> Topsent, 1932 *	Br		+						
<i>Cliona celata</i> Grant, 1826	Br						+		
<i>Cliona schmidtii</i> (Ridley, 1881)	Br	+	+			+	+		
<i>Cliona viridis</i> (Schmidt, 1862)	Br		+						
<i>Cliothesa hancocki</i> (Topsent, 1888)	Br		+						
<i>Spiroxya heteroclita</i> Topsent, 1896	Br		+						
<i>Spiroxya sarai</i> (Melone, 1965)	Br		+						
<i>Diplastrella bistellata</i> (Schmidt, 1862)	Ec	+	+						
<i>Diplastrella boeroi</i> Bertolino, Costa & Pansini sp. nov.	Ec		+						
<i>Spirastrella cunctatrix</i> Schmidt, 1868	Ec	+	+						
<i>Spirastrella angulata</i> Bertolino, Costa & Pansini sp. nov.	Ec		+						
<i>Haliclona (Gellius)</i> <i>angulata</i> (Bowerbank, 1866)	CD			+					
<i>Haliclona (Gellius)</i> sp.	Ec					+			
<i>Haliclona (Halichoclona)</i>	Ec					+			

<i>fulva</i> (Topsent, 1893)									
<i>Haliclona</i> (<i>Reniera</i>) <i>cratera</i> (Schmidt, 1862)	ME					+			
<i>Haliclona</i> (<i>Reniera</i>) <i>mediterranea</i> Griessinger, 1971	ME					+			
<i>Haliclona</i> (<i>Rhizoniera</i>) <i>sarai</i> (Pulitzer-Finali, 1969)	ME					+			
<i>Haliclona</i> (<i>Soestella</i>) <i>mucosa</i> (Griessinger, 1971) *	ME					+			
<i>Haliclona</i> (<i>Soestella</i>) <i>valliculata</i> (Griessinger, 1971) *	Ec					+			
<i>Gelliodes fibulata</i> (Carter, 1881) *	ME							+	
<i>Petrosia</i> (<i>Petrosia</i>) <i>clavata</i> (Esper, 1794)	ME		+						
<i>Petrosia</i> (<i>Petrosia</i>) <i>ficiformis</i> (Poiret, 1789)	ME	+	+	+	+	+	+		
<i>Petrosia</i> (<i>Strongylophora</i>) <i>pulitzeri</i> Pansini, 1996 *	ME					+			
<i>Petrosia</i> (<i>Strongylophora</i>) <i>vansoesti</i> Boury-Esnault, Pansini & Uriz, 1994 *	ME					+			
<i>Oceanapia perforata</i> (Sarà, 1960) *	ME					+			
<i>Lissodendoryx</i> (<i>Anomodoryx</i>) <i>cavernosa</i> (Topsent, 1892)	CD		+						
<i>Crambe crambe</i> (Schmidt, 1862)	Ec							+	
<i>Crella</i> sp.	Ec		+						
<i>Ulosa stuposa</i> (Esper, 1794)	ME					+			
<i>Hamigera hamigera</i> (Schmidt, 1862)	Ec							+	
<i>Hemimycale columella</i> (Bowerbank, 1874)	Ec						+	+	

<i>Hymedesmia</i> (<i>Hymedesmia</i>) <i>paupertas</i> (Bowerbank, 1866) *	Ec					+			
<i>Phorbis dives</i> (Topsent, 1891)	Ec		+						
<i>Phorbis fictitius</i> (Bowerbank, 1866)	Ec		+						
<i>Phorbis tenacior</i> (Topsent, 1925)	Ec	+	+	+					
<i>Clathria</i> (<i>Clathria</i>) <i>coralloides</i> (Scopoli, 1772)	ME								+
<i>Clathria</i> (<i>Clathria</i>) <i>toxistricta</i> Topsent, 1925	Ec								+
<i>Clathria</i> (<i>Microciona</i>) <i>toxitenuis</i> Topsent, 1925	Ec							+	
<i>Clathria</i> (<i>Clathria</i>) <i>toxivaria</i> (Sarà, 1959)	Ec		+						
<i>Mycale</i> (<i>Mycale</i>) <i>lingua</i> (Bowerbank, 1866)	Ec		+						
<i>Mycale</i> (<i>Mycale</i>) <i>massa</i> (Schmidt, 1862)	ME		+						
<i>Axinyssa aurantiaca</i> (Schmidt, 1864)	ME		+						
<i>Halichondria</i> (<i>Halichondria</i>) cf. <i>panicea</i> (Pallas, 1766)	Ec		+						
<i>Halichondria</i> (<i>Halichondria</i>) <i>contorta</i> (Sarà, 1961) *	ME					+			
<i>Spongosorites intricatus</i> (Topsent, 1892)	CD		+						
<i>Aaptos aaptos</i> (Schmidt, 1864)	ME					+	+		
<i>Protosuberites epiphytum</i> (Lamarck, 1815)	Ec	+	+						
<i>Terpios gelatinosus</i> (Bowerbank, 1866)	Ec		+				+		
<i>Tethya aurantium</i> (Pallas, 1766)	ME		+						

<i>Tethya citrina</i> Sarà & Melone, 1965	ME		+						
<i>Timea stellata</i> (Bowerbank, 1866)	CD		+						
<i>Timea unistellata</i> (Topsent, 1892)	CD		+						
<i>Ancorina cerebrum</i> Schmidt, 1862 *	CD		+						
<i>Dercitus (Stoebe) plicatus</i> (Schmidt, 1868)	CD	+	+						
<i>Jaspis incrustans</i> (Topsent, 1890)	CD		+						
<i>Jaspis johnstonii</i> (Schmidt, 1862)	CD	+	+						
<i>Stelletta grubii</i> Schmidt, 1862	CD		+						
<i>Stelletta mediterranea</i> (Topsent, 1893) *	CD		+						
<i>Stelletta stellata</i> Topsent, 1893	CD		+						
<i>Calthropella (Corticellopsis) stelligera</i> (Schmidt, 1868) *	CD						+		
<i>Calthropella</i> sp.	CD		+						
<i>Erylus discophorus</i> (Schmidt, 1862)	CD	+	+						
<i>Penares helleri</i> (Schmidt, 1864)	CD	+	+						
<i>Penares euastrum</i> (Schmidt, 1868)	CD	+	+						
<i>Geodia cydonium</i> (Linnaeus, 1767)	CD		+						
<i>Geodia conchilega</i> Schmidt, 1862	ME	+							
<i>Pachastrella monilifera</i> Schmidt, 1868	CD	+	+						
<i>Triptolemma simplex</i> (Sarà, 1959)	CD		+						
<i>Poecillastra compressa</i> (Bowerbank, 1866)	CD		+						

<i>Tetilla</i> sp.	ME		+						
<i>Alectona millari</i> Carter, 1879	Br		+						
<i>Delectona madreporica</i> Bavestrello, Calcinai, Cerrano & Sarà, 1997 *	Br		+						
<i>Chondrilla nucula</i> Schmidt, 1862	ME	+	+			+	+		
<i>Chondrosia reniformis</i> Nardo, 1847	ME	+	+				+		
<i>Aplysina aerophoba</i> (Nardo, 1833)	ME	+	+						
<i>Aplysina cavernicola</i> (Vacelet, 1959)	ME								+
<i>Aplysina</i> sp.	Ec					+			
<i>Hexadella racovitzai</i> Topsent, 1896	Ec						+		
<i>Dysidea avara</i> (Schmidt, 1862)	ME		+						
<i>Dysidea fragilis</i> (Montagu, 1814)	ME		+						
<i>Dysidea incrustans</i> (Schmidt, 1862)	Ec	+							
<i>Ircinia variabilis</i> (Schmidt, 1862)	ME					+			
<i>Sarcotragus foetidus</i> Schmidt, 1862	ME							+	
<i>Sarcotragus spinosulus</i> Schmidt, 1862	ME					+	+		
<i>Spongia</i> (<i>Spongia</i>) <i>virgultosa</i> (Schmidt, 1868)	CD	+							
<i>Fasciospongia cavernosa</i> (Schmidt, 1862)	CD	+	+	+	+	+	+		
<i>Scalarispongia scalaris</i> (Schmidt, 1862)	ME							+	
<i>Oscarella</i> cf. <i>tuberculata</i> (Schmidt, 1868) *	ME							+	
<i>Oscarella</i> sp.	ME							+	
<i>Corticium candelabrum</i> Schmidt, 1862	ME	+	+						

<i>Plakina bowerbanki</i> (Sarà, 1960)	Ec					+			
<i>Plakina dilopha</i> Schulze, 1880 *	Ec		+						
<i>Plakina reducta</i> (Pulitzer-Finali, 1983)	Ec	+	+						
<i>Plakina trilopha</i> Schulze, 1880	Ec	+	+						
<i>Plakortis simplex</i> Schulze, 1880	Ec		+						

Table 1 List of sponge species collected at Tricase Porto sampled in the two periods with indication of their habit and type of habitat and the new finding for the Ionian Sea (*)

Oceanapia perforata (Sarà, 1960) and *Plakina reducta* (Pulitzer-Finali, 1983) have been recorded for the second time after their original descriptions. Two species are new for science and are here described together with a detailed description of *P. (S.) pulitzeri* and *P. (S.) vansoesti* which cannot be distinguished according to their external morphology (Figures 4–6). Moreover, several specimens of *Aplysina* sp. recently recorded from a semi-submerged cave on the Ligurian coast (Costa et al., 2018) were recorded (Table 1). This species, living in the intertidal level, is composed of small cushion-shaped sponges, often connected by a net of stolons. The species is probably new but a genetic analysis is necessary for a definitive determination.

SYSTEMATICS

Class DEMOSPONGIAE Sollas, 1885

Subclass HETEROSCLEROMORPHA Cárdenas,

Pérez & Boury-Esnault (2012)

Order CLIONAIDA Morrow & Cárdenas, (2015)

Family SPIRASTRELLIDAE Ridley & Dendy, 1886

Genus *Diplastrella* Topsent, 1918

Diplastrella boeroi

Bertolino, Costa & Pansini, sp. nov.

(Figure 2)

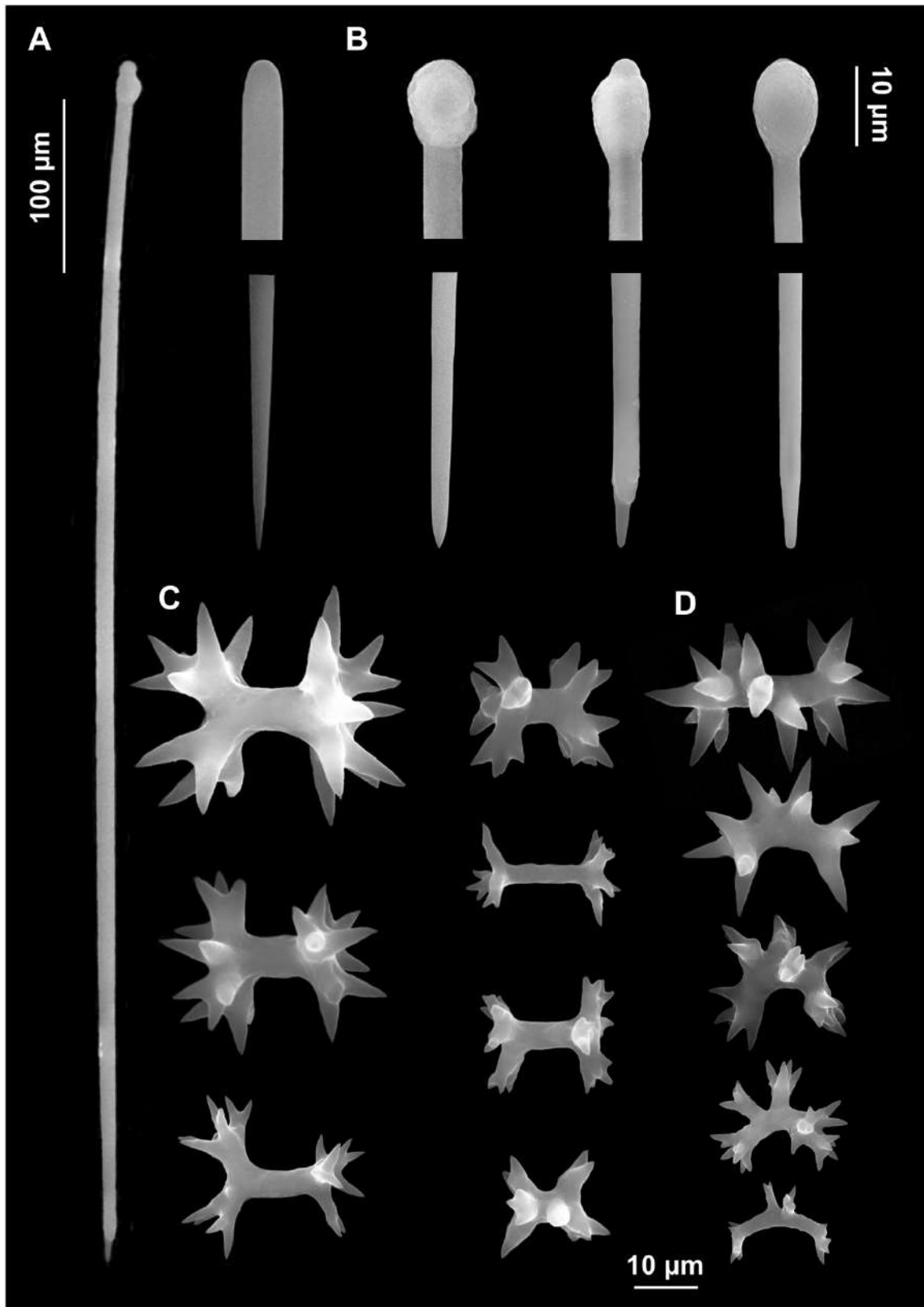


Fig. 2. *Diplastrella boeroi* sp. nov. (A) Long style; (B) style heads and tips; (C) diplasters to amphiasters; (D) spirasters.

