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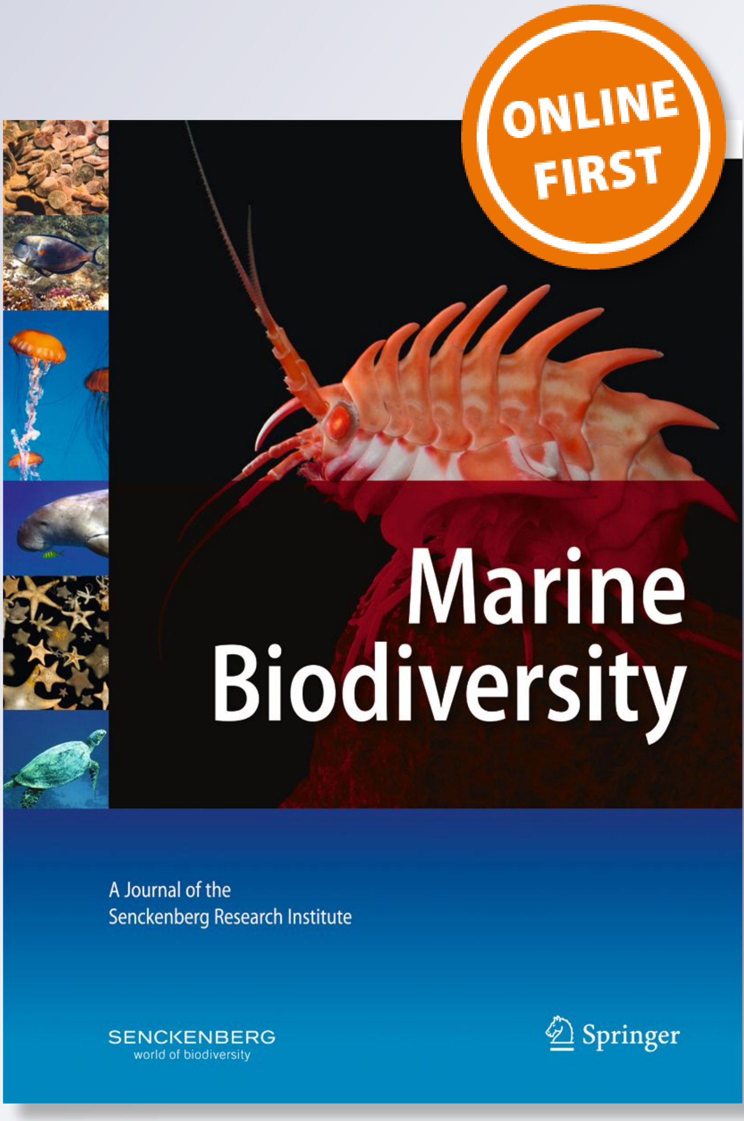


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# Sponges associated with coralligenous formations along the Apulian coasts

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**Abstract** Sponge assemblages associated with coralligenous outcrops were studied with the aim of describing and comparing their composition, morphological features and distribution at different depths (shallow vs. deep) along the Apulian coasts. In addition, image analysis enabled the description of the main features of coralligenous outcrops and the detection of structuring species. The paper provides a significant contribution in terms of supplying new taxa of sponges associated to coralligenous assemblages and emphasising the importance of invertebrates in realising calcareous constructions. Most of the new finding came from deep sites, thus underlining the need to improve taxonomic studies on coralligenous communities at greater depths. A total of 153 taxa of sponges were recorded: 4 Calcarea, 6 Homoscleromorpha and 143 Demospongiae. Two species, *Clathria (Microciona) macrochela* and *Thoosa armata*, are new records for the Italian sponge fauna, with *C. (M.) macrochela* representing a new record for the whole Mediterranean. New findings for the Ionian and Adriatic Seas totalled 25 and 8 species, respectively. Thirty-nine species are endemic for the Mediterranean. Data analyses clustered sites into two groups, separated according to the depth. Deep sites, characterised by animal dominance, exhibit a heterogeneous substrate texture richer in cavities than the shallow and homogeneous algal ones. Differences in sponge species composition also correspond to differences in the distribution of sponge growth forms, with the insinuating cryptic species more abundant in deeper communities. Ten of 15 sponge species included in national and international wildlife protection laws and policy have been detected in the present study.

**Keywords** Coralligenous community · Bathymetric range · Structuring species · Ionian and Adriatic Seas · Sponge-growing formC. Longo and F. Cardone contributed equally to this work.

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## Introduction

The coralligenous habitats are among the richest and most characteristic marine habitats of the Mediterranean Sea, ranging from about 10 to 120 m of depth (UNEP-MAP-RAC/SPA 2003; Ballesteros 2006; Cánovas Molina et al. 2016). They are the most important biogenic structures in the Mediterranean (Boudouresque 2004; Ballesteros 2006; Bertolino et al. 2013), usually characterised by a well-defined community. However, due to their peculiarities and great structural, biological and geographical heterogeneity, it seems more appropriate to consider them as a puzzle of communities rather than a single community (Ballesteros 2006; Cánovas Molina et al. 2016).

Light plays a fundamental role in the structure of this mosaic affecting the distribution of benthic organisms along a bathymetric gradient on rocky bottoms and the development of different coralligenous communities (Laubier 1966; Martí et al. 2004, 2005). In addition, the temperature range influences most coralligenous benthic species. Some organisms

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living in coralligenous assemblages in deep waters seem to be highly stenothermal since they were never found in shallow waters (Ballesteros 2006). The above parameters along with the topography affect the nature of the outcrops, leading to coralligenous banks on the horizontal seafloor and rims of vertical cliffs, the latter usually being shallower (Pérès and Picard 1964; Laborel 1987).

The main bioconstructors of the coralligenous substrate are coralline algae growing at low light levels; the shallower coralligenous habitats are dominated by erect and foliaceous forms, which, as the water deepens, are progressively replaced by encrusting species (Ballesteros 2006). Regarding the associated fauna, the abundance of suspension feeders depends on the average current intensity and availability of food. Gorgonians dominate the community in areas rich in suspended organic matter, while sponges, bryozoans and scleractinian corals are the dominant suspension feeders in more oligotrophic waters (Gili and Ballesteros 1991; Ballesteros 2006). With respect to their position, role and ecological functioning, Hong (1982) distinguishes four different categories of invertebrates in the coralligenous habitats, all of them contributing to the turnover of the calcareous concretion: fauna contributing to build up, cryptofauna, epifauna and endofauna, and eroding species.

All the four categories include sponge species, either as constructors by agglomerating carbonate particles or as eroders (Hong 1980; Cerrano et al. 2001; Cánovas Molina et al. 2016). Endolithic and digging sponges are commonly found in coralligenous habitats (Bertolino et al. 2013) where they usually show higher species richness and biomass with respect to those in the epibenthic layer (Calcinai et al. 2015). To date, the sponge fauna associated with coralligenous formations constitute about 45% of the total known Mediterranean sponge species (Voultsiadou 2009; Coll et al. 2010; Gerovasileiou and Voultsiadou 2012).

