Marine rocky reef assemblages and lithological properties of substrates are connected at different ecological levels

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Abstract
Recent studies suggest that the lithological properties of hard substrates play an important role in influencing the diversity and structure of marine assemblages involving macroalgae, sessile organisms and vagile animals like heterobranchs gastropods and fishes. The present study aims at exploring whether the influence of different substrates (limestone vs granite) could drive the occurrence of different vagile groups (crustacean decapods, echinoderms and fishes). The study was carried out at the “Tavolara-Punta Coda Cavallo” Marine Protected Area (NE Sardinia, Mediterranean Sea) where substrates of different lithology, namely granites and limestones, occur on a local spatial scale. The diversity and the abundance of 16 vagile species (four crustaceans, seven echinoderms and five fishes) were investigated by the analysis of photographs (2352 images) collected in 20 sites (10 limestones and 10 granites), between 30 and 50 m depth. Statistical analyses showed a clear-cut separation between the assemblages assessed on the two lithological substrate types, with assemblages on granites that were tightly grouped and those on limestones more dispersed. The total species richness did not significantly vary between limestones and granites. Galathea strigosa and Marthasterias glacialis were exclusively recorded on granites, while Palmaria palmata, Scyliorhinus canicula, Arbacia lixula, Ophiaster ophiidiatus and Serranus scriba were exclusively found on limestones. The observed patterns could be partially explained by multiple factors related to lithology: i) the different availability of preferred food sources, potentially influenced by substrate type; ii) the site geomorphology, that could provide different dens and refuges (in terms of quantity and types of shelters) suitable for different species; iii) the colour of different substrates enhancing the mimicry of different species according to their livery and camouflage ability. Our and literature data suggest that the substrate type in rocky reefs could interact with other environmental factors (i.e., light intensity related to depth) in shaping the structure of rocky-reef assemblages.

Keywords: Lithology, rocky-reef assemblages, limestone, granite, Mediterranean Sea

Introduction
Structure and diversity of hard-bottom benthic assemblages are known to be shaped by a wide variety of bio-ecological processes (e.g., prey/predator relationships, competition/cooperation) (Dayton 1971; Jones et al. 1994) as well as chemical-physical factors (e.g., depth, water column variables, light intensity, rugosity, pH) that may act at different spatial and temporal scales (Gaston 2000).

Among the abiotic factors, the substrate features can play a primary role in affecting early colonization stages and development of the algal canopy and sessile zoobenthos, which in turn determine a wide variety of seascapes (McCoy et al. 1991; Cerrano et
al. 1999; Bavestrello et al. 2000; Diez et al. 2003). Although it is not easy to disentangle the relative and/or interacting effects of geomorphology, surface texture at macro and microscale, and chemical composition of the rocks (Coombes et al. 2013, 2015), it is nowadays clear that the rocky substrate type is one of the main drivers in determining the diversity and the structure of associated assemblages. Besides the evidence reported for ophiolithic rocks (Bavestrello et al. 2018), most of the available data concern the differences between assemblages associated with limestones and granites (Guidetti et al. 2002, 2004; Schiaparelli et al. 2003; Canessa et al. 2020a, 2020b, 2021a, 2021b). Thanks to the presence of the limestones of the Tavolara Island and the granites of the surrounding Molara Island and Molarotto islet, the Tavolara-Punta Coda Cavallo Marine Protected Area (TPCCMPA) (North-eastern Sardinia, western Mediterranean Sea) is the ideal setting to investigate the effect of lithology on the composition and structure of associated assemblages. Literature data show that, in this area, the most impressive difference between the two substrate types (namely, limestone and granite) is due to the encrusting coralline algae. On limestone these algae build a consistent coralligenous basal bioherm that have a key role in the stabilization of the surface and in the increasing of 3D complexity. On the contrary, on granites, algal bioherms are only occasionally present (Canessa et al. 2020a).

Focusing on epibenthic species, the large, massive and erected sponges such as Sarcotragus foetidus Schmidt, 1862, Axinella polyoides (Schmidt, 1862) and Axinella spp. characterize the granitic seascape. The gorgonian Eunicella cavolini (Koch, 1887) is far more common on limestone than on granite, while Paramuricea clavata (Linnaeus, 1758) is the most common on granite rocks (Canessa et al. 2020a, 2021a).

Finally, some attempts were done to test if differences in the assemblages settled on the two substrate types scaled also up to higher trophic levels in the food web. Distribution patterns of fish assemblages at shallow rocky reefs (around 5 m depth) are reported to significantly differ according to the substrate type. Labrids of the genus Symphodus and the serranid Serranus scriba (Linnaeus, 1758) tend to be more abundant on granite, while Serranus cabrilla (Linnaeus, 1758), the blennid Parablennius rouxi (Cocco, 1833), the gobid Gobius incognitus Kovačić & Šanda, 2016 and the labrid Thalassoma pavo (Linnaeus, 1758) showed greater densities on limestone. Also, the distribution of echinoids was investigated, without recording significant differences between the two substrates (Guidetti et al. 2002, 2004).

A recent study examined the diversity and the abundance of stenophagous predators like heterobranch gastropods associated with granite and limestone, suggesting that their distribution patterns reflect the variety and availability of the preferred food items, in their turn affected by the substrate features (Canessa et al. 2021b).

The present study is aimed at exploring, through an observational-correlative approach (sensu Underwood 1997), if the lithology of the substrate can drive the diversity and abundance of different groups of vagile organisms thriving in circalittoral rocky reefs, exploiting a wide variety of food items and shelter features. In particular, we have investigated more in depth the distribution patterns of filter feeders like ophiuroids and cirriods, grazers like sea urchins, active predators of benthic organisms like starfishes and crustaceans and vagile predators such as fishes.

