Herbivory in a Rhodolith Bed: a Structuring Factor?

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Abstract: Rhodolith beds are widespread along the Brazilian coast, being important marine environments supporting a high biodiversity. Although studies on rhodolith beds have increased since the last decade, little is known about the role of herbivory on these environments. We evaluated the influence of herbivory on the distribution and abundance of the epiphytic algal community occurring in a rhodolith bed in southern Brazil through a grazers exclusion experiment. Fully, partially meshed and unmeshed cages, in addition to control samples, were randomly distributed at two different depths. Lower values of epiphytic algal biomass were found within the fully, partially and unmeshed cages comparing to control areas. The increase of herbivory by mesograzers within the cages is suggested as cause for the lower values of biomass. The role of other factors potentially contributing to the structure of the rhodolith bed community is also discussed.

Key words: coralline algae, epiphytic algae, grazers exclusion, mesograzers.

Resumo: Herbivoria em um Banco de Rodolitos: um Fator Estruturador? Bancos de rodolitos estão amplamente distribuídos ao longo da costa brasileira, sendo importantes ecossistemas de ambientes marinhos, possuindo uma alta biodiversidade. Embora estudos em bancos de rodolitos tenham aumentado desde a última década, pouco se sabe sobre o papel da herbivoria nesses ambientes. Nós avaliamos a influência da herbivoria na distribuição e abundância da comunidade algal epifítica ocorrendo no banco de rodolitos no sul do Brasil, por meio de um experimento de exclusão de herbívoros. Gaiolas totalmente e parcialmente teladas e gaiolas sem tela, além de áreas controle, foram aleatóriamente distribuídas em duas profundidades diferentes. Menores valores de biomassa de algas epifíticas foram encontrados nas gaiolas comparativamente aos controles. O aumento de herbivoria por mesoherbívoros é sugerido como causa para os menores valores de biomassa dentro das gaiolas. O papel de outros fatores que potencialmente contribuem para a estrutura do banco de rodolitos também é discutido.

Palavras chave: algas calcárias, algas epífitas, exclusão de herbívoros, mesoherbívoros

Introduction

The biological interactions in marine environments have traditionally been studied through predators, competitors and/or grazers manipulations experiments (Coyer & Witman 1990; McClanahan et al. 2002). Some studies on succession involved manipulation of consumers (Lubchenco & Gaines 1981) and grazers exclusion experiments have largely been adopted in studies of biological relations in different environments (Hixon & Brostoff 1996, McClanahan et al. 2002). However, in soft bottom environments the biological interactions are still not well understood (Thrush 1999, Eriksson et al. 2005).

The corallines algae (Corallinales, Rhodophyta) form a group of over 1000 species with a wide geographical distribution, frequently abundant in areas with high grazing intensity

(Woelkerling 1988) and chronic physical disturbance (Hinojosa-Arango et al. 2009). The forms growing unattached are known as rhodoliths, nodules or maërl and form large beds in different latitudes and depths (Foster 2001). This biogenic substratum supports a high diversity of organisms, including rare, endemic (De Grave 1999) or economically important species (Bosence 1979, Wilson et al. 2004). However, although maerl beds support such diversity, little is known about the interactions among the associated species (Hinojosa-Arango et al. 2009).

Several biotic, and non-biotic, factors are known to influence the diversity, distribution and abundance of the macrobenthic community associated to the rhodolith beds (Ballesteros 1988, Keats et al. 1997, Suzuki et al. 1998, Daume et al. 1999, De Grave 1999, Steller et al. 2003, Villas Bôas & Figueiredo 2004, Riul et al. 2008). Some authors suggested that crustose corallines are appropriate substratum for epiphytic macroalgae (i.e. Figueiredo et al. 1996), which depend on herbivores to prevent fouling (Steneck 1983a). Factors such as sloughing of epithelial cells (Johnson & Mann 1986) and hydrodynamics (Littler & Littler 1984) also play a role on preventing fouling. However, in spite of their importance, studies on the roles of herbivory, a recognized component on the determination of spatial-temporal patterns of species diversity and abundance on hard substratum (Worm & Chapman 1998) are rare in coralline beds, where the physical and biological dynamics are very peculiar (Foster 2001). Here we tested if herbivory has a key role on the abundance of the macrophytobenthos associated to a rhodolith bed in southern Brazil and provided qualitative data on the zoobenthic groups that may contribute to explain the observed patterns.

