

Bio-mineralogy as a structuring factor for marine epibenthic communities

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ABSTRACT: The mineralogical features of the substrate were generally considered a minor factor in structuring marine benthic communities. The aim of this work is to verify whether the presence of quartz minerals in rock may explicate differences, usually explained in terms of substrate roughness or other factors, in epibenthic communities. Laboratory tests on the hydroid *Eudendrium glomeratum* showed that its planulae settle preferentially on carbonatic, rather than quartzitic, substrates. To test the influence of quartz on established communities, we analysed the species composition and quantitative structure of sublittoral sessile assemblages on different rocks in several localities of the Ligurian and Tyrrhenian seas. The observed differences appeared to be related to the presence of quartz in the substrate rock. The interactions between organisms and minerals (bio-mineralogy) might play a significant role on benthic communities, affecting not only the initial colonisation, but also later assemblages. This potential role has been largely neglected to date and further studies are needed to prove its importance.

KEY WORDS: Substrate colonisation · Mineral composition · Marine benthos distribution · Hard substrates · Bio-mineralogy

INTRODUCTION

The spatial distribution and structure of marine benthic communities are due to numerous abiotic and biotic factors which, in turn, are influenced by the presence of the organisms, in a mutual exchange of inputs. Among the abiotic factors, the mineralogical features of the substrate were generally considered of scarce importance, but recent studies by Cerrano et al. (1998) have shown that the presence of quartz in the sand may affect the initial steps of infauna colonisation. Cerrano et al. (1998) introduced the term bio-mineralogy to explicate the interrelationships between biological systems at different hierarchies (cell, organism, species, community) and minerals.

Bio-mineralogy could influence hard-bottom assemblages and explain some 'anomalies' in the structure of

communities growing on rocks of different nature. A species assemblage, which may be slightly more attracted to a particular substrate, could affect succession by its subsequent interaction with later assemblages. A similar effect was evidenced in the colonisation of artificial substrates, with respect to both species composition and abundance (Anderson & Underwood 1994, Holm et al. 1997). Less information is available for natural substrates (McGuinness 1989), but it is common knowledge that the softness and asperity of a rock can favour or hamper biotic colonisation through selective larval settling, retention of water (in the littoral) and organic matter, and provision of refuges from predation or grazing (Den Hartog 1972, Levinton 1982, Walters & Wethey 1996).

More is known about the influence of substrate mineralogy on bioboring, which is prevented by high percentages of quartzitic or pelitic components in the rock. Sublittoral endolithic communities are charac-

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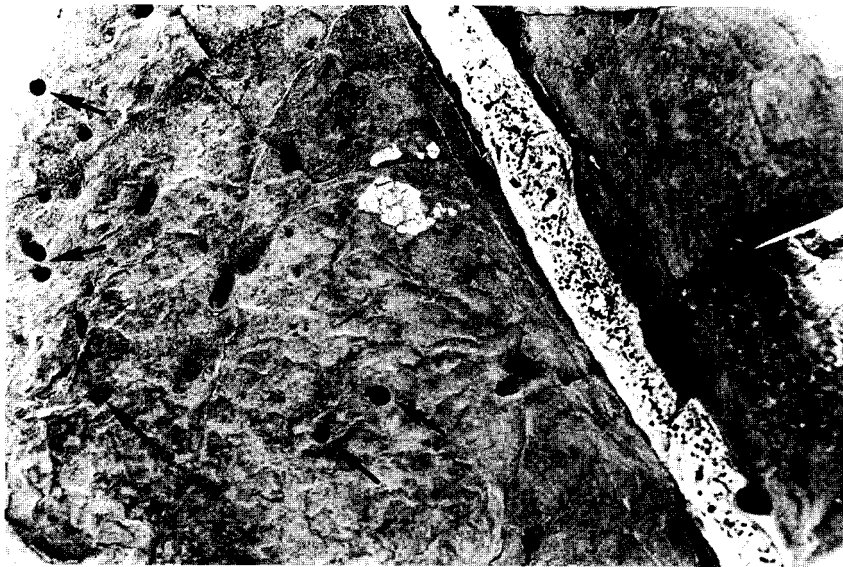


Fig. 1. Sublittoral rock showing differences in the distribution of borers due to the mineral composition of the substrate. The white calcitic vein is widely bored by the sponge *Cliona celata* which is absent on marl limestone (grey). Herein only the date-mussel *Lithophaga lithophaga* is able to penetrate (arrows)

terised mainly by clionid sponges and bivalves. Clionid sponges use hatching cell pseudopodes and the production of carbonic acid to penetrate limestone (Rützler & Rieger 1973, Pomponi 1979), but *Cliona celata* Grant preferentially bores, in the Mediterranean Sea, substrates richer than 60% in carbonates (unpubl. obs.). Bivalves, such as species of *Lithophaga*, bore with the help of sulphuric acid and/or neutral mucoproteins (Russo & Cicogna 1992), and are also able to penetrate marl limestone, which is impenetrable by clionids (unpubl. obs., Fig. 1). All this has important consequences on the rock texture and roughness and, ultimately, on the community structure.

