Lithology could affect benthic communities living below boulders

M. Canessa[1] (iD), G. Bavestrello[1], E. Trainito[2], A. Navone[2] and R. Cattaneo-Vietti[1]

[1]Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università di Genova, Corso Europa, 26 –16132 Genova, Italy and [2]Tavolara-Punta Coda Cavallo MPA, Via San Giovanni, 14 – 07026 Olbia, Italy

Abstract

Structure and diversity of sessile zoobenthic assemblages seem to be driven not only by chemical-physical constraints and biological interactions but also by substrate lithology and its surface features. Nevertheless, broadly distributed crustose epilithic corallines could mask the role of substrate on animal settling. To evaluate the direct influence of different rocky substrates, occurrence and coverage of several sessile species, growing on the dark (i.e. coralline-free) face of sublittoral limestone and granite boulders were compared in the Tavolara MPA (Mediterranean Sea). The analysis of photographic samples demonstrated significant differences in terms of species composition and coverage, according to lithology. Moreover, limestone boulders were widely bare, while the cover per cent was almost total on granite. The leading cause of observed patterns could be the different level of dissolution of the two types of rocks, due to their different mineral composition and textural characteristics. Limestone has previously been shown to have higher dissolution compared with granite, and consequently, a more unstable surface. Our results suggest that, in dark habitats, the absence of the crustose coralline layer allows more rock dissolution and consequent lower stability of the limestone compared with granite, which, in turn, reduces the zoobenthos colonization.

Introduction

The lithological characteristics of the substrate may influence the richness and dynamics of hard-bottom benthic assemblages (Cerrano *et al.*, 1999; Bavestrello *et al.*, 2000, 2018; Cattaneo-Vietti *et al.*, 2002; Faimali *et al.*, 2004; Johansen, 2018; Canessa *et al.*, 2019, 2020). In fact, under comparable edaphic conditions, several communities were found to be structurally different on substrates of different lithology, in terms of presence and abundance of some sessile species (Coombes, 2011). However, there is a general scarcity of studies on this topic. During tests performed using experimental blocks of different rocks along the coast of Cornwall, barnacle settling was higher on granites and concrete than on limestones, suggesting that the roughness of the substrate could positively influence settling (Coombes, 2011). The influence of different rock types was particularly evident also for the supralittoral barnacle *Chthamalus* spp. which, in the Ligurian Sea, appeared more abundant on limestones than on marly substrates (Canessa *et al.*, 2019). Also, comparing barnacle populations living on different ophiolitic rocks, differences in density arose: they were abundant on serpentinite rocks and virtually absent on metagabbros (Bavestrello *et al.*, 2018).

In the subtidal zone of the Mediterranean, the species richness of sponges, anthozoans, serpulids and sessile gastropods living on hard bottoms characterized by different lithologies showed differences in density or covering capacity (Cattaneo-Vietti *et al.*, 2002; Bavestrello *et al.*, 2003; Schiaparelli *et al.*, 2003; Guidetti *et al.*, 2004). For example, in coralligenous habitats of north-east Sardinia, some sponges (*Axinella* sp., *Axinella polypoides* and *Sarcotragus foetidus*), although present on both granite and carbonate, showed a clear preference for granite (Canessa *et al.*, 2020).

The bulk of evidence suggests an intricate pattern of interactions exists between sessile organisms, rock morphology and composition, together with several local environmental factors (Aguilera *et al.*, 2014; Angiolillo *et al.*, 2016). In particular, the structure and diversity of algal assemblages seem particularly sensitive to substrate lithology (McGuinness, 1989; Hadfield & Paul, 2001; Bavestrello *et al.*, 2018). Crustose epilithic red algae may act as ecosystem engineers, modifying conditions, creating habitat, but also competing for space with sessile animals (Bressan, 1974; Steneck, 1986; Johansen, 2018). Comparing the development of calcareous algae on two contiguous ophiolitic rocks in the upper tidal zone, it was evident that *Neogoniolithon brassica-florida* was only present on serpentinites, while virtually absent on metagabbros (Bavestrello *et al.*, 2018). Moreover, in subtidal habitats within the area of Tavolara Island (north-east Sardinia), the thickness of the crustose calcareous red algae was higher on limestone rocks than on granite ones (Canessa *et al.*, 2020). Here, it is possible that two different genotypes of 'Lithophyllum stictiforme' colonized these two different lithotypes, as stated by Pezzolesi *et al.* (2019).

Table 1. Per cent occurrence of each species/OTU in each site and average occurrence on limestone (Ol) and granite (Og) boulders

