

# Community structure of rhodolith-forming beds on the central Brazilian continental shelf

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**Abstract** The community structure of rhodoliths beds in the central Brazilian continental shelf was studied under the hypothesis that nongeniculate coralline algae are the major contributors of the individual rhodoliths. Samples were collected from five localities within a single area at 17–18 m depth. At each locality, rhodoliths were collected in 10 random quadrat samples along a 20-m transect. Our results show that dead cores of rhodoliths were significantly composed by nongeniculate coralline red algae rather than bryozoans, corals, or inorganic material. The live outer layers of the rhodoliths are composed mainly of 7 species of nongeniculate red coralline algae (*Lithophyllum coralline*, *L. johansenii*, *L. depressum*, *L. stictaeformis*, *Neogoniolithon brassica-florida*, *Spongites fruticosus*, and *Lithothamnion muellerii*) associated with other encrusting organisms such as bryozoans, sponges, corals, barnacles, and *Peyssonnelia* red algae. Significant differences were found in the proportion of *Lithophyllum* species in relation to other red coralline algae found in this study. Our results show that on the Brazilian continental shelf, the rhodolith-

forming species are quite higher in size than in any other studied areas in the world. There was no difference in the proportion of live-to-dead rhodolith materials, suggesting an old bed deposit. Also, the amount of calcium carbonate material in the specimens is relevant to take in account in terms of the CO<sub>2</sub> balance worldwide.

**Keywords** Coralline red algae · Community structure · Encrusting organisms · Rhodolith bed

## Introduction

Rhodolith beds support subtidal communities around the world relevant in many ecological processes (Foster 2001). The rhodolith skeleton is composed of carbonate components, commonly encrusted, abraded, and bioeroded (Checconi et al. 2006). Rhodolith sphericity (Bosence 1976; Foster et al. 1997), branch density (Steller and Foster 1995; Basso et al. 2009), and species composition (Steller et al. 2003, 2009) are influenced by water motion and depth. Substratum stability can be one of the main forces that drive rhodolith community composition, as demonstrated for some other environments (Littler and Littler 1984). Consequently, one or more encrusting species may become part of an individual rhodolith (Bosellini and Ginsburg 1971; Bosence 1983a, b, c; Reyes-Bonila et al. 1997; James et al. 2006). In any of the above cases, live material is fixed on the most external pigmented layer (Steller et al. 2003), strongly suggesting that proportions of live and dead material are unequal (Bahia et al. 2010). The settlement and survival of competing organisms can be limited by negative interactions with the coralline algae (Figueiredo et al. 1997; Villas-Boas and Figueiredo 2004).

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The structure of individual rhodoliths may vary from being composed of a single coralline species (Riosmena-Rodriguez et al. 1999, 2010; Steller et al. 2003) to a structure with a composition of multiple species termed “boxwork rhodolith” Bosence (1983a, b; Basso 1998; Baarli et al. 2012). This structure can result from the fragmentation of corals, reef rock, bivalve, and gastropod shells or coralline algae alone (Bosence 1985; Piller and Rasser 1996). Little is known about their community structure and whether beds are dominantly composed by individual or multispecific rhodoliths.

Our present knowledge of species composition within rhodolith beds is limited to few studies in European waters (Basso 1998; Birkett 1998; Sciberras et al. 2009), the Red Sea (Piller and Rasser 1996), the Gulf of California (Steller et al. 2003, Yabur-Pacheco and Riosmena-Rodriguez 2007), Canada (Gagnon et al. 2012), Southern Australia (Harvey and Bird 2008), and New Zealand (Nelson 2012). In the North Atlantic Ocean, some of the most common sessile elements within the rhodolith framework are bivalves, gastropods, serpulids, bryozoans, foraminifera, sponges, and tunicates (e.g., Florida Keys in Bosence 1985) with only limited data available about their relative abundance. In the South Atlantic, however, little is known about the relative abundance of encrusting organisms on rhodoliths, although their relevance for seaweed richness and biomass has been shown (Riul et al. 2009).