Type material

Holotype: (Specimens and slides) Tr.BL1_48 (MSNG 60884), Ionian Sea, Tricase Porto, (Otranto Strait) 39°55'32.1''N 18°24'00.7''E, depth 20 m, on a coralligenous concretion, 10.6.2017.

Paratype: Tr.BL2_39. Adriatic Sea, Torre Guaceto, 40°42'57.51''N 17°48'12.61''E.

Other examined material:

(Specimens and slides) Tr.BL1_F15_3A_351; Tr.BL1_F9B_273; Tr.BL2_39; Ionian Sea, Tricase Porto, (Otranto Strait) 39°55'32.1'' N 18°24'00.7''E, depth 20m, on a coralligenous concretion, 10.6.2017. TG.BL1_42; TG.BL1_F10A_14; Adriatic Sea, Torre Guaceto, 40°43'00.61'' N 17°48'34.50''E, depth 24 m, on a coralligenous concretion, 12.6.2017.

Description

The specimens are small (about 2 cm in length) and thin (1– 3 mm), encrusting on coralligenous concretions. The surface is slightly hispid. The colour in life is red and fades to orange after alcohol preservation. Live specimens are soft and show small elevated oscula.

Skeleton. Typical spirastrellidae structure consists of a base layer of spongin and microscleres. The tylostyles are erect, arranged in bouquets, with the heads embedded in the basal spongin layer. Some of them protrude through the sponge surface producing its hispidation. The ectosomal crust is mainly formed by diplasters.

Spicules.

Megascleres: styles to tylostyles, straight or slightly curved, with circular or oval heads characterized by irregular or corrugate surface. Tips may be stepped, blunt, hastate and acerate (Figure 2A, B). They measure 250 (350) 450 × 2.5 (6.25) 10 µm.

Microscleres: most spicules are diplasters with a smooth shaft and regular or sometimes irregular whirls of spines, 3.5 (15.5) 27.5 × 1 (3) 5 µm (Figure 2C). Spines are often bifid. Other microscleres are spirasters that sometimes show bouquets of spines on the shaft, 9 (17) 25 × 2.5 (5) 7.5 µm (Figure 2D) (Table 2).

Etymology

The new species is named after Prof. Ferdinando Boero in recognition of his relevant contribution to biodiversity of the Salento coasts.

Habitat

Specimens recorded at 20–25 m depth encrusting the surface of coralligenous concretions and their superficial cavities.

Remarks

The species is assigned to the genus *Diplastrella* Topsent, 1918 according to the skeletal arrangement and the presence of diplasters. Seven species of the genus are known and two of them, *D. bistellata* (Schmidt, 1862) and *D. ornata* Rützler & Sarà, 1962, are recorded in the Mediterranean Sea. Both differ from the new species. *D. bistellata* has bigger microscleres (both

spirasters and diplasters) than the new species: 45 µm in length vs 27.5 µm. *D. ornata* has large diplasters (56–76 µm) with characteristic multi-branched rays. The medium-sized ones may rarely assume the shape of thick spirasters but they do not represent a separate category of microscleres. In *D. gardineri* Topsent, 1918, a species with tropical distribution (Red Sea; Maldives; Zanzibar; Madagascar), the spirasters, 45 µm long, are much more

numerous than the diplasters. *D. megastellata* Hechtel, 1965 and *D. spiniglobata* (Carter, 1879) have small asters and spheraster. *D. spirastrelloides* Van Soest, 2017 from the North Atlantic has spirasters twice as large as the new species. *D. yongmeoriensis* Kim & Sim, 2009 from the East China Sea has long and very thin spirasters similar to those found in the genus *Cliona*.

<i>Diplastrella boeroi</i> sp. nov.	Tylostyles (µm)	Diplasters (µm)	Spirasters (µm)
Tr. Bl1_48	250(312.5)375 x 2.5(5)7.5	4(13.5)27.5 x 2.5(3.75)5	10(15)20 x 5(6.25)7.5
TR. Bl1_F15_3A_351	250(430)610 x 2.5(21.5)2.5	10(16.25)25 x 2(3.75)5	10(16.5)23 x 5(6.25)7.5
TR. Bl1_F9B_273	287.5(313.7)340 x 4.5(6)7.5	3.5(14.6)25 x 2(3.75)5	12.5(16.25)20 x 2.5(3.75)5
TR. Bl2_39	287.5(313.7)340 x 4.5(6)7.5	3.5(14.6)25 x 2(3.75)5	12.5(16.25)20 x 2.5(3.75)5
TG. Bl1_42	310(370)430 x 5(7.5)10	5(14.4)25 x 1(3.4)5	9(15.5)22 x 5(6.25)7.5
TG. Bl1_F10A_14	330(390)450 x 5(7.5)10	5(15)27.5 x 1(3.4)5	10(17.5)25 x 5(6.25)7.5
<i>Spirastrella angulata</i> sp. nov.	Tylostyles (µm)	Spirasters (µm)	
Tr. Bl1_37	500(674)800 x 5(5.5)7.5	7.5(18.5)25 x 2.5(7.5)17.5	
Tr.BL1_F15_1A_342	500(694)900 x 5(5.5)7.5	7.5(18.5)25 x 2.5(7.5)17.5	
Tr.BL1_F18_3A_441	480(660)750 x 5(5.5)7.5	7.5(18.5)25 x 2.5(7.5)17.5	

Table 2. Spicule measures of specimens of *Diplastrella boeroi* sp. nov. and *Spirastrella angulata* sp. nov.

Genus *Spirastrella* Schmidt, 1868
Spirastrella angulata
Bertolino, Costa & Pansini, sp. nov.
(Figure 3)

Type material

Holotype. (Specimens and slides) Tr.BL1_37, (MSNG 60885), Tricase Porto, 39°55'32.1''N 18°24'00.7''E, depth 20 m, on a coralligenous concretion, 10.6.2017.

Paratypes: (Specimens and slides) Tr.BL1_F15_1A_342; Tr.BL1_F18_3A_441, Tricase Porto, depth 20 m, on a coralligenous concretion, 10.6.2017, dry preserved.

Description

The three specimens were thinly encrusting (1–2 mm thick) on a coralligenous concretion, covering small surfaces (1–2 cm²). The colour in life is red and becomes orange in alcohol. The surface is slightly hispid. Live specimens are soft and show small elevated oscula.

Skeleton. The skeleton is typical of the genus *Spirastrella* with dense layers of spirasters in both ectosomal and basal choanosomal regions and bundles of a few tylostyles with the points directed outward. The smaller spirasters are concentrated at the surface, the larger ones close to the substrate, and many microscleres of both types are strewn in between. Tylostyles heads are embedded in the basal spongin layer. Some tylostyles protruding from the sponge surface cause a faint hispidation.

Spicules. Megascleres: Tylostyles to sub-tylostyles to styles, straight or curved and

sometimes sinuous. Heads round to oval (sometimes showing malformations) and shafts with sharp points (Figure 3A, B). They measure 480 (690) 900 × 5 (5.5) 7.5 μm. Microscleres: all the microscleres are spirasters, 7.5 (18.5) 25×2.5 (7.5) 17.5 μm. The spiraster axis is generally twisted, angulate and sometimes curved and often once or twice bent (Figure 3C). The conical spines, always sharp, may be more or less evenly distributed or confined to the spicule extremities. A reduction in the number of spines may be observed in some of the spicules with a thin axis (Figure 3C) (Table 2).

Etymology

The species is named after the peculiar shape of the small angulate spirasters.

Habitat

Specimens were recorded at 20–25 m depth encrusting coralligenous concretions characterized by a pillar structure.

Remarks

Among the 17 known species of *Spirastrella*, only *S. cunctatrix* Schmidt, 1868 is until now recorded in the Mediterranean Sea and the Eastern Atlantic. *S. cunctatrix* differs from the new species for the morphology and the size of spicules. The tylostyles of *S. angulata* sp. nov. are remarkably longer than those of *S. cunctatrix*, whereas the spirasters of *S. cunctatrix* (28–50 μm in length) may be twice as big and different in shape from those of the new species. The two species present in the

Red Sea: *S. decumbens* Ridley, 1884 and *S. pachyspira* Lévi, 1958, differ from *S. angulata* sp. nov. in the shape and size of spicules. *S. decumbens* has shorter tylostyles, *S. pachyspira* has very large spirasters up to 110 μm in length. The other known *Spirastrella* species have different characters in spicular complement (shape and measures) and live in

geographically distant areas such as the Eastern Atlantic and the Caribbean, the Indian Ocean, the coast of Japan and a few Pacific areas.

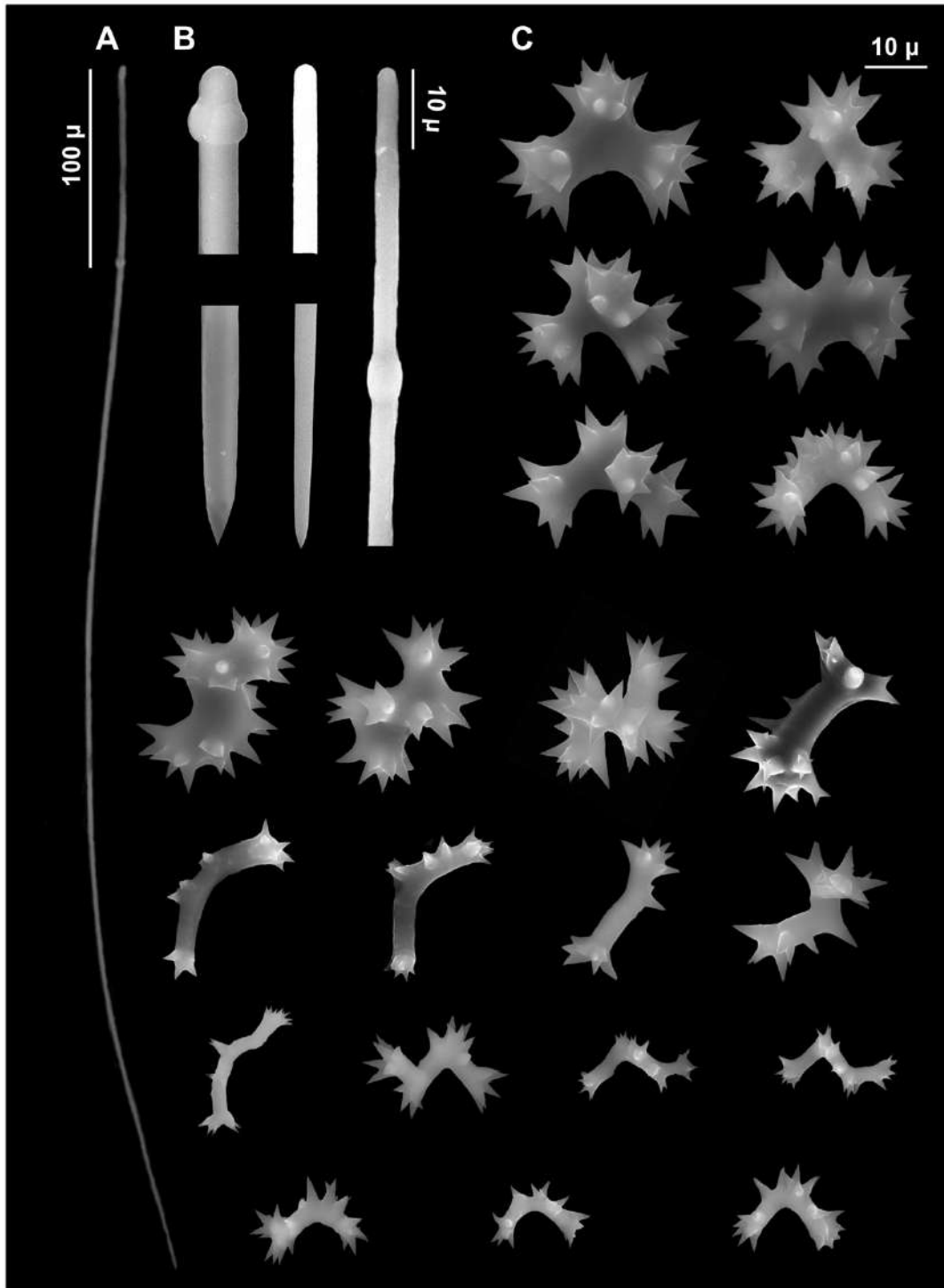


Fig. 3. *Spirastrella angulata* sp. nov. (A) Long style; (B) style heads and tips; (C)

