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# Rhodolith Morphology and the Diversity of Polychaetes Off the Southeastern Brazilian Coast

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## ABSTRACT

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Rhodoliths modify the physical characteristics of their environment, producing a habitat that can support diverse, associated fauna, where polychaetes often achieve high richness expressed in density and trophic diversity. Nevertheless, there are few studies that describe and identify the fauna associated with this habitat. In this research, specimens were collected from 6 to 18 m depth in Brazilian rhodolith beds: two off the southern coast of Espírito Santo, Brazil, and one in the Arolhos bank, Brazil. The most common rhodoliths were *Lithophyllum corallinae*, *Neogoniolithon* sp., and *Mesophyllum erubescens*. The rhodoliths ranged from large with short branches to small with long branches. Polychaetes at Espírito Santo, Brazil were predominately infaunal, whereas in Bahia, Brazil, they were mainly epifaunal living among finely branched structure. Twenty-six families were identified, four exclusive to Espírito Santo, Brazil, and nine in the Arolhos, Brazil. The most common families registered different species composition in both rhodolith beds, except for *Eunice multicylindris* and *Arabella mutans* found in both regions. Syllidae was the most abundant and species-rich family in Arolhos, Brazil. Rhodoliths off Espírito Santo, Brazil, hosted polychaetes dominated by burrowers, such as the Lumbrineridae, which were favored by their boxwork structure, built of invertebrates and inorganic material. Rhodoliths on the Arolhos, Brazil, hosted polychaetes dominated by carnivorous or herbivores families, such as the Syllidae. There is a significant difference between Espírito Santo, Brazil, and the Arolhos, as reflected by the polychaete taxocoenosis. This is demonstrated by a clear differentiation in species and family composition and also by feeding guilds, indicating how different rhodolith morphologies can affect community structure.

**ADDITIONAL INDEX WORDS:** Biodiversity, rhodolith growth-forms, feeding guilds, bioeroders, community structure.

## INTRODUCTION

Rhodoliths are formed by calcareous algae known as coralline algae (Corallinales, Rhodophyta), and they usually build large beds; some of which, located off the Brazilian coast, are the largest known in the world (Foster, 2001; Kempf, 1970). The rhodolith beds can stimulate increased local species diversity because of their spatial heterogeneity, often associated with the calcareous algae complex, branched structure that offers a great variety of ecological niches for associated fauna (Amado-Filho *et al.*, 2007; Figueiredo *et al.*, 2007; Foster, 2001; Sciberras *et al.*, 2009; Steller *et al.*, 2003). The interaction of physical and biological factors, such as water currents, light, depth, and action of bioturbators (*e.g.*, polychaetes), is reflected in the diversity of different growth-forms showed by these calcareous algae. Among the fauna

that inhabit rhodoliths, polychaete worms are often the most abundant and richest taxa (Bordehore, Ramos-Esplá, and Riosmena-Rodríguez, 2003; Grall *et al.*, 2006; Harvey and Bird, 2008; Sciberras *et al.*, 2009).

Most likely, abundance is affected in a positive way because polychaetes present a great diversity of feeding strategies occupying several different ecological niches (Fauchald and Jumars, 1979; Gaston, 1987; Paiva, 2006; Sciberras *et al.*, 2009). Polychaetes play a key role in the structural makeup and function of communities by contributing to the recycling of organic matter through their feeding habits and through bioturbation of the marine bottoms, which consequently, increases primary production by remineralization of nutrients (Lana *et al.*, 1996; Paiva, 2006). In addition, polychaetes are used as food for several commercially valuable fish (Amaral and Migotto, 1980; Petti, Nonato and Paiva, 1996) and are useful to marine biologist as environmental bioindicators (Reish, 1979). Because of their diverse feeding strategies, polychaetes are usually used to assess community structure through the analysis of their “feeding guilds” as conceptually proposed by Fauchald and

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Jumars (1979). This concept reflects more than the grouping of various taxonomic characteristics and should reflect the ecological habits of polychaetes because it includes several characteristics associated with feeding behavior, including motility, type of buccal apparatus, and trophic levels (Antoniadou and Chintiroglou, 2006). Feeding guilds might also reflect functional redundancy, expressed as the number of species within a given functional group that could prove useful for investigating the functional stability of a community in the face of environmental change (Wahl, 2009).

