

RHODOLITH BED STRUCTURE ALONG A DEPTH GRADIENT ON THE NORTHERN COAST OF BAHIA STATE, BRAZIL

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ABSTRACT

The aim of this study was to determine the structure of a rhodolith bed along a depth gradient of 5 to 25 m in the shelf in front of Salvador City, a region of northeastern Brazil. The dimensions, morphology and coralline algae composition of the rhodoliths were analyzed, as well as the vitality, density, and associated flora of the bed at three depths: 5, 15 and 25 m. Samples were obtained by SCUBA divers in summer 2007. Five rhodolith-forming taxa were identified: *Sporolithon episporum*, *Lithothamnion brasiliense*, *Lithothamnion superpositum*, *Mesophyllum erubescens*, and *Lithophyllum* sp. The encrusting growth form and the spherical shape were predominant at all depths. Rhodolith dimensions and vitality decreased and the density increased from the shallow to the deepest zones. Fifty-six macroalgal species were found as rhodolith-associated flora. The shallower depth presented higher values for macroalgal biomass and number of species. These results associated with other recent rhodolith bed descriptions indicate that the pattern of Brazilian rhodolith bed structure along depth gradients may be related to a combination of the extent and slope of the continental shelf.

RESUMO

O objetivo deste estudo foi determinar a estrutura de um banco de rodolitos ao longo de um gradiente de profundidade na plataforma em frente à cidade de Salvador, nordeste brasileiro. Foram analisadas as dimensões, a forma e composição das algas calcárias dos rodolitos, bem como a vitalidade, densidade e flora associada ao banco, em três profundidades: 5, 15 e 25 m. As amostras foram obtidas por meio de mergulho autônomo no verão de 2007. Cinco espécies de algas calcárias formadoras de rodolito foram identificadas: *Sporolithon episporum*, *Lithothamnion brasiliense*, *Lithothamnion superpositum*, *Mesophyllum erubescens* e *Lithophyllum* sp. A forma de crescimento incrustante e a forma esférica foram predominantes em todas as profundidades. Houve uma redução da dimensão e vitalidade dos rodolitos e um aumento da densidade com a profundidade. Cinquenta e seis espécies de macroalgas foram encontradas como flora associada aos rodolitos. A profundidade mais rasa apresentou os maiores valores de biomassa e número de espécies de macroalgas. Esses resultados, associados com outras descrições recentes de bancos de rodolitos, indicam que o padrão estrutural desses bancos no Brasil, ao longo de gradientes de profundidade, pode estar relacionado a uma combinação da extensão e da inclinação da plataforma continental.

Descriptors: Coralline Algae, Benthic Community, Continental Shelf, Depth Gradient, *Lithothamnion brasiliense*, *Lithothamnion superpositum*.

Descritores: Algas coralíneas, Comunidade Bentônica, Plataforma Continental, Gradiente de Profundidade, *Lithothamnion brasiliense*, *Lithothamnion superpositum*.

INTRODUCTION

Rhodoliths are free-living calcareous structures composed mostly (>50%) of non-geniculate coralline red algae (Corallinales, Rhodophyta) (STENECK, 1986; FOSTER, 2001). Rhodolith beds are distributed worldwide, from the tropics to the poles, from the intertidal zones to depths of over 200 m (LITTLER et al., 1991; FOSTER, 2001; KONAR et al., 2006).

They are ecologically important benthic algal communities. The rhodolith structure provides a tri-dimensional hard-substrate and serves as microhabitat for a great diversity of invertebrates and associated algae (FOSTER et al., 1997; STELLER et al. 2003; LITTLER; LITTLER, 2008; NELSON, 2009). For this reason and because of their susceptibility to damage caused by human activity, rhodolith beds are protected habitats in Europe (BIRKETT et al., 1999; WILSON et al., 2004).