Order HAPLOSCLERIDA Topsent, 1928

Family PETROSIIDAE van Soest, 1980

Genus *Petrosia* Vosmaer, 1885

Subgenus *Petrosia (Strongylophora)* Dendy, 1905

Petrosia (Strongylophora) pulitzeri Pansini, 1996

(Figures 4A–5)

Type material

(Specimens and slides) TRP64, Tricase Porto, Ionian Sea, semi-submerged ‘Matrona’ Cave (39°54’20.02’’N 18°23’25.76’’E), depth 2 m, 11.6.2017.

Description

Massive sponge with anastomosing horizontal irregular branches and with vertical irregular digitiform processes up to 1.5–2 cm high. Scattered round oscules are 1–5 mm wide. The surface is smooth with a cribose aspect due to the presence of ostia (0.2– 0.3 mm) (Figure 4A). Consistency is hard and colour is white in vivo and in alcohol preserved specimens.

Skeleton. The ectosomal skeleton is a network of irregular triangular or quadrangular meshes with sides formed by single strongyles or oxeas. At the angular points (‘corners’) of the strongyle-tracts are groups of very short strongyles which form surface nodes that produce the granular-aspect of the surface (Figure 5A). Choanosomal skeleton is a very dense, compact sub-rectangular network with small meshes formed by stout spicular tracts of closely packed strongyles and free spicules (Figure 5B, C). Toward the surface there are stout multispicular tracts formed by radiating

bundles of closely packed strongyles, without visible spongin.

Spicules. Megascleres: oxeas, measure 30 (152.4) 300×2 (6.1) 20µm; styles measure 30 (106.7) 375×2.5 (12.5) 20µm and strongyles with intermediate forms, measure 50 (162.5) 300× 2.5 (9.7) 20 µm (Figure 5D).

Geographical distribution

Tyrrhenian Sea (Gulf of Naples), Aegean Sea (Crete), coasts of Turkey (Marmara Sea) (Pansini, 1996).

Petrosia (Strongylophora) vansoesti Boury-Esnault, Pansini & Uriz (1994) (Figures 4B–6)

Type material

(Specimens and slides) TRP32, Tricase Porto, Ionian Sea, semi-submerged ‘Matrona’ Cave (39°54’20.02’’N 18°23’25.76’’E), depth 2 m, 11.6.2017.

Description

Massive sponge with external morphology similar to that of *P. (Strongylophora) pulitzeri* sampled by us (Figure 4B).

Skeleton. The ectosomal skeleton is a network of irregular triangular or quadrangular meshes with sides formed by single strongyles or oxeas (Figure 6A). At the angular points (‘corners’) of the strongyle-tracts are groups of very short strongyles which form surface nodes that produce the granular-aspect of the surface. Choanosomal skeleton very dense: compact sub-rectangular network of small meshes formed by stout tracts of closely packed strongyles and free spicules (Figure

6B, C). Toward the surface there are stout multispicular longitudinal tracts formed by radiating bundles of single strongyles, closely packed, without visible spongin.

Spicules. Megascleres: oxeas, measure 42.5 (164) 242.5 × 1 (5.25) 12.5 μm, styles, measure 50 (162.14) 212.5 × 5 (8.6) 12.5 μm and strongyles with intermediate forms, measure 14 (190) 235 × 5 (8.21) 12.5 μm (Figure 6D).

Geographic distribution

Saharan upwelling within the outflow of Mediterranean seawater in the Atlantic (Strait of Gibraltar), coast of Greece (Youra Island) and coast of Turkey.

Remarks

In the Matrona Cave, three species of the genus *Petrosia* (*P. ficiformis*, *P. pulitzeri* and *P. vansoesti*) were recorded. The external morphology does not allow their specific separation (Figure 4). While the spicules of *P. ficiformis* are well known, the other two species were less studied. In Table 3 we have compared data about morphological characters and ecology of *P. (Strongylophora) pulitzeri* Pansini, 1996 and *P. (Strongylophora) vansoesti* Boury-Esnault, Pansini & Uriz, 1994 specimens hitherto recorded in the Mediterranean Sea and in Table 4 we have compared data about the spicules of our specimens with those reported by previous description. Study of the skeleton (Figure 5A–C) of *P. (Strongylophora) pulitzeri* confirms that this species can be

attributed to the subgenus *Strongylophora* as suggested by Lévi & Lévi (1983), de Weerd & van Soest (1986) and Pansini (1996). *Petrosia (Strongylophora) pulitzeri* is known for the Gulf of Naples, the Island of Crete (Pansini, 1996) and the Marmara Sea (Topaloğlu, 2001). *Petrosia (Strongylophora) vansoesti* was described by Boury-Esnault et al. (1994) from the Saharan upwelling within the outflow of Mediterranean seawater in the Atlantic (Strait of Gibraltar) and later recorded on the coast of Greece (Youra Island) by Voultziadou & Vafidis (2004) and Turkey by Evcen & Cinar (2012).

Species	Shape	Colour	Surface	Consistency	Skeleton	Spicules (μm)	Habitat and Depth
<i>P. pulitzeri</i> after the original description	Specimens: ML29 cushion-shaped CRT10 cylindrical CRT43 small incrustations Rather coarse, with rounded tubercles less than 1 mm high, or with series of low ridges arranged to form roundish meshes. Oscules are scattered, round, 1–2 mm wide and bordered by a low rim. Other minor vents (0.2–0.3 mm across) are scattered on the sponge surface.	White or yellowish	Smooth	Specimen: ML29 stony hard CRT10-CRT43 slightly softer	Ectosome as a felt-work of tangentially arranged oxeads (of different sizes), which do not form any reticulation, supported by the choanosomal spicule tracts. The choanosome is a dense reticulation of stout tracts of closely packed spicules, mostly strongyles of the bigger size, forming roundish meshes rather variable in size.	CRT10 Oxeads and strongyles with intermediate forms. (See Tab. 4)	ML29 submerged cave, 15 m CRT10 submerged cave, 2–5 m CRT43 submerged cave, 0.5–1 m
<i>Petrosia (Strongylophora) vansoesti</i> after the original description	DR40-E10 DR111-48 Massive spherical An oscule 5 mm in diameter opens at the top of the sphere on a flattened area. The minor vents are grouped into small groups each corresponding to an inhaling canal.	Ochre after preservation	Smooth	Hard	Ectosomal skeleton is polygonal. Mesh of the network is 200 μm wide on average and the bundles of the spicules constituting it, 30–35 μm in diameter. This primary mesh is subdivided into smaller meshes by unispiculated lines. Choanosomal complex is also a network with an average mesh size of 340 μm . Bundles of strongyles constituting these meshes have a diameter of 85 μm . No visible spongin.	DR40-E10 DR111-48 Strongyles and oxeads. (See Tab. 4)	Saharan upwelling within the outflow of Mediterranean Sea water in the Atlantic, between 285 and 362 m.
<i>Petrosia (Strongylophora) vansoesti</i> after Voultsiadou & Vafidis, 2004	Massive spherical It bears an oscule, having a diameter of 0.5 cm, in the middle of a depression, on its upper surface. Small ostia are arranged in groups around the body.	Light	Smooth	Hard	Ectosomal skeleton is made of a reticulation of spicules, while the choanosomal skeleton is characterized by thick spicule tracts, having a mean width of 200 μm , forming meshes with a mean diameter of 500 μm , obscured in some places by irregular masses of spicules.	Oxeads, strongyles and styles (See Tab. 4)	Cave wall at 20 m depth, Youra Island (Greece)
<i>Petrosia (Strongylophora) vansoesti</i> after Evcen et al. 2012	ESFM-POR/2005-59,05.10.2005, K44 Undetermined	Undetermined	Undetermined	Undetermined	Ectosomal skeleton has a reticulation of spicules. The choanosomal skeleton has thick tracts, obscured by irregular masses of spicules in some places.	Oxeads and strongyles (See Tab. 4)	On rocks 0.1–3 m depth, southern Turkey coast

Table 3. Morphological characters and ecology of *P. (Strongylophora) pulitzeri* Pansini, 1996 and *P. (Strongylophora) vansoesti* Boury-Esnault, Pansini & Uriz, 1994 specimens hitherto recorded in the Mediterranean Sea

<i>Petrosia (Strongylophora) pulitzeri</i> Pansini, 1996	Oxeas (µm)	Strongyles (µm)	Styles (µm)
Specimen CRT10 Pansini, 1996	57.5(143.4)285 x 2.5(8.15)15	32.5(108.6)245 x 5(11)20	45(171)245 x 5(10.75)15
Specimen TRP64 present paper	30(152.4)300 x 2(6.1)20	30(106.7)375 x 2.5(12.5)20	50(162.5)300 x 2.5(9.7)20
<i>Petrosia (Strongylophora) vansoesti</i> Boury-Esnault, Pansini & Uriz, 1994	Oxeas (µm)	Strongyles (µm)	Styles (µm)
Specimen Boury-Esnault <i>et al.</i> 1994	54(90)140.4 x 2.7(4)5.4	21.6(128)337.5 x 8.1(12)21.6	-
Specimen Voultziadou & Vafidis 2004	(Oxeas) 50(-)200 x 3(-)8 (Large oxeas) 200(-)320 x 20(-)32	200(-)320 x 20(-)32 (Small strongyles) 50(-)100 x 12(-)28	200(-)320 x 20(-)32
Specimen Evcen and Çinar 2012	120(-)300 x 5(-)8	65(-)360 x 8(-)20	-
Specimen TRP32 present paper	42.5(164)242.5 x 1(5.25)12.5	50(162.14)212.5 x 5(8.6)12.5	140(190)235 x 5(8.21)12.5

Table 4. Spicule measures of specimens of *P. (Strongylophora) pulitzeri* and *P. (Strongylophora) vansoesti* recorded in the Mediterranean Sea.