One of the most extensive areas for rhodolith beds in the world is on the Brazilian continental shelf ranging from

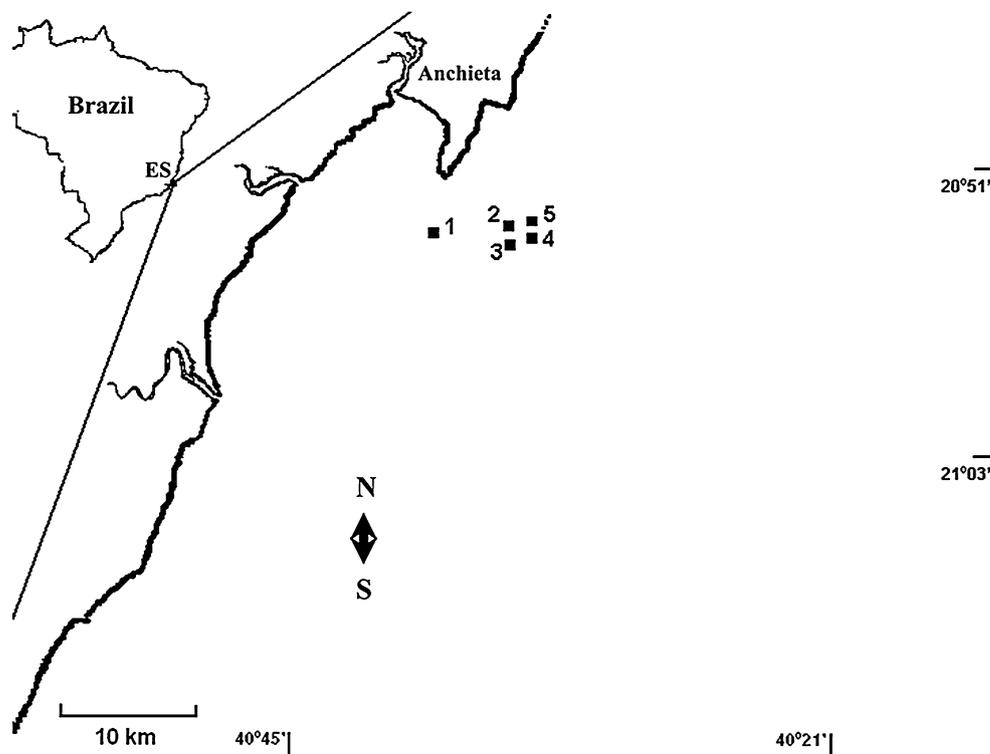
2°N to 25°S (Kempf 1970; Foster 2001), with a coastal length of 4,000 km. It has been documented as one of the most important calcium carbonate-producing bio-factories in the tropical South Atlantic (Amado-Filho et al. 2012c). Most of the known rhodolith beds in Brazilian waters are situated between 20- and 100-m depth (Kempf 1970), most of the known beds are in the north part of the country (Testa 1997; Amado-Filho et al. 2012a, b), and a single bed is at the south end of Brazil (Gherardi 2004; Pereira-Filho et al. 2012). However, little information is available about the composition of encrusting communities that build these rhodolith beds. Therefore, our goals are to (1) describe rhodolith-forming community structure; (2) identify the proportion of the main coralline algae genera that build rhodoliths; (3) determine the proportion of live and dead material in rhodoliths.

## Materials and methods

### Study area

The studied localities are located in Banco do Índio (BI) in Espírito Santo State. This state has a coastline of 421 km on the central Brazilian continental shelf (Fig. 1). Winds are predominantly and stronger from the east to northeast directions. However, southeastern winds are commonly associated with storms from June to September. Heavy rainfall occurs from October to January. The continental

**Fig. 1** Study site and localities of the studied rhodolith bed (Banco do Índio) on the central Brazilian continental shelf



**Table 1** Location and depth of the sample sites at central Brazilian continental shelf

Sites	Location	Depth (m)
1	20°54'09"S–40°38'46"W	18
2	20°54'14"S–40°34'50"W	18.3
3	20°54'12"S–40°34'50"W	18.8
4	20°54'32"S–40°35'05"W	18
5	20°53'23"S–40°34'07"W	17.7

shelf of Espírito Santo is influenced by the Brazilian Current that runs along the coast from north to south. This current is described in the literature as a weaker current compared to the Gulf Current in the North Atlantic (Silveira et al. 2000). The studied beds are situated at 18-m depth and 16 km offshore (Fig. 1; Table 1). Local oceanographic conditions feature high-speed currents at the sea surface, but slow bottom currents. Maximum at the bottom irradiance levels is about  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$  on the sea surface and  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the bottom with occasional turbidity. Average water temperature is 27 °C at the surface and 20–21 °C at the bottom, with a salinity of 37 ‰.