Polychaetes have an important role in carbonate production because of their capacity to bore through calcareous, hard substrates by forming growth reaction rims on live calcareous algae thalli or by boring inward, as seen in fossil rhodoliths (Bosence, 1979). The boring action of these worms includes both chemical attacks and mechanical abrasion with chaetae and mandibles (Hutchings, 2010; Schönberg and Wilkinson, 2001). Their boring activities are likely to erode calcareous reefs at higher rates, producing large amounts of calcium-carbonate sediment around and within reef formation (Leão, Dutra, and Spanó, 2006). Nevertheless, there are few studies that identify polychaete faunas associated with rhodoliths and especially that compare the relation between rhodolith morphology, faunal composition, and function. Exceptions are noted for a study on the coast of Ireland (Bosence, 1979), California (Hinojosa-Arango and Riosmena-Rodríguez, 2004), and another off the Australian coast (Harvey and Bird, 2008). The main goal of this survey is to evaluate the influence of rhodolith morphology on the composition and diversity of polychaete taxocoenosis.

## MATERIALS AND METHODS

### Study Area

Faunal specimens were collected from selected rhodolith beds: two off the southern coast of Espírito Santo State (20°49' S, 40°34' W and 20°55' S, 40°45' W) and one in the Abrolhos Marine National Park (20°51' S, 40°45' W and 17°59' S, 38°42' W) in Brazil (Figure 1). The most common algae in these rhodolith beds were *Lithophyllum corallinae*, *Neogoniolithon* sp., and *Mesophyllum erubescens*. The rhodoliths ranged in diameter from large (>50 mm) with short branches (warty growth-form *sensu* Woelkerling, Irvine, and Harvey, 1993) dominant in Espírito Santo, Brazil, to small (<10 mm) with long branches (fruticose maerl), in Abrolhos, Brazil. Details on the geographic location of these rhodolith beds and morphological description of coralline algae are given by Figueiredo *et al.* (2007) and Villas-Boas *et al.* (2009).

### Field Activities and Data Analysis

Sampling on the Espírito Santo, Brazil, rhodolith beds was carried out by scuba diving in April 2005. All rhodoliths were collected in 10 quadrats (0.25 m<sup>2</sup>) randomly placed along each of 20-m transects, in five different localities that were 200 to 300 m from each other at 18 m deep and one near shore at 6 m deep. The biggest rhodolith was collected from each quadrat. Polychaetes worms were then extracted through fragmentation of each rhodolith sample. On the Abrolhos bank, sampling

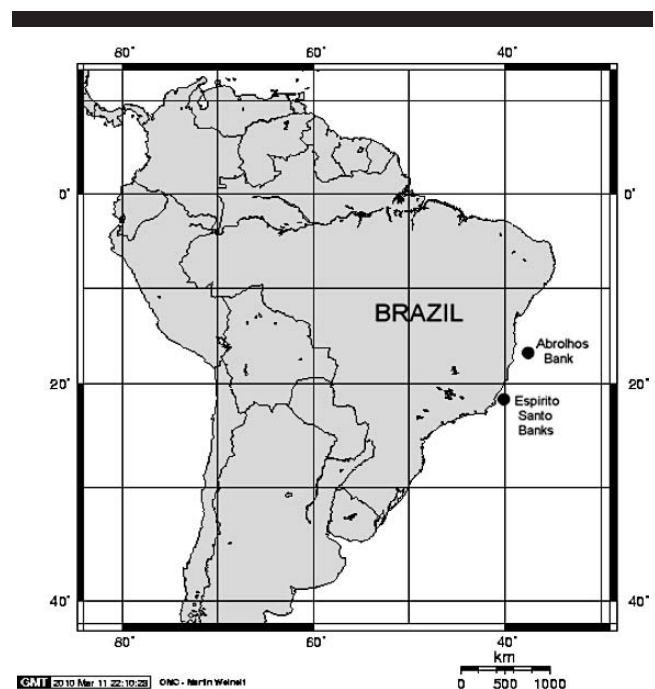


Figure 1. Map showing the locations of the Espírito Santo and Abrolhos regions of Brazil.

was carried out in April, August, and November 2000 using core samples 10 cm in diameter drilled 20 cm deep into the bed surface. Five random core samples were taken along each of four 10-m transects placed at right angles to the fringing reef at 9 m of depth ( $n = 20$ ). Core content was transferred to plastic buckets, and the biological content anesthetized using isotomic magnesium chloride, fixed in 10% formalin, and later preserved in 70% ethanol.