Material and Methods

Study site - The experiment was carried out at the Arvoredo Marine Biological Reserve, which is formed by Galés, Deserta and Arvoredo Islands. The rhodolith bed is located at Rancho Norte Bay, on the west side of Arvoredo Island (48° 22,00' W, 27° 17,5' S). The site is protected from southern winds and relatively protected from waves (Fig. 1). The area of the bed is of approximately 10 ha and the shallowest and deepest parts are respectively at 5 and 16 m depth. According to the Brazilian law, biological reserves are fully protected, thus fishing is prohibited within the studied area.

Experimental design - Following Chapman (1998), two sets of 12 cages were randomly placed on the rhodolith bed, spaced 2 m from each other, at the depths of 7 and 13 m. The cages were 50x50x20

cm (covering area of 0,25 m^2) and 1 cm mesh aiming to exclude grazers larger than 1 cm, such as urchins, fish and large molluscs. These organisms are important herbivores in marine environments (Creese 1988, James 2000, Stimson 2001). Each experimental set was separated into three subsets with four cages each: i) fully meshed (F), to evaluate the grazers exclusion effect; ii) partially meshed (one side open) (P); and iii) unmeshed (only frame) (U), these two subsets were designed to test for possible artifacts caused by the experimental apparatus, such as light attenuation and water motion. In addition, areas of the same size of the cages were randomly placed near the cages, also spaced 2 m from them, and used as control plots (C).

The experiment was carried out from August to October 2002. Every month a set of treatments was sampled at each depth. Samples consisted of seven rhodoliths being randomly taken from each cage and control areas (n=14 rhodoliths) and kept in labelled plastic bags with sea water/formalin 4%. The samples were analysed and identified in laboratory and the epiphytes from each rhodolith were separately dried at 50oC until constant weight was observed.

Along with the experiments the zoobenthos with potential to be foraging inside the cages were surveyed. Twenty samples (15 cm diameter X 10 cm height) were taken along the whole batimetric extension of the rhodolith bed. The samples were fixed in sea water/formalin 4%, and at the laboratory the samples were sieved (0.5 mm), sorted under microscope and identified.

Material identification - Chlorophyta, Rhodophyta and Phaeophyceae were identified to the species level and colonial diatoms to the order level. The macroalgae followed the nomenclature proposed by Wynne (2005). The Corallines (Corallinales, Rhodophyta) identification followed the methodology and bibliography described by Horta (2002).

Zoobenthic specimens were identified to class, order or family levels and classified according to their preferential feeding habits following Fauchald & Jumars (1979) for Polychaeta, Arruda et al. (2003) for molluscs. Feeding-types of scarce macrofauna taxa (e.g. Sipunculida, Phoronida, Chaetoptera and Nemertea), Crustacea, Cnidaria and Echinodermata taxa were divided according to the main habit of the group after Barnes (1980). Due to the high level of identification used here the feeding habits were classified according to most likely and less likely guilds.

Statistical analysis - We evaluated the grazers exclusion effect on the abundance of the

phytobenthos associated to rhodoliths by comparing the dry epiphytic biomass (g) among the different treatments.

After assessing homogeneity of variances using the Cochran test, we performed a Factorial