In 2008, due to the ecological importance of the coralligenous habitats, the Contracting Parties of the Barcelona Convention adopted a specific "Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea" (UNEP-MAP-RAC/SPA 2008). One of the priority actions identified by this Action Plan was to improve the knowledge of Mediterranean bioconstructions by encouraging research on their characteristics and distribution. Recently, the Italian project BIOMAP (Biocostruzioni Marine in Puglia: AA VV 2014), granted by the Apulia Region, has promoted actions to map and characterise the coralligenous systems surrounding Apulia (SE Italy).

The Apulian region, with a coastline of 900 km, is one of the areas of regional interest listed by the UNEP-MAP-RAC/SPA (2008) for the Mediterranean Sea for which the knowledge about the occurrence and distribution of species is still not exhaustive. Apulian coralligenous outcrops were firstly reported by Sarà (1968, 1969), who described these assemblages as a complex and peculiar biocoenosis dominated by calcified algae and where sponges are highly represented. Further research focused on distribution and taxonomy of some sponge taxa (Corriero and Scalera Liaci 1997; Pansini and Pesce 1998; Corriero et al. 2004; Cocito and Lombardi 2007).

Notwithstanding the increasing research effort on Mediterranean coralligenous formations, the core of our knowledge comes from shallow sites, while few studies describe the structure and the patterns of distribution of biological communities at greater depths (UNEP-MAP-RAC/SPA 2015; Giakoumi et al. 2013; Martin et al. 2014). Therefore, this scientific knowledge still needs to be improved, particularly with regard to the components deeper than 40 m. In this scenario, the present work aims at increasing the knowledge on heterogeneity of coralligenous habitats and describing and comparing the sponge community at different depths along the Apulian coasts.

## Materials and methods

### Study sites

Data were collected during the period 2011–2013 by SCUBA divers specialised in biological sampling. The study was performed at 10 sampling sites, distributed along more than 200 km of the Apulian coast, in areas where coralligenous formations had already been recorded during previous surveys (Fig. 1). Two different bathymetric intervals were considered: −25/−30 m (shallow coralligenous formations) at the sites of Torre Guaceto (TGU), Cerano (CER), Porto Miggiano (PMI), Torre Inserraglio (TIN) and Taranto (TAR), and −55/−60 m (deep coralligenous formations) at Otranto (OTR), Santa

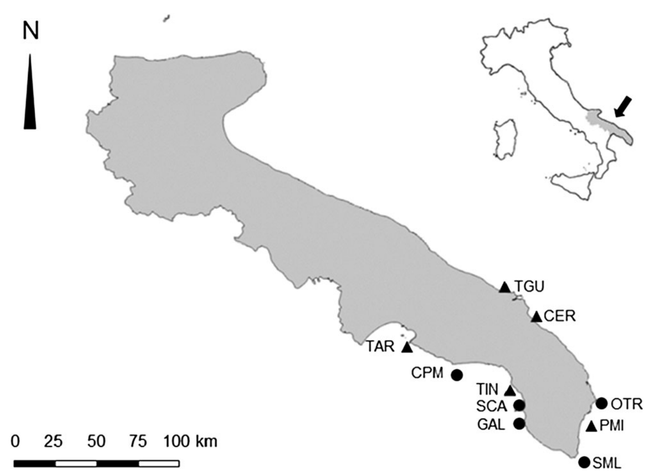


**Fig. 1** Distribution of the coralligenous sites studied. *Triangles* shallow sites; *circles* deep sites. Sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*), Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*)

Maria di Leuca (SML), Gallipoli (GAL), Santa Caterina (SCA), and Campomarino (CPM).

For each site, sampling was performed at two stations about 50 m apart. At each station, samples were collected by scraping off the substrate from 20 × 20 cm quadrats (two replicates per station), avoiding cavities and crevices. In addition, to detect the habitat-structuring macro-species in the sites of observation, ten videos within each station were taken using a waterproof digicam with a frame of 40 × 50 cm, covering a total area of 2 $m^2$. They were examined using the ImageJ software and the conspicuous algal and animal species were annotated. In order to obtain an overview of the coralligenous communities within the investigated areas, data on the biological coverage, nature, inclination and height of the outcrops were directly collected in situ by SCUBA divers and/or on the basis of the video material.

### Sponge identification

Samples were immediately fixed in a buffered 4% formaldehyde solution and brought to the laboratory for subsequent sorting and identification procedures.

Taxonomic revision and nomenclature up-date was carried out according to World Porifera Database (van Soest et al. 2016).

Endemic traits of sponge species were evaluated according to literature data from the World Porifera Database (van Soest et al. 2016), Medifaune (Fredj et al. 2002), and authors' expertise. The geographic distribution of sponges was compared with that reported by Pansini and Longo (2003, 2008).

In order to compare the study sites in terms of morphological composition (morphological dominance) of the sponge communities associated with coralligenous outcrops, the growth form of each species sampled was recorded. Six morphological categories were chosen (Boury-Esnault and Rützler 1997): boring, insinuating, insinuating/encrusting, encrusting, massive, and erect.

### Statistical analysis

To minimise the weight of the dominant species and to balance the role of rare species, data were reduced to a presence/absence matrix, on which a Bray-Curtis similarity matrix was applied.

Analysis of variance (ANOVA) was used to assess differences in the sponge specific richness in relation to depth (25/30 vs. 55/60 m). Prior to running analyses, the homogeneity of variances was tested by Levene's test; whenever necessary, data were transformed and re-tested (Underwood 1997).

Bray-Curtis similarity was calculated and data were analysed with ANOSIM and Principal Component Analysis (PCoA). All analyses were performed using the statistical program PRIMER (Clarke 1993).

## Results

### Main features of studied coralligenous communities (Fig. 2)

In situ observations, together with the analysis of photographs and videos, allowed description of the main features of coralligenous communities and identification of structuring species at the investigated sites.

– TGU (Torre Guaceto, Adriatic Sea; 40.7507°N, 18.7566°E; shallow site), Fig. 2a.

Coralligenous outcrops grow on pinnacles 1–2 m high, with dominance of red calcified algae. Conspicuous invertebrate species are mainly represented by large erect and massive sponges, calcified bryozoans (*Myriapora truncata*, *Reteporella* spp.) and scleractinians (*Cladocora caespitosa*).

– CER (Cerano, Adriatic Sea; 40.5670°N, 18.1309°E; shallow site).

Pinnacles about 2 m high, rich in holes and crevices, scattered on a sand-muddy bottom. The main builders are represented by encrusting Corallinales algae associated with sciaphilic green algae. The most conspicuous invertebrates are represented by encrusting bryozoans, solitary ascidians, serpulid polychaetes, numerous specimens of the echinoid *Echinus melo*, and different species of sponges.

– OTR (Otranto, Ionian Sea; 40.1348°N, 18.5237°E; deep site), Fig. 2b.