**Materials and methods**

**Sampling procedure**

Twenty sites were chosen based on their comparable depths within the TPCCMPA. Ten sites were characterised by limestone cliffs and outcrops, located along all the eastern coast of Tavolara Island (Occhio di Dio (OdD), Tegghja Liscia (TL), Cala Cicale (CC), Grottone (Gr), Papa Shoal 1 (P1), Papa Shoal 2 (P2); Archetto (Ar), Picchi della Mandria (PdM)) Papa Point (PP), Punta Timone (PT). The other ten sites were granitic outcrops located in the middle of the Tavolara Channel (NEW 01 (N1), Mandria Shoal (N26), NEW 27 (N27), NEW 34 (N34), Angelo Shoal (N35), Lu lu Shoal (N36), NEW 38 (N38), NEW41 (N41), NEW 118 (N118), Pinnacolo (N151) (Table I; Figure 1).

We examined photographs making part of the personal collection of one of us (ET) taken at these sites by SCUBA diving between 2016 and 2019 in the 30–50 m depth range. A total of 2352 images (942 and 1410 from limestones and granites, respectively) were selected and the vagile species in each image were classified and counted. Photographs were obtained by a Sony A6000 camera, 24 megapixels, 2 Inon S2000 flashes, color temperature 5000° K; Sony 16–50 lens; Sea & Sea MDX-a6000 underwater case with flat porthole with Wide Wet Lens Nauticam WWL1. The images correspond to wide-angle close-ups taken to make it possible for the identification of the organisms at the species level. Photographs were analysed by Photoshop CS6 at maximum screen resolution using the short-cut cmd 1. Each original image,
Figure 1. A, Location of the Tavolara–P. ta Coda Cavallo Marine Protected Area (MPA). B, the position of the investigated limestone (white spots) and granite (grey spots) sites. White spots: limestone sites (Archetto (Ar); Cala Cicale (CC); Occhio di Dio (OdD); Papa Shoal 1 (P1); Papa Shoal 2 (P2); Papa Point (PP); Punta Timone (PT); Grottone (Gr); Picchi della Mandria (PdM); Tegghja Liscia (TL)). Grey spots: granite sites (NEW 01 (N1), Mandria Shoal (N26), NEW 27 (N27), NEW 34 (N34), Angelo Shoal (N35), Lulù Shoal (N36), NEW 38 (N38), NEW41 (N41), NEW 118 (N118), Pinnacolo (N151)). The colored polygons are the boundaries of the zones with different levels of protection. Red, fully protected (no entry-no take) zones; yellow and green (partially protected) buffer zones. WGS84 reference coordinate systems.

Table I. Position and depth range of the investigated sites within the Tavolara–P. ta Coda Cavallo Marine Protected Area, with the relative number dives, photos and species found and average specific richness found on the two substrates. The geographical coordinates can be consulted on the AMP GIS platform.

| Substrate | ID  | Site            | Depth range (m) | N Dives | N Photos | N Species | Avg N species ± SE |
|-----------|-----|-----------------|-----------------|---------|----------|-----------|---------------------|
| Limestone | Ar  | Archetto        | 30–40           | 6       | 19       | 5         | 5.9 ± 1.1           |
|           | CC  | Cala Cicale     | 30–37           | 18      | 122      | 10        |                     |
|           | OdD | Occhio di Dio   | 30–37           | 22      | 116      | 11        |                     |
|           | P1  | Papa Shoal 1    | 30–45           | 20      | 208      | 5         |                     |
|           | P2  | Papa Shoal 2    | 30–45           | 18      | 64       | 6         |                     |
|           | PP  | Papa Point      | 40–45           | 1       | 74       | 1         |                     |
|           | PT  | Punta Timone    | 35–40           | 1       | 20       | 0         |                     |
|           | Gr  | Grottone        | 30–37           | 6       | 81       | 7         |                     |
|           | PdM | Picchi della Mandria | 30–39 | 4 | 83 | 6 |                     |
|           | TL  | Tegghja Liscia  | 30–37           | 14      | 155      | 8         |                     |
| Granite   | N1  | NEW 01          | 37–44           | 4       | 174      | 6         | 5.7 ± 0.5           |
|           | N26 | Mandria Shoal   | 36–45           | 15      | 141      | 6         |                     |
|           | N27 | NEW 27          | 39–47           | 13      | 173      | 8         |                     |
|           | N34 | NEW 34          | 38–45           | 1       | 70       | 3         |                     |
|           | N35 | Angelo Shoal    | 36–42           | 11      | 132      | 7         |                     |
|           | N36 | Lulù Shoal      | 36–40           | 5       | 104      | 4         |                     |
|           | N38 | NEW 38          | 37–42           | 4       | 186      | 7         |                     |
|           | N41 | NEW 41          | 32–39           | 3       | 151      | 6         |                     |
|           | N118| NEW 118         | 47–52           | 2       | 87       | 5         |                     |
|           | N151| Pinnacolo       | 38–46           | 5       | 192      | 5         |                     |
measuring 50 × 34 cm at 300 dpi, was examined three times larger at 72. This methodology was illustrated in Canessa et al. (2021b). Abundance data were obtained for crustaceans, echinoderms and fishes. Concerning the latter group, the species taken into account in this study were chosen on the base either of their remarkable conservation relevance (e.g., the dusky grouper Epinephelus marginatus and the brown meagre Sciaena umbra) or for the previously available data collected at this study area (Guidetti & Cattaneo-Vietti 2002; Guidetti et al. 2004).

For the analysis, only the species present in at least three sites out of 20 were considered. Species abundance, expressed as the number of specimens normalized on the number of photos collected per site, was calculated (Table II). The feeding strategies and food items of the considered species were summarized from the available literature (Table III).