To check the influence of substrate mineralogy on the larval settling, a series of laboratory tests was conducted using planulae of the hydroid *Eudendrium glomeratum* (Picard), a very common species of the sublittoral Mediterranean zoobenthos (Boero et al. 1986). In order to seek a relation between the mineralogy of natural substrates and the structure of sessile epibenthic communities, the species composition and percent cover of assemblages living on different kinds of rock in the western Mediterranean Sea were compared.

MATERIAL AND METHODS

Laboratory. Planulae of the hydroid *Eudendrium glomeratum* were obtained from female colonies collected on the rocky cliff of the Portofino Promontory

during November 1998 at 20 to 25 m depth. The fertilised eggs develop in verticils of 5 to 10 fixed to a rudimentary polyp, the blastostyle, deprived of mouth and tentacles. Each egg is enveloped by a non-branched spadix. The verticils of eggs were mechanically detached from the mother colony and placed in 250 ml cups filled with filtered natural sea water at a temperature of 15°C.

Cerrano et al. (1997) demonstrated that light exposure is necessary to trigger egg hatching and therefore we reared the eggs in lit conditions for 3 d. New released planulae were divided into 4 stocks of 60 specimens and each stock was placed for 12 d in an experimental Petri dish in complete darkness to avoid problems related to their very high phototrophy. Petri dishes were prepared by sticking a uniform layer

of sand grains with Eukitt; half of the surface was covered by quartz sand, and half by sand derived from Carrara marble. The 2 sand types have the same granulometric (125 to 250 µm) and morphological features (roundness, 0.35 to 0.7; projection of sphericity, 0.8 to



Fig. 2. Geographic layout of the field-study sites in the Ligurian and Tyrrhenian seas (NW Mediterranean)

Table 1. Localities for field studies on sublittoral rocky bottoms

Locality	Contrasted mineralogies			Depth range (m)	No. of stations	No. of species
Ligurian Sea	Quartzite (Gallinaria Island)	vs	Puddingstone, marl limestone and sandstone (Portofino region)	5–7	14	60
Giglio Island	Granite (most of the island)	vs	Limestone (western part of the island)	6–10	16	54
Northeast Sardinia	Granite (most of the coast and small islands)	vs	Limestone-dolomite (Tavolara Island)	18–34	20	44

0.9). Both kinds of sand were previously stored at 100°C for 24 h, which enabled us to obtain an artificial hard bottom on the entire Petri dish surface, with very similar physical features but with 2 different mineralogies.

Field. The data matrices were produced using unpublished data sets on subtidal epibenthic communities of the Ligurian Sea (Gallinaria Island and Portofino region) and Tyrrhenian Sea (Giglio Island and northeast Sardinia) (Fig. 2). The data sets were chosen in order to be able to contrast communities from an equal number of stations on rocks rich in quartz, such as quartzite and granites, or deprived of that mineral (Table 1). All data sets consist of percent cover data of conspicuous species (Hiscock 1987), derived from underwater visual inventories by SCUBA divers using quadrats (Bianchi et al. 1991). Cover data for a total of 96 species (Table 2) were available, but each data set was analysed separately according to depth zone and geographical location, so that communities only showed differences in the mineralogical nature of the substrate and possibly exposure. To avoid the influence of sedimentation, which may alter the effects of mineralogical composition at the rock surface (Bavestrello et al. 1995a), vertical stations (70 to 95° slope) were selected. Matrices of species cover data were compared by correspondence analysis (Legendre & Legendre 1998), and species numbers and total cover by 1-way ANOVA. Prior to analysis, percentage cover values were arcsine transformed to meet the assumption of homogeneity of variances (Underwood 1997).

Field-study sites. The Ligurian Sea data derive from surveys carried out in shallow water at Gallinaria Island in the summer of 1991 and in the region of Portofino Promontory in the summer of 1993. The Tyrrhenian Sea data include information taken at infralittoral depths around Giglio Island in September of 1988 to 1991 and at circalittoral depths in north-eastern Sardinia in June 1990 (Table 1).