Coralligenous concretions in the form of rims growing on a rocky cliff that rises from the sandy bottom. The biogenic framework is mainly composed by the aggregation of the deep-sea oyster *Neopycnodonte cochlear*, which constitutes a thick secondary substrate of high structural complexity and heterogeneity of microhabitats. Several colonial and solitary scleractinians (*Leptopsammia pruvoti*, *Cladopsammia rolandi*, *Phyllangia americana mouchezii*), together with encrusting bryozoans also contribute significantly to build up such concretions. Cavities and crevices are colonised by a remarkable population of *Corallium rubrum*, characterised by slender and well-branched colonies. Massive and erect sponge species are uncommon, mainly represented by horny sponges and small demosponges.

– PMI (Porto Miggiano, Ionian Sea; 40.0329°N, 18.4641°E; shallow site).

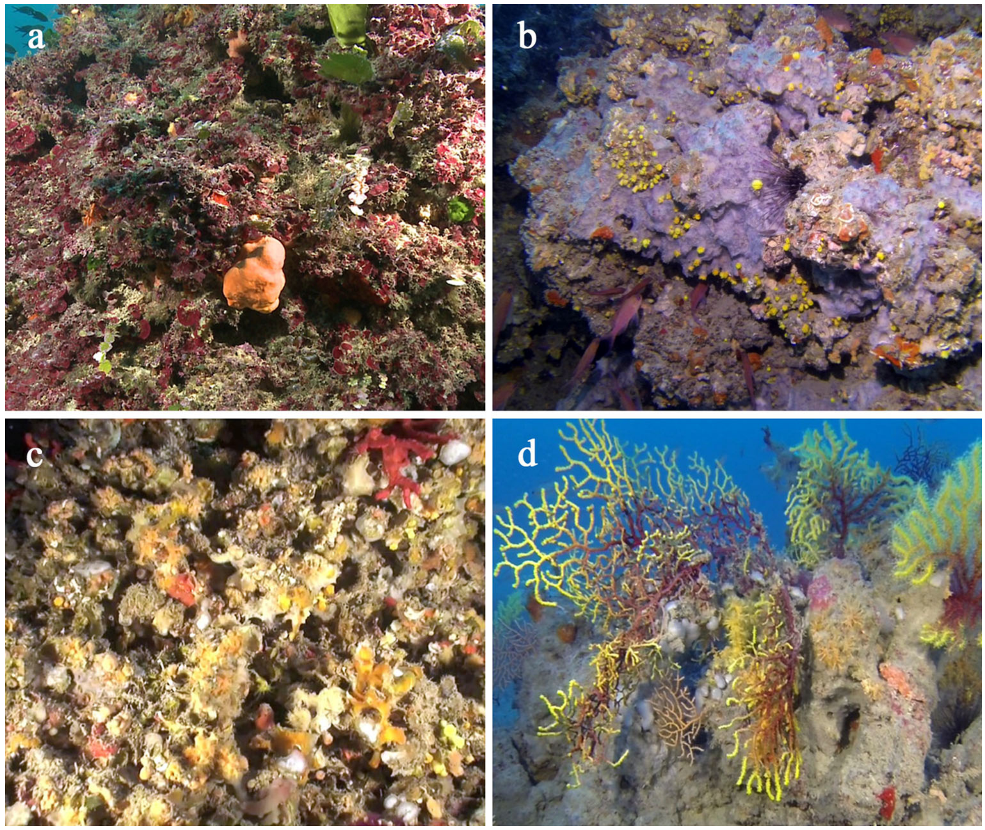


**Fig. 2** Coralligenous communities along Apulian coasts. **a** Torre Guaceto, secondary hard substrate formed by multilayers concretion of calcified algal thalli; **b** Otranto, biogenic framework composed by the aggregation of the deep-sea oyster *Neopycnodonte cochlear* and scleractinian corals (*Leptopsammia pruvoti*, *Cladopsammia rolandi* and *Phyllangia americana mouchezii*); **c** Santa Maria di Leuca, vertical cliffs concretions built by the oyster *N. cochlear*. Note the contribution of the diversified associated fauna; **d** Gallipoli, rocky outcrops characterised by three-dimensional structure due to a mixed assemblage of the sea fans *Eunicella cavolini* and *Paramuricea clavata*

The coralligenous substrate consists of high vertical rims and is relatively poor in cavities and holes. The main framework builders are represented by encrusting Corallinales algae, whereas the contribution of invertebrates is low. Erect and massive species are poorly represented and consist of small colonies of bryozoans (*M. truncata*), sponges (*Acanthella acuta*, *Agelas oroides*, *Axinella* spp., *Sarcotragus spinosulus*), scleractinians (*C. caespitosa*) and solitary ascidians.

– SML (Santa Maria di Leuca, Ionian Sea; 39.8191°N, 18.3943°E; deep site), Fig. 2c.

Rocky shoals steeply arising from a sandy bottom. The coralligenous community shows two different structural patterns. On the flat and sub-horizontal surface of the shoal head, the concretions are characterised by a thick basal layer of encrusting red algae on which erect invertebrates develop (the bryozoan *Pentapora fascialis*; the gorgonians *Paramuricea clavata* and *Eunicella cavolini*), often forming dense facies. On vertical cliffs, the structural framework of the concretion is mainly built by the oyster *N. cochlear*, which forms a very irregular and jagged surface rich in small crevices and cavities. The biogenic substrate hosts a mixed community characterised by encrusting bryozoans, numerous species of Porifera, usually of small size, solitary Anthozoa and, within crevices and cavities, scattered colonies of *C. rubrum*.

– GAL (Gallipoli, Ionian Sea; 40.0299°N, 17.9062°E; deep site), Fig. 2d.

Carbonate rocky outcrops, distributed over gently sloping muddy/sandy grounds. Rocks are irregular in shape and rich in crevices and cavities. The main builders are encrusting Corallinales algae, whereas the contribution of the animal component is provided primarily by encrusting bryozoans. Erect bryozoans are very rare. Solitary scleractinians also occur, but constitute a minor component in the structuring of the biogenic frame. Large facies of the Zoantharia *Parazoanthus axinellae* settle directly on the carbonate substrate. The sponge community is mainly dominated by species with encrusting habitus. Several individuals of the echinoid *Centrostephanus longispinus* occupy the cavities. The main contribution to the three dimensional structure of the community is conferred by a mixed assemblage of the sea fans *Savalia savaglia* and *P. clavata*.

– SCA (Santa Caterina, Ionian Sea; 40.1659°N, 17.8241°E; deep site).

The study site consists of sparse rocky cliffs, up to about 200 m long and 6 m high, arising from a sandy bottom. Coralligenous concretions are cavernous, rich in large cavities and crevices. The basal framework is mainly built by encrusting calcified Rhodophyta, together with different species of scleractinian corals (*P. americana mouchezii*, *Polycyathus muellerae*, *Hoplangia durotrix*, *L. pruvoti* and the solitary *Thalamophyllia gasti*), encrusting bryozoans, serpulid polychaetes, and widespread colonies of *C. rubrum*. The seascape is characterised by rich facies of the gorgonian *P. clavata*, which widely cover the walls of the cliffs. Sponges are mainly represented by encrusting forms together with numerous specimens of the massive *Chondrosia reniformis*.