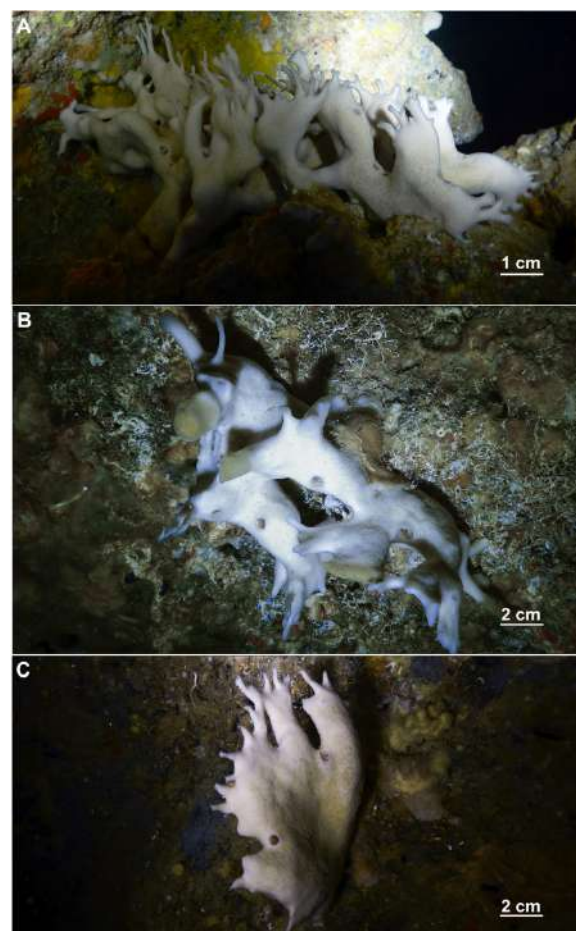


Fig. 4. (A) *P. (Strongylophora) pulitzeri*; (B) *P. (Strongylophora) vansoesti*; (C) *P. ficiformis* with similar habit in the ‘Matrona’ cave at Tricase Porto

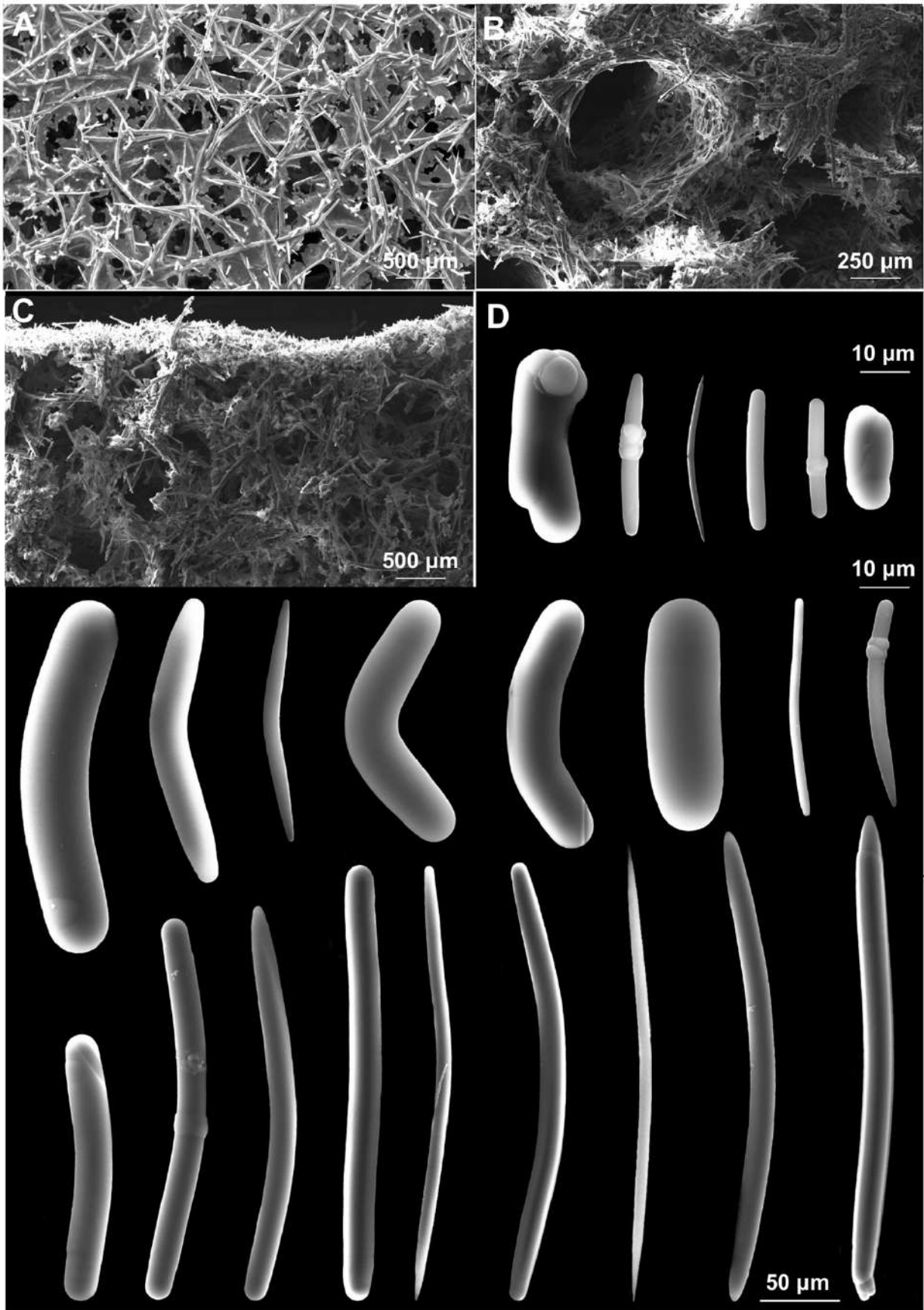


Fig. 5. *P. (Strongylophora) pulitzeri*. (A) Ectosomal skeleton; (B) detail of a canal in the choanosomal skeleton; (C) choanosomal skeleton; (D) oxeas, strongyles and styles.

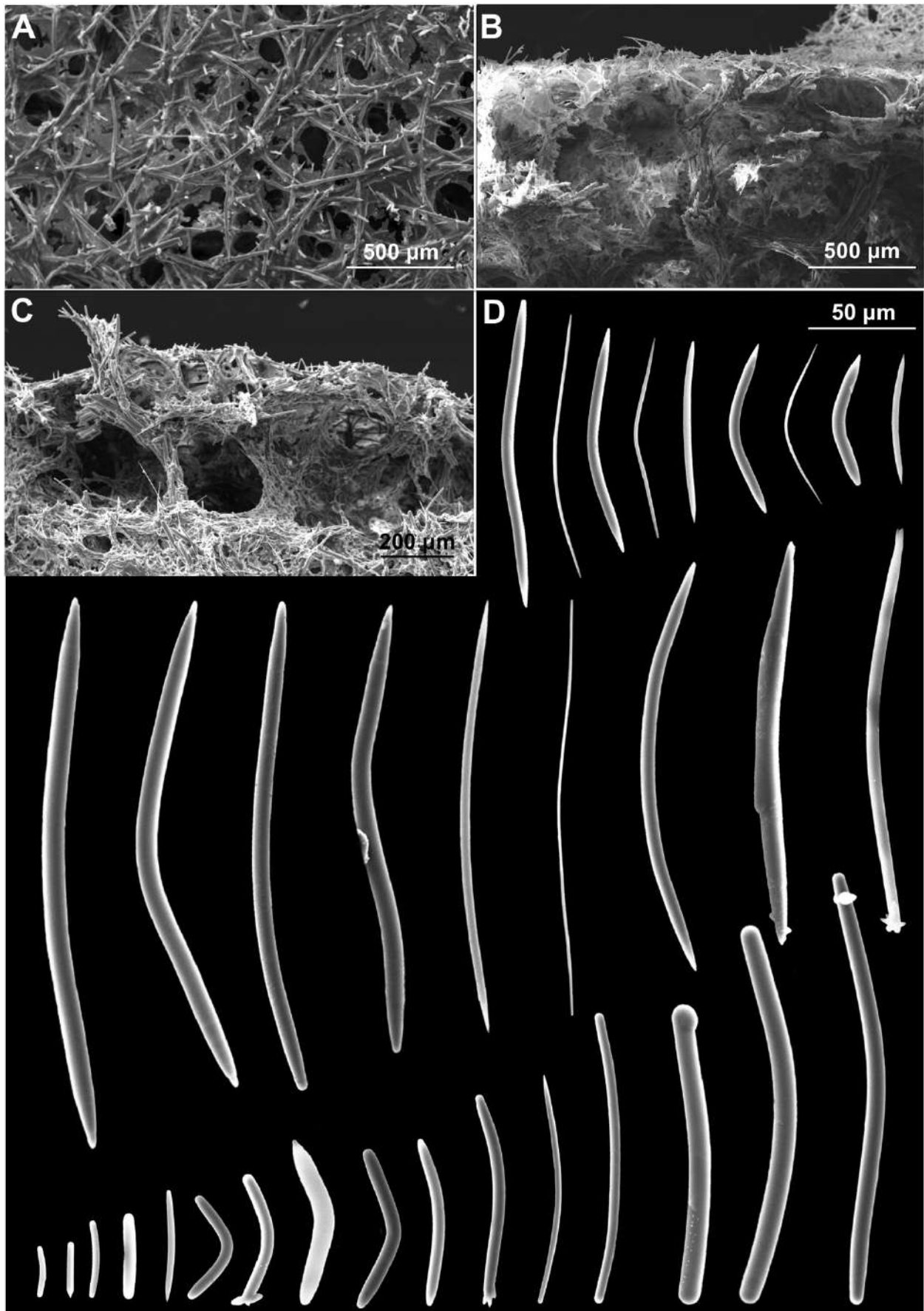


Fig. 6. *P. (Strongylophora) vansoesti*. (A) Ectosomal skeleton; (B) choanosomal skeleton; (C) detail of the choanosomal skeleton; (D) oxeas, strongyles and styles.

4. Discussion and conclusions

In recent decades, marine ecosystem composition and functioning, especially in the Mediterranean Sea, have headed toward deep modifications driven by climate variations. It is well known that the biology of marine organisms can be altered by climate changes due to both a higher frequency of short-term extreme events and long-term temperature increases (Lejeusne et al., 2010).

Long-term biodiversity monitoring and observations are essential for understanding the changes over time of the marine benthic communities (Roberts, 2009; Boero et al., 2015). In this context, sponges, due to their high biodiversity and long persistence of their spicular remains, are a suitable group to check putative differences occurring over a number of temporal scales (Bertolino et al., 2016, 2017a, 2017b; Costa et al., 2018). Thanks to the data of Pulitzer-Finali (1983) recorded about 50 years before the present survey, a first comparative investigation of the sponge assemblages present in four habitats of Tricase Porto coastal area was possible.

The number of sponge species recorded in the Tricase area was about twice that observed 50 years before in the same stretch of coast (Table 1 and Figure 7). Thirty-one species (62% of the species recorded in the period 1967–70) are shared by the two surveys (Figure 7).

The dramatic increase of the species recorded in the recent sampling is probably due to several factors. Firstly, during the recent survey we examined in detail two habitats, marine caves and deep cliffs (finding 13 and five species respectively), that were only sporadically visited by Pulitzer-Finali who found four species in each of them. Moreover, it is very likely that our survey could have been more accurate compared with that of Pulitzer-Finali which collected only discrete and large specimens. On the other hand, if we compare only the species recorded by Pulitzer-Finali in the two most species-rich habitats, the rocky cliffs and the coralligenous, we see that 64.7 and 75% of the species recorded in the period 1967–70 are present currently, indicating a significant resilience of the past communities.

Nevertheless the increase in the number of recorded species should not be considered only in relation to differences in the sampling accuracy. In the two more species-rich habitats, rocky cliffs and coralligenous, the number of species increased from 17 to 26 and from 36 to 77 respectively. This impressive increase was approximately the same in all the considered sponge growth forms (Figure 8).

Thibaut et al. (2005) had hypothesized that, under the recent seawater warming, the Mediterranean benthic communities experienced a strong decrease in biodiversity. Our data indicate that sponge communities do

not confirm this assumption. Nevertheless, the strong increase of biodiversity recorded in the present survey may be partially biased by the more accurate sampling method (with coralligenous slices), but very likely indicates a real trend of the community. These data match well with previous evidence from other Mediterranean localities. For example, Costa et al. (2018) have recently shown that the number of sponge species present in semi-submerged caves of the Ligurian Sea surveyed 50 years ago is now almost doubled. Certainly Porifera, and particularly the horny sponges, suffered many massive epidemic diseases that have brought entire populations of some species to the brink of extinction (Gaino & Pronzato, 1991; Rizzello et al., 1997; Pronzato, 1999; Cerrano et al., 2000; Pronzato & Manconi, 2008; Pronzato et al., 2012; Di Camillo & Cerrano, 2015). Nevertheless, evidence coming from comparative studies at pluri-decennial scale, from several areas of the Mediterranean Sea, shows a clear increasing trend of sponge diversity in this period of water warming (Bianchi et al., 2014; Bertolino et al., 2016). These hypotheses are in agreement with data on a millennial time span, obtained through the analysis of the spicular remains present in dated core samples of coralligenous concretions, indicating an increase of sponge diversity in correspondence with periods of increasing water temperature (Bertolino et al., 2017b).