The Ligurian Sea has been the object of much research in marine biology, and many studies have

taken into account the epibenthic communities on the rocky bottom (Bianchi et al. 1987, Cattaneo-Vietti et al. 1988). One of the most studied sites is the region around Portofino (Tortonese 1958, 1962, Morri et al. 1988), but recent research has also been done on the Island of Gallinaria (Balduzzi et al. 1994). These studies underlined that epibenthic communities on sublittoral rocks at Portofino are dominated by flourishing gorgonian populations, whereas at Gallinaria, gorgonians are scarce and sponges dominate. From a mineralogical point of view, Gallinaria Island is exclusively quartzitic (Orsino 1975), whereas the coast around Portofino is characterised by puddingstone, marl limestone and sandstone, none of which has a significant quartz component (Boni et al. 1969).

The Giglio Island is included in the southern group of the Tuscan Archipelago, at the border between Ligurian and Tyrrhenian seas. Its rocky coast is mostly granite, but a small portion on the western side is composed of limestone (Alvisi et al. 1994). The subtidal epibenthic communities of Giglio Island were first described by Balduzzi et al. (1996).

The northeast corner of Sardinia is mostly composed of granite. A striking exception is the Tavolara Island made by a gigantic limestone-dolomite slab (Lorenzoni & Chiesura-Lorenzoni 1973). Together with Molara, Molarotto and other minor islets and rocks (all granitic), Tavolara forms a small archipelago, the epibenthic communities of which have been studied by Navone et al. (1992).

RESULTS

Laboratory

After hatching, the *Eudendrium glomeratum* planulae crawled on the bottom of culture vessel for 2 to 3 d. Then, they fixed to the substrate by the anterior pole and metamorphosed into a planular polyp. Data showed that crawling planulae had a strong selectivity for the substrate, being always about 5 times more abundant on the

Table 2. List of the species in inventories of field studies on sublittoral rocky bottoms. Species codes are those used in Figs. 4, 6 & 7