**Statistical analyses**

Putative differences in the abundance patterns of the whole vagile assemblages and single groups associated with limestones and granites were investigated by means of multivariate methods. Data were appropriately transformed (cubic root) to reduce the influence of dramatically abundant and gregarious taxa (e.g., Periclimenes scriptus) in the analyses.

The non-metric Multi-Dimensional Scaling (nMDS) plot was used to possibly visually represent clustering patterns between the assemblages associated with the two considered lithologies using the species abundance dataset. PERMutational ANalysis Of Variance (PERMANOVA) was performed to test for putative differences attributable to the factor “Substrate” (two levels, fixed) and “Site” (20 levels, random and nested in each level of “Substrate”) (Anderson 2005). The significant PERMANOVA result about the “Substrate” factor was further analysed with PERUtational analysis of Multivariate DISPersions (PERMDISP) to determine the difference in dispersion (variance) among a priori groups, considering the mean distance of samples from centroids as measure of the heterogeneity of assemblages (Euclidean Distance similarity Index measure, permutation = 9999) (Anderson 2006) (Table IV). Finally, the SIMPER (SIMilarity PERcentage) routine was conducted to assess species contribution to the dissimilarity between groups (here the two substrate types), both for the whole assemblages and single groups (Bray–Curtis similarity Index measure, permutation = 9999) (Clarke 1993) (Table V). All statistical analyses were performed using PRIMER-e 7 with PERMANOVA+ Add On package.

**Results**

On the whole, 16 species, four crustaceans, seven echinoderms and five fishes, occurred in at least three sites. Total species richness did not significantly vary between limestones and granites (14 vs 11 species, respectively), with two species exclusive of granites (Galathea strigosa and Marthasterias glaciatus) and five of limestones (Palinurus elephas, Scyllarides latus, Arbacia lixula, Ophidiaster ophidius, Serranus scriba). The species richness per site ranged from 0 to 11 (5.9 ± 1.1, mean ± SE) and from 3 to 8 (5.7 ± 0.5, mean ± SE) on limestone and granites, respectively (Tables I, 2).

The nMDS plots performed on the abundance data showed a clear-cut separation between the vagile assemblages associated with the two substrate types, with assemblages associated with granites that were tightly grouped, whereas those associated with limestone were more dispersed (Figure 2). PERMANOVA showed a significant effect of the factor “Substrate” (Table IV) besides a significant variability at the scale of “Site”. PERMDISP detected a significant difference in dispersion between the two substrates (P = 0.0127) (Table IV). Also, the SIMPER analysis highlighted a far lower average similarity among limestones than among granites (Table V).

Considering the whole assemblages of vagile species, granites were mainly characterised by Periclimenes scriptus (Risso, 1822), while Serranus cabrilla, Epinephelus marginatus (Lowe, 1834) and Sciaena umbra Linnaeus, 1758 were the most representative species on limestones (Table V; Figure 3).

Considering the single taxonomic groups, the two substrates hosted two fairly different assemblages, as showed by values of average dissimilarity between groups (Table V). Among crustaceans, P. scriptus and Galathea strigosa (Linnaeus, 1761) were found only in granites, while Palinurus elephas (Fabricius, 1787) and Scyllarides latus (Latreille, 1803) were recorded only on limestones (Table V, Figure 3A). This scenario revealed the dramatic difference in occurrence and abundance among species associated with the two substrates (99.53%).

This pattern was mirrored by echinoderms (89.85% average dissimilarity between granite and limestone): two species (Arbacia lixula (Linnaeus, 1758) and Ophidiaster ophidius (Lamarck, 1816)) were exclusively found on limestones, Marthasterias glacialis (Linnaeus, 1758) was recorded only on
granites, *Astrospartus mediterraneus* (Risso, 1826) was mostly associated to granite, while *Antedon mediterranea* (Lamarck, 1826), *Centrostephanus longispinus* (Philippi, 1845) and *Echinaster sepositus* (Retzius, 1783) were ubiquitous (Table V, Figure 3B).

Finally, the average dissimilarity between granite and limestone in occurrence and abundance of fishes was slightly lower if compared with other groups (77.33%): *Serranus scriba* occurred only in limestone sites while no species were exclusively found on granites. *E. marginatus* and *S. umbra* were strongly associated with limestone, while the other recorded fishes showed similar abundance on both substrates (Table V, Figure 3C).

**Discussion**

Recent studies conducted in the TPCCMPA provided evidence about the importance of the lithology of the hard substrates in structuring benthic assemblages through the selection of macroalgae and sessile zoobenthos under different environmental conditions (Canessa et al. 2020a, b, 2021a). Moreover, in this study area, it was strongly suggested that specialised vagile predators, like hetero-branches, are associated with different substrates, generally according to their benthic prey occurrence (Canessa et al. 2021b).

In the present study, it was explored whether the lithological nature of the substrate can drive diversity and abundance of other vagile groups, composed of species that exploit a wide variety of food items and shelter features.

At the assemblage level, our data revealed a different dispersion pattern but also a clear separation according to substrate lithology, due to the exclusive or preferential occurrence and different relative abundance of several species making part of the assemblages associated with granite or limestone.

The sea urchins *Arbacia lixula* is one of the most common echinoids on shallow subtidal rocky habitats in the Mediterranean and is considered a key species capable of modifying macroalgae assemblages (Benedetti-Cecchi et al. 1998; Sala et al. 1998; Bulleri et al. 1999; Boudouresque & Verlaque 2001; Guidetti 2006). In the Tavolara area, around 5 m depth, this species did not show significant differences related to rock lithology (Guidetti et al. 2004). On the contrary, at 30–50 m depth, this sea urchin was recorded only on limestones. This pattern is more than likely related to the paucity of macroalgae on granitic substrates at deeper stands, while on limestone coralline algae are abundant (Canessa et al. 2020a). Literature data about gut contents report that encrusting coralline algae are a primary food source for *A. lixula* (Chiantore et al. 2008; Privitera et al. 2008) (Table III). The other sea urchin recorded in this study, *Centrostephanus longispinus*, is characterised by a wide feeding plasticity (the diet includes benthic invertebrates such as bryozoans, tunicates and sponges; Table III), was equally distributed and abundant on both substrate types.