– TIN (Torre Inserraglio, Ionian Sea; 40.1776°N, 17.9250°E; shallow site).

The investigated site consists of rocky outcrops up to 1.5 m in height, sparsely distributed on a detritic/sandy bottom. The main coralligenous framework builders are represented by encrusting Corallinales algae with the support of erect bryozoans. Among epibenthic organisms, large ascidians (*H. papillosa*, *Aplidium conicum*, *A. tabarquensis*, *Pallusia mammillata*), together with erect (*Axinella polypoides*, *A. cannabina*), massive (*Dysidea avara*, *Fasciospongia cavernosa*, *Spongia* (*Spongia*) *officinalis*, *Sarcotragus foetidus*) and encrusting sponges (*Phorbas tenacior*, *Crambe crambe*) are also present.

– CMP (Campomarino, Ionian Sea; 40.2678°N, 17.5062°E; deep site).

Isolated large banks growing upon rocky outcrops, about 2–3 m in height, irregularly scattered on a detrital bottom. Encrusting and laminar calcified Rhodophyta build the upper framework of the concretion. Coralligenous animal builders contributing to the structure of concretions are relatively uncommon and are mainly represented by encrusting and erect bryozoans, often in association with serpulid polychaetes. Slender, erect forms of *Eunicella singularis*, *Axinella verrucosa*, *A. damicornis* and the tunicate *H. papillosa* also occur. The vertical walls and small cavities of the outcrops sustain a complex and structured animal community dominated by suspension feeders. The encrusting sponge *Dendroxea lenis*, the erect *A. verrucosa* and the Scleractinia *L. pruvoti* are the most common species. Small and stubby colonies of *C. rubrum* are found in a patchy distribution

– TAR (Taranto, Ionian Sea; 40.4336°N, 17.1377°E; shallow site).

The substrate consists of the basal portion of vertical walls together with large rocky outcrops irregular in shape and rich in cavities. The main coralligenous framework builders are represented by encrusting Corallinales algae, whereas the contribution of invertebrates is low. Massive and erect species are uncommon and mainly represented by small specimens of sponges (*A. verrucosa* and *A. damicornis*), anthozoans (*P. axinellae*), serpulids (*Filograna implexa*) and bryozoans (*P. fascialis*).

**Coralligenous sponge community**

A total of 153 taxa of sponges were recorded (147 identified at species level and 6 at genus level: 143 Demospongiae, 4 Calcarea and 6 Homoscleromorpha) (Table 1). Two species, *Clathria (Microciona) macrochela* and *Thoosa armata* are new records for the Italian sponge fauna. In particular, *C. (M.) macrochela* represents a new record for Mediterranean sponge fauna. For the Ionian and Adriatic Italian seas, respectively, 25 and 8 species are new findings. The endemic Mediterranean species found are 39, corresponding to almost 25% of the total (Table 1).

All three subclasses of Demospongiae (Verongimorpha, Keratosa and Heteroscleromorpha) are represented, and, among the 22 orders currently considered to be valid (van Soest et al. 2016), 16 are represented in the study sites (Fig. 3). The order Poecilosclerida is the most represented, with 11 families, 15 genera, and 27 species. The orders Tetractinellida, Clionaida, Dictyoceratida, Haplosclerida and Axinellida are also well represented, with the number of species ranging between 21 and 14. The orders Suberitida, Tethyida, Bubarida, Agelasida, Dendroceratida and Verongida are present with a few species each. Finally, Biemnida, Chondrillida, Chondrosiida and Trachycladida are present with just one species each. Within the Calcarea, both the known subclasses of Calcinea and Calcaronea are represented, with one order each (Clathrinida and Leucosolenida, respectively) of the five currently considered to be valid (van Soest et al. 2016). The order Clathrinida is represented by three species while the order Leucosolenida is represented by just one species. The class Homoscleromorpha is represented by the only one known order (Homosclerophorida), two families (Oscarellidae, Plakinidae) and 6 species.

Four of the species found (*Acanthella acuta*, *Crambe crambe*, *Jaspis johnstonii* and *Phorbas tenacior*) were present at all the study sites. Totals of 97 species were found at deeper sites, 47% of them exclusively recorded at these depths, 107 at shallower sites, 52% of them exclusive to such depths, and 35 species (about 23% of the whole list) were shared between the two depth groups (Table 1).

The results of ANOVA statistical test on the depth factor, even if significant ($p < 0.05$), did not afford a proper evaluation model for the specific richness among sites. A more detailed analysis is provided by the a posteriori test that highlighted only two significant differences between the two levels of depth, one referring to the shallow Torre Inserraglio (TIN), the other to the deep Santa Caterina (SCA) site (Fig. 4).

With regard to the qualitative comparisons between depth groups, the ANOSIM showed significant differences between the specific composition of the coralligenous assemblages at different depths (test for difference between depth groups, $R = 0.964$; $p < 0.01$).

**Table 1** Sponge species identified along the Apulian coralligenous concretion with an annotation on Growing Form (*GF*); Endemic species (*E*); Protected species (*P*); new findings for Mediterranean (*), Italian (§), Adriatic (#) and Ionian seas (φ). Sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*), Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*). Growing Forms: Boring (*BO*), Encrusting (*EN*), Erect (*ER*), Insinuating (*IN*), Massive (*MA*)