It is presumed that the largest rhodolith beds in the world are to be found on the Brazilian coast. Estimates indicate that these beds cover extensive areas of the N-NE Brazilian continental shelf (KEMPF, 1970; MILLIMAN, 1977; TESTA; BOSENCE, 1999; FOSTER, 2001; AMADO-FILHO et al. 2007; FIGUEIREDO et al., 2007). However, there is still much to be done in terms of the systematic surveying of the latitudinal distribution and community structure of rhodolith beds on the Brazilian continental shelf (GHERARDI, 2004). Most studies on rhodoliths in Brazil have investigated the sedimentary character of the Brazilian shelf and the prospects for their potential for commercial exploitation (KEMPF et al., 1967/9; KEMPF, 1970; MABESSONE et al., 1972; MILLIMAN; AMARAL, 1974; MILLIMAN, 1977; VICALVI; MILLIMAN, 1977; DIAS, 2000). Very few published studies on rhodolith beds in Brazil have approached these communities from a biological point of view and included consistent information on rhodolith bed structure, associated organisms and non-geniculate coralline red algae identification (TESTA, 1997; TESTA; BOSENCE, 1999; GHERARDI, 2004; ROCHA et al., 2006; AMADO-FILHO et al., 2007; FIGUEIREDO et al., 2007; HORTA et al., 2001; RIUL et al., 2009; VILLAS-BOAS et al., 2009). These studies have shown the great diversity of the organisms associated with rhodolith beds as well as highlighting their ecological relevance. Most rhodolith beds in Brazil, however, still remain unexplored or poorly known within this biological context.

Of more than 300 macroalgae species quoted as present on the Brazilian northeastern coast, about 70% are referred specifically to Bahia State (NUNES, 2005). However, most of these taxa were collected in the intertidal and shallow subtidal zones. Studies focusing on benthic communities below 5 m depth are lacking in Brazil. In addition, rhodolith beds have been cited as one of the most promising subtidal habitats for

Brazilian marine diversity surveys (HORTA et al., 2001; AMADO-FILHO et al., 2007).

It has been demonstrated that the rhodoliths' distribution, dimensions and morphology can vary with depth (LITTLER et al., 1991; STELLER et al., 2003; AMADO-FILHO et al., 2007; RIUL et al., 2009). The environmental conditions that normally vary with depth, such as light, sedimentation and water motion, can affect the rhodolith beds' characteristics such as vitality, associated fauna/flora diversity and benthic abundance directly (STELLER; FOSTER, 1995; BASSO, 1998; RIOSMENA-RODRIGUEZ et al., 1999; WILSON et al., 2004; HINOJOSA-ARANGO et al., 2009).

The relatively narrow continental shelf distinguishes the northern coast of Bahia State from other tropical areas where rhodolith beds have been studied along depth gradients in Brazil (see Amado-Filho et al., 2007; Riul et al., 2009). This study describes the structure, composition and associated flora of a rhodolith bed on the northern coast of Bahia State to discover whether its structure is affected by depth, and to compare these results with those of the studies of other Brazilian rhodolith beds.

MATERIAL AND METHODS

Study Area

The study area is located in the Itapuã region, in the city of Salvador, on the northern coast of Bahia State, Brazil (12°57'S, 38°22'W) (Fig. 1). Water salinity there ranges from 35.5‰ to 37 ‰ (DHN, 1993) and the sea-surface temperature (SST) from 20°C to 27°C (NUNES, 2005). It is a place exposed to the action of waves and wind, with prevailing easterly winds. The extension of the continental shelf in the study area is of about 10 km. The sea bottom of the subtidal zone is composed mainly of coralline reefs and rhodoliths interspersed with sand and gravel.

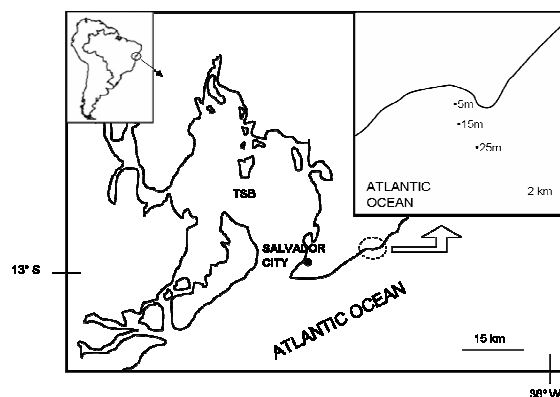


Fig. 1. Map of the study area on the northern coast of Bahia State with sampling sites along a depth gradient. TSB = Todos os Santos Bay.

Samples were obtained in summer 2007, at the end of the dry season, by Scuba divers from three depth zones about 1 km apart: at 5 m (12°57'33"S, 38°22'21"W); at 15 m (12°58'01"S, 38°22'13"W) and at 25 m (12°58'28"S, 38°21'53"W) (Fig. 1). In each of these zones, three 20 m long transects were randomly positioned on the sea bottom and fifteen (25 cm x 25 cm) quadrats on them (five per transect) were sampled at random. All the superficial rhodoliths in each quadrat - those found within a layer down to 5 cm below the bottom - were transferred to separate collection bags.