In this study, three species of starfishes were considered, and their distribution resulted almost in agreement with their known food preferences. Starfishes are generally classified as obligate herbivores, omnivores and carnivores, depending on the species (Coleman 2017). Field studies and stable isotope analyses indicated that crustose coralline algae and * Peyssonnelia* spp. are an essential part of the diet of *Ophidiaster ophidianus* (Trapani et al. 2017), while the keratose sponge *Ircinia variabilis* resulted in its second most frequent food item (Di Trapani et al. 2020) (Table III). The record of this starfish almost exclusively on limestones is, therefore, in agreement with the distribution of its preferred food items. The opportunistic *Echinaster sepositus*, exploiting a wide variety of food sources (mainly coralline algae and sponges), was equally recorded on both substrates (Vasserot 1961; Sarà & Vacelet 1973; Garcia-Raso et al. 1992; Villamor and Becerro (2010). The large predator and scavenger *Marthasterias glacialis* was recorded only in granite sites. The observed affinity of this species for granitic substrates is hardly explained just based on its feeding strategies (Verling et al. 2003) (Table III). In any case, due to the low number of recorded specimens, the observed distribution could include some stochastic components.

The two filter feeder species *Astrospartus mediterraneus* and *Antedon mediterranea* displayed different distribution patterns in relation to the substrate type. *A. mediterraneus* was virtually exclusively recorded on granite sites, while *A. mediterranea* was equally abundant on limestones and granites (Table II). Even though the SIMPER analysis indicates that *A. mediterranea* is more associated with limestones, this output is biased by its extremely high abundance at the P2 site (Table V). *A. mediterraneus* is a typical acrophylic species associated with erected organisms, such as gorgonians and erected sponges that, in the abovementioned site, were mainly found on granitic substrates (Canessa et al. 2020a, 2021a).

The most impressive differences in distribution patterns according to substrates concern the four species of studied decapod crustaceans. The shrimp *Periclimenes scriptus* was typically found in large groups associated with the purple gorgonian *Paramuricea clavata* (Ledoyer 1968; Manconi &
Table II. List of species found in the photographic samples, specimen abundance per site normalised on the number of available photos, average abundance ± SE on granites (GA) limestones (LA) and on the whole dataset (TA).

| Species                        | N1 | N26 | N27 | N35 | N35 | N36 | N38 | N41 | N118 | N151 | Ar | CC | OdD | Gr | PdM | PP | PT | P1 | P2 | TL | GA ± SE | LA ± SE | TA ± SE |
|--------------------------------|----|-----|-----|-----|-----|-----|-----|-----|-----|------|----|----|-----|----|-----|----|----|----|----|----|-----|------|-------|--------|
| Galathea stenografa            | 0.6| 2.1 | 1.7 | 1.4 | 2.3 | 1.1 | 1.1 |    |     |      |    |    |     |    |     |    |    |    |    |    |    | 1.0 ± 0.3 |      | 0.5 ± 0.2 |
| Palinurus elephas              |    |     |     |     |    |     |     | 5.7 | 6.0 |      |    |    |     |    |     |    |    |    |    |    | 1.3 | 1.3 ± 0.8 | 0.7 ± 0.4 |
| Periclimenes scriptus          | 21.8| 11.3| 37.0| 35.7| 15.9| 26.0| 0.5 | 20.7| 36.5|      |    |    |     |    |     |    |    |    |    |    | 20.5 ± 4.4 | 0.1 ± 0.1 | 10.3 ± 3.2 |
| Scyllarides latus              |    |     |     |     |    |     |     | 0.8 | 6.0 |      |    |    |     |    |     |    |    |    |    |    | 0.6 | 0.7 ± 0.6 | 0.4 ± 0.3 |
| Echinoderms                    |    |     |     |     |    |     |     |    |     |     |    |    |     |    |     |    |    |    |    |    |    |    |    |    |
| Antedon mediterranea           |    |     |     |     |    |     |     | 2.3 | 1.2 | 2.3  | 1.1 | 0.7 | 1.0 | 1.6 | 2.4 | 3.1 | 7.1 | 0.3 | 0.7 | 0.3 | 0.7 ± 0.3 | 0.7 ± 0.4 | 0.7 ± 0.2 |
| Arbacia lxxula                 |    |     |     |     |    |     |     |    |     |     |    |    |     |    |     |    |    |    |    |    |    |    |    |    |
| Asteroaster mediterraneus      |    |     |     |     |    |     |     | 2.6 | 0.8 | 0.9  | 1.2 | 1.2 | 1.2 | 1.2 | 1.2 | 1.2 | 9.7 | 0.7 | 0.1 | 0.1 | 0.5 ± 0.3 | 0.5 ± 0.3 | 0.5 ± 0.3 |
| Centrostephanus longispinus    | 2.3| 1.2 | 2.3 | 1.1 | 0.7 | 1.0 | 1.6 | 2.4 | 3.1 | 7.1  | 0.3 | 0.7 |     |    |    |    |    |    |    |    |    |    |    |
| Echinaster sepositus           |    |     |     |     |    |     |     |    |     |     |    |    |     |    |     |    |    |    |    |    |    |    |    |    |
| Marthasterias glacialis        |    | 0.7 | 1.2 | 0.5 | 0.7 | 0.5 | 0.5 |     |     |     |    |    |     |    |    |    |    |    |    |    | 0.4 ± 0.1 | 0.2 ± 0.1 | 0.2 ± 0.1 |
| Ophiidiaster ophidiamus        |    |     |     |     |    |     |     | 0.8 | 1.9 | 2.2  | 0.7 | 1.1 |     |    |    |    |    |    |    |    | 2.4 | 32.8 | 0.4 ± 0.2 | 0.2 ± 0.1 |
| Fishes                         |    |     |     |     |    |     |     |    |     |     |    |    |     |    |     |    |    |    |    |    |    |    |    |    |
| Epinephelus marginatus         | 0.6| 0.7 | 0.8 | 0.8 | 0.8 | 0.5 | 0.5 | 10.7| 8.6 | 4.9  |    |    |     |    |     |    |    |    |    |    | 36.1| 70.3 | 13.5 | 0.2 ± 0.1 | 14.5 ± 7.1 | 7.3 ± 3.8 |
| Serranus cabrilla              | 10.3| 12.1| 4.6 | 6.1 | 5.8 | 2.7 | 7.9 | 1.1 | 3.1 | 0.5  | 4.9 | 6.9 | 6.2 | 3.6 | 1.4 | 7.2 | 1.6 | 5.8 | 5.4 | 1.2 | 3.8 ± 0.9 | 4.6 ± 0.8 |
| Serranus scriba                |    |     |     |     |    |     |     | 2.1 | 0.8 | 2.6  | 1.2 |    |     |    |    |    |    |    |    |    |    | 5.8 | 1.3 ± 0.6 | 0.6 ± 0.3 |
| Parabramius rouxi              | 9.2| 5.7 | 20.2| 6.8 | 1.0 | 2.2 | 4.6 |    | 2.1 | 3.3  | 2.6 | 2.5 | 1.2 |    |    |    |    | 1.9 | 4.7 | 3.2 | 5.2 ± 0.5 | 1.9 ± 0.5 | 3.6 ± 1.0 |
| Sciaena umbra                  |    | 0.6 |     |     |    |     |     | 0.6 |     |     |    |    |     |    |    |    |    |    |    |    | 17.2| 19.0 |    | 9.1 ± 0.1 | 17.4 ± 10.0 | 8.7 ± 5.3 |
Table III. Feeding strategies and food items according to literature of each investigated species.