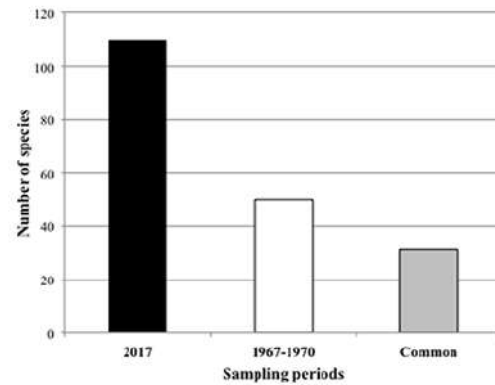


Fig. 7. Number of sponge species recorded during the two sampling periods. The grey bar represents the species in common between the two sampling periods.

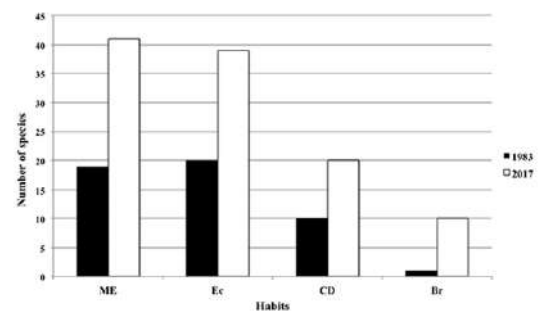


Fig. 8. Number of sponge species recorded during the two sampling periods divided according to their habit. ME: massive habit, Ec: encrusting habit, CD: cavity dwelling habit, Br: boring habit.

Supplementary material.

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315419000651>.

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Evolution on a millennial temporal scale of a Mediterranean coralligenous sponge assemblage (Tricase Porto, Otranto's Canal), preliminary results

Abstract

Studying sponge assemblages present in two coralligenous build-ups in Tricase Porto (Otranto's Channel), we are able to reconstruct the changes in species composition and abundance occurred over a pluri-millennial span of time (6207–1767 yr B.P.) in this area, similarly to the studies conducted in other areas by Bertolino et al (2014, 2017a, b 2019). Thus, the detection, description and evaluation, both from a quantitative and a qualitative point of view, of the living sponges and of the siliceous spicules entrapped in these microenvironments, is crucial to describe the actual and the ancient community types of Porifera and to define the climatic changes through the differences among them.

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Additional Resources

The study is in progress and therefore the results are preliminary

1. Materials and methods

Ancient and present sponge assemblages were studied in two coralligenous bioherms (outcrops 1 and 2, with a volume of about 50 to 70 cm in height respectively) collected at 20 m depth off Tricase Porto (Apulia - Ionian Sea) (Fig. 1 preliminary). Samplings of coralligenous conglomerates were performed by SCUBA diving during summer 2017. After collection, the build-ups were divided into horizontal slices and 1 vertical of about 4 cm thick by a stone saw. All the living sponges present on the surface of the conglomerates and those boring or cavity dwelling — detected by a visual analysis of the slice— were collected and identified.

Finally, from the central slice of each build-up, a longitudinal transect (50 cm height, block 1 and 70 cm height, block 2), oriented from the apex to the bottom, was conducted and divided in serial sub-samples about 5 cm thick. The thin sediments filling the crevices among algal strata were released by soaking each piece in hydrogen peroxide (60 wt%), changed three times at 24h intervals. The sponge spicules present in the released sediments were concentrated by dissolving the carbonate fraction with boiling nitric acid. For each sample of sediment, three replicates of 10 mg each were mounted on a microscope slide. Microscopic analysis of the spicules extracted from the sediment was performed to investigate the sponge communities up to the lower possible taxonomic level. After the

sediment extraction, each portion of the conglomerate was ¹⁴C dated by accelerator mass spectrometry (AMS) at the Center of Dating and Diagnostic (CEDAD) of the University of Salento (Calcagnile et al, 2005). Calibrated radiocarbon ages were expressed as calBP and used in the chronological discussion and interpretation.

The diversity of genera observed in the past (8000-2000 YBP) was estimated as presence/absence (Table 1).

The species found in the living assemblage but devoid of siliceous spicules, were not considered in the analysis, because it was impossible to detect their presence in the ancient assemblages.

Core Genera	Growth forms	YBP							
		8000-6000	6000-4000	4000-2000	2000-0	8000-6000	6000-4000	4000-2000	2000-0
		BL1-1	BL1-5	BL1-9	BL1-13	BL2-1	BL2-5	BL2-9	BL2-13
<i>Plakina</i>	Ec	X	X	X	X		X	X	X
<i>Petrosia</i>	ME	X	X	X	X	X	X	X	X
<i>Protosuberites</i>	Ec	X				X			
<i>Spirastrella</i>	Ec	X	X	X	X	X	X	X	X
<i>Rhabdermia</i>	Ec	X	X	X	X	X	X	X	X
<i>Diplastrella</i>	Ec	X	X	X	X	X	X	X	X
<i>Spiroxya/Dotona</i>	Br	X	X	X	X	X	X	X	X
<i>Ciona</i>	Br	X	X	X	X		X	X	X
<i>Cliothosa</i>	Br	X							
<i>Carticium</i>	ME					X			
<i>Erylus</i>	CD	X		X			X		
<i>Geodia</i>	CD	X		X	X	X	X	X	X
<i>Pachastrella</i>	CD		X			X	X		
<i>Dercitus</i>	CD	X	X	X	X	X	X	X	X
<i>Tethya</i>	ME	X	X	X	X		X	X	X
<i>Chondrilla</i>	ME	X	X	X	X		X	X	X
<i>Delectona</i>	Br	X	X	X		X	X	X	
<i>Didiscus</i>	Ec		X		X				
<i>Acamus</i>	CD		X			X			X
<i>Aaptos</i>	CD	X							
<i>Agelas</i>	ME	X	X		X		X	X	X
<i>Antho</i>	Ec	X							
<i>Thoosa</i>	Br	X	X	X	X		X	X	
<i>Thrombus</i>	CD	X							
<i>Trachycladus</i>	ME				X	X		X	
<i>Alectona</i>	Br	X			X		X	X	
<i>Alveospongia</i>	ME	X	X		X	X	X	X	X
<i>Eurypon</i>	Ec	X				X			
<i>Crella</i>	Ec	X			X	X	X	X	X
<i>Bubaris</i>	Ec	X						X	X
<i>Cerbaris</i>	Ec	X				X			X
<i>Mycale</i>	Ec	X							
<i>Placospongia</i>	Ec								X
TOTAL RECORDED GENERA		26	16	14	18	17	18	19	18

Table 1. Presence/absence of the genera in different ancient time spans

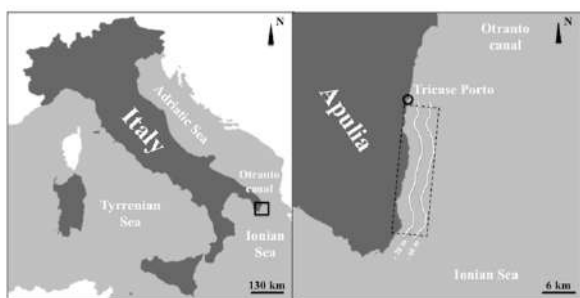


Fig. 1 Studied area in front of Tricase Porto (Ionian Sea)

2. Preliminary results

The studied coralligenous build-ups measured from 50 to 70 cm in height and about 30 cm in diameter. They were irregular in shape and with several holes and crevices. The sponge fauna settled inside and on the surface of these bioherms was studied by Costa et al 2019. Considering recorded species, some differences in sponge abundance were observed according to the different kinds of growth form (massive/erect, ME; encrusting, Ec; cavity dwelling, CD; boring, Br). The most represented growth form, in term of species richness, belongs to the category of the encrusting sponges (34 species), followed by the cavity dwelling sponges (20 species), the massive erect sponges (14 species) and the boring sponges (9 species) (Fig. 2). While concerning the most represented growth form in term of specimens abundances, an opposite trend was showed (Fig. 3). The cavity dwelling *Jaspis johnstonii* and *Jaspis incrustans* were the most frequent having a presence percentage of almost 42.8% of the total samples (*J. johnstonii* 21.4% and *J. incrustans* 21.4%). Other common species

with major samples percentage were *Cliona schmidtii* (Br), *Halichondria* sp. (Ec), *Dercitus (Stoeba) plicatus* (CD), *Diplastrella bistellata* (Ec), *Axinella verrucosa* (M/E), *Cliona viridis* (Br), *Erylus discophorus* (CD) and *Plakina reducta* (Ec) (Fig. 4).

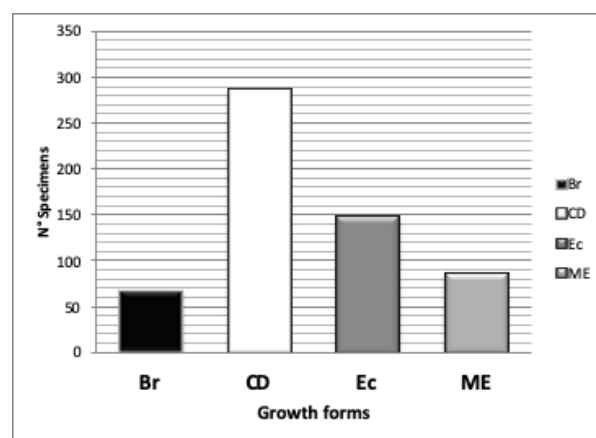


Fig. 2 Species number divided into different growth forms; (Br) Boring sponge, (CD) cavity dwelling, (Ec) encrusting, (ME) Massive/Erect

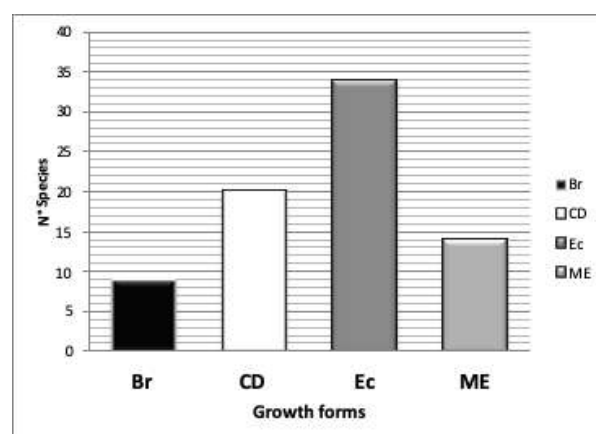


Fig. 3 Specimens number divided into different growth forms; (Br) Boring sponge, (CD) cavity dwelling, (Ec) encrusting, (ME) Massive/Erect

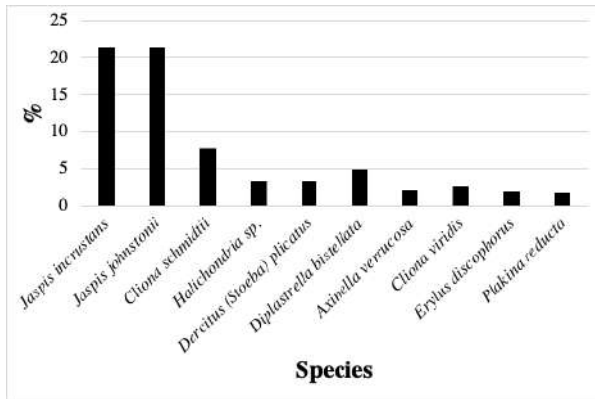


Fig. 4 Percentage of the most common species in terms of specimens abundance

Thus, from a general point of view, the endolithic forms are more abundant in terms of number of specimens respect to the epilithic ones (Fig. 5), but are less abundant in terms of number of species respect to the epilithic ones (Fig. 6).