Sites	Archetto	Cala Cicale	Occhio di Dio	Isola Rossa	Punta Arresto	Mezzo Canale	Limestone occurrence (Ol)	Granite occurrence (Og)
Substrate	Limestone	Limestone	Limestone	Granite	Granite	Granite		
Latitude	9.69662E	9.7056E	9.7072E	9.67345E	9.73665E	9.66603E		
Longitude	40.8892N	40.8953N	40.89653N	40.87731N	40.87707N	40.88487N		
Average total boulder area (cm^2) ± SE	783.2 ± 71.9	820.4 ± 101.1	820.3 ± 75.7	720.3 ± 60.7	941.9 ± 110.3	613.5 ± 47.6	808.0 ± 47.1	758.6 ± 49.3
Average algal-free boulder area (cm^2) ± SE	413.5 ± 72.5	431.1 ± 63.1	521.9 ± 68.6	438.6 ± 66.0	588.1 ± 83.8	519.2 ± 40.2	455.5 ± 39.0	515.3 ± 38.3
Miniacina miniacea[a]	66.6	91.6	75	58.3	100	83.33	77.7 ± 7.3	80.6 ± 12.1
Acanthella acuta[b]	–	–	8.3	–	–	–	2.8 ± 2.8	–
Hemimycale columella[b]	41.6	8.3	–	–	–	–	16.7 ± 12.7	–
Ircinia sp.[a]	8.3	–	–	–	8.3	–	2.8 ± 2.8	2.8 ± 2.8
Chondrosia reniformis[a]	8.33	–	–	–	–	16.67	2.8 ± 2.8	5.5 ± 5.5
Clathrina sp.[c]	–	–	–	33.3	8.3	–	–	13.9 ± 10
Cliona spp.[b]	58.0	75.3	83.3	–	–	–	72.3 ± 7.5	–
Corticium candelabrum[b]	8.3	8.3	–	–	–	–	5.5 ± 2.7	–
Haliclona fulva[a]	–	16.6	–	8.3	16.6	–	5.5 ± 5.5	8.3 ± 4 0.8
Haliclona mucosa[a]	8.3	75	16.6	25	33.3	8.3	33.3 ± 20.9	22.2 ± 7.3
Oscarella lobularis[b]	8.3	–	–	–	–	–	2.8 ± 2.8	–
Petrobiona massiliana[c]	–	–	–	–	25	8.3	–	11.1 ± 7.3
Petrosia ficiformis[a]	–	8.3	–	16.6	41.6	16.6	2.8 ± 2.8	25 ± 8.3
Phorbas tenacior[c]	–	8.3	–	8.3	16.6	25	2.8 ± 2.8	16.7 ± 4.8
Spirastrella cunctatrix[c]	–	–	–	33.3	–	25	–	19.4 ± 10
Terpios fugax[a]	16.6	–	–	25	16.6	16.6	5.6 ± 5.6	19.4 ± 2.7
Massive sponges[a]	8.3	16.6	–	33.3	8.3	–	8.3 ± 4.8	13.9 ± 10
Encrusting sponges[a]	75	66.6	75	91.6	100	91.6	72.2 ± 2.7	94.4 ± 2.7
Balanophyllia europea[b]	16.67	8.33	–	–	–	–	8.3 ± 4.8	–
Caryophyllia inornata[c]	–	–	–	–	8.3	41.6	–	16.7 ± 12.7
Scleractinians[a]	16.67	8.33	16.6	–	8.3	–	13.9 ± 2.7	2.8 ± 2.8
Beania magellanica[c]	–	–	–	–	–	8.3	–	2.8 ± 2.8
Myriapora truncata[c]	–	–	–	75	66.6	16.6	–	52.7 ± 18.2
Patinella radiata[c]	–	–	–	–	8.3	–	–	2.8 ± 2.8
Reptadeonella violacea[a]	8.3	16.6	–	25	25	–	8.3 ± 4.8	16.6 ± 8.3
Reteporella sp.[c]	–	–	–	–	33.3	–	–	11.1 ± 11.1

Encrusting bryozoans[a]	97.2±2.7	72.2±7.4	100	100	91.6	83.3	58.3	75
Novocrania anomala[a]	22.2±7.3	5.5±2.7	33.3	25	8.3	–	8.3	8.3
Serpulids[a]	97.2±2.7	88.8±7.3	100	100	91.6	91.6	100	75
Terebellidae[a]	5.6±5.6	8.33	16.6	–	–	8.3	8.3	8.3
Didemnids[a]	19.4±10	5.5±2.8	25	33.3	–	8.3	–	8.3
Halocynthia papillosa[b]	–	2.8±2.8	–	–	–	–	–	8.3
Polycitor adriaticus[b]	–	2.8±2.8	–	–	–	–	–	8.3
Phallusia fumigata[c]	5.5±2.7	–	8.3	8.3	–	–	–	–

[a]Species found on both substrates.
[b]Species/OTU exclusive of limestone.
[c]Species/OTU exclusive of granites.

This paper aims to verify the open hypothesis that the settlement of sessile zoobenthic organisms and the consequent development of the assemblage in terms of richness and occurrence could be directly driven by the substrate lithology, without interference due to encrusting calcareous algae. This was achieved by carrying out research in dark habitats, where algae are absent. Although marine caves are the most obvious option, it is virtually impossible to find close caves with similar ecological characteristics but different lithology. A more practical choice has been the study of the sessile fauna settled under boulders, comparable to that of the caves (Harmelin et al., 1985), even if influenced by the faunistic characteristics of the surrounding communities (Bellan-Santini, 1962).

Herein, we present the results obtained by evaluating the species richness and coverage of the sessile zoobenthic assemblage, growing under large boulders of different lithology, without algal presence and assuming the invariance of all other ecological variables.

Materials and methods

Study area and sampling methods

In this study, aiming to describe the diversity and coverage of benthic communities directly settled on two different kinds of substrates, we investigated the lower surface of granite and limestone boulders, characterized by a progressive decrease of algal covering, following the reduction of solar light.

A total of 72 boulders with comparable size at 15–20 m depth were randomly selected and their dark side photographed at six sites, three carbonatic (Archetto (Ar), Occhio di Dio (OD) and Cala Cicale (CC)) and the other three granitic (Isola Rossa (IR), Mezzo Canale (MC) and Punta Arresto (PA)) inside the Marine Protected Area of Tavolara-Punta Coda Cavallo in the north-east coast of Sardinia (Tyrrhenian Sea) (Table 1; Figure 1). The selected sites are characterized by calcareous-dolomitic limestone of Tavolara Island and by granitic granular red pegmatite (Orrù & Pasquini, 1992). Very likely, each boulder has its own specific position with respect to the bottom and therefore specific micro-environmental conditions affecting the development of the benthic communities. Nevertheless, we think that it was reasonable to assume that, due to the number of replicates, the average conditions under boulders of comparable size of the two lithologies can be considered similar.

During scuba diving performed in July 2019, we turned the boulders upside down and the lower side was photographed by a Sony A6000 camera, 24 megapixels, 2 Inon S2000 flashes, colour temperature 5000° K; Sony 16-50 at 16 mm focal length; Sea & Sea MDX-a6000 underwater case with a flat porthole. A twin laser pointer, calibrated at 10 cm, was used as a metric reference. The lower surface was evaluated for each image, separating the algal-free portion used for the study from the total area (Figure 2).

Data analysis

The sessile zoobenthic organisms present under the boulders were tentatively classified at a specific level, and their per cent coverage, in terms of main taxonomic groups, calculated by a superimposed grid, using ImageJ Software. When specific or generic identification was not possible, other taxonomic and morphological units (OTUs) were adopted. Also, the bare surface present on the dark side of the boulders was measured.