| Cladistics | Feeding strategy/Food items | References |
|------------|----------------------------|------------|
| Crustaceans | G. strigosa | detrital deposit feeding and scavenging | De Grave & Turner 1997 |
| | P. elephas | bivalves, sea urchins, small crustaceans, coralline algae | Goñi & Latrouite 2005; Goñi et al. 2001 |
| | P. scriptus | mucus of the octocoral host | Manconi & Mori 1992 |
| | S. latus | limpets, squids, mussels, Haliotis spp. | Rost Martins 1985; Romeo et al. 2004 |
| Echinodermes | A. mediterranea | passive suspension feeder | Leonard 1989 |
| | A. lissula | grazer of encrusting corallines | Chiantore et al. 2008; Privitera et al. 2008; Zibrowius 1978 |
| | C. longispinus | suspension feeders on gorgonians and sponges | Andrew & Byrne 2007 |
| | E. sepositus | algae, seagrass, tunicates, encrusting bryozoans, encrusting sponges | Vasserot 1961; Garcia-Raso et al. 1992; Villamor & Becerro 2010 |
| | M. glacialis | juveniles: algae, epifaunal turfs, small gastropods; adults: bivalves, carrions | Frid 1992; Penney & Griffiths 1984 |
| | O. ophidianus | crustose coralline algae, Irinina variabilis | Trapani et al. 2017; Di Trapani et al. 2020 |
| | E. marginatus | crustaceans (amphipods, isopods, shrimps, crabs), cephalopods, fishes | www.fishbase.org |
| | P. rouxi | algae, barnacles, other crustaceans, sponges | |
| | S. cabrilla | crustaceans (decapods, mysidaceans), teleost | |
| | S. scriba | crustaceans, mollusks, fishes | |
| | S. umbra | algae, seagrasses, nematodes, mollusks, annelids, bryozoans, crustaceans, echinoderms, fishes | |

Mori 1992) (Table III) that was mainly recorded in association with granite substrates. Remarkably, the shrimp was never found on the gorgonians settled on limestone. A possible explanation for this pattern may be the higher number of colonies of P. clavata affected by local diseases at limestone sites P1 and P2 (Huete-Stauffer et al. 2011). P. scriptus essentially feeds on the mucus of octocorals (Manconi & Mori 1992), whose production is strongly reduced by the stress due to periodical diseases (Mistri & Ceccherelli 1994).

The biology and ecology of the genus Galathea are poorly studied but it is generally accepted that species belonging to this genus obtain food by detrital deposit feeding and scavenging (De Grave & Turner 1997) (Table III). These feeding strategies, however, are hardly attributable to the observed affinity of G. strigosa for granitic substrates. Nevertheless, the quality of the sediment in limestone and granite sites is different: the wide presence of corallinales on limestone drives the structure of the detritus that is mostly coarse, while the sediments that surround

Table IV. PERMANOVA and PERMDISP analysis performed on the species abundance matrix, showing the significative effect of the factor “Substrate” (Fixed, two levels) and “Site” (twenty levels, random) reported in bold. Data cubic-root transformed. Bray-Curtis index and Euclidean Distance Index used for resemblance matrix calculation, respectively, for PERMANOVA and PERMDISP; permutation N: 9999.

| Source | Df | SSS | MS | Pseudo-F | P(perm) | Unique perms |
|--------|----|-----|----|----------|---------|-------------|
| Substrate | 1  | 48,238 | 48,238 | 7.4045 | 0.0002 | 9914 |
| Site (Substrate) | 18 | 2.56E+05 | 14,224 | 3.8251 | 0.0001 | 9713 |
| Res | 555 | 2.06E+06 | 3718.5 | | | |
| Total | 574 | 2.53E+06 | | | | |
| Deviation from centroids | | | | F: 4.7439 | DF1: 1 | DF2: 18 | 0.0127 |
Table V. SIMilarity PERcentage (SIMPER) routine for species contributions to the dissimilarity between limestone and granite, performed overall (ALL) and on single taxonomic group (Echinoderms, Crustaceans and Fishes) abundance dataset. Permutation N: 9999.