### Sampling

Samples were collected in the fall (April 2005). The five studied localities are separated by a distance of 200–1,000 m from each other (Fig. 1). SCUBA was used to cover a standard area of  $30 \text{ m}^2$  at each site by diving. Ten random  $0.25 \text{ m}^2$  quadrats in a 20-m transect were surveyed at each site, in total 50 quadrants. All rhodoliths were collected from each quadrat in order to measure size and sphericity and to quantify the relative abundance of coralline algae and other associated encrusting organisms.

### Rhodolith morphology

Sampled rhodoliths were measured and classified into five size classes for volume: 1 = (0.1–100 ml); 2 = (101–200 ml); 3 = (201–300 ml); 4 = (301–400 ml); 5 = (401–500 ml). The average size was also estimated based on the largest diameter and dry mass. Rhodolith shapes were analyzed following the classification according to Sneed and Folk (1958). Their degree of sphericity was estimated based on three diameters, where “S” is equivalent to the smallest rhodolith diameter, “I” refers to the intermediate measure, and “L” to the largest measure. These data were analyzed by the Tri-Plot Program (Excel, Microsoft) using the formulas:  $S/L$ ;  $L-I/L-S$  and  $(S^2/LI)^{1/3}$  which determines the degree of sphericity for each rhodolith sample and represents them on a triangular graph for each sampled site.

### Community structure

Live encrusting organisms from the superficial layer were taken from the rhodolith “boxwork” core. These were separated into high-order taxonomic groups and oven-dried at 60 °C prior to dry mass measurement. Samples were not decalcified in order to estimate their contribution to the bulk of the rhodolith structure. The biomass of each group was converted to a percentage of total rhodolith mass.

Taxonomic identification of nongeniculate coralline red algae was based on the paper by Villas-Boas et al. (2009) for *Lithophyllum*. The frequency of nongeniculate coralline algae (NG) genera (in the case of *Lithophyllum*, all four species were commonly present in the samples, and in the case of Masthoporoideae and Melobesioideae, one species was identified) was estimated for each rhodolith.

Normality and homoscedasticity were tested after percentage data were arcsin-transformed before analysis of variance (ANOVA) was used to test differences among organism abundance by groups. The Tukey test was used to detect differences among means when the ANOVA results with a probability of 0.05 (Zar 1984). Pearson’s correlation was used to examine the association between the abundance of calcareous algae and other groups of encrusting organisms.