Polychaetes were separated from the rhodolith samples by washing them with freshwater and by elutriation using a net sample of 0.5-mm mesh size. All polychaetes were counted and identified to species level, whenever possible. Polychaetes worms were grouped in feeding guilds. This procedure followed the concept and classification established by Fauchald and Jumars (1979) as further revised by Gaston (1987), based on feeding apparatus, motility, and feeding strategies.

Because of differences in sampling procedures that were necessary given the nature of the bottom types at each locality, the observed richness and density of polychaetes did not allow a straightforward explanation of diversity patterns. To circumvent these problems, comparisons were performed by means of k-dominance curves (Lambshhead, Platt, and Shaw, 1983) through plotting the cumulative percentage of abundance against species rank on a log scale. Functional structure, as assessed by feeding-guilds, was compared between each rhodolith bed studied and to a third rhodolith bed studied by Martin (1987) in the Mediterranean. Goodness-of-fit for feeding-guild structure (*i.e.*, density of each guild for each locality and between each pair of localities) was assessed by means of a  $\chi^2$  test (Zar, 1996). For such a purpose, the abundance of each trophic group was previously log-transformed.

Table 1. Density of polychaete taxa exclusive to Espírito Santo and Abrolhos, Brazil, rhodolith beds.

Espírito Santo Rhodolith Beds			Abrolhos Rhodolith Beds		
Families	Taxa	Density	Families	Taxa	Density
Aphroditidae	<i>Pontogenia chrysocoma</i>	6	Acoetidae	<i>Acoetes pleei</i>	1
Euphrosinidae	<i>Euphrosine triloba</i>	3	Opheliidae	<i>Armandia maculata</i>	17
Polynoidae	<i>Chaetacanthus magnificus</i>	3	Sigalionidae	<i>Pelogenia kinberg</i>	1
	<i>Thormora cf. jukesii</i>	21	Spionidae	<i>Prionospio cristata</i>	6
	<i>Lepidonotus caeruleus</i>	32		<i>Prionospio heterobranchia</i>	96
	<i>Harmothoë macginitiei</i>	8		<i>Prionospio cf. light</i>	6
<i>Sabellaria sp.</i>	1	<i>Laonice petersenae</i>		1	
Sabellaridae			Paraonidae	<i>Arcidea (Acmira) simplex</i>	137
				<i>Cirrophorus sp.</i>	46
			Capitellidae	<i>Notomastus hemipodus</i>	1
				<i>Notomastus tenuis</i>	17
				<i>Neopseudocapitella brasiliensis</i>	1
				<i>Pseudocapitella sp.</i>	1
			Cirratulidae	<i>Tharyx sp.</i>	10
				<i>Caulleriella cf. alata</i>	15
			Goniadidae	<i>Goniada teres</i>	5
			Hesionidae	<i>Hesione sp.</i>	1
				<i>Podarke sp.</i>	1

## RESULTS

### Composition, Abundance, and Diversity of Polychaetes

Among 26 polychaete families found in this survey, four occurred exclusively in Espírito Santo, Brazil, and nine in the Abrolhos bank, Brazil (Table 1). Even those families common to both areas (Table 2) showed different specific composition, except for *Eunice multicylindri* and *Arabella mutans*, which were found to be shared by both. Among the families identified, Syllidae was the most abundant in Abrolhos followed by Paraonidae, whereas on Espírito Santo, the Polynoidae and Lumbrineridae were found to be dominant, but with much lower densities. In general, Espírito Santo had a much lower density with 167 individuals compared with 1361 from the Abrolhos bank, reflecting differences in sampling effort between both areas. Nevertheless, even though the Abrolhos bank was found to be richer, presenting 45 species against only 30 from the Espírito Santo rhodolith beds, the later was more diverse as shown in the plot of k-dominance curves where the curve for Espírito Santo is practically always below the curve for Abrolhos (Figure 2).

### Functional Structure

Functional diversity was also high with 16 feeding guilds found, which were coded with the following characteristics: surface-deposit feeders (S), subsurface-deposit feeders (B), suspension feeders (F), carnivores (C), herbivores (H), motile (M), discretely motile (D), sessile (L), tentaculate (T), jawed (J), and soft proboscis (X). There were six guilds of surface deposit feeders (SDJ, SDT, SMJ, SMX, SLX, and SLT), four guilds of subsurface deposit feeders (BDJ, BMJ, BLX, and BSX), three guilds of carnivores (CDJ, CMJ, and CDX), two guilds of herbivores (HMJ and HMX), and two suspension feeder guilds (FDT and FLT) (Table 3).