**ALL**

| Species                      | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.%  |
|------------------------------|----------|--------|--------|----------|--------|
| **Granites Average similarity: 49.53** |          |        |        |          |        |
| *P. scriptus*                | 20.55    | 30.34  | 1.16   | 61.25    | 61.25  |
| *S. cabrilla*                | 5.38     | 9.42   | 1.13   | 19.02    | 80.28  |
| *P. rouxi*                   | 5.17     | 5.75   | 0.90   | 11.62    | 91.90  |
| *G. strigosa*                | 1.04     | 1.50   | 0.79   | 3.03     | 94.93  |
| *A. mediterraneus*           | 0.73     | 0.98   | 0.48   | 1.97     | 96.90  |
| *C. longispinus*             | 0.75     | 0.74   | 0.48   | 1.49     | 98.39  |
| *M. glacialis*               | 0.36     | 0.44   | 0.47   | 0.90     | 99.28  |
| *A. mediterraneus*           | 0.92     | 0.24   | 0.36   | 0.49     | 99.77  |
| *E. marginatus*              | 0.20     | 0.11   | 0.26   | 0.23     | 100.00 |
| **Limestones Average similarity: 21.46** |          |        |        |          |        |
| *S. cabrilla*                | 3.81     | 6.56   | 0.96   | 30.56    | 30.56  |
| *E. marginatus*              | 14.47    | 5.21   | 0.67   | 24.30    | 54.85  |
| *S. umbra*                   | 17.42    | 4.49   | 0.47   | 20.90    | 75.76  |
| *P. rouxi*                   | 1.94     | 1.95   | 0.76   | 9.10     | 84.86  |
| *A. lissula*                 | 0.68     | 1.15   | 0.39   | 5.38     | 90.24  |
| *S. scriba*                  | 1.26     | 0.99   | 0.43   | 4.62     | 94.86  |
| *P. elephas*                 | 1.31     | 0.35   | 0.21   | 1.65     | 96.51  |
| *A. mediterranea*            | 3.73     | 0.25   | 0.34   | 1.14     | 97.65  |
| *C. longispinus*             | 0.72     | 0.20   | 0.22   | 0.94     | 98.59  |
| *O. ophidianus*              | 0.43     | 0.18   | 0.36   | 0.83     | 99.42  |
| *S. latus*                   | 0.75     | 0.09   | 0.26   | 0.41     | 99.83  |
| *E. sepositus*               | 0.15     | 0.04   | 0.15   | 0.17     | 100.00 |

**Granites vs Limestones Average dissimilarity: 86.57**

| Species                      | Granite Av.Abund | Limestone Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.%  |
|------------------------------|------------------|-------------------|--------|---------|----------|--------|
| *P. scriptus*                | 20.55            | 0.09              | 31.20  | 1.27    | 36.03    | 36.03  |
| *S. umbra*                   | 0.06             | 17.42             | 12.32  | 0.85    | 14.23    | 50.26  |
| *E. marginatus*              | 0.20             | 14.47             | 11.80  | 0.92    | 13.63    | 63.89  |
| *S. cabrilla*                | 5.38             | 3.81              | 7.81   | 0.83    | 9.02     | 72.91  |
| *P. rouxi*                   | 5.17             | 1.94              | 7.40   | 0.91    | 8.55     | 81.46  |
| *A. mediterranea*            | 0.73             | 3.73              | 3.13   | 0.69    | 3.62     | 85.08  |
| *S. scriba*                  | —                | 1.26              | 1.90   | 0.73    | 2.20     | 87.28  |
| *G. strigosa*                | 1.04             | —                 | 1.90   | 0.88    | 2.19     | 89.47  |
| *A. mediterraneus*           | 0.92             | 0.12              | 1.82   | 0.43    | 2.10     | 91.57  |
| *C. longispinus*             | 0.75             | 0.72              | 1.81   | 0.80    | 2.09     | 93.66  |
| *P. elephas*                 | —                | 1.31              | 1.55   | 0.54    | 1.79     | 95.45  |
| *A. lissula*                 | —                | 0.68              | 1.51   | 0.59    | 1.74     | 97.19  |
| *S. latus*                   | —                | 0.75              | 0.85   | 0.42    | 0.99     | 98.18  |
| *M. glacialis*               | 0.36             | —                 | 0.74   | 0.67    | 0.52     | 99.03  |
| *O. ophidianus*              | —                | 0.43              | 0.49   | 0.70    | 0.57     | 99.60  |
| *E. sepositus*               | 0.08             | 0.15              | 0.34   | 0.53    | 0.40     | 100.00 |

**ECHINODERMERS**

| Species                      | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.%  |
|------------------------------|----------|--------|--------|----------|--------|
| *A. mediterranea*            | 0.73     | 8.20   | 0.43   | 32.98    | 32.98  |
| *C. longispinus*             | 0.75     | 7.78   | 0.46   | 31.28    | 64.26  |

(Continued)
Table V. (Continued).

ALL.