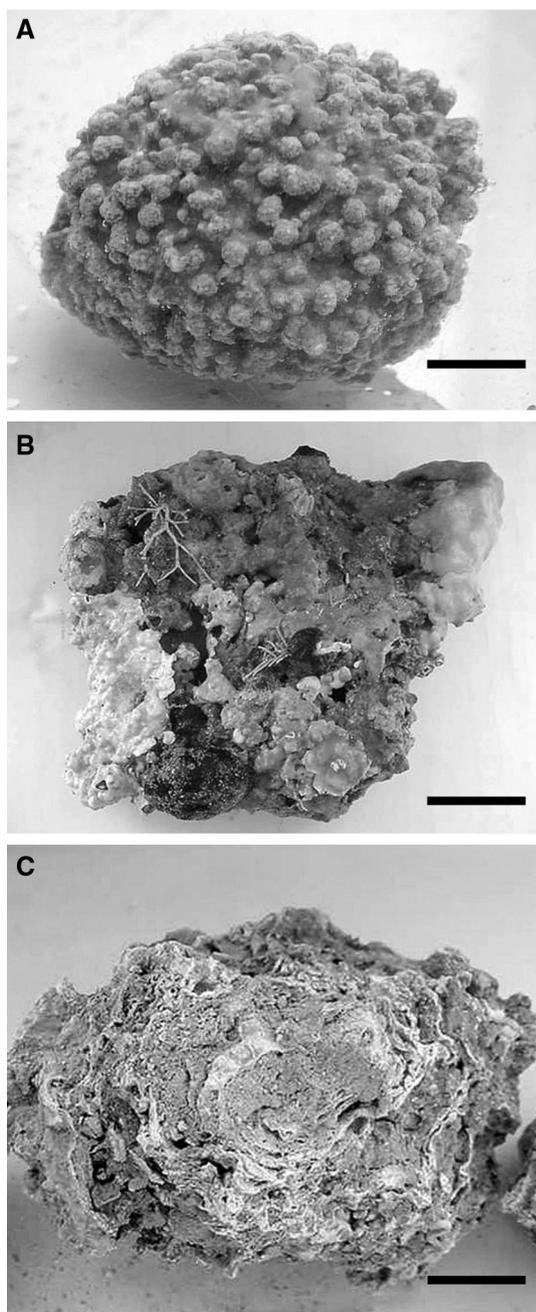
## Results

### Rhodolith morphology

A total of 50 individual rhodoliths were evaluated on site. The average and range size of rhodoliths in all the studied sites were (4)–10–(24) cm based on the largest diameter. The dry mass was (27)–162–(886) g, and the volume was (10)–165 (500) ml. Spherical forms included the compact, compact foliose, and compact elongated. These forms were composed by one nongeniculate species (Fig. 2a). Boxwork were composed by up to four nongeniculate genera (and one main species each) plus other encrusting organisms (Fig. 2b, c).

In most studied sites, the smallest size class (up to 100 ml) dominated except site 4 where there was also a high frequency of the size class immediately above (up to 200 ml). At site 5, there was no difference among size classes (Fig. 3: 1a to 5a).

In relation to degree of rhodolith sphericity, there was a high frequency of foliose forms (70 %) at sites 1, 3, 4, and 5, and only in site 2, there was a high frequency of both spherical and foliose forms (Fig. 3: 1b to 5b).



**Fig. 2** Individual rhodolith forms, according to Bosence (1983a, b, c), found in the studied bed: **a** spherical and monospecific rhodolith. Scale bars 2 cm; **b** “boxwork” rhodolith composing by up to four genera. Scale bars 3 cm; **c** “boxwork” rhodolith showing the concentric nature of core material. Scale bars 1.7 cm

### Community structure

The studied area is mostly composed by large, foliose, and nongeniculate multispecific rhodoliths with a “boxwork” internal structure and by smaller, spherical, and monospecific rhodoliths. *Lithophyllum* was the most frequent nongeniculate genus, including four species (*Lithophyllum*

*coralline*, *L. johanseni*, *L. depressum*, *L. stictaeformis*), followed in frequency by *Neogoniolithon brassica-florida*. Both genera were present in at least half of the rhodolith samples. *Spongites fruticulosus* and *Lithothamnion muellerii* were less frequent species (Fig. 4). Among the analyzed rhodoliths, 54 % were built by two nongeniculate genera, 32 % had only one genus, 13 % had three genera, and 1 % had four genera. All the material was examined based on external features confirmed by thin histological sections.