In a comparison among both regions and a similar study by Martin (1987) in the Mediterranean Sea (Figure 3), no differences were found for feeding guilds densities (in log scale)

between each Brazilian rhodolith beds and the Mediterranean example according to a goodness-of-fit adjustment ( $\chi^2$ ;  $p = 0.57$  and  $p = 0.66$ ). Nevertheless, there were significant differences between Espírito Santo and Abrolhos regions ( $\chi^2$ ;  $p = 0.02$ ). The dominant feeding guilds from the Abrolhos region were mainly herbivores (HMJ and HMX), carnivores (CMJ and CMX), and suspension feeders (FDT), whereas the Espírito Santo region was dominated by carnivores (CMJ and CDJ), surface deposit feeders (SDJ and SLX), and subsurface deposit feeders (BDJ, BMJ, and BLX). The rhodolith beds of Espírito Santo were dominated by families known to be borers like members of *Eunicea* (Eunicidae, Lumbrineridae, Oeonidae), composed mainly of carnivores and some subsurface deposit feeders, such as some members of the Eunicidae. On the other side, those from the Abrolhos were dominated by nonboring families, mainly herbivores or carnivorous, such as the family Syllidae or suspension feeders/deposit feeders, such as the Spionidae and Paraonidae.

## DISCUSSION

High species diversity is known from benthic systems associated with biogenic substrates, such as corals, bryozoans, and calcareous algae. The heterogeneity and structural complexity offered by these key players provide a variety of microhabitats and resources that organisms can use (Foster, 2001; Thompson *et al.*, 1996). Among these biogenic substrates, reefs formed by calcareous algae (rhodoliths) can play a key role on local benthic-community structure because of their ability to modify the physical characteristics of the environment. Hence, they are often called *bioengineers* (Bruno and Bertness, 2001; Jones, Lawton, and Shachak, 1997; Steller *et al.*, 2003). In these environments, polychaete worms are often one of the dominant taxonomic groups, as shown in a study on the Western Port rhodolith bed in Australia, with polychaetes comprising (89%) of the community (Harvey and Bird, 2008). In addition, polychaetes were also the most abundant taxon in the maerl bed community from the Bay of Brest, France,

Table 2. Density of polychaete taxa common to Espírito Santo and Abrolhos, Brazil, rhodolith beds.

Espírito Santo Rhodolith Beds			Abrolhos Rhodolith Beds			
Families	Taxa	Density	Families	Taxa	Density	
Amphinomidae	<i>Eurythoe complanata</i>	6	Amphinomidae	<i>Eurythoe complanata</i>	287	
	<i>Notopygos crenita</i>	1		Chrysopetalidae	<i>Chrysopetalum</i> sp.	1
Chrysopetalidae	<i>Chrysopetalum occidentale</i>	3	Dorvilleidae		<i>Schistomeringos rudolphi</i>	82
	<i>Dorvillea sociabilis</i>	3		<i>Protodorvillea kefersteini</i>	31	
Oeononidae	<i>Oenone fulgida</i>	1	Oeononidae	<i>Arabella mutans</i>	18	
Eunicidae	<i>Eunice imogena</i>	8	Eunicidae	<i>Eunice filamentosa</i>	1	
	<i>Eunice fucata</i>	1		<i>Eunice multicylindri</i>	1	
	<i>Eunice multicylindri</i>	2		Lumbrineridae	<i>Lumbrineris</i> sp.nov1	4
	<i>Marphysa</i> sp	4			<i>Lumbrineris</i> sp.nov2	1
	<i>Lysidice collaris</i>	4			<i>Lumbrineris coccinea</i>	1
Lumbrineridae	<i>Lumbrineris perkinsi</i>	37	<i>Clymenella</i> sp.		2	
	<i>Scoletoma cf maine</i>	1	<i>Mystides</i> sp.1		1	
	<i>Lumbrineris cf floridana</i>	1	<i>Mystides</i> sp.2	1		
Maldanidae	<i>Lumbriclymene</i> sp.	19	Maldanidae	<i>Phyllodoce</i> sp	1	
Phyllodocidae	<i>Phyllodoce madeirensis</i>	3		<i>Laonereis</i> sp	4	
				<i>Ceratonereis singularis</i>	19	
Nereididae	<i>Platynereis dumerilii</i>	11	Nereididae	<i>Nereis riisei</i>	1	
	<i>Ceratonereis hircinicola</i>	5		<i>Branchioma</i> sp.	7	
Sabellidae	<i>Hypsicomus</i> cf <i>circumspicines</i>	1	Sabellidae	<i>Fabriciola trilobata</i>	1	
				<i>Chone</i> sp.	6	
Serpullidae	<i>Pomatoceros</i> sp.	3	Serpullidae	<i>Vermiliopsis</i> sp.	2	
Syllidae	<i>Trypanosyllis zebra</i>	3	Syllidae	<i>Exogone</i> cf <i>arenosa</i>	278	
	<i>Langerhansia</i> sp.	1		<i>Syllis (Typosyllis) variegata</i>	116	
Terebellidae	<i>Streblosoma</i> sp.	3	Terebellidae	<i>Sphaerosyllis cf hystrix</i>	119	
				<i>Polycirrus abrolhensis</i>	6	
				<i>Polycirrus paivai</i>	22	