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *M. glacialis*  | 0.36     | 6.29   | 0.47   | 25.30    | 89.56 |
| *A. mediterraneus* | 0.92   | 2.60   | 0.37   | 10.44    | 100.00|

Limestones Average similarity: 14.07

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *A. lixula*     | 0.68     | 6.83   | 0.50   | 48.54    | 48.54 |
| *O. ophidianus* | 0.43     | 3.64   | 0.34   | 25.86    | 74.39 |
| *A. mediterranea* | 3.73  | 2.01   | 0.34   | 14.28    | 88.68 |
| *C. longispinus* | 0.72     | 1.25   | 0.22   | 8.90     | 97.57 |
| *E. sepositus*  | 0.15     | 0.34   | 0.15   | 2.43     | 100.00|

Granites vs Limestones

| Species         | Granite Av.Abund | Limestone Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|-----------------|-----------------|-------------------|---------|---------|----------|-------|
| *A. mediterranea* | 0.73       | 3.73            | 25.50   | 0.84    | 28.39    | 28.39 |
| *C. longispinus* | 0.75       | 0.72            | 12.27   | 0.73    | 14.19    | 61.61 |
| *A. lixula*     | —             | 0.68            | 12.30   | 0.60    | 13.69    | 75.30 |
| *M. glacialis*  | 0.92         | 0.12            | 9.75    | 0.57    | 10.85    | 86.16 |
| *O. ophidianus* | —             | 0.43            | 8.91    | 0.62    | 9.91     | 96.07 |
| *E. sepositus*  | 0.08         | 0.15            | 3.53    | 0.54    | 3.93     | 100.00|

CRUSTACEANS

Granites Average similarity: 48.48

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *P. scriptus*   | 20.55    | 45.75  | 1.25   | 94.36    | 94.36 |
| *G. strigosa*   | 1.04     | 2.74   | 0.73   | 5.64     | 100.00|

Limestones Average similarity: 5.79

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *P. elephas*    | 1.31     | 4.44   | 0.33   | 76.76    | 76.76 |
| *S. latus*      | 0.75     | 1.35   | 0.35   | 23.24    | 100.00|

Granites vs Limestones

| Species         | Granite Av.Abund | Limestone Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|-----------------|-----------------|-------------------|---------|---------|----------|-------|
| *P. scriptus*   | 20.55           | 0.09              | 78.82   | 2.90    | 79.20    | 79.20 |
| *G. strigosa*   | 1.04            | —                 | 9.98    | 0.58    | 10.03    | 89.23 |
| *P. elephas*    | —               | 1.31              | 7.16    | 0.45    | 7.19     | 96.42 |
| *S. latus*      | —               | 0.75              | 3.57    | 0.42    | 3.58     | 100.00|

FISHES

Granites Average similarity: 40.42

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *S. cabrilla*   | 5.38     | 26.19  | 1.43   | 64.78    | 64.78 |
| *P. rouxi*      | 5.17     | 14.00  | 1.01   | 34.62    | 99.41 |
| *E. marginatus* | 0.20     | 0.24   | 0.26   | 0.59     | 100.00|

Limestones Average similarity: 23.84

| Species         | Av.Abund | Av.Sim | Sim/SD | Contrib% | Cum.% |
|-----------------|----------|--------|--------|----------|-------|
| *S. cabrilla*   | 3.81     | 8.65   | 0.87   | 36.30    | 36.30 |
| *E. marginatus* | 14.47    | 6.16   | 0.68   | 25.84    | 62.14 |
| *S. umbra*      | 17.42    | 5.39   | 0.46   | 22.61    | 84.75 |
| *P. rouxi*      | 1.94     | 2.40   | 0.75   | 10.05    | 94.80 |
| *S. scriba*     | 1.26     | 1.24   | 0.43   | 5.20     | 100.00|

Granites vs Limestones

| Species         | Granite Av.Abund | Limestone Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|-----------------|-----------------|-------------------|---------|---------|----------|-------|
| *S. cabrilla*   | 5.38            | 3.81              | 19.65   | 0.86    | 25.40    | 25.40 |
| *S. umbra*      | 0.06            | 17.42             | 18.70   | 0.90    | 24.18    | 49.58 |
| *E. marginatus* | 0.20            | 14.47             | 18.48   | 1.06    | 23.89    | 73.47 |
| *P. rouxi*      | 5.17            | 1.94              | 15.92   | 0.88    | 20.59    | 94.06 |
| *S. scriba*     | —               | 1.26              | 4.59    | 0.49    | 5.94     | 100.00|
granite outcrops are fine and often silty (ET personal observation). Moreover, *G. strigosa* prefers horizontal crevices, where it stands both on the vault and on the bottom (ET personal observation): this kind of crevices is typical of granite cracks.

On the contrary, the spiny lobster *Palinurus elephas* and the slipper lobster *Scyllarides latus* were recorded only in limestone sites. This evidence can be explained by two possible factors related to food preferences and substrate morphology. The food sources of these two large decapods mainly include bivalves, sea urchins, small crustaceans and coralline algae (Goñi & Latrouite 2005) (Table III) that are typically recorded in limestone sites and are scarce or absent on granitic substrates (Canessa et al. 2020a). On the other hand, also the 3D complexity of the substrate can be invoked to explain a differential presence in the two different lithological situations. Lobsters prefer dens with small, multiple openings to those with larger entrances (Spanier & Almog-Shtayer 1992; Spanier & Lavalli 2006). Limestones sites, due to the presence of coralligenous bioherms, are characterized by a greater variety of structures, ravines, overhangs and crevices, which
are likely to provide more suitable shelters. Differences in the distribution of juveniles of *P. elephas* related to the rocky substrate were studied by Diaz et al. (2001). These Authors observed a more intense settlement on limestones in comparison with metamorphic and siliceous rocks. This selection was explained by the presence on the limestone of empty holes of the date mussel *Lithophaga lithophaga* (Linnaeus, 1758) providing daytime refuge for young specimens. Similar patterns in the use of empty holes of endolithic molluscs on limestone were observed for juvenile sea urchins (Guidetti 2011) and some small cryptobenthic fishes (Parravicini et al. 2008).