Values of relative occurrence (Ol and Og, respectively for limestone and granite) were calculated for each species/OTUs, as per cent presence on the 12 photographs shot per site (Table 1). For
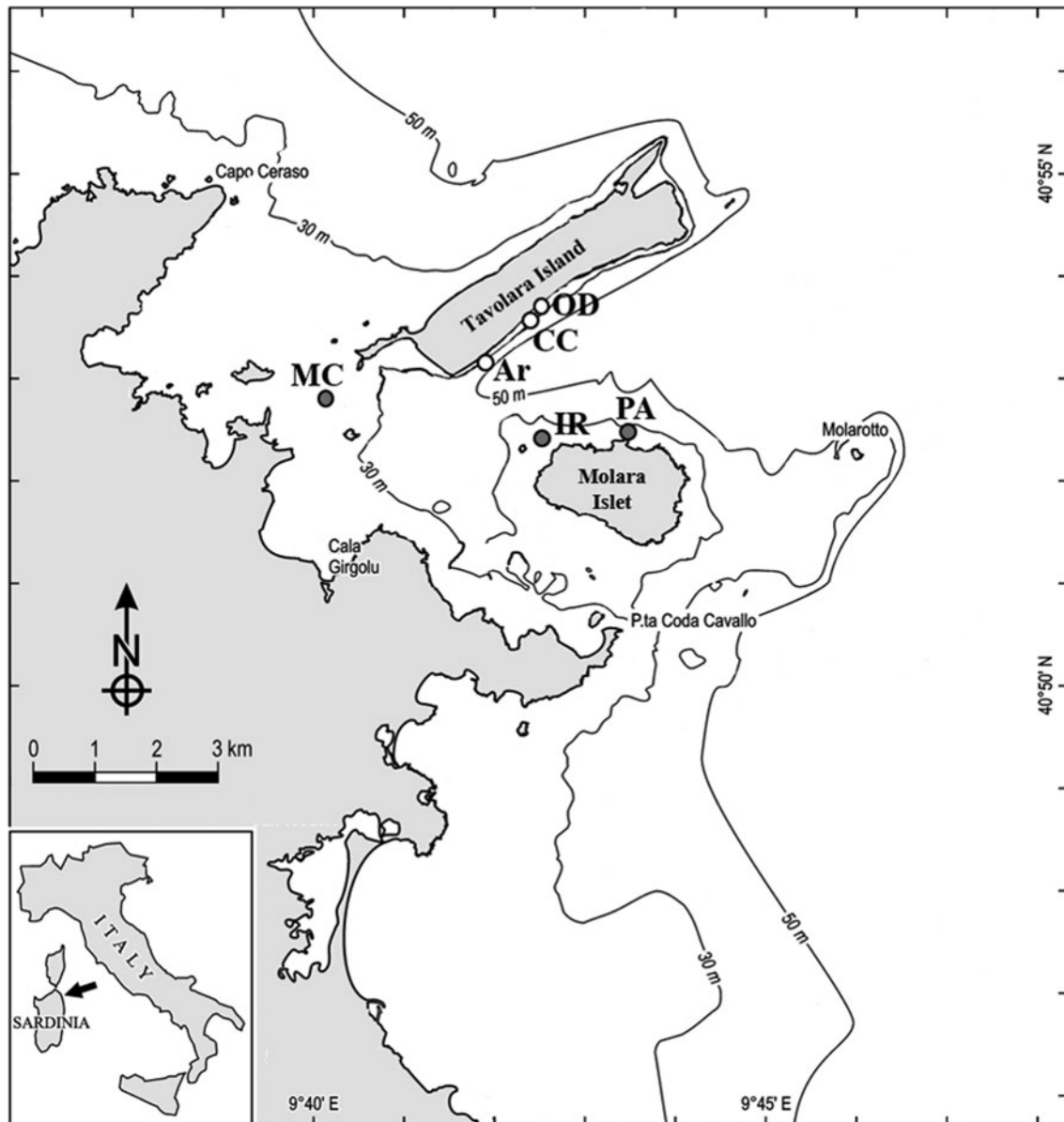
Fig. 1. Study area and sample sites within the Tavolara-Punta Coda Cavallo MPA. White dots, limestone, grey dots, granite. Ar, Archetto; CC, Cala Cicale; OD, Occhio di Dio; MC, Mezzo Canale; IR, Isola Rossa; PA, Punta Arresto.

the statistical analysis, we considered only the species/OTUs present in all the three sites of at least one substrate.

Resemblance similarity matrices, based on the Bray–Curtis index, were constructed for species/OTUs occurrence and per cent coverage of the main taxonomic groups (Anderson, 2001). The multivariate configuration of both the datasets was visualized through non-metric multi-dimensional scaling (nMDS).

Permutational analysis of variance (PERMANOVA) (Anderson, 2001) was performed using a two-way experimental design, with 'Substrate' (Su) as a fixed factor with two levels (Limestone (L) and Granite (G)) and 'Site' (Si), a random factor with six levels nested within the substrate. Each analysis used 9999 random permutations; Monte Carlo test was performed for deficient order of permutations; pairwise tests were used to compare condition levels when significant differences were detected by PERMANOVA (Table 2).

Similarity percentages analysis (SIMPER) (Clarke, 1993) was performed to identify the percentage contribution of each descriptor to the Bray–Curtis similarity among the two substrates (Table 3).

All the statistics were performed using PRIMER_E (Version 7).

Results

The sessile zoobenthic communities settled on the dark side of large boulders were investigated according to the substrate lithology.

The total area of the lower face of the boulders was, on average, $808 \, cm^2 \pm 47.1$ SE for limestone and $758.6 \, cm^2 \pm 49.3$ SE for granite. The average area wholly deprived of algae (the suitable boulder portion for the investigation) was $455.5 \, cm^2 \pm 39$ SE for limestone and $515.3 \, cm^2 \pm 38.3$ SE for granite (Table 1). No correlation between the number of species/OTUs and the considered surfaces was found ($R = 0.17$).