Code	Species/family name	Phylum	Code	Species/family name	Phylum
Aab	<i>Acetabularia acetabulum</i> (Linnaeus) P. C. Silva	Chlorophyta	Ior	<i>Ircinia oros</i> (Schmidt)	Porifera
Aac	<i>Acanthella acuta</i> Schmidt	Porifera	Irc	<i>Ircinia</i> sp.	Porifera
Acr	<i>Amphiroa cryptarthrodia</i> Zanardini	Rhodophyta	Iva	<i>Ircinia variabilis</i> (Schmidt)	Porifera
Ada	<i>Axinella damicornis</i> (Esper)	Porifera	Jru	<i>Jania rubens</i> (Linnaeus) Lamouroux	Rhodophyta
Ali	<i>Arbacia lixula</i> (Linnaeus)	Echinodermata	Lfr	<i>Lithophyllum frondosum</i> (Dufour) Furnari, Cormaci et Alongi	Rhodophyta
Aor	<i>Agelas oroides</i> (Schmidt)	Porifera	Lin	<i>Lithophyllum incrustans</i> Philippi	Rhodophyta
Ari	<i>Amphiroa rigida</i> Lamouroux	Rhodophyta	Lob	<i>Laurencia obtusa</i> (Hudson) Lamouroux	Rhodophyta
Ave	<i>Axinella verrucosa</i> (Esper)	Porifera	Lpr	<i>Leptopsammia pruvoti</i> Lacaze-Duthiers	Cnidaria
Beu	<i>Balanophyllia europaea</i> (Risso)	Cnidaria	Lva	<i>Leucosolenia variabilis</i> Haeckel	Porifera
Bpe	<i>Balanus perforatus</i> Bruguière	Arthropoda	Mli	<i>Mesophyllum lichenoides</i> (Ellis) Lemoine	Rhodophyta
Cad	<i>Codium adhaerens</i> C. Agardh	Chlorophyta	Mtr	<i>Myriapora truncata</i> (Pallas)	Bryozoa
Cbo	<i>Caberea boryi</i> (Audouin et Savigny)	Bryozoa	Mvu	<i>Microcosmus vulgaris</i> Heller	Chordata
Cbu	<i>Codium bursa</i> (Linnaeus) C. Agardh	Chlorophyta	Pax	<i>Parazoanthus axinellae</i> (Schmidt)	Cnidaria
Ccl	<i>Clathrina clathrus</i> (Schmidt)	Porifera	Pcl	<i>Paramuricea clavata</i> (Risso)	Cnidaria
Cco	<i>Clathrina contorta</i> (Bowerbank)	Porifera	Pco	<i>Parerythropodium coralloides</i> (Pallas)	Cnidaria
Ccr	<i>Crambe crambe</i> (Schmidt)	Porifera	Pcr	<i>Palmophyllum crassum</i> (Naccari) Rabenhorst	Chlorophyta
Cde	<i>Clavelina dellavallei</i> (Zirpolo)	Chordata	Pfa	<i>Pentapora fascialis</i> (Pallas)	Bryozoa
Cel	<i>Corallina elongata</i> Ellis et Solander	Rhodophyta	Pfi	<i>Petrosia fificiformis</i> (Poirer)	Porifera
Cfi	<i>Cellaria fistulosa</i> (Linnaeus)	Bryozoa	Pft	<i>Phorbas fictitius</i> (Bowerbank)	Porifera
Cfr	<i>Codium fragile</i> (Suringar) Hariot	Chlorophyta	Pfu	<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	Chlorophyta
Cgr	<i>Corallina granifera</i> Ellis et Solander	Rhodophyta	Pli	<i>Paracentrotus lividus</i> (Lamarck)	Echinodermata
Cin	<i>Caryophyllia inornata</i> (Duncan)	Cnidaria	Pne	<i>Phyllophora nervosa</i> (De Candolle) Greville ex J. Agardh	Rhodophyta
Cla	<i>Cladophora</i> sp.	Chlorophyta	Ppa	<i>Padina pavonica</i> (Linnaeus) Lamouroux	Phaeophyta
Cln	Clonidae spp.	Porifera	Psq	<i>Peyssonnelia squamaria</i> (Gmelin) Decaisne	Rhodophyta
Cmu	<i>Cutleria multifida</i> (Smith) Greville	Phaeophyta	Pte	<i>Phorbas tenacior</i> (Topsent)	Porifera
Cni	<i>Cliona nigricans</i> (Schmidt)	Porifera	Ptr	<i>Pomatoceros triqueter</i> (Linnaeus)	Annelida
Cnu	<i>Chondrilla nucula</i> Schmidt	Porifera	Ptu	<i>Protula tubularia</i> (Montagu)	Annelida
Cpa	<i>Chartella papyrea</i> (Pallas)	Bryozoa	Rfu	<i>Reniera fulva</i> Topsent	Porifera
Cpr	<i>Cladophora prolifera</i> (Roth) Kützing	Chlorophyta	Rhy	<i>Rhyncozoon</i> sp.	Bryozoa
Cre	<i>Chondrosia reniformis</i> Nardo	Porifera	Rvi	<i>Reptadeonella violacea</i> (Johnston)	Bryozoa
Csp	<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	Phaeophyta	Sar	<i>Serpulorbis arenaria</i> (Linnaeus)	Mollusca
Czo	<i>Cystoseira zosteroides</i> (Turner) C. Agardh	Phaeophyta	Sau	<i>Schizomavella auriculata</i> (Hassall)	Bryozoa
Ddi	<i>Dictyota dichotoma</i> (Hudson) Lamouroux	Phaeophyta	Sce	<i>Smittina cervicornis</i> (Pallas)	Bryozoa
Dpo	<i>Dictyopteris polypodioides</i> (De Candolle) Lamouroux	Phaeophyta	Sco	<i>Sphaerococcus coronopifolius</i> (Goodenough et Woodward) C. Agardh	Rhodophyta
Dve	<i>Dasycladus vermicularis</i> (Scopoli) Krasser	Chlorophyta	Scu	<i>Spirastrella cunctatrix</i> Schmidt	Porifera
Dvr	<i>Dudresnaia verticillata</i> (Withering) Le Jolis	Rhodophyta	Sdy	<i>Salmacina dysteri</i> (Huxley)	Annelida
Eca	<i>Eunicella cavolinii</i> (Koch)	Cnidaria	Sel	<i>Sertularella ellisii</i> (Deshayes et Milne-Edwards)	Cnidaria
Era	<i>Eudendrium racemosum</i> (Gmelin)	Cnidaria	ser	Unidentified serpulids	Annelida
Esi	<i>Eunicella singularis</i> (Esper)	Cnidaria	Sla	<i>Savignyella lafontii</i> (Audouin et Savigny)	Bryozoa
Fpe	<i>Flabellia petiolata</i> (Turra) Nizamuddin	Chlorophyta	Slo	<i>Schizoporella longirostris</i> Hincks	Bryozoa
Fru	<i>'Falkenbergia rufolanosa'</i> (Harvey) Schmitz	Rhodophyta	spi	Unidentified spirorbids	Annelida
Gob	<i>Galaxaura oblungata</i> (Ellis et Solander) Lamouroux	Rhodophyta	Ssc	<i>Stypocaulon scoparium</i> (Linnaeus) Kützing	Phaeophyta
Hco	<i>Hemimycale columella</i> (Bowerbank)	Porifera	Sse	<i>Sertella septentrionalis</i> Harmer	Bryozoa
Hdi	<i>Halopteris diaphana</i> (Heller)	Cnidaria	Sve	<i>Serpula vermicularis</i> Linnaeus	Annelida
Hfi	<i>Halopteris filicina</i> (Grateloup) Kützing	Phaeophyta	Svu	<i>Sargassum vulgare</i> C. Agardh	Phaeophyta
Hpa	<i>Halocynthia papillosa</i> (Linnaeus)	Chordata	Vst	<i>Vermiliopsis striaticeps</i> (Grube)	Annelida
Htu	<i>Halimeda tuna</i> (Ellis et Solander) Lamouroux	Chlorophyta	Vut	<i>Valonia utricularis</i> (Roth) C. Agardh	Chlorophyta
hyd	Unidentified hydroids	Cnidaria	Wpe	<i>Wrangelia penicillata</i> C. Agardh	Rhodophyta