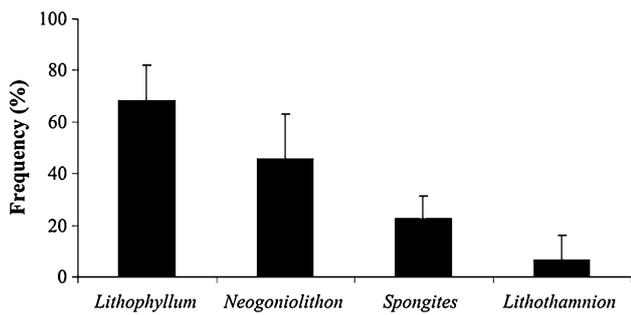
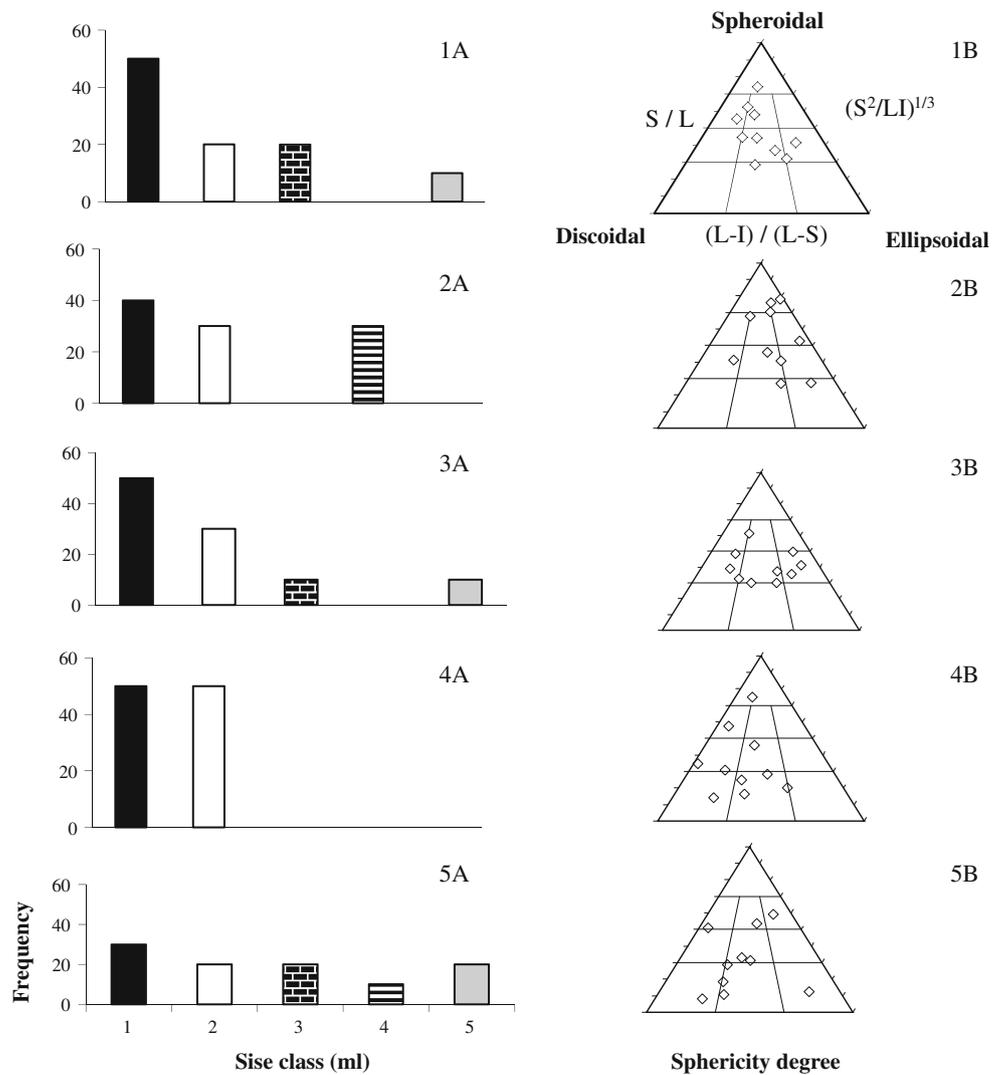
Comparing live encrusting organisms on the surface with the dead core of rhodoliths, it was observed that half the dry mass was composed of live organisms (including carbonate skeletons, shells, and sponge spicules) and the other half by a core formed by dead nongeniculate, dead bryozoans, dead corals, and mineral substrata (Fig. 2c). There was no significant difference between the percentage of live and dead materials that built rhodoliths at most studied sites (ANOVA,  $p > 0.05$ ), except for site 5 (ANOVA,  $p = 0.005$ ) (Fig. 5).

The abundance of live encrusting organisms and their contribution to rhodolith bulk structures differed significantly among rhodoliths, independent of the studied site. Nongeniculate coralline red algae were the dominant group of organisms in the rhodolith composition. Bryozoans and crustaceans (barnacles) were less abundant groups, considering that their material represents 3 % or less of the total biomass against 5 % of nongeniculate coralline algae. Sponges were found but represented the least important group. There was a significant difference in encrusting organism’s dry mass among studied sites and among all groups of organism, independent of each other (Fig. 6; Table 2). However, there was no significant correlation between nongeniculate coralline red algae abundance and other encrusting groups of organism (Pearson’s correlation,  $p = 0.14$  for sponges;  $p = 0.07$  for bryozoans; and  $p = 0.2$  for crustaceans). Among rare organisms, mollusk bivalves, corals, and the red calcareous alga *Peyssonmelia* were found that together represented 1 % of the total biomass among all the studied sites.