comprising 61 polychaete species, followed in decreasing dominance by crustaceans (55 species) and molluscs (33 species), according to Grall *et al.* (2006). Polychaetes comprised about (45%) of the cryptofauna in the El Requeson bed from Bahía Concepción in the Gulf of California (Steller *et al.*, 2003). However, Hinojosa-Arango and Riosmena-Rodríguez (2004) found the most abundant taxon to be the crustaceans in the same region. In another study, conducted on two maerl beds in Spain, polychaetes were the dominant taxon in the Tabarca and Benidorm beds, comprising 65% and 78%, respectively (Bordehore *et al.*, 2003). In the Mannin Bay maerl bed of Galway, Ireland, however, the most abundant phylum was found among the Mollusca, especially the bivalve, followed by the Polychaeta (Bosence, 1979). In another maerl bed from Scotland, the community was dominated by the crustacean *Upogebia deltaura*, whereas the next-most-abundant group was bivalve molluscs (Hall-Spencer and Atkinson, 1999). These variations in cryptofauna density associated worldwide with rhodolith beds can be due to biogeographic differences or variations in rhodolith morphology or different methods of sampling (Steller *et al.*, 2003). Therefore, further studies will be necessary to elucidate what factors can influence the cryptofaunal distribution and density in rhodolith beds (Harvey and Bird, 2008). In addition, there are few studies that assess community structure through trophic-groups analysis in this habitat (Bosence, 1979; Grall *et al.*, 2006;

Sciberras *et al.*, 2009), especially studies considering polychaetes only (Martin, 1987).

In this survey, polychaetes species recorded for both regions were carnivores, herbivores, suspension feeders, and subsurface-deposit feeders; however, their feeding guild distribution was found to be rather different among these rhodolith beds. Indeed, the prevalence of carnivores is very common in communities associated with hard substrates, and generally, the Syllidae are one of the most common polychaete taxon in this kind of substrata, including calcareous algae, coral reefs, bryozoans, *etc.* (Antoniadou and Chintiroglou, 2006; Figueiredo *et al.*, 2007; Grall *et al.*, 2006, Martin, 1987; Morgado and Tanaka, 2001; Nogueira, 2000). This relationship is likely to occur because of the range of body dimensions in this family (from <1 mm to >90 mm) (Serrano, San Martin, and López, 2006), multiple feeding strategies (Fauchald and Jumars, 1979; Giangrande, Licciano, and Pagliara, 2000), their reproduction strategies, and probably because of high motility that allows for shelter within calcareous rami. Even though the Syllidae occur in both regions, they were more abundant and richer on the Abrolhos bank. This is probably because they do not possess mandibles for boring into rhodoliths, such as those of members of the Lumbrineridae, which dominate the Espírito Santo rhodolith beds. In those beds, a *boxwork* structure is predominant, characterized by a nucleus built internally by bryozoans or other invertebrates that create holes. Further, the cavities

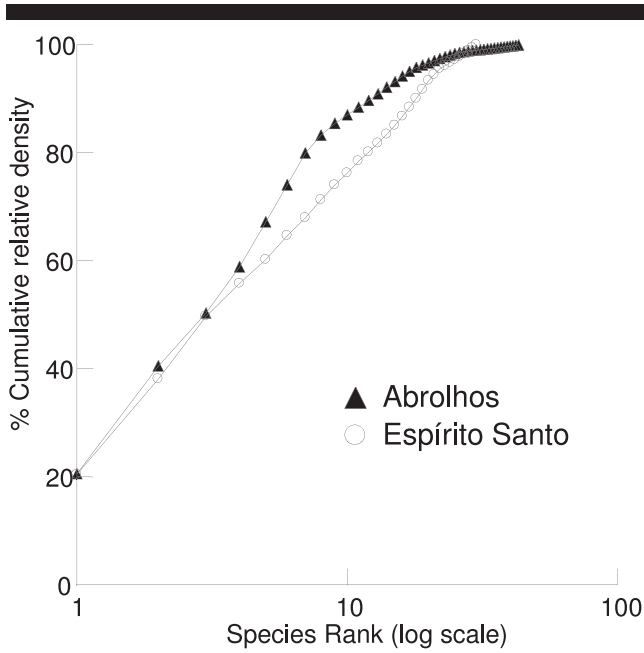


Figure 2. K-dominance curves for Espírito Santo and Abrolhos, Brazil, rhodolith beds.