carbonatic sediments (Fig. 3a). During the experimental time (11 d), about one-third of the planulae metamorphosed and the number of planular polyyps reflected the number of planulae present in the different sections of

the dishes (Fig. 3b). The ratio between metamorphosed (settled) and crawling planulae was not significantly different in the 2 sections (43.3 ± 14.6 and $45.6 \pm 6\%$ for quartz and carbonate respectively).

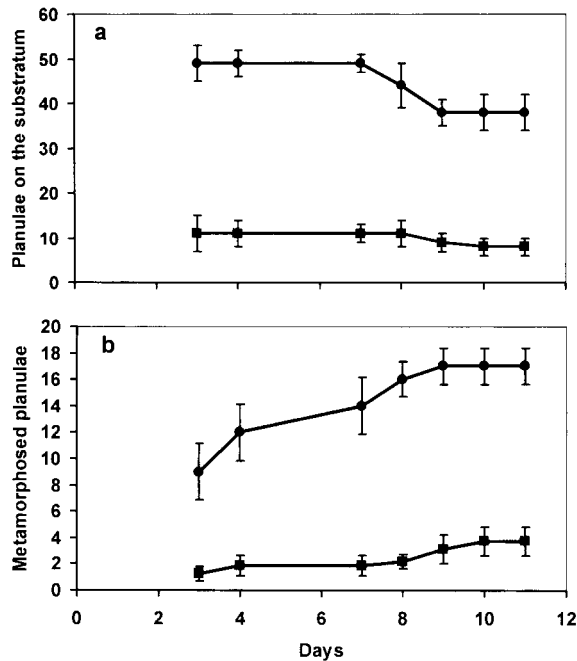


Fig. 3. Response of *Eudendrium glomeratum* planulae to differences in the mineral composition of the substrate. (a) Number of crawling planulae on marble (●) and quartz (■) sands. (b) Number of metamorphosed planulae on the same substrates. Data are the means \pm SE of 4 replicates

Field

The first 2 axes extracted from the correspondence analyses on the 3 data sets were significant in all cases ($p < 0.05$ according to the tables of Lebart 1975). The fraction of the total variance represented on the plane formed by the first 2 axes was 45.73% for the Ligurian Sea data set, 43.84% for Giglio Island, and 32.00% for northeast Sardinia.

Correspondence analysis on Ligurian Sea infralittoral epibenthic communities showed, along the 1st axis, a clear-cut separation of the stations of Gallinaria Island from those of the Portofino region, the first site being mainly characterised by quartzitic rock and the second by different rock types (Fig. 4). Along the 2nd axis, the station points of Portofino region tended to spread around according to the nature of their rocky bottoms, marl limestone separating at one extreme and sandstone at the other. This last arrangement might also reflect an exposure gradient, sandstone stations being located at more exposed sites than the limestone ones. However, there were station points of equally exposed sites of Gallinaria, all on quartzitic rock, which remained well separated from the corresponding ones of Portofino. Mean species richness on the quartzitic rocks of Gallinaria was lower than on the non-quartzitic rocks of the Portofino region (Fig. 5a):

