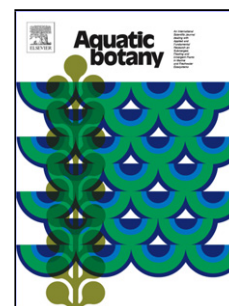


## Accepted Manuscript



Title: Seasonal and depth-driven changes in rhodolith bed structure and associated macroalgae off Arvoredo island (southeastern Brazil)

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*Lithothamnion crispatum* was the dominant rhodolith species

The predominance of spherical rhodoliths indicate high movement

Rhodoliths density were higher in summer decreasing with increasing depth

Associated macroalgae increased abundance and richness in the summer

The assemblages differed between seasons and depths

Accepted Manuscript

Seasonal and depth-driven changes in rhodolith bed structure and associated  
macroalgae off Arvoredo island (southeastern Brazil)

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**Abstract**

Rhodoliths are formed by coralline red algae and can form heterogeneous substrata with high biodiversity. Here we describe a rhodolith bed at the southern limit of the known distribution of this habitat in the western Atlantic. We characterized rhodolith and macroalgal assemblages at 5, 10 and 15 m depth during summer and winter.

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*Lithothamnion crispatum* was dominant amongst the six rhodolith-forming species present. Most rhodoliths were spheroidal in shape indicating high mobility due to water movement. Rhodolith density decreased with increasing depth and during winter. Turf-forming seaweeds accounted for 60% of the biomass growing on rhodoliths. Macroalgae increased abundance and richness in the summer, but was similar between 5 to 15 m depth. They were less abundant and diverse than that recorded in rhodolith beds further north in Brazil. Both, season and depth, affected the structure of the macroalgae assemblages. We conclude that *Lithothamnium* is the most representative genus of Brazilian rhodolith beds. Summer is responsible for increasing the diversity and richness of macroalgae, as well as increasing rhodolith density.

**Keywords:** Coralline algae, macroalgae, marine biodiversity, marine protected area, *Lithothamnion crispatum*

## 1. Introduction

Rhodoliths are of conservation interest as they provide long-lived, complex coralline algal habitat for diverse communities (Foster et al., 2001). Rhodoliths are non-renewable resources and particularly interesting for conservation (Barbera et al., 2003; Blake and Maggs, 2003). In Brazil, rhodolith beds cover extensive areas of the continental shelf and also occur on seamounts and oceanic islands (Amado Filho et al., 2007; Riul et al., 2009, Bahia et al., 2010; Amado Filho et al., 2012a, b, Pereira-Filho et al., 2012). Brazilian rhodolith beds are dredged intensively (Riul et al., 2008) and a lack of information on their ecological role has hindered conservation and management strategies. Rhodolith dredging is causing on-going environmental problems in the NE Atlantic and is now banned in the UK (Grall and Hall-Spencer, 2003; Hall-Spencer,

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2005). It has been assumed that rhodolith beds have a continuous distribution along the Brazilian shelf (Kempf, 1970), but there are considerable gaps in their known distribution from 23° to 27°S (Horta, 2002) and very little information is available on the southernmost beds (Gherardi, 2004; Rocha et al., 2006; Metri et al., 2008; Scherner et al., 2010).

Here we describe a rhodolith bed and associated macroalgal assemblage at the southernmost known limit of this habitat in the western Atlantic. We assess the influence of season and depth on i) rhodolith density, (ii) rhodolith volume, (iii) number of species and biomass of associated macroalgae and (iv) the structure of associated assemblages.

## 2. Material and Methods

The Marine Biological Reserve of Arvoredo (Rebio Arvoredo) is a 176 km<sup>2</sup> “no take” marine protected area. In summer this reserve is influenced by warm coastal waters (22°C), in winter the influence of Prata River and the Falklands current decrease water temperatures to 17°C (Piola et al., 2005). The seabed has a mixture of calcareous sediment, biodebris and calcareous nodules, covering an area of approximately 1000 m<sup>2</sup> (Gherardi, 2004). Samples were collected at Rancho Norte (27°17'S 48°22'W) in February (summer) and August (winter) 2008 at 5, 10 and 15 m depth by SCUBA diving. At each depth, nine samples (quadrats 25x25 cm) were distributed haphazardly and all specimens inside the quadrats were collected.