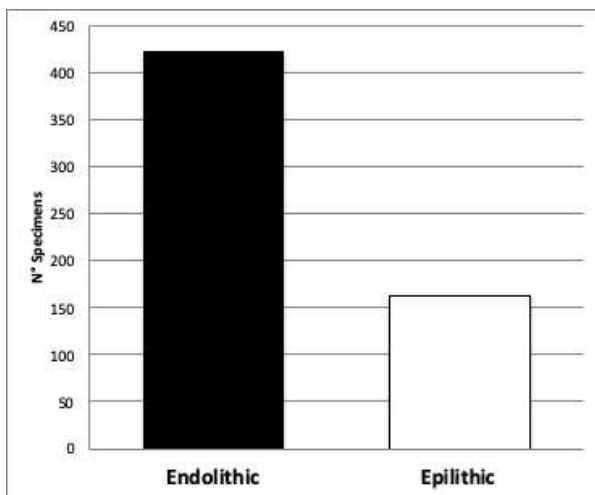


Fig. 5 Specimens number divided into Endolithic and Epilithic sponges

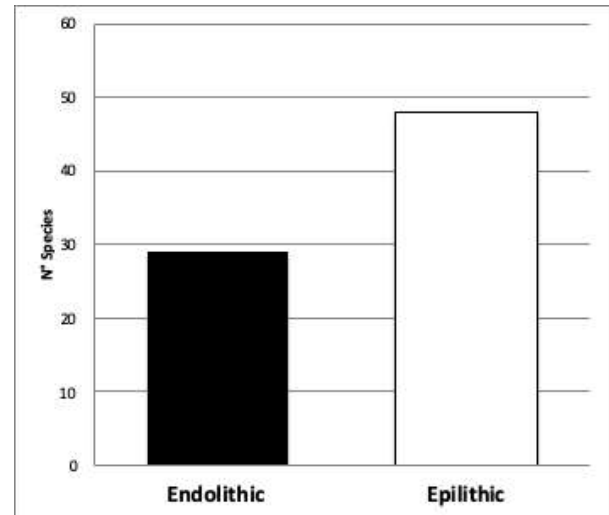


Fig. 6 Species number divided into Endolithic and Epilithic sponges

Analysing the siliceous spicules embedded in the sediments trapped into the pith of these bioherms, a total of 33 genera have been recognized, 9 of these genera were absent in the modern sponge fauna recorded in the two pillars (Table 1).

The temporal study of the sponge richness variation shows stable values along the four timespans analysed. Four recorded genera appear to be persistent and thus present in all the timespans (*Petrosia*, *Spirastrella*, *Diplastrella*, *Spiroxya/Dotona*). While others as *Cliothosa*, *Corticium*, *Aaptos*, *Antho*, *Mycale* and *Placospongia* are almost ore exclusively present in one of the four periods analysed (Table 1). Particularly significant is the record of sinuous acanthomicrostrongyles referable to the genus *Alveospongia*, recently described from Brazil (Santos et al, 2016), and already found in the similar studies of Bertolino et al (2017a, b; 2019). The quantitative contribution of different kinds of

spicules was estimated, focusing on the most representative genera and neglecting the genera having the least spicules abundances (Fig. 7).

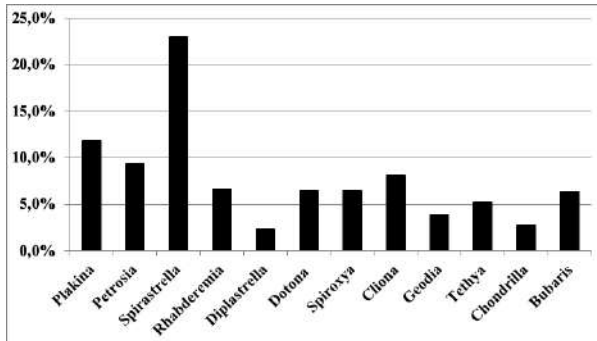


Fig. 9 Percentage of spicules abundance of most representative ancient genera

3. Preliminary discussion

Tricase Porto sponge community, from a quantitative point of view, is dominated by cavity dwelling (CD) sponges. It is intriguing that the genera *Spirastrella*, *Diplastrella* and *Petrosia* are constantly recorded during the entire life of the bioconcretions whereas other cavity dwelling sponges are not more recorded in the living assemblage. A similar situation was also recently observed in the coralligenous formations from the Ligurian Sea (Bertolino et al, 2017), recalling the observations of Wiedenmayer (1994) from tropical coral reefs. From a biogeographical point of view, it is worth stressing the wide presence of sinuous acanthomicrostrongyles belonging to *Alveospongia*, a genus of Heteroxyidae family, recently described by Santos et al (2016) from the tropical Atlantic and also found in ancient embedded

sediments of the coralligenous build-ups of the Ligurian Sea (Bertolino et al, 2017) and in this study; from the comparison of the appearance pattern of *Alveospongia* in the build-ups of the Ligurian sea and of Tricase Porto, point out a sort of analogy: in both the studies *Alveospongia* results to be absent in the same time span (between 2500 and 3000 YBP in the Ligurian build-up and between 2000 and 4000 YBP in the Apulian build-up) Moreover, the conspicuous finding of *Plakina reducta* (Pulitzer-Finali, 1983) among the endolithic species is important to be underlined; this encrusting species is never been found by other authors after Pulitzer-Finali in 1983 and Longo et al. in 2017, whose found it exclusively in studies concerning the same biogeographical area of this work, in particular Pulitzer-Finali described it from the stretch of coast of Tricase Porto, and Longo et al. (2017) found it at Torre Inserraglio (Jonian coast), this observations can bring to suppose *P. reducta* is endemic of this biogeographic zone.

By comparing past and modern periods of the study areas of Ligurian Sea, Jonian Sea and that one of the present work, a significant change in biodiversity is evident in both the areas, whereas the loss in genus richness could be related to sharp variations of seawater temperature. In the light of these results, it can be confirmed that a better interaction between the paleoecological and geophysical studies in the Mediterranean area

might contribute to improve our knowledge on the evolution of the littoral benthic communities in the last millennia as underlined by Pirazzoli (2005).

4. References

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Final discussion

Porifera, with over 300 species (Longo et al, 2017; Costa et al, 2019), are today one of the most diversified groups in the entire coralligenous community. Thanks to the analysis of the slices pinnacles (Bertolino et al, 2014) it is possible to study the sponges that live inside the bio-concretion, indeed, with this method, for example Costa et al, 2019 discovered two new sponge species (*Diplastrella boeroi* and *Spirastrella angulata*) in the Tricase coralligenous and increasing the number of species associated with this habitat.

Instead thanks to the taxonomic analysis of the siliceous spicules trapped in the sediments that accumulate over millennial time in the cavities of the conglomerate, it is possible to evaluate the dynamic variation of the specific wealth of this community during the entire evolutionary history of bioconstruction.

The analyses conducted on the coralligenous of Bogliasco, Porto Cesareo and Tavolara, have shown a substantial millennial temporal stability of the sponge community: most of the ancient spicules observed belong to genera still present today in and on bioconstructions. An important exception is represented by the genus *Alveospongia*, once widespread in all the studied communities and today totally absent from the entire Mediterranean basin, since it makes us

suppose an extinction of this taxon after a certain period. Other genera, in the past variously represented, today can be found only in deep faunas such as those associated to white corals.

Despite this basic stability, the wealth of the sponge community shows evident variations over the millennia that seem to be in agreement with the climatic variations known for the northern hemisphere (Bertolino et al, 2019). In particular, the highest levels of biodiversity were found during the Holocene Climatic *Optimum*. The temporal trend shows a rapid reduction during the Bronze Age Crisis to rise again during the Roman Empire's *Optimum*, still tending to decrease during the small Medieval Glaciation.

From a spatial point of view, these communities seem to have been much more similar to each other in the past millennia (8000-2000 YBP), when all bio-constructions were in an active growth phase, while today they show a greater degree of differentiation, probably in relation to the different conditions of vitality of the coralligenous itself.

The method developed by Bertolino et al (2014), and improved during this PhD work, is therefore excellent for the study of the sponge communities present and past associated with coralligenous.

Furthermore, the study of the Porifera siliceous spicules trapped in sediments datable in the Mediterranean coralligenous proved to be an effective tool for analysing

the temporal variations of the sponge biodiversity, also in light of the great climatic changes that characterized the recent Holocene.

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Questions for future projects and works

(“Growth dynamics and conservation of mediterranean coralligenous bioherms”. Presented in: “Il coralligeno dei Mari Italiani, Workshop Ustica, 5-8 Settembre 2017.”)

During this period of work, questions arose concerning mainly the age and growth dynamics of these bioconstructions.

Taking into consideration the coralligenous constructions studied along the Italian coasts, different growth dynamics are noted:

- as regards the substrate, the main differences are related to the depth and inclination (cliff or platform coralligenous);
- the formation age can be very variable (8000-2000 YBP);
- some structures are still actively growing while others seem to be totally inactive.

For example:

- **Porto Cesareo** (Apulia, Ionian Sea – 20 m depth)

What determines the upward growth of the Apulian coralligenous (Fig. 1)? These structures contain a high amount of serpulid tubes, they also show very regular growth (Fig. 2). Could the tubes determine a directionality of the structures?

Why coralline algae, which are the main builders of coralligenous, have been replaced by a photophilic algae community?

Could it be related to changes in depth or changes in temperature and trophic?

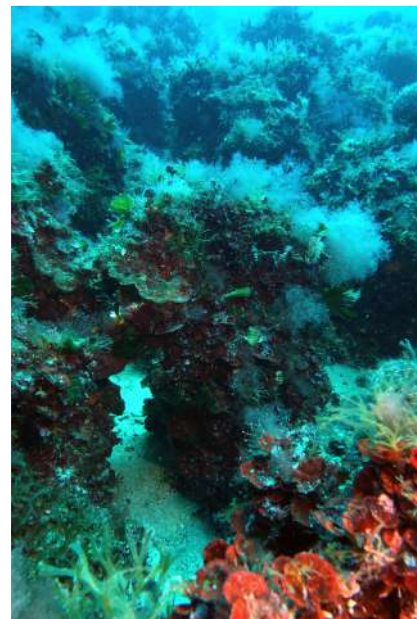


Fig. 1 Typical Apulian coralligenous pinnacle covered by photophilous algae

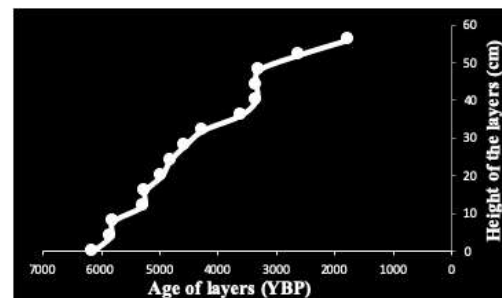


Fig. 2 Age of Porto Cesareo coralligenous layers linked to height growth.

- **Marine Protected Area Tavolara**

(Sardinian, Tyrrhenian Sea – 40 m depth)

The living corallin algae seem very scarce and leave room for an algal coating with scarce presence of sponges in the shady areas. This structure, which forms cushions on the platform (Fig. 3), had a very fast growth of between 6000 and 4000 approximately YBP (Fig. 4).



Fig. 3 Typical Tavolara cushion coralligenous covered by photophilous algae

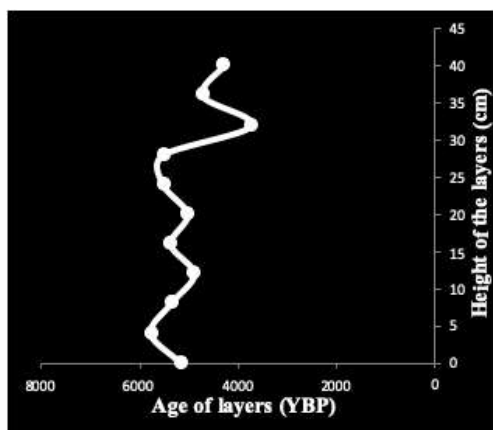


Fig. 4 Age of Tavolara coralligenous layers linked to height growth.

- **Bogliasco** (Ligurian Sea – 15 m depth)

Similarly to Tavolara, the structure is made up of cushions grown on the platform (Fig. 5). Also here, the living corallin algae seem very scarce and leave room for an algal coating. This structure had a very fast growth (between 2000 and 1000 YBP) and apparently inconsistent (Fig. 6). The possible explanation of the non-linear growth of the Bogliasco coralligenous is present in the study by Bertolino et al (2017).