The analysis of the photographic sampling allowed the identification of 34 species/OTUs: 24 of them were observed under granitic boulders (9 exclusives) and 25 under limestone boulders (10 exclusives). The number of species/OTUs recorded on granite ranged from 4 to 10 per image, and that recorded on limestone from 2 to 10; 44.1% of the species were found in common,
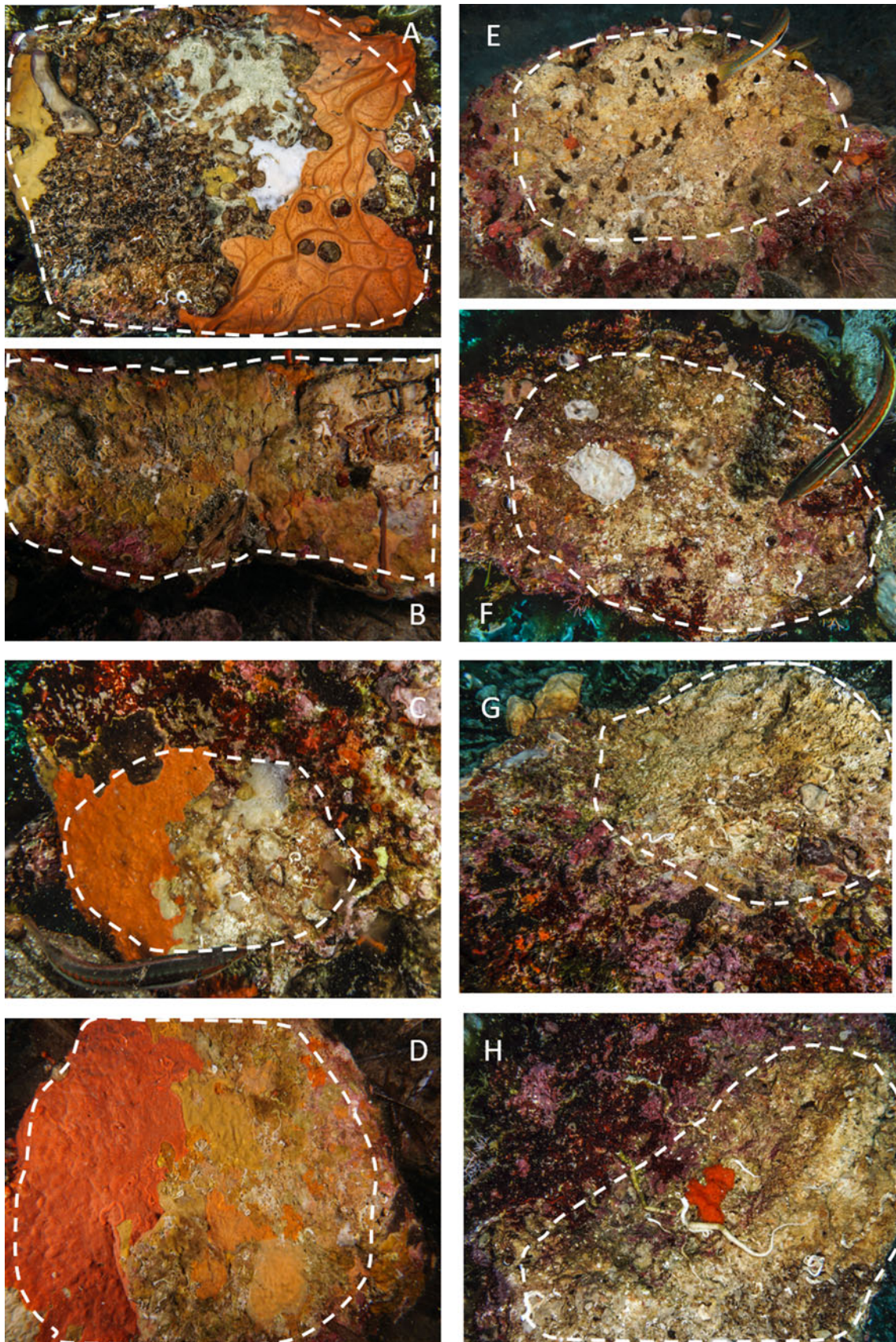
Fig. 2. Examples of limestone and granite boulders photographed during the sampling activity. The stacked lines include the algal-free surfaces on the dark side of the boulders selected for the analysis. A–D, granites; E–H, limestones. Note the extensive coverage of sponges and bryozoans on granites and the sizeable bare area, often bored by date-mussels, recorded on limestones.

Table 2. PERMANOVA performed on the occurrence for the species /OTUs recorded in all the sites of at least one lithology, and coverage of the main taxonomic groups

Occurrence	df	SS	MS	Pseudo-*F*	P(perm)	Unique Perm	P(MC)
Su	1	6118	6118	6.0018	0.0986	10	**0.0174**
Si (Su)	4	4077.5	1019.4	1.8901	**0.0392**	9933	**0.0463**
Res	66	35,595	539.31				
Total	71	45,790					
Coverage							
Su	1	96,581	96,581	76.001	0.1026	10	**0.0001**
Si(Su)	4	5083.1	1270.8	1.7505	0.0674	9914	0.0764
Res	66	47,914	725.97				
Total	71	1.50×10^5					

Bray–Curtis similarity index used for the resemblance matrix construction; permutation N = 9999. Monte Carlo test applied for insufficient unique permutations. Significant values are in bold.