Analysis of Variance to test for significant differences comparing biomass under different months (2), depths (2) and treatments (4). Whenever significant differences were found ($p<0.05$), the Newman-Keuls test was used.
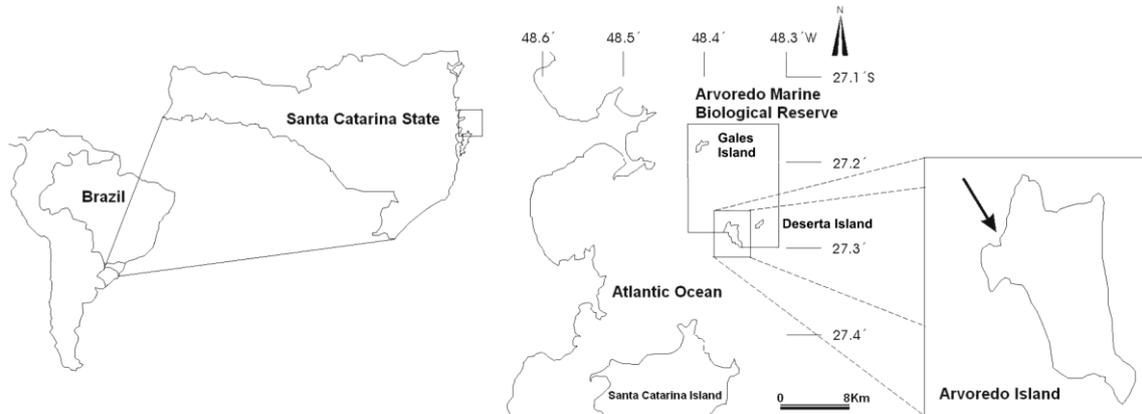

Figure 1. Map showing the location of the Arvoredo Marine Biological Reserve. The rhodolith bed, where the experiments were carried out, is indicated by the arrow in detail.

Results

Six species of corallines were identified: *Lithophyllum margaritae* (Hariot) Heydr., *L. stictaeformis* Hauck and *Hydrolithon* sp. of the family Corallinaceae, and *Lithothamnion heteromorphum* (Foslie) Foslie, *L. rugosum* Foslie and *Mesophyllum erubescens* (Foslie) M. Lemoine of the family Hapalidiaceae (Harvey *et al.*, 2003).

Among the epiphytes, 16 species were identified to the species level, of which 11 Rhodophyta, one Phaeophyceae and two Chlorophyta. One colonial diatom of the order

Pennales (Bacillariophyta) and one non identified cyanobacteria was found. The operational taxonomic unit (O.T.U) more frequent at both depths was a mucilaginous material (MM), which was formed by Cyanophyta and bio-debris (Table I).

The Factorial ANOVA demonstrated that the biomass was not affected by month and depth, and that there was no interaction between these factors and treatments. However, the analysis revealed significant differences on the biomass when comparing the exclusion treatments and control samples (Table II; Fig. 2).
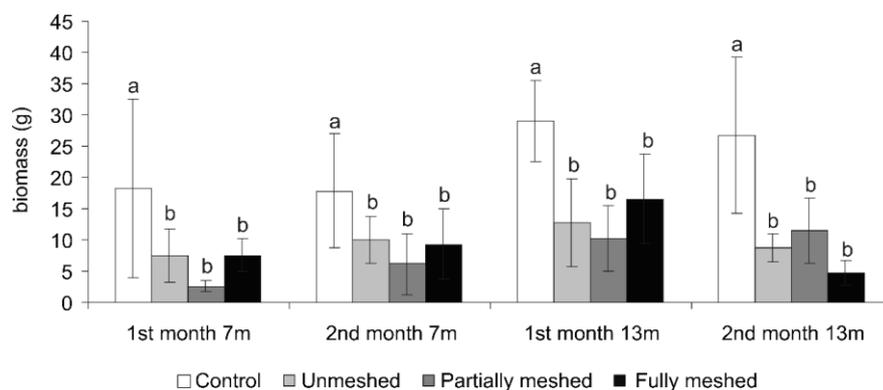

Figure 2. Means (±S.E.) for biomass (g/rhodolith) of fresh macroalgae (dry weight) associated to rhodoliths at Arvoredo Marine Reserve under the different treatments (n=14) at the depths of 7 and 13 meters. Data from the first and second month are shown. Different letters mean significant differences according to the Newman-Keuls test ($p<0.05$).

Table I. Summary of qualitative data (epiphytes on rhodoliths) from different treatments (where: C, control plots; U, unmeshed, P, partially meshed; F, fully meshed).