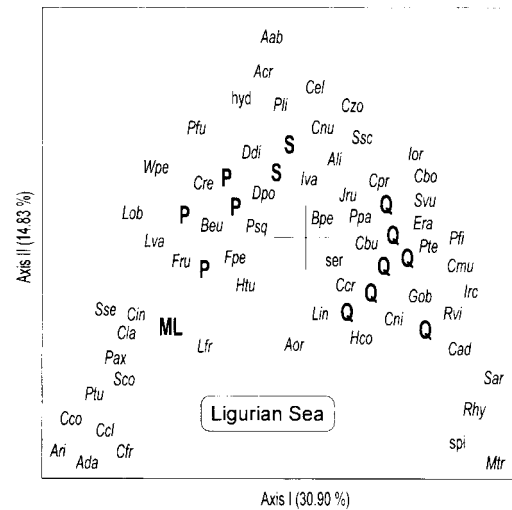


Fig. 4. Correspondence analysis on sublittoral rocky bottom data in the Ligurian Sea (Portofino region and Gallinaria Island). The variance fraction explained by the first 2 axes is indicated. Station points are identified by bold capital letters according to the nature of the rock: Q: quartzite; S: sandstone; ML: marl limestone; P: puddingstone. Species points are identified by codes as in Table 2

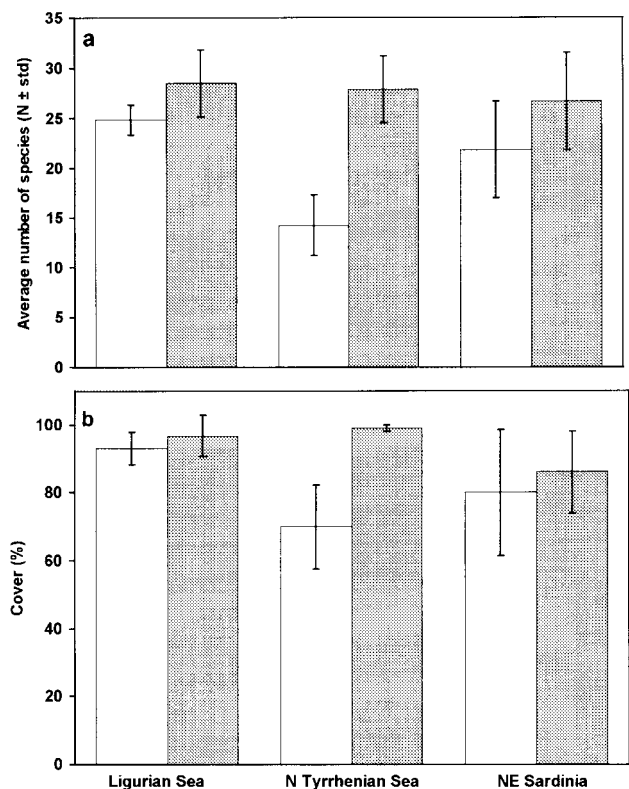


Fig. 5. Mean (± 1 standard deviation) number of species (a) and total substratum cover (b) of the epibenthic assemblages in the 3 study sites, according to rock mineralogy. For each site, quartz-rich rocks (quartzite or granites) (□), and rocks poor in or deprived of quartz (■) are represented

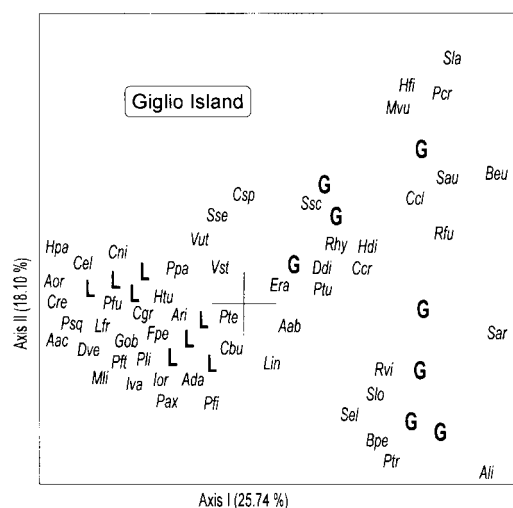


Fig. 6. Correspondence analysis on sublittoral rocky bottom data at Giglio Island (northern Tyrrhenian Sea). The variance fraction explained by the first 2 axes is indicated. Station points are identified by bold capital letters according to the nature of the rock. G: granite; L: limestone. Species points are identified by codes as in Table 2

this difference is significant (1-way ANOVA, $p = 0.024$). On the contrary, total substratum cover (Fig. 5b) was not significantly different ($p = 0.119$).