Rhodolith identification followed Woelkerling (1988) and Horta (2002). When rhodoliths were formed by more than one species only the dominant (highest cover) was identified. Shorter (S), intermediate (I) and longer (L) axes of each rhodolith were

1 measured using a caliper ( $\pm 0.1$  mm). Rhodolith volumes (volume of water displaced by  
2 the rhodolith) were measured in a graduated beaker. Epiphytes were removed from  
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4 rhodoliths, identified, and weighed with a balance (0.01 g precision) after drying at 60°  
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6 C for 48 h. Species with weights below 0.01 g were considered as presenting 0.001 g  
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9 We used the degree of sphericity to describe variations in rhodolith shape, this  
10 method uses the relationships rhodolith axes to classify them as discoidal (D),  
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12 ellipsoidal (E) or spheroidal (S) (Bosence and Pedley 1982). After assessing  
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14 homogeneity of variances using Cochran's Test we performed a Two-Way Analysis of  
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16 Variance to test differences on rhodolith density and volume (square root transformed),  
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18 and number of species and biomass of associated macroalgae (log transformed) between  
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20 the seasons and depths. Whenever significant differences were found, the Newman-  
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22 Keuls test was applied. To describe the spatial distribution of samples we employed  
23  
24 non-metric Multi Dimensional Scaling nMDS (Clarke and Warwick, 1994).  
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26 Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test for  
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28 simultaneous responses of species biomass to seasons and depths (Anderson, 2001;  
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30 McArdle and Anderson, 2001). Similarity matrices used in MDS and PERMANOVA  
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32 were calculated with the Bray-Curtis index and abundance values were transformed  
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34 (square root). PERMANOVA was made on unrestricted permutation raw data using 999  
35  
36 random permutations. To describe the variations in rhodolith shape we used the  
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38 TRIPLLOT spreadsheet (Graham and Midgley, 2000). Analyses of Variance were  
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40 performed in General ANOVA Designs package (GAD - Sandrini-Neto and Camargo,  
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42 2012) under the R language and environment for statistical computing (R Core Team,  
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44 2012). nMDS and PERMANOVA were performed in PRIMER 6 + PERMANOVA  
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46 (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, United Kingdom).  
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### 3. Results

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5 Six rhodolith-forming species were found; *Lithothamnion crispatum* Hauck  
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7 dominated the assemblage (Table 1). More than 75% of the rhodoliths in both seasons  
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9 and all depths were spherical in shape (Table 2; Figure S1). Significant differences were  
10  
11 observed when comparing the mean density and volume of rhodoliths between seasons  
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13 and depths (Table S1). Density of rhodoliths (mean  $\pm$ SE) was higher in the summer  
14  
15 ( $25\pm 2$  individuals per sample) than winter ( $22\pm 3$ ) and different between all depths,  
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17 decreasing from  $36\pm 2$  individuals per sample at 5 m to  $27\pm 2$  and  $9\pm 1$  at 10 and 15 m  
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19 respectively. Volume was also higher in summer ( $0.55\pm 0.06$  l per sample) than winter  
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21 ( $0.42\pm 0.05$ ). Rhodolith volumes were similar at 5 and 10 m ( $0.72\pm 0.03$  and  $0.63\pm 0.04$  l  
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23 per sample) but lower at 15 m ( $0.11\pm 0.02$ ).

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25 A total of 44 macroalgal infrageneric taxa was recorded (Table S2). *Cladophora*  
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27 *vagabunda*, *Anotrichium tenue*, *Ceramium luetselburgii* and *Erythrotrichia carnea*  
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29 where found at all depths sampled and in both seasons. Regarding the biomass the algal  
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31 turf (composed mostly of *Gelidium crinale*, *Bryopsis pennata* and *C. vagabunda*) was  
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33 the most abundant morpho-functional unit accounting for 61% of the total biomass,  
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35 followed by *P. simulans* and *Hypnea spinella* with 18% and 9% respectively.  
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37 Significant differences were observed when comparing the mean number of species and  
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39 biomass of macroalgae associated to rhodoliths between seasons but not between depths  
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41 (Table S3). Mean number of species and biomass of macroalgae were significantly  
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43 higher in summer ( $10\pm 1$  species and  $0.09\pm 0.01$  g per sample) when compared to the  
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45 winter ( $4\pm 1$  species and  $0.01\pm 0.01$  g per sample).  
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56 The MDS based on macroalgal biomass suggested differences in assemblages  
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58 from 5, 10 and 15 m and between summer and winter (Figure 1). When comparing  
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1 seasons PERMANOVA indicated that assemblages differed between summer and  
2 winter. Comparison among depths indicated that macroalgal assemblages at 5 and 10 m  
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4 depths were similar and both differed from 15 m (Table S4). Additionally,  
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6 PERMANOVA demonstrated that assemblages at all depths were different during the  
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8 summer. During the winter the assemblages at 5 and 10 m were similar but different  
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10 from those at 15 m (Table S4).  
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#### 16 4. Discussion