### Discussion

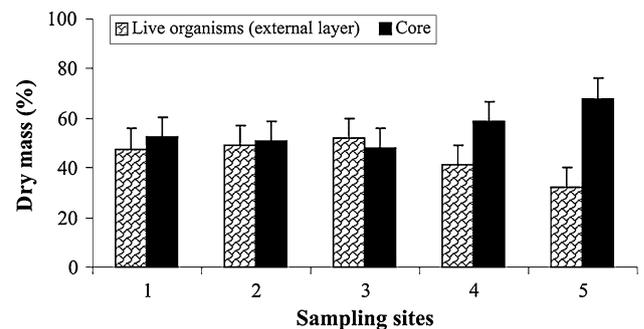
The results have shown that nongeniculate coralline red algae are the most abundant external layer component in the rhodolith structure. Other studies mentioned the presence of other encrusting organisms; however, they did not estimate their relative contributions to the rhodolith composition (Bosence 1985; Basso 1998; Prager and Ginsburg 1989; Gherardi 2004). In the studied area, spherical rhodoliths were usually composed of only one nongeniculate coralline red algal species and genus, while foliose

**Fig. 3** Size class volume frequency (a) and sphericity degree (b) of rhodoliths among studied sites (1–5;  $n = 10$  per site)



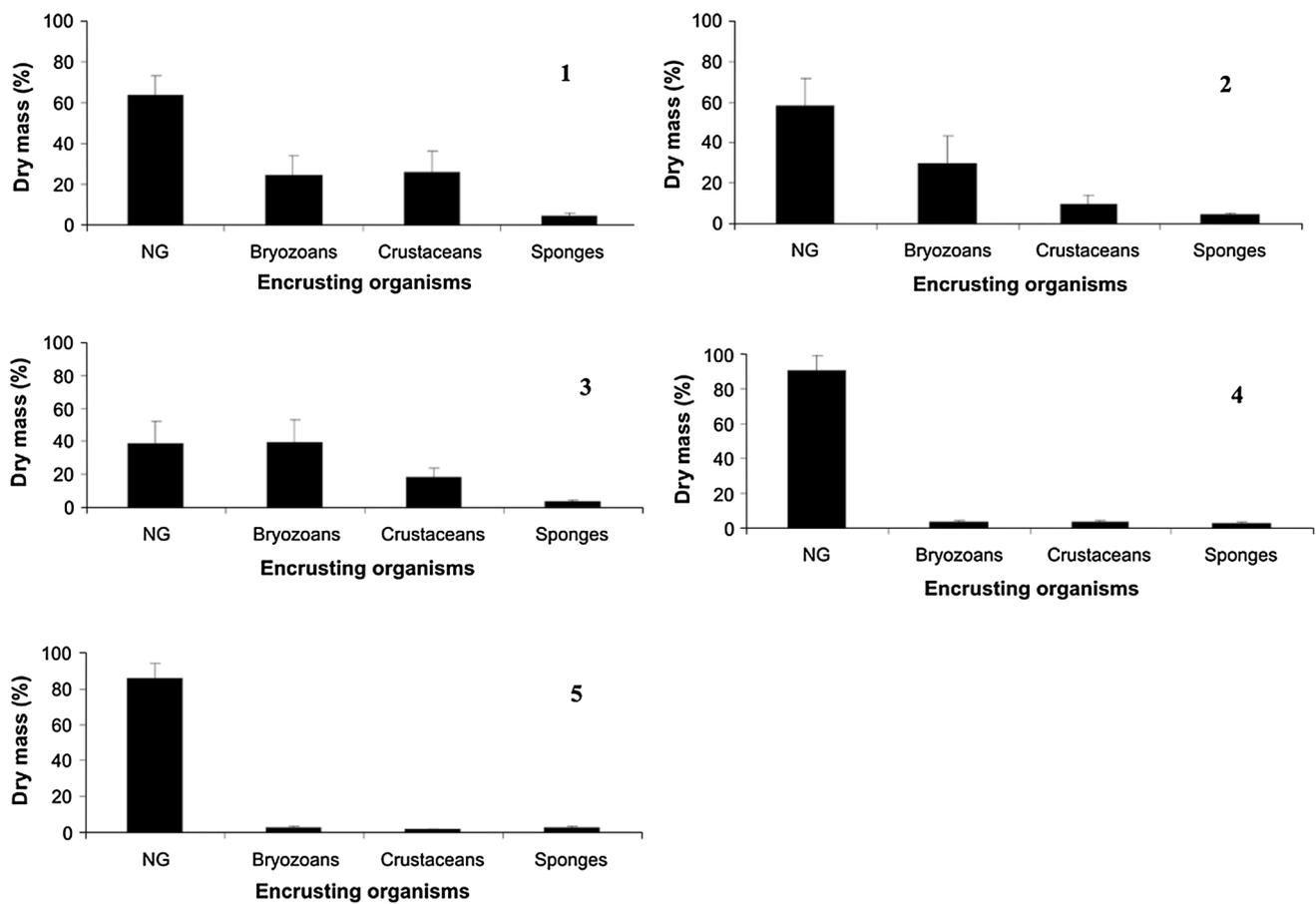
**Fig. 4** Mean and std of frequency of each coralline algal genus found in rhodoliths ( $n = 50$ )