Results from correspondence analysis on infralittoral communities of Giglio Island showed a separation of stationpoints along the 1st axis that was consistent with the mineralogical nature of the rock, opposing limestone to granite (Fig. 6). On the 2nd axis, limestone station points were closely grouped, whereas granite station points were more scattered. Looking at the species points (see Table 2 for decoding species names), the 2nd axis opposed encrusting invertebrates to algae and erect or massive invertebrates: the first assemblage was considered the result of excess sea-urchin grazing by Balduzzi et al. (1996). Both the number of species (Fig. 5a) and total cover (Fig. 5b) were severely reduced on granite as compared with limestone (1-way ANOVA, $p < 0.001$ in both cases).

Correspondence analysis on circalittoral epibenthic communities of northeastern Sardinia (Tavolara and Molara Archipelago) showed again the separation between carbonate (limestone-dolomite) and granite station points (Fig. 7). On the contrary, no relationship was evident with depth, notwithstanding the comparatively great range investigated (18 to 34 m). Also in this case, the number of species on granite was lower than on limestone-dolomite (Fig. 5a) and, although small, the difference was significant (1-way ANOVA, $p = 0.043$). In contrast, no difference was found for total cover ($p = 0.717$).

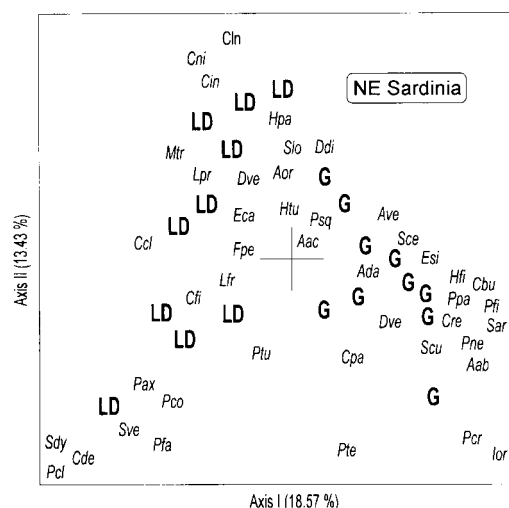


Fig. 7. Correspondence analysis on sublittoral rocky bottom data in northeastern Sardinia (Tavolara and Molara Archipelago). The variance fraction explained by the first 2 axes is indicated. Station points are identified by bold capital letters according to the nature of the rock. G: granite; LD: limestone-dolomite. Species points are identified by codes as in Table 2

DISCUSSION

The structure of hard bottom communities has been traditionally interpreted as mainly the result of complex biotic interactions within adult assemblages (Connell 1983, Schoener 1983). Only in the last decade has the importance of external factors, such as physical processes and recruitment vagaries, been fully recognised (Barry & Dayton 1991, Bingham 1992, Bianchi 1997, Guichard & Bourget 1998, Smith & Witman 1999). However, our knowledge about the role of the nature of substratum remains anecdotal. Many general papers on marine ecology report on the influence of hard substratum surface texture and physico-chemical properties upon community composition and structure (Den Hartog 1972, Levinton 1982), but studies providing direct evidence are scarce. Comparing the epibiotic communities of different types of substratum, Connell & Glasby (1999) found differences in the identity of species and the abundance of individual taxa. The same authors observed that the characteristics of the substratum surface were an important determinant in the structure of assemblages and that certain physical or chemical properties (e.g. alkalinity) may affect the settlement, growth or survival of organisms. On the other hand, Caffey (1982) found no effect of rock types on the settlement or survival of the intertidal barnacle *Tessieropora rosea* (Krauss).

Our experiments with the subtidal hydroid *Eudendrium glomeratum* suggest that the larvae of benthic organisms could be selected, other environmental con-

ditions being equal, by the mineral composition of the substrate and by the presence of quartz in particular. Most hydroids are substrate generalists (Gili & Hughes 1995) and species of *Eudendrium* are probably not exceptions (Sommer 1992). Our data for the first time demonstrate a strong choice of hydroid larvae against mineral substrates. In this choice no biological (presence of a bacterial film) or physical (roughness, grain shape) features may be invoked. The fact that after 11 d the ratio metamorphosed/crawling planulae in each dish section was not significantly different showed that, while the mineral nature of the substrate affects the larval behaviour, the metamorphosis into planular polyps was not influenced. It is possible that the production of a perisarcal cover avoids any kind of negative interaction between the polyp and the substrate.