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18 Here we have described the structure of a rhodolith bed and its associated  
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20 macroalgae at the currently known southern limit of distribution of this habitat in  
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22 western Atlantic. *Lithothamnion* appears to be the most important genus of rhodolith-  
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24 forming species in the SW Atlantic since *L. crispatum* is dominant at the southern limit  
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26 of this habitat and also dominates the largest rhodolith deposit in the world, off eastern  
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28 Brazil (Amado-Filho et al., 2012b) with *Lithothamnion* sp. dominant off NE Brazil  
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30 (Riul et al., 2009). We found that most of the rhodoliths off SW Brazil were spheroidal,  
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32 as is the case off E Brazil (Amado-Filho et al., 2007; Bahia et al., 2010), reflecting high  
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34 seabed mobility since rhodolith shape changes from discoidal to spheroidal as water  
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36 movement increases (Prager and Ginsburg 1989).  
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46 We found that winter storms spreading rhodoliths apart and reducing their volume  
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48 by fragmentation or due to the burial of larger and heavier specimens. Reduction in  
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50 rhodolith density and/or volume with an increase in depth was also observed in other  
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52 studies (Steller and Foster, 1995; Riul et al., 2009; Amado-Filho et al., 2010; Bahia et  
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54 al., 2010). Increasing depth is followed by a reduction in temperature, irradiance and  
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56 increased sedimentation. These factors lead to physiological limitations affecting  
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1 rhodolith growth (Wilson et al., 2004). We also observed a reduction in number of  
2 species and biomass of associated macroalgae during the winter which is likely to be  
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4 due to lower irradiance and temperatures, as observed on other rhodolith beds (Steller  
5 and Foster, 1995; Amado-Filho et al., 2007, 2010). This seasonality could be also  
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7 related to increased water movement (Hinojosa-Arango et al., 2009) promoting  
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9 sediment suspension and causing epiphytes to be scraped off as the rhodoliths are  
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11 moved. As expected from studies in northeastern Brazil (Riul et al., 2009; Bahia et al.,  
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13 2010) we found seasonal and depth-driven changes in the structure of the assemblages  
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15 of macroalgae associated with rhodoliths. We believe these differences reflect  
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17 synergistic effects of herbivory, irradiance and hydrodynamics, promoting differences  
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19 in species abundance and composition (Breitburg, 1985; Scherner et al., 2010).  
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21 The Arvoredo bed had a relatively low number of species and biomass of associated  
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23 macroalgae compared with another Brazilian rhodolith beds reflecting the  
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25 biogeographic trend of decreasing species richness with increasing latitude in the warm  
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27 temperate SW Atlantic (Horta et al., 2001). Nevertheless, the no-take reserve status of  
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29 Rebio Arvoredo makes this environment particularly interesting for ecological  
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31 comparisons with other rhodolith beds worldwide. We believe further work should  
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33 focus on manipulative experiments regarding effects of movement on rhodolith shape  
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35 and growth rates and also broader scales investigations on connectivity between these  
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37 ecosystems, including population structure of rhodolith-forming species to assess the  
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39 factors shaping rhodolith distribution.  
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## 53 **5. Acknowledgements**