| Species no. | Calcarea | Status[a] | TGU | CER | PMI | TIN | TAR | OTR | SML | GAL | SCA | CAM | GF[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Clathrina clathrus* (Schmidt, 1864) | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | MA |
| 2 | *Clathrina coriacea* Montagu, 1818 | | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | MA |
| 3 | *Clathrina rubra* Sarà, 1958 | | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | MA |
| 4 | *Sycon elegans* Bowerbank, 1845 | φ | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ER |
| Homoscleromorpha | | | | | | | | | | | | | |
| 5 | *Corticium candelabrum* Schmidt, 1862 | | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | MA |
| 6 | *Plakina monolopha* Schulze, 1880 | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 7 | *Plakina reducta* (Pulitzer-Finali, 1983) | E, # | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 8 | *Plakina trilopha* Schulze, 1880 | | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | EN |
| 9 | *Plakortis simplex* Schulze, 1880 | | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | EN |
| 10 | *Oscarella lobularis* (Schmidt, 1862) | | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | MA |
| Demospongiae | | | | | | | | | | | | | |
| 11 | *Aaptos aaptos* (Schmidt, 1864) | | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | MA |
| 12 | *Acanthella acuta* Schmidt, 1862 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | MA |
| 13 | *Acarnus tortilis* Topsent, 1892 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | EN |
| 14 | *Agelas oroides* (Schmidt, 1864) | E | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | MA |
| 15 | *Alectona millari* Carter, 1879 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | BO |
| 16 | *Antho (Antho) involvens* Schmidt, 1864 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 17 | *Aplysilla rosea* (Barrois, 1876) | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | EN |
| 18 | *Aplysina aerophoba* (Nardo, 1833) | P | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | ER |
| 19 | *Aplysina cavernicola* Vacelet, 1959 | E, P | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | ER |
| 20 | *Axinella cannabina* (Esper, 1794) | E, P | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | ER |
| 21 | *Axinella damicornis* (Esper, 1794) | | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | ER |
| 22 | *Axinella polypoides* Schmidt, 1862 | P | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | ER |
| 23 | *Axinella rugosa* (Bowerbank, 1866) | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ER |
| 24 | *Axinella verrucosa* (Esper, 1794) | | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | ER |
| 25 | *Axinyssa aurantiaca* (Schmidt, 1864) | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | MA |
| 26 | *Batzella inops* Topsent, 1891 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 27 | *Bubaris carcisis* Vacelet, 1969 | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | ER |
| 28 | *Bubaris vermiculata* (Bowerbank, 1866) | | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | EN |
| 29 | *Cacospongia mollior* Schmidt, 1862 | φ | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | EN |
| 30 | *Calyx nicaeensis* Risso, 1826 | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ER |
| 31 | *Chondrilla nucula* Schmidt, 1862 | | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | MA |
| 32 | *Chondrosia reniformis* Nardo, 1847 | | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | MA |
| 33 | *Clathria (Clathria) toxistricta* (Topsent, 1925) | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | EN |
| 34 | *Clathria (Microciona) armata* Bowerbank, 1862 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 35 | *Clathria (Microciona) gradalis* Topsent, 1925 | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | EN |
| 36 | *Clathria (Microciona) macrochela* (Lévi, 1960) | * | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | EN |
| 37 | *Clathria (Microciona) spinarcus* (Carter & Hope, 1889) | φ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | EN |
| 38 | *Clathria* sp. | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 39 | *Cliona celata* Grant, 1826 | | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | BO |
| 40 | *Cliona copiosa* sensu Sarà, 1959 | | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 41 | *Cliona janitrix* Topsent, 1932 | φ | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | BO |
| 42 | *Cliona nigricans* sensu Schmidt, 1862 | | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 43 | *Cliona rhodensis* Rutler & Bromley, 1981 | E | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 44 | *Cliona schmidti* Ridley, 1881 | | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |

**Table 1** (continued)

| Species no. | Calcarea | Status[a] | TGU | CER | PMI | TIN | TAR | OTR | SML | GAL | SCA | CAM | GF[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 45 | *Cliona* sp. | | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | BO |
| 46 | *Cliona topsenti* (Lendenfeld, 1896) | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | BO |
| 47 | *Cliona tremitensis* sensu Sarà, 1961 | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 48 | *Cliona vermifera* Hancock, 1867 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 49 | *Cliona viridis* Schmidt, 1862 | | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | BO |
| 50 | *Crambe crambe* (Schmidt, 1862) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | EN |
| 51 | *Crella (Pytheas) fusifera* (Sarà, 1969) | φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 52 | *Crella (Pytheas) sigmata* Topsent, 1925 | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 53 | *Delectona ciconiae* Bavestrello et al., 1996 | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | BO |
| 54 | *Dendroxea adumbrata* Corriero et al., 1996 | E, φ | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 55 | *Dendroxea lenis* (Topsent, 1892) | | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | EN |
| 56 | *Dercitus (Stoeba) dissimilis* (Sarà, 1959) | E | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | IN |
| 57 | *Dercitus (Stoeba) plicatus* (Schmidt, 1868) | | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | IN |
| 58 | *Dercitus* sp. | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | IN |
| 59 | *Dictyonella incisa* (Schmidt, 1880) | | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | MA |
| 60 | *Dictyonella marsilii* Topsent, 1893 | E, φ | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | MA |
| 61 | *Didiscus stylifer* Tsurnamal, 1969 | E, # | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 62 | *Diplastrella bistellata* (Schmidt, 1862) | | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | EN |
| 63 | *Dotona* cf. *pulchella mediterranea* Rosell & Uriz, 2002 | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | BO |
| 64 | *Dysidea avara* (Schmidt, 1862) | | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | MA |
| 65 | *Dysidea fragilis* (Montagu, 1818) | | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | MA |
| 66 | *Dysidea incrustans* Schmidt, 1862 | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | EN |
| 67 | *Erylus discophorus* Schmidt, 1862 | | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | EN |
| 68 | *Eurypon denisae* Vacelet, 1969 | E | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 69 | *Eurypon topsenti* Pulitzer Finali, 1983 | E | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | EN |
| 70 | *Eurypon vescicularis* Sarà & Siribelli, 1960 | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | EN |
| 71 | *Eurypon viride* (Topsent, 1889) | # | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 72 | *Fasciospongia cavernosa* (Schmidt, 1862) | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 73 | *Forcepia* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 74 | *Geodia anceps* (Vosmaer), 1894 | E, # | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 75 | *Geodia conchilega* Schmidt, 1862 | E | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | MA |
| 76 | *Geodia cydonium* (Jameson, 1811) | P | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | MA |
| 77 | *Halichondria semitubulosa* Lieberkühn, 1859 | E | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ER |
| 78 | *Haliclona (Gellius) angulata* (Bowerbank, 1866) | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 79 | *Haliclona (Gellius)* cf. *dubia* (Babic, 1922) | φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 80 | *Haliclona (Gellius) flagellifera* (Ridley & Dendy, 1886) | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | EN |
| 81 | *Haliclona (Halichoclona) fulva* (Topsent, 1893) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 82 | *Haliclona (Reniera) cratera* Schmidt, 1862 | | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 83 | *Haliclona (Reniera) mediterranea* Griessinger, 1971 | | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ER |
| 84 | *Haliclona (Reniera)* sp. | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | MA |
| 85 | *Haliclona (Rhizoniera) sarai* Pulitzer-Finali, 1969 | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 86 | *Haliclona (Soestella) mucosa* (Griessinger, 1971) | φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | MA |
| 87 | *Hemimycale columella* (Bowerbank, 1874) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 88 | *Holoxea furtiva* Topsent, 1892 | φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | IN |
| 89 | *Hymedesmia (Hymedesmia) peachii* Bowerbank, 1882 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | EN |
| 90 | *Hymedesmia (Hymedesmia) versicolor* Topsent, 1893 | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |

**Table 1** (continued)

| Species no. | Calcarea | Status[a] | TGU | CER | PMI | TIN | TAR | OTR | SML | GAL | SCA | CAM | GF[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 91 | *Hymeniacidon perlevis* Montagu, 1818 | | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | MA |
| 92 | *Ircinia dendroides* (Schmidt, 1862) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | MA |
| 93 | *Ircinia variabilis* (Schmidt, 1862) | | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | MA |
| 94 | *Jaspis johnstonii* (Schmidt, 1862) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | IN/EN |
| 95 | *Lissodendoryx (Anomodoryx) cavernosa* Topsent, 1892 | E | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 96 | *Mycale (Aegogropila)* cf. *tunicata* (Schmidt, 1862) | φ | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | MA |
| 97 | *Mycale (Mycale) lingua* (Bowerbank, 1866) | | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | MA |
| 98 | *Mycale (Mycale) massa* (Schmidt, 1862) | | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | MA |
| 99 | *Myrmekioderma spelaeum* Pulitzer-Finali, 1983 | E | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 100 | *Negombata corticata* (Carter, 1879) | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ER |
| 101 | cf. *Nethea amygdaloides (*Carter, 1876) | φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | EN |
| 102 | *Pachastrella monilifera* Schmidt, 1868 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | MA |
| 103 | *Paratimea oxeata* Pulitzer-Finali, 1978 | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | IN |
| 104 | *Penares euastrum* (Schmidt, 1868) | φ | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | MA |
| 105 | *Penares helleri* Schmidt, 1868 | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 106 | *Petrosia (Petrosia) ficiformis* (Poiret, 1789) | | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | MA |
| 107 | *Phorbas fibulatus* (Topsent, 1893) | E, φ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | EN |
| 108 | *Phorbas fictitius* (Bowerbank, 1866) | | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | EN |
| 109 | *Phorbas tenacior* (Topsent, 1925) | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | EN |
| 110 | *Phorbas topsenti* Vacelet & Perez, 2008 | E | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 111 | *Pione vastifica* (Hancock, 1849) | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | BO |
| 112 | *Pleraplysilla spinifera* (Schulze, 1878) | | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | EN |
| 113 | *Prosuberites longispinus* Topsent, 1893 | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | EN |
| 114 | *Protosuberites denhartogi* van Soest & de Kluijver, 2003 | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | EN |
| 115 | *Pseudosuberites sulphureus* Bowerbank, 1866 | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 116 | *Raspaciona aculeata* (Johnston, 1842) | | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | EN |
| 117 | *Raspailia (Raspailia) virgultosa* (Bowerbank, 1866) | φ, # | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ER |
| 118 | *Rhabderemia topsenti* van Soest & Hooper, 1993 | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 119 | *Sarcotragus foetidus* Schmidt, 1862 | P | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | MA |
| 120 | *Sarcotragus spinosulus* Schmidt, 1862 | | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | MA |
| 121 | *Scalarispongia scalaris* (Schmidt, 1862) | | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | MA |
| 122 | *Sceptrella insignis* (Topsent, 1890) | # | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | EN |
| 123 | *Siphonodictyon infestum* (Johnson, 1889) | | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | BO |
| 124 | *Siphonodictyon* sp. | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 125 | *Spirastrella cunctatrix* Schmidt, 1868 | | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | EN |
| 126 | *Spiroxya heteroclita* Topsent, 1896 | E, # | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | BO |
| 127 | *Spiroxya sarai* (Melone, 1965) | E, φ | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | BO |
| 128 | *Spongia (Spongia) lamella* (Schulze, 1879) | E, P | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | ER |
| 129 | *Spongia (Spongia) nitens* (Schmidt, 1862) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | MA |
| 130 | *Spongia (Spongia) officinalis* Linné, 1759 | P | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 131 | *Spongia (Spongia) virgultosa* Schmidt, 1868 | | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 132 | *Spongionella gracilis* (Vosmaer, 1883) | E, φ | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | MA |
| 133 | *Spongosorites intricatus* Topsent, 1892 | E | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | IN/EN |
| 134 | *Stelletta grubii* Schmidt, 1862 | | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | MA |
| 135 | *Stelletta simplicissima* Schmidt, 1868 | E | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 136 | *Stelletta stellata* Topsent, 1893 | E | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 137 | *Suberites carnosus* Johnston, 1842 | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 138 | *Suberites domuncula* Olivi, 1792 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |

**Table 1** (continued)

| Species no. | Calcarea | Status[a] | TGU | CER | PMI | TIN | TAR | OTR | SML | GAL | SCA | CAM | GF[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 139 | *Suberites syringella* (Schmidt, 1868) | E, φ | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | EN |
| 140 | *Tedania (Tedania) anhelan*s Vio in Olivi, 1792 | | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 141 | *Terpios gelatinosa* (Bowerbank, 1866) | | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | EN |
| 142 | *Tethya aurantium* Pallas, 1766 | P | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | MA |
| 143 | *Tethya citrina* Sarà & Melone, 1965 | P | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | MA |
| 144 | *Thoosa armata* Topsent, 1888 | § | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | BO |
| 145 | *Thoosa mollis* Volz, 1939 | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |
| 146 | *Timea crassa* Topsent, 1900 | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | EN |
| 147 | *Timea fasciata* Topsent, 1934 | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 148 | *Timea simplistellata* Pulitzer-Finali, 1983 | # | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 149 | *Timea stellata* Bowerbank, 1866 | | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 150 | *Timea unistellata* (Topsent, 1892) | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | EN |
| 151 | *Trachycladus minax* Topsent, 1888 | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | EN |
| 152 | *Triptolemma simplex* (Sarà, 1959) | E, φ | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | IN |
| 153 | *Volzia albicans* Volz, 1939 | E | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | BO |

Sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*), Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*)

[a] Endemic species (*E*); protected species (*P*); new findings for Mediterranean (*), Italian (§), Adriatic (#) and Ionian seas (φ)

[b] *GF* Growing forms: boring (*BO*), encrusting (*EN*), erect (*ER*), insinuating (*IN*), massive (*MA*)

Both cluster (reported in the figure as dotted lines) and PCoA analyses showed the same strong outcome: sampling stations cluster into two groups (Fig. 5) with global similarity depending on depth. The PCoA described with the first two axes accounts for about 50% of the total variance of the system, and the studied sites group together with similarities ranging from 40 to 80%. Along the first axis, the shallower sites are separated from the deeper ones, the latter contributing to 34.5% of the total variance. The second axis explained 14.4% of the variance, further dividing the two groups: Santa Maria di Leuca (SML) and Otranto (OTR) were both characterised by vertical rim coralligenous formations and shared about 60% of the species; and Gallipoli (GAL), Campomarino (CPM) and Santa Caterina (SCA) were characterised by coralligenous outcrops scattered on soft bottoms at the same depth and also had about 60% of the species in common. With respect to shallow sites, Porto Miggiano (PMI) and Taranto (TAR) showed sponge assemblages with 50% similarity, and the same value was obtained between the two Adriatic sites of Torre Guaceto (TGU) and Cerano (CER). Torre Inserraglio (TIN) differed from the other sites with a similarity value among replicates close to 80%. PMI was characterised by vertical cliffs while TAR showed mixed features such as platform biocoenosis and tall outcrops, sometimes fused together, with steep bathymetric drops.