O.T.U	Samples															
	7 meters								13 meters							
	First month				Second				First month				Second month			
	C	U	P	F	C	U	P	F	C	U	P	F	C	U	P	F
Acrochaetium spongicola Weber-van Bosse												X				
Asparagopsis taxiformis (Delile) Trevis.												X				
Ceramium brasiliense A.B. Joly					X	X										
Ceramium comptum Børgesen										X	X	X			X	
Ceramium flaccidum (Kütz.) Ardiss.										X		X				
Ceramium sp.										X					X	
Ceramium tenerrimum (G. Martens) Okamura						X										
Codium sp.														X		
Codium taylorii P.C. Silva														X		
Colpomenia sinuosa (Roth) Derbès & Solier	X	X			X											
Champia sp.					X	X						X		X		X
Colonial diatom										X		X				
Gelidium crinale (Turner) Gaillon						X										
Herposiphonia secunda (C. Agardh) Ambronn						X										
Lomentaria corallicola Børgesen											X					
Muscilaginous mat	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Discussion

The bed is characterized by a low fresh algae abundance if compared to other northeastern Brazilian rhodolith beds (Riul *et al*. 2008) which has been suggested to be related to the corallines physiological strategies such as epithelial sloughing, and herbivory (Keats *et al*. 1997). It is in accordance with a previous survey carried in January 2003 when the low abundance of epiphytic fresh macroalgae was observed in the rhodolith bed (Horta et al. 2008).

In our study the algal turf presented the highest frequency in all samples at the two depths, while species of the genera *Ceramium* presented the second highest frequency. However, Horta *et al*. 2008 found *Dictyota pulchella*, *Asparagopsis taxiformis* and *Sebdenia flabellate* were the most abundant species at depths of 5, 10 and 15 m, respectively. These differences in composition can be related to seasonal variations, since our study was carried out in the winter (Horta et al. 2008).

The lower biomass found within the cages in all treatments, when compared to the control areas can be related to an increase of herbivory within the cages. The treatments might have excluded the bigger herbivores (urchins, fish and molluscs) but not the smaller ones, such as small gastropods, isopods and other mesograzers (see Table III) that are naturally abundant in these environments, occurring in a similar number of species to that observed in other marine systems like corals, maerl and kelp beds (Hinojosa-Arango & Riosmena-Rodríguez 2004). In addition, the treatments may have acted as refuges for these smaller organisms which, in turn, found safety from their larger natural predators within the cages (Sala 1997). Mesograzers play an important role on removing epiphytic algae (Brostoff 1988) (also see video available at: www.ccb.ufsc.br/bot/ficologia/videos.php). An herbivores exclusion experiment taken in the Mediterranean Sea demonstrated an increase on the mesograzers biomass inside the cages in the 15th week of experiment, when the biomass of gastropods and decapods were 4.6 and 4.9 times larger than in the control quadrats, respectively (Sala 1997). They point out that the migration of mezograzers into the cages is a major issue on

exclusion experiments, due to the fact that the rate of immigration and emigration through the cages is normally unknown (Sala & Boudouresque 1997). In our study, the small differences on epiphyte biomass observed in a comparison among the treatments and a higher biomass found in the control areas suggest that the simple presence of the experimental structures seemed to be enough to provide an increase in the grazing intensity within the structures.

Table III. Summary of macrozoobenthic groups from the studied rhodolith bed and their most likely (▲) and less likely (Δ) feeding habit.

Class	Order/family	Abundance (%)	Feeding habit			
			Predator	Detritivore	Filter feeder	Herbivore
Chaetoptera	Chaetopteridae	0,08		Δ	▲	
Cnidaria	Zoanthidea	40,43	▲			
Crustacea	Amphipoda	14,27		▲	Δ	
	Caridea	0,33	▲	Δ		Δ
	Decapoda	2,47	▲	Δ		Δ
	Isopoda	3,20	▲	▲		▲
	Mysidacea	0,03			▲	
	Stomatopoda	0,17	▲			
	Tanaidacea	7,73	Δ	Δ	▲	
Echinodermata	Ophiuroidea	12,63		▲	▲	
Mollusca	Bivalvia	1,39			▲	
	Gastropoda *	0,19	▲	▲	▲	▲
Nemertea	-	0,19	▲			
Phoronida	-	0,03	▲		▲	
Polychaeta						
	Amphinomidae	0,31	▲			
	Arabellidae	0,03	▲	▲		
	Capitellidae	0,08		▲		
	Chrisopetallidae	0,17	▲			
	Cirratulidae	0,89		▲		
	Dorvileidae	0,08	▲	▲		▲
	Eunicidae	2,28	▲			▲
	Hesionidae	0,50	▲			Δ
	Lumbrineridae	2,36	▲	▲		▲
	Maldanidae	0,36		▲		
	Nephtyidae	0,03	▲			
	Nereididae	0,61	▲	▲		▲
	Opheliidae	1,11		▲		
	Orbiniidae	0,72		▲		
	Paraonidae	0,33		Δ		▲
	Phyllodocidae	0,03	▲	Δ		
	Pilargidae	0,03	▲			
	Poecilochaetidae	0,06		▲		
	Polynoidae	0,11	▲			
	Sabellidae	4,20		Δ	▲	
	Sigalionidae	0,03	▲			
	Spionidae	0,39		▲	Δ	
	Syllidae	0,81	▲			Δ
	Trichobranchidae	0,03		▲		
Sipuncula	-	1,31	▲	▲		