Table 3. SIMPER analysis performed for occurrence of the main species/OTUs recorded in all the sites for almost one substrate, and coverage datasets

Occurrence	Average dissimilarity = 34.95					
OTUs	Limestone Av.Abund	Granite Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Cliona spp.	0.72	0.00	7.08	1.56	20.25	20.25
Myriapora truncata	0.00	0.53	5.04	1.03	14.42	34.67
Haliclona mucosa	0.33	0.19	3.89	0.80	11.13	45.80
Encr. sponges	0.72	0.94	3.18	0.65	9.10	54.89
Miniacina miniacea	0.78	0.92	3.06	0.59	8.75	63.64
Novocrania anomala	0.06	0.22	2.42	0.57	6.92	70.56
Phorbas tenacior	0.03	0.17	1.84	0.47	5.25	75.81
Spirastrella cunctatrix	0.00	0.19	1.83	0.48	5.24	81.05
Scleractinians	0.14	0.03	1.51	0.43	4.32	85.37
Serpulids	0.89	1.00	1.38	0.34	3.96	89.33
Terebellidae	0.08	0.06	1.35	0.38	3.87	93.20
Clatrina sp.	0.00	0.14	1.33	0.40	3.80	97.00
Encr. bryozoans	0.92	1.00	1.05	0.29	3.00	100.00
Coverage	Average dissimilarity = 76.51					
	Limestone Av.Abund	Granite Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	70.58	0.47	35.42	10.96	46.29	46.29
Sponges	7.42	49.06	21.05	5.21	27.51	73.80
Bryozoans	6.81	37.42	15.45	7.20	20.19	93.99
Serpulids	12.42	9.00	3.64	1.25	4.76	98.75
Tunicates	2.89	1.97	0.96	1.05	1.25	100.00

Bray–Curtis similarity index used for the resemblance matrix construction.

although with variable occurrences, between the two substrates. Twenty-one species/OTUs were occasional or rare, being recorded in less than 10% of the samples. The most represented taxonomic group was the sponges (with 17 OTUs) (Table 1).

Only considering the species/OTUs recorded in all of the sites of at least one lithology, it is possible to evidence a group of ubi-quitarians, OTUs recorded with a high occurrence on both sub-strata and comprising the encrusting bryozoans, serpulids and encrusting sponges together with the benthic foraminifera *Miniacina miniacea*. Also, the sponge *Haliclona mucosa*, although present with lower occurrences, did not show any particular

preference for a substratum. In contrast, the boring sponges of the genus *Cliona* showed, as expected, a complete preference for the limestone, while the brachiopod *Novocrania anomala*, the sponges *Terpios fugax*, *Phorbas tenacior*, *Petrosia ficiformis* and the branched bryozoan *Myriapora truncata* were virtually recorded only on granites (Figure 3). Among species recorded with lower frequency, the bryozoan *Reptadeonella violacea* was similarly recorded on both substrates while the behaviour of the two identified scleractinians was particularly interesting: *Balanophyllia italica* was recorded only on limestone and *Caryophyllia inornata* only on granite. Ascidians showed similar
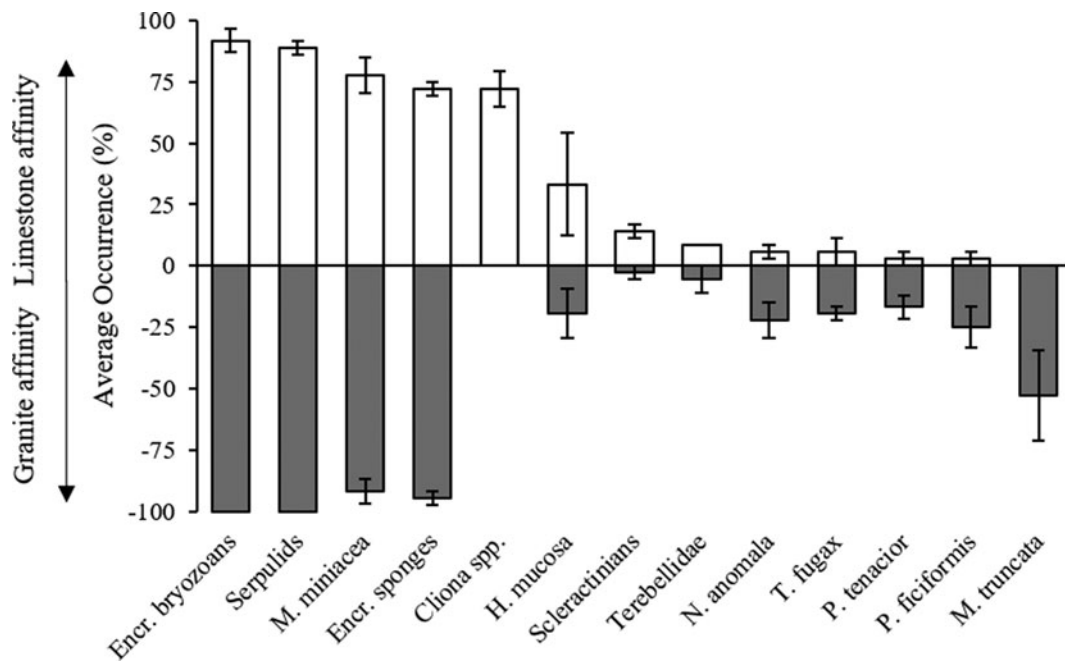
Fig. 3. Lithological affinity of species/OTUs ± SE present in all the sites of at least one substrate. White bars, limestone; grey bars, granite.

trends, with *Halocyntia papillosa* and *Polycitor adriaticus* exclusive to limestone and *Phallusia fumigata* present only on granite (Table 1).

Only considering the species/OTUs recorded in all the sites of at least one lithology, nMDS and PERMANOVA showed significant differences for both the factors ('Substrate' and 'Site'), with a marked effect of 'Substrate' in clustering sites (Figure 4A, Table 2). According to the SIMPER analysis, the percentage occurrence of the boring sponge *Cliona* spp., of the bryozoan *M. truncata* and the sponge *H. mucosa* contributed 20.25%, 14.42% and 11.13% respectively to the dissimilarity between the two substrates. At the same time, the contribution of the other OTUs was lower (Table 3).

Also, the comparison of the cover per cent on the two different substrata confirmed this trend. On limestone, a large portion of the substrate was bare (on average 70%), while granite was always completely bio-covered (Figures 2 & 5; Table 1).

Considering the per cent coverage of the main taxonomic groups, the nMDS (Figure 4B) and PERMANOVA (Table 2) highlighted two well-defined clusters, according to 'Substrate' factor, but not for 'Site'.

SIMPER analysis reported the contribution of sponges (27.51%) and bryozoans (20.19%) to describe the dissimilarity between the two assemblages and marked the critical contribution of bare substrate (46.29%) (Table 3).