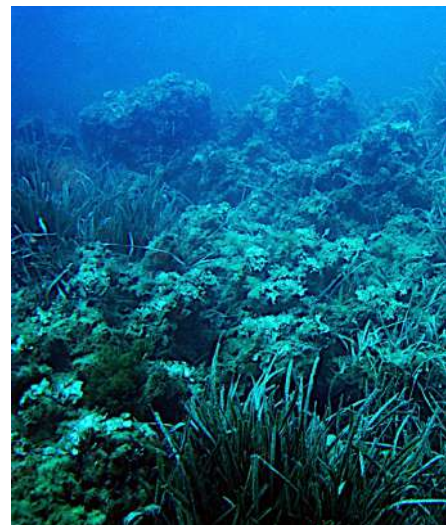


Fig. 5 Typical Bogliasco cushion coralligenous covered by photophilous algae

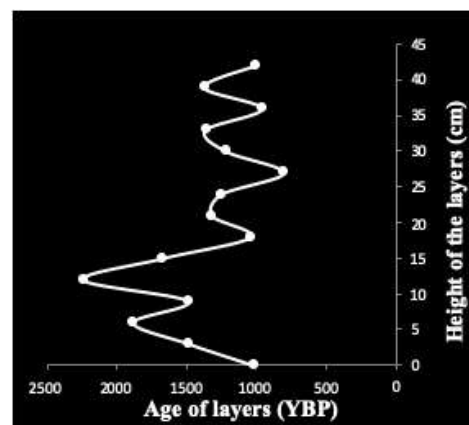


Fig. 6 Age of Bogliasco coralligenous layers linked to height growth.

- **Cala Burantino** (Alghero, Sardinia – 1.5 m depth)

This structure very close to the coast forms single or fused cushions to a depth of about 1.5 meters (Fig. 6). Despite the very low depth, it could be considered one of the most superficial coralligenous known, it seems totally inactive.



Fig. 7 Cala Burantino (Sardinia) cushion coralligenous totally inactive

From our studies and observations, it would appear that the coralligenous platform structures (pinnacles, cushions, platforms) have been inactive and probably eroded for many thousands of years. In other cases, however, the complex community established on the structures counteracts their erosion.

The Ballesteros paradigm

The development of these deep coralligenous formations occurred a long time ago, when the depth of the overlying water layer probably did not exceed 10-15 m, and from their period of settlement

(8500-7000 years ago) the rate of accumulation it is progressively decreased.

This diminution in accumulation rates could be explained by the stable but rather unfavourable environmental conditions deriving from the decrease in solar radiation in relation to the increase in the depth of the water.

It is also worth noting that coral structures below a depth of 30 m in the Marseille area are now inactive and almost free of living coral algae. On the contrary, those present in Corsica at a depth of 50 m and less (up to 65 m) are completely covered by living corals and are in an active period of growth; this difference must be related to the clear waters present in Corsica.

But the problem is certainly more complex; in fact, the history of the Mediterranean coralligenous shows us that, in past epochs, most of the Italian marine waters are divided from conditions favourable to coralline algae to conditions favourable to photophilous algae.

These conditions are therefore linked to different aspects such as water transparency, sedimentation, trophy, CO² concentration and other elements that are certainly the subject of study to better understand the still unclear growth dynamics of the coralligenous.

Other published or submitted (and published below) paper during the PhD**Production, Characterization and Biocompatibility Evaluation of Collagen Membranes Derived from Marine Sponge *Chondrosia reniformis* Nardo, 1847****Abstract**

Collagen is involved in the formation of complex fibrillar networks, providing the structural integrity of tissues. Its low immunogenicity and mechanical properties make this molecule a biomaterial that is extremely suitable for tissue engineering and regenerative medicine (TERM) strategies in human health issues. Here, for the first time, we performed a thorough screening of four different methods to obtain sponge collagenous fibrillar suspensions (FSs) from *C. reniformis* demosponge, which were then chemically, physically, and biologically characterized, in terms of protein, collagen, and glycosaminoglycans content, viscous properties, biocompatibility, and antioxidant activity. These four FSs were then tested for their capability to generate crosslinked or not thin sponge collagenous membranes (SCMs) that are suitable for TERM purposes. Two types of FSs, of the four tested, were able to generate SCMs, either from crosslinking or not, and showed good mechanical properties, enzymatic degradation resistance, water binding capacity, antioxidant activity, and biocompatibility on both fibroblast and keratinocyte cell cultures. Finally, our results demonstrate that it is possible to adapt the extraction procedure in order to alternatively improve the mechanical properties or the antioxidant performances of the derived biomaterial, depending on the application requirements, thanks to the versatility of *C. reniformis* extracellular matrix extracts.

Authors

Marina Pozzolini, Sonia Scarfi, Lorenzo Gallus, Maila Castellano, Silvia Vicini, Katia Cortese, Maria Cristina Gagliani, Marco Bertolino, **Gabriele Costa** and Marco Giovine

Additional Resources

Available online 29/03/2018 Marine Drugs, <https://doi.org/10.3390/md16040111>

Mediterranean sponges from shallow subtidal rocky reefs: *Cystoseira* canopy vs barren grounds

Abstract

Porifera richness was investigated in *Cystoseira* canopies vs barren grounds considering different substrates at 6 areas in the Central-Western Mediterranean Sea. In total 31 sponge taxa were recorded at 2–7 m depth and the sponge community structure and composition were characterized by a notably low richness with 25 taxa in the *Cystoseira* forest and 15 in the barren area. As for the sponge habitus, the massive sponges were dominant in both facies, whereas encrusting, and cavity dwelling sponges were found in higher numbers in the *Cystoseira* forest. Results revealed that rocky substrata seem to play a key role in driving the sponge community composition and diversity in both facies. In this work we explore the role of *Cystoseira* canopy as a suitable facies for sponges. Sponge assemblages were persistent, strongly resilient in space occupation and consequently support stability in both facies. Some species seem to be pre-adapted to live under the sub-optimal conditions of the barren grounds, i.e. the absence of the *Cystoseira* fronds shelter. This focus on sponge successful eco-etological performances in 'submarine deserts' such as barren areas shows features as shown in a few other sessile benthic invertebrates.

Authors

Gabriele Costa, Marco Bertolino, Stefania Pinna, Chiara Bonaviri, Andrea Padiglia, Matteo Zinni, Roberto Pronzato, Renata Manconi

Additional Resources

Available online 22/04/2018 Estuarine and Coastal Shelf Science,
<https://doi.org/10.1016/j.ecss.2018.04.002>

Biodiversity in canopy-forming algae: Structure and spatial variability of the Mediterranean *Cystoseira* assemblages

Abstract

In the Mediterranean Sea, *Cystoseira* species are the most important canopy-forming algae in shallow rocky bottoms, hosting high biodiverse sessile and mobile communities. A large scale study has been carried out to investigate the structure of the *Cystoseira*-dominated assemblages at different spatial scales and to test the hypotheses that alpha and beta diversity of the assemblages, the abundance and the structure of epiphytic macroalgae, epilithic macroalgae, sessile macroinvertebrates and mobile macroinvertebrates associated to *Cystoseira* beds changed among scales. A hierarchical sampling design in a total of five sites across the Mediterranean Sea (Croatia, Montenegro, Sardinia, Tuscany and Balearic Islands) was used. A total of 597 taxa associated to *Cystoseira* beds were identified with a mean number per sample ranging between 141.1 ± 6.6 (Tuscany) and 173.9 ± 8.5 (Sardinia). A high variability at small (among samples) and large (among sites) scale was generally highlighted, but the studied assemblages showed different patterns of spatial variability. The relative importance of the different scales of spatial variability should be considered to optimize sampling designs and propose monitoring plans of this habitat.

Authors

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Additional Resources

Available online 05/04/2018 Estuarine and Coastal Shelf Science,
<https://doi.org/10.1016/j.ecss.2018.04.001>

Project “Biodiversity MARE Tricase”: biodiversity research, monitoring and promotion at MARE Outpost (Apulia, Italy)

Abstract

The project “Biodiversity MARE Tricase” aims to research and promote coastal and marine biodiversity at the MARE Outpost (Avamposto MARE), a marine station established in Tricase (Lecce, Italy) in 2015. From March 2016 to September 2017, the first biodiversity inventory of the Tricase coastal area (Ionian Sea) was realized with the aid of citizen scientists (e.g. local fishermen, divers, bathers, and tourists). Preliminary results include 556 taxa, of which the 95% were identified at the species level. Despite the broad knowledge on Mediterranean coastal biodiversity, 71 species represented new records for the Ionian Sea. In parallel with the research activities, people’s awareness of the value of biodiversity was raised with scientific dissemination initiatives, involving about 1700 people. The “Biodiversity MARE Tricase” project realized a first small-scale species inventory contributing to the distributional, taxonomic, and ecological knowledge of the present Mediterranean biota. The coastal area of Tricase will be soon included in a new Marine Protected Area and this project represents a step forward for the sustainable development of the community of this coast.

Authors

Valerio Micaroni, Francesca Strano, Davide Di Franco, Joachim Langeneck, Cinzia Gravili, Marco Bertolino, **Gabriele Costa**, Fabio Rindi, Carlo Froggia, Fabio Crocetta, Adriana Giangrande, Luisa Nicoletti, Pietro Medagli, Vincenzo Zuccarello, Stefano Arzeni, Marzia Bo, Federico Betti, Francesco Mastrototaro, Loretta Lattanzi, Stefano Piraino, Ferdinando Boero

Additional Resources

Available online 19/06/2018 Rendiconti Lincei. Scienze Fisiche e Naturali, <https://doi.org/10.1007/s12210-018-0726-3>

A first preliminary study of the shallow water sponge fauna from Cyprus Island (Eastern Mediterranean)

Abstract

Currently, more than 8,500 valid sponge species are reported in the World Porifera Database ([http:// www.marinespecies.org/porifera/](http://www.marinespecies.org/porifera/)) (van Soest et al. 2018). The Mediterranean Sea sponge fauna, counting almost 700 species, is one of the best documented in the world (Pronzato 2003; Pansini et al. 2011; van Soest et al. 2018) but the eastern part of the basin is by far less studied, in comparison with other Mediterranean areas (Pansini et al. 2000; Voultziadou & Vafidis 2004; Topaloğlu & Evcen 2014). A small number of species, mainly belonging to the cosmopolitan genus *Spongia* (Dictyoceratida), are commonly used as bath sponges. Aim of this work is to provide further information on Cyprus Island sponges in general and on species that had commercial importance in the past.

Authors

Costa Gabriele, Giussani Valentina, Kletou Demetris, Kleitou Periklis, Pansini Maurizio, Setti Alexia, Pronzato Roberto & Bertolino Marco

Additional Resources

Available online 27/07/2018 Zootaxa, DOI: <http://dx.doi.org/10.11646/zootaxa.4450.5.7>

Sponge community variations within two semi-submerged caves of the Ligurian Sea (Mediterranean Sea) over a half-century time span

Abstract

In the last few decades, macrobenthic community structures and their species abundances have shown significant changes in the Mediterranean Sea, whose causes were attributed to anthropogenic activities and to global warming effects. The Mediterranean sponges have shown a peculiar sensitivity to these changes: the populations of some species showed significant decreases, while others, more thermophilous, increased. Therefore, sponges may be a good proxy for evaluating the effects of environmental changes. Thanks to the observations conducted by Sarà about 55 years ago, a comparative analysis of the sponge populations present within two semi-submerged caves in the Ligurian Sea was possible. The two sponge assemblages re-studied in 2016 showed an increase in terms of specific richness and a significant change in their structural aspects, since the three-dimensional growth forms were mostly replaced by two-dimensional ones, a process observed also in other littoral communities. Consequently, the sponge communities inside the semi-submerged caves may be considered poorly resilient: the massive sponges were hit by the positive thermal anomalies occurring in the Ligurian Sea in the last decade and were replaced by encrusting forms, within a possible phase of cave recolonisation.