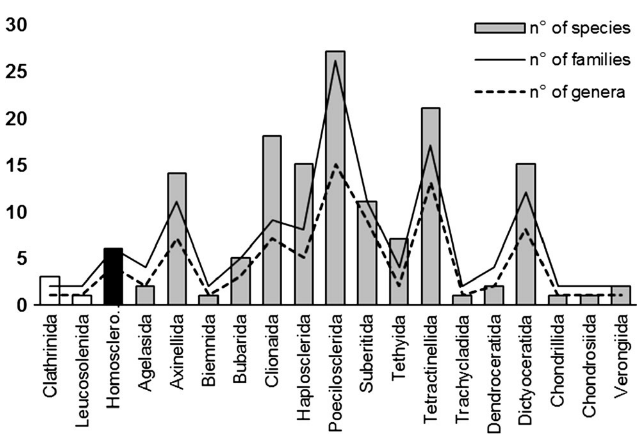


**Fig. 3** Distribution of the sponge species/genera/families among orders; *white bar* Orders of the Class Calcarea; *black bar*: Orders of the Class Homoscleromorpha; *grey bar* Orders of the Class Demospongiae

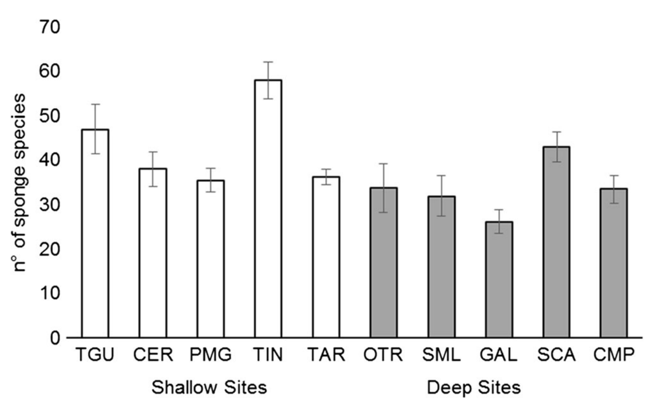


**Fig. 4** Sponge species richness computed as average values in each site. Sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*), Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*)

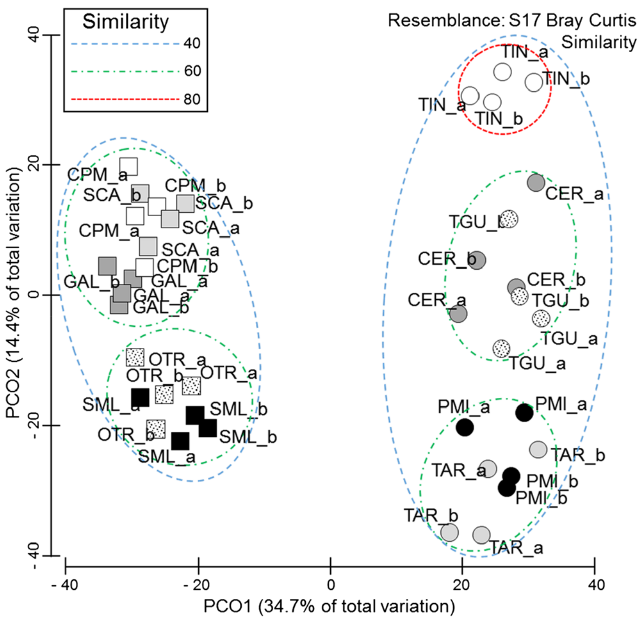


**Fig. 5** Results of PCoA and Bray–Curtis clustering analysis (*dotted lines*) on the sponge dataset. Shallow sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*). Deep sites: Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*)

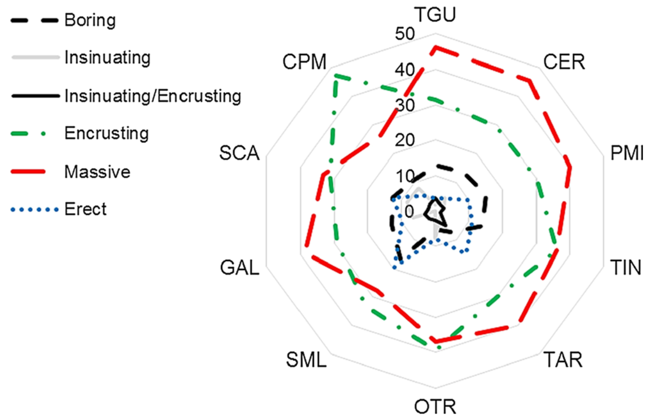


**Fig. 6** Distribution of the sponge species among sites according to their growing form (on the *right* shallow sites, on the *left* deep sites). Sites: Torre Guaceto (*TGU*), Cerano (*CER*), Porto Miggiano (*PMI*), Torre Inserraglio (*TIN*), Taranto (*TAR*), Otranto (*OTR*), Santa Maria di Leuca (*SML*), Gallipoli (*GAL*), Santa Caterina (*SCA*), Campomarino (*CPM*)

Of the over 153 sponges recorded in the present research, 123 (about 80%) were epibenthic species, whereas 28 (about 18%) had cryptic habitus. Only 2 species (*Jaspis johnstonii* and *Spongosorites intricatus*) showed specimens belonging to both categories. All sponge assemblages were characterised by the dominance of encrusting and massive epibenthic forms (Fig. 6), regardless of depth and geographical location. Shallow sites (TGU, CER, PMI, TIN, TAR) showed the highest percentage of massive forms, with an average of 43% and values ranging from 35% (TIN) to 47% (TGU and CER). Even in deep stations, massive forms (32% of the total) were well represented, with values from 27% at CMP to 38% at GAL. The wide distribution of encrusting forms did not allow the determination of a pattern separating shallow from deep environments. At shallow sites, they represented, on average, about 31% of the assemblage, with values ranging from 30% at CER, PMI and TAR and 36% at TIN. At deep stations, the average is 37%, with values between 29% at GAL and 47% at CMP. Endobenthic (both boring and insinuating) and erect forms were represented with similar mean values (about 10%) in the two groups of sites.

## Discussion

### General traits of coralligenous communities

Coralligenous concretions cover an area of at least 2763 km$^2$ in the Mediterranean Sea (Martin et al. 2014). According to recent surveys (BIOMAP Project 2007–2013; AA VV et al. 2014), they extend for more than 400 km$^2$ along the Apulian region, representing one of the most relevant regional marine habitats together with seagrass meadows (Campiani et al. 2014).

According to literature data, the investigated coralligenous bottoms are a heterogeneous mosaic, also varying at small spatial scale, allowing several different assemblages to coexist in a reduced space (Ferdeghini et al. 2000; Balata et al. 2005; Virgilio et al. 2006). To date, different types of coralligenous communities have been indentified with marked differences in the relative dominance of animal or algal structuring species. In the present research, the analysis of photographic images revealed two main categories of coralligenous macro-builders: coralline algae, building smooth organogenous structures where the distribution of invertebrates is patchy, occurring in shallow sites; and invertebrates, largely represented in deeper outcrops, some of them contributing to realise a substrate texture rich in cavities and crevices.