Discussion

In several hard-bottom communities of the photic zone, the presence of secondary substrates of biological origin frequently prevents the direct contact of larvae with the rock. In particular, the development of the epilithic corallines is often so broad that it produces a virtually continuous secondary substrate on which other organisms grow (Johansen, 2018). Consequently, the presence of crustose red algae can mask the influence of the primary substrate on zoobenthos settling. Several invertebrate larvae, in fact, recruit in response to chemical traits of specific crustose coralline algae (Hadfield & Paul, 2001). In this situation, some conclusions previously obtained about the influence of rock composition on the development of benthic communities could

be biased by the interference due to the coralline coverage. It was, in fact, generally stated that, when comparing benthic communities settled on limestone and granite, the latter is less abundant in species diversity and the bio-coverage is lower (Bavestrello *et al.*, 2000; Canessa *et al.*, 2020). The present study was planned to evaluate, in the field, the direct effect of limestone and granite on the settling and development of zoobenthic species, without the influence of the epilithic crustose corallines. The dark sides of large boulders turned out to be particularly fit for this purpose, providing light conditions comparable to those found in caves, as the presence of the sponge *Petrobiona massiliana*, considered exclusive to the biocenosis of dark caves, confirms (Harmelin *et al.*, 1985; Manconi *et al.*, 2009).

The results obtained were mostly unexpected. In fact, we have shown that the dark sides, coralline-free, of limestone boulders, were widely bare, while the cover per cent was almost total on granite. The only exclusive species with a high occurrence recorded on limestones were clionids, able to bore carbonates due to acid secretions of their etching cells (Ruetzler, 1975). In contrast, several species, mainly sponges and bryozoans, were almost exclusive to granite. A pool of other species or morphological OTUs indifferently occupied both substrates, although with different occurrences.

The leading cause that might explain these findings could be the different level of chemical stability of the two types of rocks, due to their different composition and textural characteristics. In the sea, carbonates precipitate in the light zone and dissolve in dark ones where the CO_2 increases, favouring a progressive bacterial-induced carbonate dissolution (Golubić & Schneider, 1979). Moreover, directed carbonate removal is carried out by specialized macroborers as bivalves (mainly *Lithophaga lithophaga*) and clionid sponges which produce a further, more in-depth erosion with a consequent increase of substrate instability (Schneider & Torunski, 1983). In contrast, granites are much more stable, as indicated by Coombes (2011). A high level of substrate superficial instability has already been demonstrated to strongly affect larval settling and assemblage development. Some friable rocks, such as chalk and sandstones, appeared much more unsuitable compared with harder granites for settling of the barnacle *Chthamalus montagui* in the English Channel,
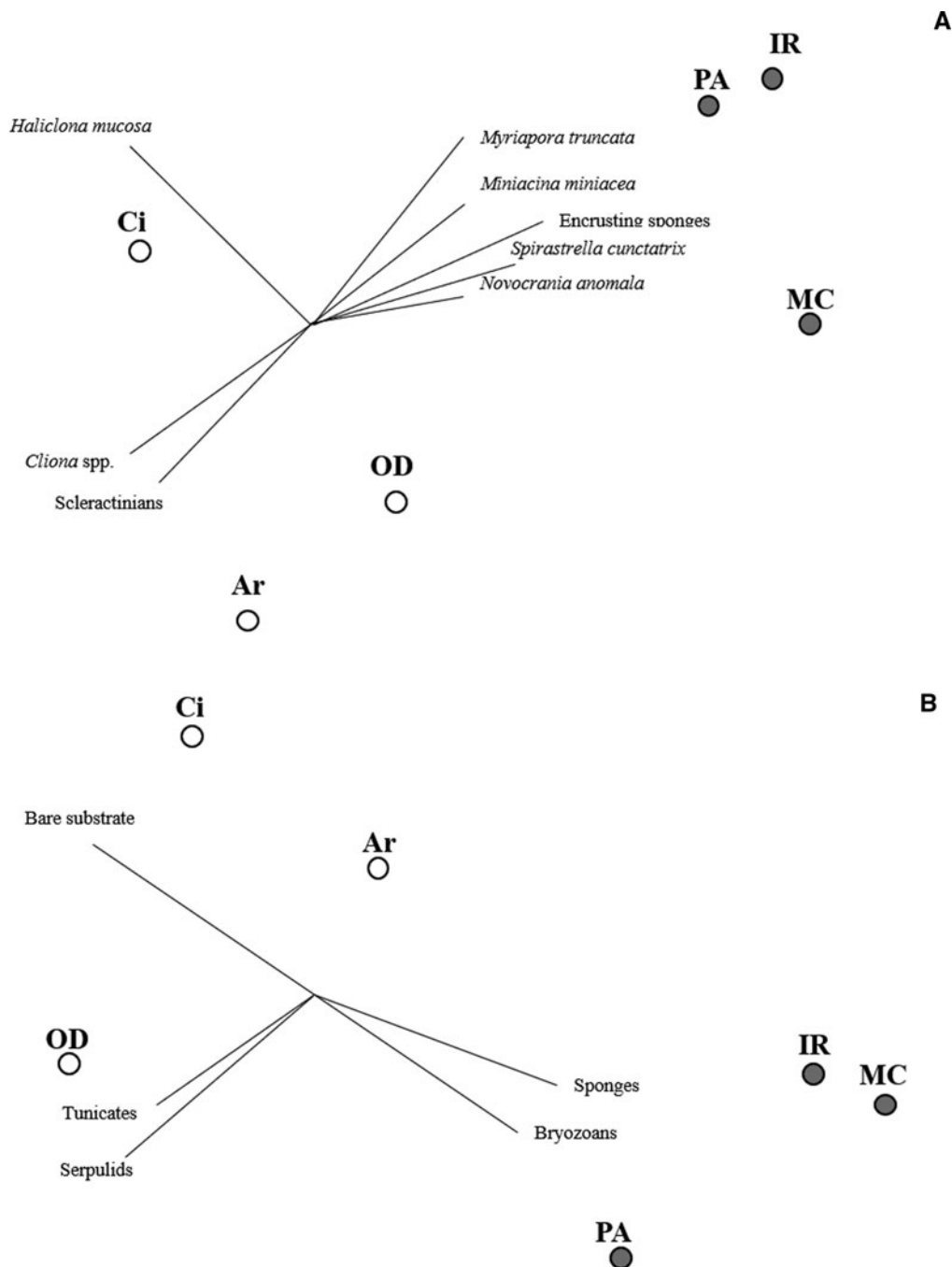
Fig. 4. Non-metric multi-dimensional scaling (nMDS) performed considering the occurrence of species/OTUs present in all the sites of at leat one substrate (A) and per cent coverage (B) of main taxonomic groups and bare substrate. White dots: limestone; grey dots: granite.

where the survival rate of its cyprids was relatively low even in the presence of high recruitment (Herbert & Hawkins, 2006).