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## Figure list

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5 Figure 1 - Multivariate distribution (nMDS) of samples of macroalgae associated with  
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7 rhodolith beds at two seasons and three depths at Arvoredo island (southeastern Brazil).  
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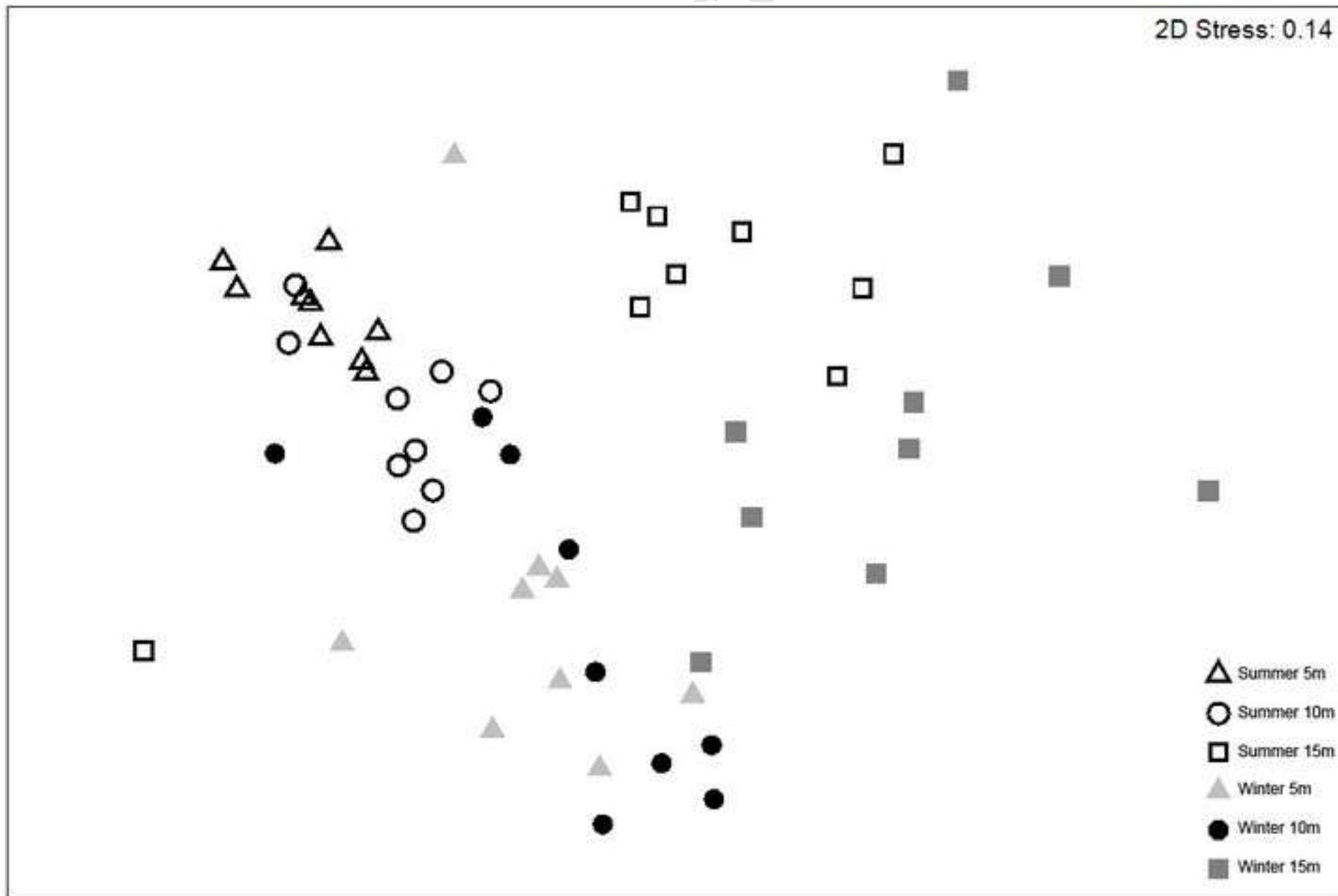




Table 1 - Mean ( $\pm$ SE) rhodolith density ( $0.625 \text{ m}^2$ ) at the Arvoredo island  
(southeastern Brazil).

Species	Summer			Winter		
	5m	10m	15m	5m	10m	15m
<i>Hydrolithon</i> sp.	0.56 ( $\pm 0.44$ )	2.11 ( $\pm 0.42$ )	1.00 ( $\pm 0.44$ )	0.78 ( $\pm 0.46$ )	1.78 ( $\pm 0.43$ )	-
<i>Lithophyllum rugosum</i>	1.67 ( $\pm 0.55$ )	1.89 ( $\pm 0.56$ )	1.33 ( $\pm 0.65$ )	0.22 ( $\pm 0.15$ )	3.00 ( $\pm 1.29$ )	0.22 ( $\pm 0.15$ )
<i>L. stictaeforme</i>	5.89 ( $\pm 1.51$ )	5.33 ( $\pm 1.50$ )	2.11 ( $\pm 0.65$ )	4.89 ( $\pm 1.70$ )	4.22 ( $\pm 0.70$ )	0.89 ( $\pm 0.26$ )
<i>L. margarettae</i>	1.00 ( $\pm 0.37$ )	0.11 ( $\pm 0.11$ )	-	0.67 ( $\pm 0.29$ )	-	-
<i>Lithothamnium crispatum</i>	24.11 ( $\pm 2.17$ )	4.44 ( $\pm 0.96$ )	6.78 ( $\pm 1.14$ )	26.67 ( $\pm 3.39$ )	11.89 ( $\pm 2.21$ )	5.11 ( $\pm 0.89$ )
<i>Mesophyllum erubescens</i>	3.00 ( $\pm 1.08$ )	14.67 ( $\pm 2.03$ )	-	2.78 ( $\pm 1.41$ )	3.67 ( $\pm 1.71$ )	0.11 ( $\pm 0.11$ )

Table 2 - Rhodolith shape and number of individuals at Arvoredo island (southeastern Brazil).

Shape	Summer			Winter		
	5 m	10 m	15 m	5 m	10 m	15 m
Discoidal	4.9%	5.5%	3%	1.9%	0.9%	5.3%
Ellipsoidal	6.1%	15.7%	9.9%	9.6%	10%	14%
Spheroidal	89%	78.8%	87.1%	88.6%	89.1%	80.7%
N	326	255	101	324	221	57