are filled with inorganic material (pebbles) (Basso, 1998). These kinds of boxwork rhodoliths probably can be eroded more easily by burrowers. In contrast, *fruticose maerl* rhodoliths, dominant in the Abrolhos bank, are formed only by coralline alga and are difficult to burrow into by bioeroders such as polychaetes. Another difference can be observed in dominant families exclusive to each region, like the Polynoidae from the Espírito Santo beds and the Paraonidae from the Abrolhos region. Members of the Polynoidae are scale worms that have pharynxes armed with jaws and are common in shallow-water settings within a wide variety of life habitats. Polynoids are considered mainly carnivores, feeding on small crustaceans, echinoderms, and other polychaetes or herbivores, especially species from the genera *Harmothoe* and *Lepidonotus* (Fauchald and Jumars, 1979; Hughes, 1975).

According to Basso (1998), boxwork rhodoliths grow under low-energy conditions, resulting in large, stable forms that allow other organisms to coexist. Thus, a wide diversity of epiphytic macroalgae was found attached on these rhodoliths, promoting the accumulation of large amounts of biodebris among the rami/thallus and attendant incorporation with rhodoliths (Villas-Boas *et al.*, 2009).

Hutchings (1981) found more nonborer, polychaete, “opportunistic” species, living into holes created by others burrowing organisms, within blocks of dead coral. According to Hutchings

Table 3. Density and feeding guilds of polychaete families in each studied area of Brazil and in the Mediterranean. Classification according to Fauchald and Jumars (1979), reviewed by Gaston (1987). Codes are surface-deposit feeder (S); subsurface-deposit feeder (B); suspension feeder (F); carnivore (C); herbivore (H); motile (M); discretely motile (D); sessile (L); tentaculate (T); jawed (J); and soft proboscis (X).

Families	Feeding Guilds	Mediterranean	Abrolhos	Espírito Santo
Achoetidae	CMJ	0	1	0
Amphinomidae	CMX	0	287	7
Aphroditidae	CMJ	0	0	6
Arenicolidae	SDX	10	0	0
Capitellidae	BMX	31	23	0
Chaetopteridae	FLT	335	0	0
Chrysopetalidae	CMX	147	1	3
Cirratulidae	SDT	242	25	0
Dorvilleidae	HMJ, CMJ, SMJ	6	113	3
Eunicidae	BDJ, CDJ, HMJ	288	2	19
Euprosinidae	?	0	0	3
Glyceridae	CDJ, BMJ	117	0	0
Goniadidae	CMJ, CDJ	0	5	0
Hesionidae	CMJ, HMJ, SMJ, BMJ	116	2	0
Lacydonidae	BMX	80	0	0
Lumbrineridae	CMJ, BMJ	90	16	39
Maldanidae	SLX, BLX	307	2	19
Nereididae	SDJ	474	16	24
Oeonidae	CMJ, SMJ	16	18	4
Opheliidae	BMX	5	17	0
Orbinidae	BMX	29	0	0
Paraonidae	SMX, HMX, BMX	311	183	0
Phyllodocidae	CMX	104	3	3
Polynoidae	CMJ	100	0	64
Sabellariidae	FFT	723	0	1
Sabellidae	FDT, FLT	1694	14	1
Scalibragmidae	BMX	9	0	0
Serpulidae	FLT	614	2	3
Sigalionidae	CMJ	0	1	0
Sphaerodomidae	BMX	5	0	0
Spionidae	FDT, SDT	424	109	0
Syllidae	CMJ, HMJ, SMJ	3.535	509	4
Terebellidae	SDT, SLT	13	28	3