Two out of the five fish species examined in this study, *Parablimnius rouxi* and *Serranus cabrilla*, displayed similar distribution patterns on limestone and granite. The remaining three fishes, namely *Epinephelus marginatus*, *Sciaena umbra* and *S. scriba*, were clearly more associated with limestone.

Many and non-mutually exclusive plausible factors (considering those intrinsically related to lithology) could explain the distribution patterns of fish observed in this study, directly or indirectly related to substrate type: i) the colour of the rocky background related to the mimetic ability of fish; ii) the different architectural structures offering shelters for juvenile and adult fish (from small holes to boulders, forming larger shelters or small caves); iii) different food sources associated to different rock types (e.g., vagile invertebrates and juvenile fish comprising most preys of the fish species studied here).

The abundance of *E. marginatus* and *S. umbra* in Mediterranean rocky reefs is known to be negatively influenced by the intensity of fishing (Di Franco et al. 2009; Guidetti & Micheli 2011) and positively influenced by the shelter availability (www.fishbase.org). In the study area, the rocky substrate 3D structure is often more complex on limestone rocky substrates, due to accumulations of boulders collapsing from the emerged cliffs. Such boulders’ accumulations form a rocky habitat rich in shelters and crevices that could support higher abundances of these two species compared to granitic rocks. This scenario is, first of all, in agreement with the observations carried out by Desiderà et al. (2021), who reported higher abundances of *E. marginatus* on limestone. Also, Guidetti et al. (2004), reported that the densities of other shelter-related fish species, namely *Chromis chromis* and *Aponon imberbis*, were higher on limestones than granites. *C. chromis* is a planktivorous fish swimming and feeding in the water column daytime but searching for shelter close to the sea bottom during the night, while *A. imberbis* is well known to be a sciaphilic fish, thriving in rocky reefs rich in crevices and caves (Bussotti et al. 2015).

In this study, *P. rouxi* was recorded as equally partitioned between limestone and granite substrates at relatively deep stands (around 30–50 m depth), while in a previous survey Guidetti et al. (2004) recorded higher abundances on limestone in shallow rocky reefs. These authors suggested that the observed distribution pattern could be the result of the camouflage of this small light-colored blennid fish over bare limestones (Guidetti 2006). Moreover, in this habitat empty holes of endolithic molluscs offer an additional opportunity for shelter (Parravicini et al. 2008). At deeper stands, “light” rocky substrates void of vegetation and endolithic molluscs are fairly rare, and this situation could explain the absence of differences in the abundance of this species between limestone and granite.

Previous studies conducted in the same area (Guidetti & Cattaneo-Vietti 2002; Guidetti et al. 2004) but at shallow stands (< 10 m) reported that *S. scriba* and *S. cabrilla* were more abundant on granite and limestone, respectively. These Authors suggested that substrate colour could again account for differences in the distribution patterns of these two territorial fishes associated with granite or limestone rocks. As already stated, limestones at shallow stands are often lighter than granites, and *S. cabrilla* could be more abundant due to mimicry offered by its paler livery. At deeper stands, limestone rocks are covered by well-developed coralligenous formations, which could nullify such a “background-camouflage” advantage for *S. cabrilla* on shallow limestones.

In a different lithological situation, i.e., the granite vs schist rocks of the Asinara Island (Sardinia, Italy), the fish community showed different species occurrence/abundance on the two substrates (Pais et al. 2004). For example, *S. cabrilla* was more abundant on schists than on granites at 24–30 m depth. For other species, like *E. marginatus*, *P. rouxi*, *S. scriba*, *S. umbra*, occurrence did not vary according to the substrate.

Generally, our data about several taxa of vagile fauna, characterized by different feeding strategies and shelter preferences, suggest that the substrate features may influence the circalittoral rocky-reef assemblages in different ways, concerning multiple trophic levels. Such an influence can be explicated by the differential presence of the preferred food source, that in turn, is directly conditioned by the type of substrate. Secondly, also the geomorphology (i.e., 3D architectural complexity) of sites could play an important
role, providing different dens and refuges suitable for different species. Field and experimental studies have demonstrated how substrate morphology, particularly the presence of holes and galleries, can affect fish species richness and abundance patterns (Risk 1972; Luckhurst & Luckhurst 1978; Grattawie & Speight 2005; Rogers et al. 2014). Finally, the colour of the substrates can enhance the mimicry of different species according to their livery. In our case, the different rugosity and bioconditioning (covering, etching) of the two substrates, deriving from different chemical properties and aptitude to support the development of coralligenous bioconstructions, is likely to create an intricate pattern of interactions that probably drives the vagile fauna assemblages (Aguilera et al. 2014).

Our data suggest that the substrate works probably in synergy with other environmental factors (i.e., light intensity changing with depth) in shaping the community structure (McGuinness 1989; Hadfield & Paul 2001; Bavestrello et al. 2018). This is clearly shown by the sea urchin A. lividus that only down to 30 m depth displays different distribution patterns related to lithology, but not in shallow waters where the algal canopy is present both on granites and limestones (Guidetti et al. 2004). The small serranid S. cabrilla, on the contrary, showed a different distribution related to lithology in infralittoral but not in circalittoral substrates (Guidetti & Cattaneo-Vietti 2002; Guidetti et al. 2004).

In conclusion, this study reported for the first time a possible interaction between lithology and “depth” (actually, the factors changing with depth) in influencing infralittoral rocky-reef assemblages compared to literature data about infralittoral assemblages. The interaction between substrate lithology and other environmental factors and processes changing with depth (e.g., light intensity), spatial scales (latitude related to climate change) and levels of human disturbance (exploitation, pollution, etc.) surely represent an interesting field for future observational and experimental studies to carry on in the field and mesocosms.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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