* Depends on species

While plants with a high growth rate depend upon this to recover from herbivory, plants that have a low growth rate allocate resources for different defence mechanisms (Coley *et al*. 1985). These defensive responses include: growth in shape and size that minimise their accessibility to herbivores; growth in textures that inhibits the herbivores manipulation and feeding; deposition of cell material such as $CaCO_3$ that decrease palatability; low nutritional values and alellochemicals production such as toxins, digestion inhibitors and unpalatable substances in the cells (Littler & Littler 1984). In our study, a cyanobacteria was abundant (found in the Muscilaginous Mat) (although its biomass was not estimated) in all treatments and control areas (Table II), which can be explained by the fact that cyanobacterias are unpalatable organisms (Nagle & Paul 1998). Thacker & Paul (2001) showed the role of feeding preferences on structuring algal communities, but other studies point out the importance of considering other factors such as the algae age (Sousa *et al*. 1981) and differences on the amount of resources among individuals of the same species (Lobban & Harrison 1994) as potential factors influencing preferential feeding. The high frequency of species of high growth rate, like those of the genera *Ceramium* (Kiirikki *et al*. 1998), both within the cages and in the control areas, suggests that the environment is characterized by a high disturbance level, either due to a high pressure of herbivores or to other factors, such as hydrodynamics (Hinojosa-Arango *et al*. 2009).

The hydrodynamics may also play an important role on the determination of the bed's structure. The hydrodynamics causes rhodoliths movement and rolling rates preventing the development of epiphytes (Steller & Foster 1995, James 2000). Steller & Foster (1995) point out that oscilatory movements and rolling are enough to keep the rhodoliths integrity and prevent epiphytes. Steller *et al*. (2003) found a higher algal biomass at deep beds in comparison to shallow ones, where the hydrodynamics is higher, during the winter. It suggests that a combination of lower hydrodinamics, lower temperature and higher levels of nutrients, which usually increases with depth, can also be important factors stimulating algal growth in deepest rather than in shallowest areas. Complementary, herbivory intensity usually decreases with depth, presenting an inverse relation with the abundance of fresh algae (van den Hoek *et al*. 1978, Steneck 1983b). Other studies have described the richness and abundance variability through substrata formed by rhodoliths of different sizes and sediment quality (i.e. Grall & Glemerac 1997). In our study no

significant differences in abundance between the shallowest
and deepest areas could be observed, which could be related to the relatively short batimetric variation of the studied bed. However, the number of species was higher in the deepest area than in the shallowest.

Other factors such as corallines epithelial cells sloughing (Keats *et al*. 1997) and production of allelopathic substances that prevent epiphytic growth (Suzuki *et al*. 1998) and/or suppresses the development of algal spores (Villas Bôas & Figueiredo 2004), are important factors that may contribute to the structure of rhodolith beds. It is suggested that the associations of corallines with herbivores, their adaptations against herbivory and their intrinsic anti-epiphytic capability, are complementary strategies to decrease the vegetative growth by other species (Morse & Morse 1984; Johnson & Mann 1986). However, here we demonstrated that mesograzers may play an important role in structuring rhodolith beds.

Acknowledgements

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