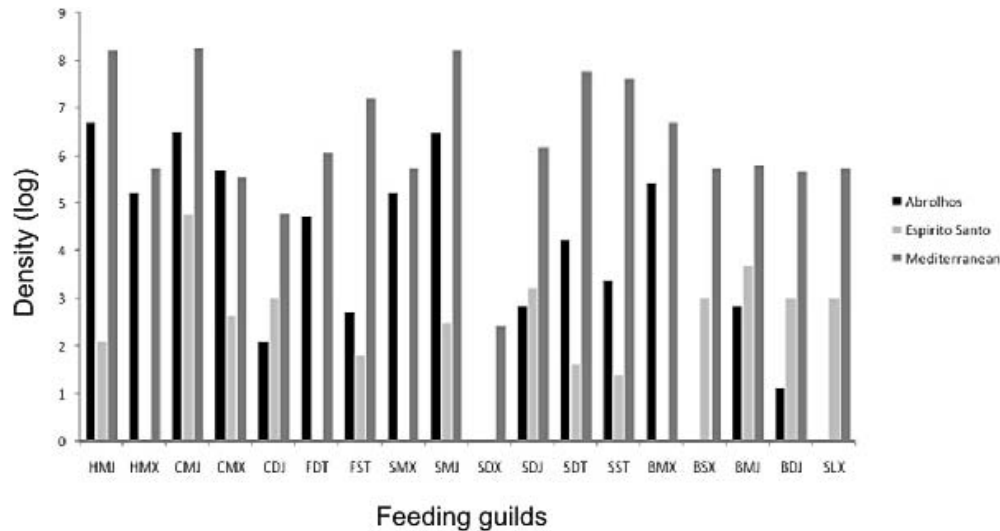


Figure 3. Density of feeding guilds in rhodolith beds in two Brazilian regions studied and one region in the Mediterranean studied by Martin (1987).

(1981) and Hutchings and Weate (1977), opportunistic species are the major component of the cryptofauna because they present great dispersion and colonization abilities that allow them to occupy coral substrata. This could also explain the dominance of the Paraonidae in the Abrolhos bank.

One possible explanation for the low polychaete density in Espírito Santo is that rhodoliths from the area are strongly colonized by sponges, bryozoans, and other organisms, and because their stability increases the competition for space among those organisms at the expense of polychaete settlement (Basso, 1998; Hutchings and Weate, 1977; Villas-Boas *et al.*, 2009). These factors may explain why the different rhodolith beds demonstrated different feeding guilds of polychaetes composition and why they were not different from the Mediterranean region studied by Martin (1987). Mediterranean rhodolith beds are formed mainly of a mix of foliose and fruticose morphotypes (*e.g.*, *Pseudolithophyllum expansum*, *Mesophyllum lichenoides*, and *Neogoniolithon mamillosum*), giving them a more complex structure and, thus, a more diversely associated community. Moreover, two studies regarding community structure of different growth forms in rhodolith species, conducted in the Gulf of California, México, (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Steller *et al.*, 2003) showed that large, complex thalli and densely branched rhodoliths are important factors that can influence the abundance patterns and serve as a predictor of richness.

In fact, Hinojosa-Arango and Riosmena-Rodríguez (2004) discovered an associated faunal abundance and a richness higher in *Neogoniolithon trichotomum* than *Lithophyllum margaritae*, so they did not see a significant difference between growth forms but found a difference between different rhodoliths-forming species. This result may be related to the fact that calcareous algae are an important source for invertebrate larval settlement and this kind of settlement cue can vary according to calcareous algae species (Morse, 1992). That variations in physical factors can strongly influence the

associated community structure should also be considered (Bosence, 1979; Steller *et al.*, 2003). In contrast, the *k*-dominance curves shown in this study (Figure 2) clearly indicate that the Espírito Santo rhodolith beds were more diverse than Abrolhos bank, although lower in density. It seems likely that the boxwork structure of some rhodoliths allows polychaetes to explore both inside and outside rhodoliths. On the other hand, rhodoliths from the Abrolhos bank offered only one restricted niche in which this interstitial habitat was developed.

In contrast with other studies, herbivores were found to be the dominant polychaete in the Abrolhos bank. It is mainly the Syllidae that correspond to 50% of the total density of polychaetes found in the Abrolhos bank. Among the more abundant species are herbivores belonging to the genera *Exogone* and *Sphaerosyllis* (Serrano, San Martín, and López, 2006). The other genus in the Syllidae common on the Abrolhos is *Syllis*. This genus has been considered carnivorous because of the work by Fauchald and Jumars (1979), but a more recent study suggests that *S. prolifera* has an omnivorous behavior (Giangrande, Licciano, and Pagliara, 2000). Furthermore, the dorvilleid *Schistomeringos rudolphi*, also one of the most abundant species, is herbivorous (Fauchald and Jumars, 1979). On the other hand, high abundances of deposit feeders/suspension feeders from members of the Paraonidae and Spionidae, living on a hard substrate, can be explained by hydrodynamic conditions (Morgado and Tanaka, 2001), which could signify an increase in sedimentation processes.