rhodoliths were composed of up to four nongeniculate coralline red algal genera. In general, foliose rhodoliths composed of two or more nongeniculate coralline red genera and other encrusting organisms were the majority in this bed. Prager and Ginsburg (1989) found that sites with strong bottom currents and wave action tend to be



**Fig. 5** Mean and std of dry mass content of live and dead material in the boxwork rhodolith samples

dominated by spherical rhodoliths, while sites with slower bottom currents tend to induce the formation of foliose shapes. However, other more recent studies have shown that water movement is not always relevant for rhodolith shape (Foster et al. 1997; Marrack 1999). Rhodoliths with



**Fig. 6** Mean and std of abundance of encrusting organism groups in the composition of external layers of rhodoliths at five studied sites (1–5). (NG) nongeniculate coralline algae

**Table 2** Analysis of variance for the dry mass of encrusting organisms at the five studied sites (S) and four groups of organisms (O)

Treatments	<i>df</i>	<i>Ms</i>	<i>F</i>	Significance
Sites	4	$2.05 \times 10^{-7}$	5.2	0.002
Groups	3	$1.14 \times 10^{-8}$	29.2	<0.001
S × G	9	$4.2 \times 10^{-6}$	1.1	0.384
Error	184	$3.9 \times 10^{-6}$		

foliose shapes suffer from different disturbance sources. These forms can be partially covered by sediments which can cause a partial death of nongeniculate coralline red thalli, thereby providing space for other encrusting organisms to settle and to compete with these algae, influencing the formation and growth of the so-called “boxwork” rhodolith structures (Basso 1998). Spherical forms allow rhodoliths to roll and experience the same degree of disturbance on all sides, thus preventing the development of other encrusting organisms. In the studied sites, foliose forms equivalent to the “boxwork” configuration described by Basso (1998) allow rhodoliths to grow sideways.

Aggregation of such rhodoliths with each other forms a stable rhodolith bed which favors the settlement of marine invertebrates. The individual crust is lost in a coalescent process.

Rhodoliths may be entirely composed by one or more species of nongeniculate coralline red algae (Bosence 1983a, b, c; Basso 1998) or may have a core composed by other material (“nucleated rhodoliths”; Freiwald and Henrich 1994), indicating that they can grow from fragments or from spore settlement on a hard substratum (Foster 2001). In the spherical form of studied rhodolith samples, the core and all live surfaces were 100 % composed of nongeniculate coralline red algae. In the foliose forms, the rhodolith core was composed of an assemblage of skeletons of nongeniculate coralline red algae, bryozoans, corals, and mineral substratum. In general, half of the rhodolith dry mass was composed of live encrusting organisms and the other half by a dead core.

The dominant organisms in the outermost rhodolith live layer were the nongeniculate coralline red algae. However, bryozoans, crustaceans (barnacles), and sponges represented an important—but not predominant—component of

the community, growing as part of this assemblage. There was a significant difference of cover of encrusting organisms on rhodoliths among the studied sites, indicating that the rhodolith bed contains a heterogeneous community structure of encrusting organisms.