Authors

G. Costa, F. Betti, E. Nepote, R. Cattaneo-Vietti, M. Pansini, G. Bavestrello, & M. Bertolino

Additional Resources

Available online 13/11/2018 European Zoological Journal, DOI:
<https://doi.org/10.1080/24750263.2018.1525439>

Biodiversity assessment in Western Mediterranean marine protected areas (MPAs): Porifera of *Posidonia oceanica* meadows (Asinara Island MPA) and marine caves (Capo Caccia–Isola Piana MPA) of Sardinia

Abstract

This paper focuses on a faunistic inventory and the biogeographic pattern of Sardinian Porifera in a scarcely investigated Italian sea belonging to the Eastern Algero-Provençal Basin. The composition and structure of sponge fauna were studied in two priority habitats in two Marine Protected Areas (MPAs) of the North-Western Sardinian Sea. Shallow-water surveys investigated *Posidonia oceanica* meadows at five sites in the Asinara Island MPA and three karstic submerged caves in the Capo Caccia–Isola Piana MPA. The annotated checklist shows notably high values of taxonomic richness, confirming that *P. oceanica* meadows and karstic caves are key habitats for Porifera assemblages. Indeed, the sponge taxa recorded (n = 77) with 59 cave-dwelling and 45 taxa in seagrass meadows represent over 10% of the total Mediterranean sponge fauna, despite the small areas investigated, restricted biotopes and low sampling effort. This suggests that species richness is underestimated in circum-Sardinia seas. Internationally protected species (n = 6), rare species (n = 5) and Mediterranean endemic species (n = 14) were recorded. Previously investigated *Posidonia* meadows and caves share comparable values of species richness and endemism with the Sardinian biotopes. The geographic range of species indicates that the biogeographic affinity of the NW Sardinian Sea sponge fauna is dominated by Atlanto-Mediterranean species. The three caves harbour a notably homogeneous sponge community, as indicated by the ca. 50% of shared species and high similarity index (> 83%). By contrast, the composition varies markedly among the five *Posidonia* meadows, which share only five species and display similarity values ranging ca. 20–60%. Unexpectedly when comparing these contrasting biotopes, faunal similarity is relatively low (< 40% shared species); indeed, *Posidonia* meadows harbour a notable number of cave-dwelling species in intermatte shaded microhabitats.

Authors

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Additional Resources

Available online 13/11/2018 European Zoological Journal, DOI: <https://doi.org/10.1080/24750263.2018.1525440>

The sponge fauna of the Seno Magdalena and Puyuhuapi Fjord (Chile), with a description of two new species

Abstract

The presence of fjords, islands and channels originating from glacial erosion and ice cap retreat, makes the Chilean benthic biodiversity difficult to explore and study. Our survey of this region allowed the identification of 29 Demospongiae species in total. Two of them are new to science and here described: *Biemna lutea* sp. nov., and *Hamigera cleistochela* sp. nov.. Two species (*Clathria* (*Clathria*) *microxa* and *Lissodendoryx* (*Ectyodoryx*) *patagonica*.) are new for the region and the Chilean fjords. *Lissodendoryx* (*Ectyodoryx*) *patagonica* was found for the second time after the original description by Ridley & Dendy, 132 years ago. These results – considering the small number of species identified on the whole – are promising and confirm that the marine biodiversity of Chilean fjords is remarkable but not well known yet.

Authors

Marco Bertolino, **Gabriele Costa**, Anna Reboa, Giorgio Bavestrello, Maurizio Pansini, Federico Betti, Marzia Bo & Giovanni Daneri

Additional Resources

Available online 25/06/2019 Zootaxa, DOI: <https://doi.org/10.11646/zootaxa.4623.2.5>

Insights into the evolution of metazoan regenerative mechanisms: roles of TGF superfamily members in tissue regeneration of the marine sponge *Chondrosia reniformis*

Abstract

Tissue repair is an adaptive and widespread metazoan response. It is characterised by different cellular mechanisms and complex signalling networks that involve numerous growth factors and cytokines. In higher animals, transforming growth factor- β (TGF- β) signalling plays a fundamental role in wound healing. In order to evaluate the involvement of TGF superfamily members in lower invertebrate tissue regeneration, sequences for putative TGF ligands and receptors were isolated from the transcriptome of the marine sponge *Chondrosia reniformis*. We identified seven transcripts that coded for TGF superfamily ligands and three for TGF superfamily receptors. Phylogenetically, *C. reniformis* TGF ligands were not grouped into any TGF superfamily clades and thus presumably evolved independently, whereas the TGF receptors clustered in the Type I receptor group. We performed gene expression profiling of these transcripts in sponge regenerating tissue explants. Data showed that three ligands (TGF1, TGF3 and TGF6) were mainly expressed during early regeneration and seemed to be involved in stem cell maintenance, whereas two others (TGF4 and TGF5) were strongly upregulated during late regeneration and thus were considered pro-differentiating factors. The presence of a strong TGF inhibitor, SB431542, blocked the restoration of the exopinacoderm layer in the sponge explants, confirming the functional involvement of the TGF pathway in tissue regeneration in these early evolved animals.

Authors

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Additional Resources

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A new sponge species of the genus *Antho* (Demospongiae, Microcionidae) from the Tyrrhenian deep sea

Abstract

The use of ROVs has greatly enhanced the possibility of obtaining information on living deep sponge communities (Bertolino *et al.* 2015). The aim of this work is to describe a new Mediterranean species, *Antho (Plocamia) sarasiri* sp. nov. (Microcionidae Carter, 1875), characterized by dumbbell spicules making up the framework of the choanosomal skeleton (Van Soest *et al.* 2013). Samples were collected by ROV during an oceanographic survey in September 2012 on board of the R/V ‘Astrea’ (ISPRA) in “Secca P.ta Fetovaia” (42°43’29.54”N 10° 9’31.64”E) (Elba Island, Tyrrhenian Sea) at 70 m depth. We compared our sample with additional material collected by Sarà & Siribelli (1960, 1962).

Authors

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Additional Resources

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Shallow-water sponge grounds along the Apulian coast (central Mediterranean Sea)

Abstract

Sponge grounds are complex three-dimensional benthic habitats dominated by sponges. These sponge-dominated assemblages have been reported worldwide, from the intertidal zone to the deep sea. In shallow euphotic waters, dense sponge aggregations have been mainly found in tropical areas, and their presence is in some cases related to environmental degradation and coral decline. The Mediterranean Sea is globally recognised as a biodiversity hotspot, where light-exposed rocky reefs are typically dominated by photophilous algae. However, high local anthropogenic pressures, coupled with climate change, are leading to the reorganisation of benthic communities and the occurrence of regime shifts in several areas. Here we report the first description of unusual, shallow-water sponge grounds in Mediterranean light-exposed rocky reefs, in an area previously impacted by the destructive date-mussel fishery. These assemblages, found along the Apulian coast (central Mediterranean Sea), are now (2017) characterised by a mean coverage of sponges ranging between 3% and 33%, with maximum values up to 85%. Variation in the structure of assemblages and in the abundance of individual taxa between depths has been tested by multivariate and univariate techniques. The spatial characterisation has been complemented with the taxonomic analysis of the sponge assemblages, which resulted in the identification of 14 sponge taxa. These findings are compared with results of previous research in the same area and discussed with particular reference to the potential variables involved in sponge dominance and spatial distribution in the present system and elsewhere.

Authors

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Additional Resources

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***Aplysina aerophoba* (Nardo, 1833) (Porifera, Demospongiae): an unexpected miniaturised growth form from the tidal zone of Mediterranean caves: morphology and DNA barcoding.**

Abstract

In the Mediterranean Sea the two sponges of the genus *Aplysina* (*A. aerophoba* and *A. cavernicola*) are identified on the basis of their external morphology and the environment in which they live. During a research program on the sponge fauna in semi-submerged caves of the Italian coasts, we have sampled an abundant very small yellow sponge, often living in the tidal zone, which were attributed to the genus *Aplysina*. Failing to assign the samples to a species through classical taxonomic methodologies (growth form and skeleton arrangement) and for the particular environment where this sponge lives, we have decided to use the COI analysis to solve the taxonomic problem offered by these miniaturized specimens. The analysis indicated that, in spite of the morphological differences, they belong to *A. aerophoba*. During old detailed surveys, conducted in the '60 years in some of the studied caves, this species was not recorded. It is possible that its abundant presence is related to the modifications occurred in the Mediterranean sponge communities occurred in the last decades in relation to global warming.

Authors

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Additional Resources

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Macroalgal forest vs sea urchin barren: patterns of macro-zoobenthic diversity in a large-scale Mediterranean study

Abstract

The study aimed at contributing to the knowledge of alternative stable states by evaluating the differences of mobile and sessile macro-zoobenthic assemblages between sea urchin barrens and macroalgal forests in coastal Mediterranean systems considering a large spatial scale. Six sites (100s kilometers apart) were selected: Croatia, Montenegro, Sicily (Italy), Sardinia (Italy), Tuscany (Italy), and Balearic Islands (Spain). A total of 531 taxa, 404 mobile and 127 sessile macro-invertebrates were recorded. Overall, 496 and 201 taxa were found in macroalgal forests and in barrens, respectively. The results of this large-scale descriptive study have met the expectation of lower macrofauna complexity and diversity in barrens rather than in macroalgal forests, and have allowed estimating the differences in levels of diversity and the consistency of variability across Mediterranean sites. Some peculiar patterns in barrens related to the abundance of specific taxa and to high values of beta diversity have been evidenced.

Authors

Pinna S., Piazzzi L., Ceccherelli G., Castelli A., **Costa G.**, Curini-Galletti M., Gianguzza P., Langeneck J., Manconi R., Montefalcone M., Pipitone C., Rosso A., Bonaviri C.

Additional Resources

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<https://doi.org/10.1016/j.marenvres.2020.104955>

Submitted paper during PhD

Keratose sponge grounds from the Ligurian Sea (NW Mediterranean Sea)

Abstract

In this study we characterized for the first time the keratose sponge aggregations dwelling on the Ligurian continental shelf by means of ROV-Imaging and Scuba diving. A peculiar assemblage of massive filter feeders, dominated by *Sarcotragus foetidus*, together with several other sponges, including *Spongia lamella* and *Axinella polypoides*, was recorded. A total of 204 sponge grounds have been characterized, mainly concentrating between 40-70 m depth. They occurred as fragmented, not continuous facies, mainly due to the heterogeneity of the hard bottoms on which they settle.

These Sponge-dominated ecosystems have an exceptionally wide distribution, with the densest aggregations (up to 7.7 individuals m⁻²) thriving along the westernmost part of the Ligurian coastline concomitant to flat hardgrounds subjected to high silting levels. The dominant sponge species reach considerable heights (up to 65 cm), greatly increasing the habitat three-dimensionality and acting as pole of attraction for a diverse sessile and vagile fauna.

Differently from the North Atlantic Ocean, only few examples of sponge grounds are known from the Mediterranean Sea, mainly in the deep-sea. So far, this represents a unique description of keratose aggregations, whose abundance at mesophotic depths might be related to both the oceanographic characteristics of the Ligurian basin as well as the mass mortality events that have stricken the shallow-water populations in the last decades.

Authors

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Additional Resources

Submitted to Marine Ecology

Exploring the diversity and metabolic profiles of bacterial communities associated with Antarctic sponges (Terra Nova Bay, Ross Sea)

Abstract

Complex cell-to-cell interactions (including the production of antibiotics and the quorum sensing phenomenon) occur between benthic marine organisms and bacteria, leading to the establishment of synergic interactions, especially in extreme and harsh environments, such as Antarctica. Despite this, current data concerning the composition, host- and site-relatedness, and biotechnological values of the bacterial community associated with Antarctic sponges are limited to a few works, resulting in a still fragmented and incomplete knowledge. In this context, a total of 11 sponge species (belonging to Demospongiae and Hexactinellida) from the Terra Nova Bay area (Ross Sea) were explored for the associated bacterial diversity by the ION Torrent sequencing. An additional predictive functional analysis on 16S rRNA gene data was performed to unravel metabolic and biotechnological potentials of the associated bacterial communities. Data obtained highlight the predominance of Proteobacteria, mainly affiliated to Alpha- and Gammaproteobacteria. Retrieved phyla were similarly distributed across samples, with dissimilarities encountered for the sponge *Haliclona (Rhizoniera) dancoi* (Topsent, 1901). The analysis of the functional prediction suggests that the associated bacterial community may be involved in the biosynthesis of antibiotics, quorum sensing and degradation of aromatic compounds.

Authors

Papale M., Rizzo C., Fani R., Bertolino M., **Costa G.**, Paytuví-Gallart A., Schiaparelli S., Michaud L., Azzaro M., Lo Giudice A.

Additional Resources

Submitted to Frontier

National and international congress, workshop and seminar during the PhD

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2. Oprandi A., **Costa G.**, Castellano M., Pansini M., Bavestrello G., Bertolino M., 2019. Studio delle comunità di spugne del passato utilizzando le spicole silicee intrappolate nella "matte" di *Posidonia oceanica*. Poster presentato al 50° Congresso della Società Italiana di Biologia Marina, 10-14 giugno 2019, Livorno.
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