In the Espírito Santo region, where rhodoliths were bigger, polychaete borers were very common, being represented by members of the Lumbrineridae, Eunicidae, and Oeonidae. All members of these families have strong mandibles, like that of the *Lysidice collaris* (Hartman, 1954), capable to boring into corals, but that does not mean that they are carnivorous. In fact, Gambi, Van Tussenbroek, and Brearley

(2003), studying mesofaunal borers in the seagrass *Thalassia testudinum*, found *L. collaris* within the dead leaves of the seagrass, suggesting this species is likely to be a detritivore. A similar dubious feeding habit can be stated for the most abundant families in Espírito Santo: Lumbrineridae and Polynoidae. According to Gaston (1987) some species, mainly of the genus *Lumbrineris*, might be carnivorous when adults, but subsurface-deposit feeders when juvenile. Furthermore, Carrasco and Oyarzún (1988) studied feeding strategies of *Lumbrineris tetraura* from polluted sediments and showed that their feeding habit was mainly carnivorous selectively, preying on polychaetes worms, especially medium-sized sigalionids (*Sthenelais helenae*). However, they can adopt other strategies secondarily (Carrasco and Oyarzún, 1988). The abundance of the deposit feeders in Espírito Santo can be explained by decomposition from epiphytic macroalgae together with the sedimentation of particulate organic matter (Grall *et al.*, 2006).

There are few studies that draw comparisons between rhodolith morphology and faunal composition. Those that do (Harvey and Bird, 2008; Hinojosa-Arango and Riosmena-Rodríguez, 2004) find no differences between fauna associations related to the morphotypes of fruticose and foliose rhodoliths. However, in our study, we found a clear difference in polychaetes species and family composition and also in feeding guilds in which the boxwork structure of rhodoliths found in Espírito Santo included sediments with internal structure. Other multispecific organisms from within the boxwork structure account for the dominance of infauna, especially the borers, carnivores, surface deposit feeders, and subsurface deposit feeders which probably feed on organic matter at the maerl layer - sediment layer interface (Grall *et al.*, 2006). Whereas, true rhodoliths from Abrolhos sediments, contain particulate organic matter, that was deposited on thallus/rami. This factor can help explain the dominance of suspensive feeders and epifaunal deposit feeders. On the other side, the dominance of herbivores from the Abrolhos bank probably can be explained by the presence of microphyto-benthos living on the rhodolith thallus (Grall *et al.*, 2006).

Differences between localities indicate that polychaete species well known as bioeroders dominate in Espírito Santo rhodolith beds. These activities normally lead to a net rate of erosion by boring and thus a carbonate production of 130 to 400 g.m<sup>-2</sup>.y<sup>-1</sup> in tropical and temperate rhodoliths beds (Bosence, 1979; Gherardi, 2004) that are close to 356 g.m<sup>-2</sup> in coral reefs (Osorno, Peyrot-Clausade, and Hutchings, 2005). Nevertheless, differences in rhodolith morphology and community structure between both areas can also be related to high sediment production in the shallow near shore. Taken together, these factors indicate that variations in rhodoliths morphology and sediment producing processes could affect community structure, as reflected by the polychaete taxocoenosis.

## CONCLUSIONS

- (1) Rhodolith morphology affects community structure and a clear difference was seen with polychaete species, family composition, and feeding guilds between regions.

- (2) In Espírito Santo, boxwork rhodoliths account for burrowing polychaetes composed of carnivores, surface deposit feeders, and subsurface deposit feeders, which probably live on organic matter of at the sediment layer interface.
- (3) On the Abrolhos bank, maerl rhodoliths account for nonburrowing polychaetes composed of herbivores, suspension feeders, and epifaunal deposit feeders, probably living on organic matter deposited within thallus/rami.
- (4) Rhodolith beds are more diverse in Espírito Santo than they are in the Abrolhos bank, probably because of their boxwork, complex structure, which offers a variety of niches for polychaetes.
- (5) Sediment-producing processes from nearshore rhodolith beds may affect community structure. Thus, polychaete feeding guilds differ between rhodolith beds, because the Abrolhos bank is located offshore and Espírito Santo is a nearshore habitat.

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