Bryozoans, the second most abundant organisms, were observed sharing space with nongeniculate coralline red algae on the surface of foliose rhodoliths. Site 3 was dominated by foliose rhodoliths, on which bryozoans and sessile crustaceans reached their greatest abundance. At the same site, nongeniculate coralline red algae presented the lowest abundance. However, there was no significant correlation between the abundance of nongeniculate coralline red, bryozoans, crustaceans, and sponges in all the studied sites. This result supports the findings of Steller et al. (2003) that rhodolith forms influence directly the diversity and abundance of associated animal taxa.

Bivalve mollusks, corals, and the calcareous red alga *Peyssonnelia* were the encrusting organisms with lower abundances. The shells of live and dead bivalve mollusks were fixed onto rhodoliths and might be incorporated into the core structure during its formation. *Peyssonnelia* might connect the structures formed by other organisms, consolidating the rhodolith structure. Corals represent the organisms with least contribution to the live layer of rhodoliths. However, many dead coral fragments were found in the rhodolith core. These may indicate that there was a replacement of the principal builder organism in the community during geological time. Bosence (1983c) observed that taxonomic composition and rhodolith structure can change through time, and these changes can be due to the increase of rhodolith shape or, alternatively, to an ecological succession from the rhodolith core to the outside reflecting a change in the benthic environment. Evidence of the ecological succession theory has been later provided by other authors (Basso and Tomaselli 1994; Basso et al. 1998).

In the studied area, four nongeniculate coralline red algal genera were found forming rhodoliths: *Lithophyllum* was the dominant genus and is one of the commonest rhodolith-forming genera worldwide. *Neogoniolithon* and *Spongites* are two other nongeniculate coralline red algae genera that greatly contribute to the composition of this area. These genera have been observed as rhodolith-forming taxa in the Mediterranean (Basso and Rodondi 2006). *Neogoniolithon* has also been identified as rhodolith-forming genus elsewhere (Riosmena-Rodriguez et al. 2010). *Lithothamnion* was the genus with lowest frequency, appearing at only two sites of the rhodolith bed, and this is different from elsewhere (Riosmena-Rodriguez et al. 2010). The presence of up to four nongeniculate coralline red algae genera and 7 species demonstrates how diverse the rhodolith beds are.

The genus *Lithophyllum* is described as one of the commonest rhodolith builders in the world. It is present in

both shallow and deep waters presenting a variety of external morphologies (Yabur-Pacheco and Riosmena-Rodriguez 2007; Riosmena-Rodriguez et al. 2010). In the Marine Biological Reserve of Arvoredo, southern Brazilian continental shelf, Gherardi (2004) described a small and isolated rhodolith bed composed of only one nongeniculate coralline red algal genus: *Lithophyllum*. In Manin Bay's Beds, Ireland, Bosence (1979) found two nongeniculate coralline red genera forming rhodoliths: *Lithothamnion* and *Phymatolithon*. In the Gulf of California, Steller et al. (2003) found up to three nongeniculate coralline red algal genera: *Lithophyllum*, *Neogoniolithon*, and *Lithothamnion* forming rhodoliths each with one species only, while in our study, we found at least 4 in *Lithophyllum* and 2 species of Mastophoroids.

The dominance of the foliose rhodolith forms indicates that this is a stable bed. There was no difference in the proportion of live and dead materials within any single rhodolith suggesting that this is an old calcareous deposit. Rhodolith cores are composed of an assemblage of skeletons of nongeniculate coralline red algae, bryozoans, corals, and a mineral substratum, suggesting that the overall rhodolith structure changed through time. The living outer layer of these rhodoliths is somehow similar, built by nongeniculate coralline red algae but associated with a higher number of groups of encrusting organisms. Rhodolith beds in the studied area have a heterogeneous community structure composed by nongeniculate coralline red algae and other encrusting organisms that serve as habitat for many other species, thus forming a complex and diverse environment that needs to be protected. There are other methodologies recently proposed (Leal et al. 2012) who might help in the understanding of rhodolith-forming structures, their associated biodiversity (Riosmena-Rodriguez and Medina-Lopez 2010), and their implications in global change (Basso 2012).

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