Our field data seem to suggest that the mineralogical properties of the substratum are long lasting, and continue to affect the established epibenthic communities. The contrast between rocks rich in or deprived of quartz always resulted evident on the first axis of correspondence analysis, indicating that this was the most important factor in differentiating the patterns of species composition and dominance. In all localities, the assemblages on quartz-rich rocks were less diverse and showed a simpler physiognomy. This could indicate the difficulty to reach a 'mature' condition in presence of quartz, which acts as an inhibiting factor. Cerrano et al. (1998) suggested that crystalline quartz has an evident negative effect on animals that colonise sands, probably due to both the oxidant properties of the crystal surface, generating silicon-based radicals, and to the formation of $\bullet\text{OH}$ radicals in the surrounding aqueous environment (Marasas & Harington 1960, Langer & Nolan 1986, Shi et al. 1988, Vallyathan et al. 1988). In the case of rocky substrates, it seems reasonable to think that this inhibitory effect acts chiefly on the early stages of colonisation, perhaps via the microbial communities of the primary film (Wahl 1989, Johnson et al. 1997), and reduces as succession goes on. Many sessile organisms lay calcareous structures that in turn offer a secondary substrate to later colonists, thus annulling the effect of quartz. Most algae, for instance, are not influenced by the mineralogical nature of the rock (Cabioc'h et al. 1992) and, once developed, operate a 'biological conditioning' of the substrate, which has been considered as the most important factor structuring faunal communities (Abbiati et al. 1987, 1991, Simbora et al. 1995). Clearly, disturbance may disrupt biological cover (Sousa 1984), re-exposing organisms to the direct influence of the original substrate. This may explain why shallow-water sessile communities on quartz-rich rocks always appear in an early developmental phase, a fact com-

monly interpreted as a consequence of intense sea-urchin grazing (Navone et al. 1992, Balduzzi et al. 1996). However, there is no reason to think that sea urchins graze more heavily on granite than on limestone; rather, sea-urchin grazing should be considered as another form of disturbance that frees patches of the original substrate (Fanelli et al. 1994). In deeper water, sea urchins are less abundant and wave effects negligible. Disturbance is therefore less frequent and/or intense, and bio-mineralogy loses importance. Perhaps this is the reason why, in the whole Mediterranean Sea, the shallowest communities dominated by gorgonians, which are typical late-successional organisms, are found at greater depths on granite than on limestone (unpubl. obs.). Also, our data on circalittoral communities of northeast Sardinia showed that the difference in the number of species was not as great as for the shallower, infralittoral communities. Obviously, substratum stability is a consequence not only of depth but also of its intrinsic hardness and consistency, which are of direct importance with respect to wave action and bio-boring. Hardness and consistency, which are in turn related to the mineralogical composition, should be higher in granite than in limestone, thus suggesting the reverse of the observed pattern.

In the study of ecological succession, Connell & Slayter (1977) proposed 3 different mechanisms of interaction between organisms colonising hard substrates: facilitation, inhibition, and tolerance. We think that similar mechanisms might be recognised in the interaction between organisms and the substrate, which can facilitate, inhibit, or be neutral, not only to borers, but also to epilithic species, therefore affecting the development of communities.

Animals colonising sands and algae on rocks, as discussed above, might provide examples of inhibition by the substrate and of neutrality, respectively. A case of facilitation may occur when an organism, requiring high concentration of silica, uptakes this mineral directly from the substrate, instead of from the water. Gemmules of *Spongilla lacustris* L. reared in silica-free water may produce a complete spicular complement using different kinds of silicates laid down on the aquarium bottom as silica source (Jørgensen 1944). Volkmer-Ribeiro (pers. comm.) maintains that this phenomenon is also common in a natural environment: Brazilian fresh water sponges produce normal spicules in temporary water pools filled only by completely silica-free rain. In this habitat the only silica source is the quartzitic sand of the bottom of the pools and sedimented diatoms and spicules. To date, the biochemical mechanism allowing the dissolution and the uptake by sponges of particulate silica is not known. Nevertheless the marine sponge *Chondrosia reniformis* is able to collect and dissolve quartz grains (Bavestrello et al.

1995b), probably due to a considerable production of ascorbic acid (Cerrano et al. 1999).

The results of this study and the above considerations suggest that bio-mineralogy is likely to play a major role on benthic communities, selecting the biota and affecting not only the initial colonisation, as seen in the experiment of *Eudendrium* settlement, but also later assemblages, as apparent from our field data. This potential role has been largely neglected to date and further studies are needed to prove its importance.

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