Substrate roughness has always been claimed as one of the main features of the rock to determine the success of larval settlement (Barnes, 1970; Raimondi, 1988; Holmes *et al.*, 1997; Berntsson *et al.*, 2000; Coombes, 2011). Our data do not support this statement. In our opinion, it is possible to hypothesize that when two substrata have comparable chemical stability, the roughness can enhance the settlement and the development of epilithic communities, but when a substrate is subject to a continuous superficial dissolution this characteristic overcomes any other surface feature. Although it is evident that some species were positively attracted by one or the other substrate, in general, the lithology did not affect the richness of the communities. Our data support, in contrast, a

profound influence of the lithology on the cover capacity of modular organisms: on limestone, a pool of 29 species produced coverage of about 30% of the available substrate. In contrast, 26 species/OTUs resulted in virtually complete coverage on granites.

In our study, the first conclusion is that the lithology and in particular the substrate stability is one of the primary drivers of colonization, also taking into account that the rock roughness is directly proportional not only to the type of lithology but also to its greater or lesser resistance to erosive processes. A second conclusion picks up on the pivotal role of epilithic corallines in the colonization of rocky substrates. Canessa *et al.* (2020) have demonstrated a strong preference of these macroalgae for calcareous substrates, and it is possible to hypothesize that their settling affects the following phases of colonization producing a
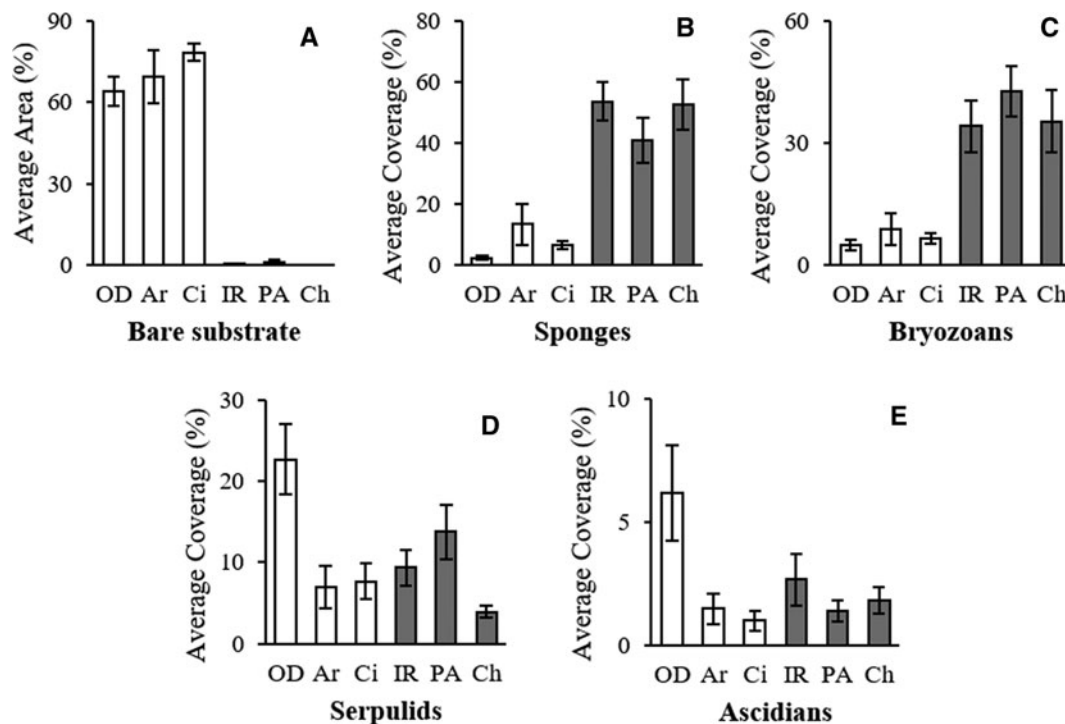
Fig. 5. Average per cent area of bare substrate ± SE (A) and average per cent coverage ± SE (B–E) of the main taxonomic groups in each site.

stabilization of the limestone, preserving it from surface dissolution. This scenario could explain the differences observed in the richness of coralligenous communities dwelling on granites and limestones within the Tavolara MPA.

Martin & Gattuso (2009) have demonstrated changes in the balance between algal carbonate production and dissolution induced by elevated pCO_2 and temperature in coralligenous communities. In light of these considerations and of our results, marine acidification, causing a loss of coralline layer, could also have an impact on the structure of zoobenthic assemblages living on limestone and, consequently, a significant adverse effect on the biodiversity of whole Mediterranean coastal ecosystems.

References

Aguilera MA, Broitman BR and Thiel M (2014) Spatial variability in community composition on a granite breakwater *vs* natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. *Marine Pollution Bulletin* **87**, 257–268.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Australian Ecology* **26**, 32–46.

Angiolillo M, Gori A, Canese S, Bo M, Priori C, Bavestrello G, Salvati E, Fabrizio E, Greenacre M and Santangelo G (2016) Distribution and population structure of deep-dwelling red coral in the Northwest Mediterranean. *Marine Ecology* **37**, 294–310.

Barnes H (1970) A review of some factors affecting settlement and adhesion in the cyprids of some common barnacle. In Manly RS (ed.), *Adhesion in Biological Systems*. New York, NY: Academic Press, pp. 89–111.

Bavestrello G, Bianchi CN, Calcinai B, Cattaneo-Vietti R, Cerrano C, Morri C and Sarà M (2000) Bio-mineralogy as a structuring factor for rocky bottom communities. *Marine Ecology Progress Series* **193**, 241–249.