Although both coralline algae and invertebrates contribute to the creation of coralligenous formations, the former are usually considered the main coralligenous builders, while the role of invertebrates is still poorly investigated (Laborel 1961; Laubier 1966; Sartoretto 1996; Peirano et al. 2001; Kersting and Linares 2012). Whereas bryozoans and polychaetes are the most abundant animal groups in coralligenous outcrops, other taxa such as cnidarians and molluscs are considered to be minor contributors (Hong 1980), with the exception of the scleractinian *Cladocora caespitosa* (Peirano et al. 2001; Kersting and Linares 2012). Conversely, present data underline that the bivalve *Neopycnodonte cochlear* and the anthozoans *Phyllangia americana mouchezii* and *Polycyathus muellerae* appear capable of forming true facies, thus showing a dominant role as builders in the deepest communities. This succession along a bathymetric range from algal to animal composition seems to be common, although it had not been previously emphasised in the literature on Apulian coralligenous outcrops, which instead focused on the structural differences between vertical and platform coralligenous formations, the latter of which is always surrounded by sedimentary substrata (Sarà 1968, 1969).

**Sponge community structure and pattern of distribution**

To date, the taxonomic revision of literature data allowed us to record 291 sponge species associated with coralligenous formations of Mediterranean Sea, 112 of them also found in the Apulian coralligenous formations (Labate 1967; Sarà 1968, 1969, 1973, Annicchiarico 1980; Corriero et al. 2004; Baldacconi and Corriero 2009; Kipson et al. 2011; Bertolino et al. 2013, 2014; Calcinai et al. 2015). Here, we increase the number of sponge species associated with the Mediterranean to 306 and those of Apulian coralligenous formations to 169. More than half (30) of the 57 sponge species added to Apulian coralligenous list come from deep sites, thus underlining the need to improve taxonomic studies on coralligenous outcrops over a huge bathymetric range.

The 153 sponge species reported in the present paper are mainly represented by demosponges. According to literature data on Ligurian coralligenous outcrops (Bertolino et al. 2013, 2014; Calcinai et al. 2015), Poecilosclerida is the most represented order. However, great differences occur in the specific pattern of the sponge assemblages associated with Apulian and Ligurian formations that share only 35% of species.

The endemic sponge species (39) represent 25% of the total recorded sponge species, a value rather low with respect to the 48% reported for the endemic coralligenous sponges at the Mediterranean scale (Pansini and Longo 2003). This difference is probably due to the recent increase of knowledge on species distribution, which also involved the new discovery of Mediterranean species in neighbouring Atlantic waters, rendering some literature data obsolete.

It must be underlined that this is the first research focusing on coralligenous sponge communities along a bathymetric range on large geographic scale (more than 400 km of coastline). Our analyses have shown substantial and significant differences between the deep and shallow sponge assemblages. About 30% (46 species) of the total sponges found are 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). The pattern of sponge distribution observed does not seem linked to the availability of nutrients, since it does not vary according to differences in the trophic regime of the investigated sites. Indeed, although nutrients differ significantly in Adriatic and Ionian waters (CMEMS 2016), we did not observe a coherent correspondence between water trophism and the distribution of sponge fauna. As for light, it is known to be an important ecological factor also able to determine the distribution of the sponges. Patterns of species substitutions are known, for example, for the Porifera assemblages of semi-submerged caves, where the reduction of the light along the outer/inner gradient exceeds other important ecological factors such as the trophic depletion (Corriero et al. 2000). The occurrence of large differences in the sponge pattern at the two examined depths should therefore be influenced by the different light penetration in shallow sites with respect to deeper ones. In the literature, data relating to the distribution of coralligenous species mainly refer to the susceptibility of communities to light and temperature as a whole and do not investigate individual taxonomic groups aside from some structuring algae (Dring 1981; Lüning 1981; Ballesteros and Zabala 1993).

The nature of substrate plays a key role in explaining the differences in the sponge distribution, as highlighted by PCoA, which also probably affects the remaining benthic community. The deep coralligenous formations characterised by animal dominance show a more heterogeneous texture and are richer in crevices and cavities than the shallow and homogeneous algal ones. These differences in sponge species composition also correspond to a difference in the distribution of growing forms, with the insinuating cryptic species more abundant in deeper coralligenous formations because of the numerous cavities. The type of substrate seems to also explain the differences in sponge assemblages within the two depth groups identified by the PCoA. Among the shallow sites, Porto Miggiano presents high walls, similarly to Taranto; at Torre Guaceto and Cerano, low coralligenous outcrops emerge from a sandy bottom; while Torre Inserraglio is characterised by a shape mosaic consisting of both walls and low coralligenous banks. Among the deep sites, Otranto and Santa Maria di Leuca are characterised by walls interspersed with large areas of sandy bottom, whereas Gallipoli, Campomarino and Santa Caterina consist of isolated large banks irregularly scattered on a detrital bottom.

On the whole, our data have shown a clear dominance of epibenthic over cryptic sponge species. This finding is in agreement with data referred to coralligenous formations in the Ligurian Sea (Bertolino et al. 2013). However, this condition is not the rule, since the importance of cryptic sponge species may increase locally in relation to different environmental conditions (Calcinai et al. 2015). As it concerns cryptic sponges, boring species represent the main component of the Apulian coralligenous community, confirming their importance in erosion dynamics of the coralligenous outcrops (Sarà 1999; Cerrano et al. 2001).

## Final remarks

The present research is in agreement with the "Updated Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in Mediterranean Sea (UNEP-MAP-RAC/SPA 2015). Indeed, the Action Plan asked for an increase in the data on coralligenous distribution, also adding new information on sites deeper than 50 m, in order to assess the real extent of this assemblage in the Mediterranean. Moreover, the Action Plan encouraged the collecting of new data on species composition of coralligenous assemblages, with a focus on the identity of algal and animal builders. In this scenario, this paper provides a significant contribution in terms of the supply of new taxa to the coralligenous species list (an increase of 5 and 34% of the sponges species recorded from Mediterranean and Apulian coralligenous, respectively).

Coralligenous formations represent one of the most interesting biological communities occurring in Apulian seas. Their wide distribution and great diversity allow the forming of a mosaic of diverse habitats in which animals tend to substitute algae in the role of main bioconstructors as the water deepens. Indeed, together with *C. caespitosa*, a well-known engineering species at lower depths, other invertebrates such as molluscs, bryozoans and cnidarians strongly contribute to building coralligenous bottoms.

Sponges represent an important component of Apulian coralligenous communities in terms of species richness, actively contributing to the mechanism of substrate creation/destruction thanks to their dual role of habitat builders and eroders. Ten of the 15 sponge species included in national and international wildlife protection laws and policy (Barcelona Convention 1978; Bern Convention 1983) have been detected in the present study. In this sense, coralligenous habitats play the role of a source of marine fauna of high conservation value.

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