Bavestrello G, Benatti U, Cattaneo-Vietti R, Cerrano C and Giovine M (2003) Sponge cell reactivity to various forms of silica. *Microscopy Research and Technique* **62**, 327–335.

Bavestrello G, Bo M, Betti F, Canessa M, Gaggero L, Rindi F and Cattaneo-Vietti R (2018) Differences in composition of shallow-water marine benthic communities associated with two ophiolitic rock substrata. *Estuarine, Coastal and Shelf Science* **200**, 71–80.

Bellan-Santini D (1962) Etude de peuplement des 'dessous de blocs non ensablés' de la partie superieure de l'etage infralittoral. *Recueil des Travaux de la Station Marine d'Endoume* **27**, 185–196.

Berntsson KM, Jonsson PR, Lejhall M and Gatenholm P (2000) Analysis of behavioural rejection of microtextured surfaces and implications for recruitment by barnacle *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology* **251**, 59–83.

Bressan G (1974) Rodoficee calcaree dei mari italiani. *Bollettino Società Adriatica Scienze Naturali* **59**, 1–132.

Canessa M, Bavestrello G, Bo M, Betti F, Gaggero L and Cattaneo-Vietti R (2019) The influence of the rock mineralogy on population density of *Chthamalus* (Crustacea: Cirripedia) in the Ligurian Sea (NW Mediterranean Sea). *European Zoological Journal* **86**, 389–401.

Canessa M, Bavestrello G, Bo M, Trainito E, Panzalis P, Navone A, Caragnano A, Betti F and Cattaneo-Vietti R (2020) Differences in coralligenous assemblages on limestone and granite in the Tavolara-Punta Coda Cavallo MPA (NE Sardinia. Mediterranean Sea). *Regional Studies in Marine Science* **35**, 101159.

Cattaneo-Vietti R, Albertelli G, Bavestrello G, Bianchi CN, Cerrano C, Chiantore M, Gaggero L, Morri C and Schiaparelli S (2002) Can rock composition affect sublittoral epibenthic communities? *Marine Ecology* **23**, 65–77.

Cerrano C, Arillo A, Bavestrello G, Benatti U, Calcinai B, Cattaneo-Vietti R, Puce S and Sarà M (1999) Organism-quartz interactions in structuring benthic communities: towards a marine bio-mineralogy? *Ecology Letters* **2**, 1–3.

Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.

Coombes MA (2011) *Biogeomorphology of Coastal Structures: Understanding Interactions Between Hard Substrata and Colonising Organisms as a Tool for Ecological Enhancement* (PhD thesis). University of Exeter, pp. 1–591.

Faimali M, Garaventa F, Terlizzi A, Chiantore M and Cattaneo-Vietti R (2004) The interplay of substrate nature and biofilm formation in regulating *Balanus amphitrite* Darwin, 1854 larval settlement. *Journal of Experimental Marine Biology and Ecology* **306**, 37–50.

Golubić S and Schneider J (1979) Carbonate dissolution. In Trudinger PA and Swaine DJ (eds), *Studies in Environmental Science*, Vol. **3**.

Biogeochemical Cycling of Mineral-Forming Elements New York, NY: Elsevier, pp. 107–129.

Guidetti P, Bianchi CN, Chiantore M, Schiaparelli S, Morri C and Cattaneo-Vietti R (2004) Living on the rocks: substrate mineralogy and the structure of subtidal rocky substrate communities in the Mediterranean Sea. *Marine Ecology Progress Series* **274**, 57–68.

Hadfield MG and Paul VJ (2001) Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. *Marine Chemical Ecology* **13**, 431–461.

Harmelin JG, Vacelet J and Vasseur P (1985) Les grottes sous-marines obscures: un milieu extrême et un remarquable biotope refuge. *Tethys* **11**, 214–229.

Herbert RJH and Hawkins SJ (2006) Effect of rock type on the recruitment and early mortality of the barnacle *Chthamalus montagui*. *Journal of Experimental Marine Biology and Ecology* **334**, 96–108.

Holmes SP, Sturgess CJ and Davies MS (1997) The effect of rock-type on the settlement of *Balanus balanoides* (L.) cyprids. *Biofouling* **11**, 137–147.

Johansen HW (2018) *Coralline Algae: A First Synthesis*. Boca Raton, FL: CRC Press.

Manconi R, Ledda FD, Serusi A, Corso G and Stocchino GA (2009) Sponges of marine caves: notes on the status of the Mediterranean palaeoendemic *Petrobiona massiliana* (Porifera: Calcarea: Lithonida) with new records from Sardinia. *Italian Journal of Zoology* **76**, 306–315.

Martin S and Gattuso JP (2009) Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biology* **15**, 2089–2100.

McGuinness KA (1989) Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama. *Marine Ecology Progress Series* **52**, 201–208.

Orrù P and Pasquini C (1992) Rilevamento geomorfologico e sottomarino della riserva marina di Tavolara e di Capo Coda Cavallo (Sardegna nord-orientale). *Giornale di Geologia* **54**, 49–63.

Pezzolesi L, Peña V, Le Gall L, Gabrielson PW, Kaleb S, Hughey JR, Rodondi G, Hernandez-Kantun JJ, Falace A, Basso D, Cerrano C and Rindi F (2019) Mediterranean *Lithophyllum stictiforme* (Corallinales, Rhodophyta) is a genetically diverse species complex: implications for species circumscription, biogeography and conservation of coralligenous habitats. *Journal of Phycology* **55**, 473–492.

Raimondi PT (1988) Rock-type effects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *Journal of Experimental Marine Biology and Ecology* **123**, 253–267.

Ruetzler K (1975) The role of burrowing sponges in bioerosion. *Oecologia* **19**, 203–216.

Schiaparelli S, Guidetti P and Cattaneo-Vietti R (2003) Can mineralogical features affect the distribution of sessile gastropods? The Vermetidae case in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **83**, 1267–1268.

Schneider J and Torunski H (1983) Biokarst on limestone coasts, morphogenesis and sediment production. *Marine Ecology* **4**, 45–63.

Steneck RS (1986) The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics* **17**, 273–303.