Coralline Algae Identification

Small pieces of fertile material were separated and prepared for both light microscope and scanning electron microscope (SEM) analyses. The samples for light microscopy were decalcified in 10% nitric acid, dehydrated in ethanol sequence, embedded in resin, and sectioned (12-15 μm thick) (for further description see Amado-Filho et al., 2007). Specimens for SEM were prepared by air drying small pieces of material and then mounting them on aluminium stubs using a double-sided conductive tape. The stubs were sputter coated with gold and investigated with a Zeiss EVO 40 SEM at 14-15 kV. The taxonomic characteristics applied were based on Womersley (1996). Species identifications were based on comparisons of vegetative and reproductive features with previously published data (see Harvey; Woelkerling, 2007 for a review).

Vitality

Rhodolith vitality was estimated based on pigmentation analysis of the coralline algae thallus surface. The rhodoliths from each quadrat were immediately photographed to record their original color. A grid with 300 points was positioned over each image. Using a table of random numbers, considering only the points over the coralline algae, 60 points per image/quadrat were analyzed. The living unit considered was the coralline algae thallus surface which presented pigmentation, i.e., of a pink, purple or reddish color. The results were expressed as a percentage cover of living coralline algae on the rhodoliths.

Morphology, Dimensions and Density

Rhodolith shape was determined in accordance with the method of Bosence and Pedley (1982), by measuring the long, intermediate and short axes of the outer surfaces of the rhodoliths. These data were plotted using the TRIPLLOT v.1.3 spreadsheet of Graham and Midgley (2000), who plotted data on the pebble-shape diagram of Sneed and Folk (1958), and

which can be used to separate rhodoliths into spheroidal, discoidal or ellipsoidal shapes (BOSENCE; PEDLEY, 1982; PERRY, 2005). In addition, the predominant coralline algae growth form was determined in rhodoliths in accordance with the criteria established by Woelkerling et al. (1993). Rhodolith mean diameter was obtained from the measurements of three axes (long, intermediate and short) of the rhodoliths. The rhodolith volume was estimated by the volume of water displaced in a graduated beaker after the removal of all epibenthic organisms. Rhodolith density was determined by counting individual rhodoliths in quadrats. Data were expressed in rhodoliths.m⁻².

Associated Flora

The seaweeds were carefully separated into different populations and identified at species level with the aid of stereoscope and microscope. Then they were dried (at 60°C for at least 48 h) and quantified with an analytical balance (precision of 0.001 g). Species with weights below 0.001 g were considered as presenting 0.001 g and quantified.

Data Analyses

After assessment of homogeneity of variances (Levene test) and normality (Kolmogorov-Smirnov), differences in rhodolith characteristics (growth forms, shape, mean diameter, density and vitality) and biomass of the associated flora among depths were tested by One-Way Analysis of Variance (ANOVA). Differences among the distinct growth forms and shape frequencies were also tested by ANOVA. Whenever significant differences were found the Tukey test was applied (ZAR, 1999). Multi Dimensional Scaling (MDS) ordination was used to summarize the associated flora similarities (Bray-Curtis) among depths, thereafter an Analysis of Similarities (ANOSIM) was performed to evaluate significant differences (CLARKE; WARWICK, 1994). The univariate statistical analyses were performed using STATISTICA (version 6.0), while the multivariate statistical analyses were carried out on PRIMER (version 6.0). All data are expressed as means (\pm 95% confidence interval) and differences were considered significant at $p < 0.05$.

RESULTS

Coralline Algae Identification

The rhodolith bed in the study area is composed of at least 5 non-geniculate coralline red algae taxa, representing the three families of the order Corallinales: Hapalidiaceae, *Lithothamnion brasiliense* Foslie, *Lithothamnion superpositum* Foslie

and *Mesophyllum erubescens* (Foslie) Lemoine; Sporolithaceae, *Sporolithon episporum* (M.A. Howe) E.Y. Dawson; and Corallinaceae, *Lithophyllum* sp. A detailed taxonomic description is provided for the *Lithothamnion* species since they are poorly described for Brazil. Brief descriptions of the other species and comments on them are presented.

Lithothamnion brasiliense was found at both 5 and 15 m depths, composing rhodoliths with encrusting to lumpy growth form (Fig. 2A). The thallus is pseudoparenchymatous, 1-2 mm thick, presenting nodular protuberances, 0.2-3 cm long and 2-5 mm in diameter. The internal organization is monomerous in the crustose portions and radial and monomerous in the protuberances. Cells of adjacent filaments connected laterally by cell fusions. Flared epithallial cells, 3-4 μm long and 5-8 μm in diameter, are arranged in a single layer (Fig. 2B). Tetrasporangial conceptacles are multiporate, 100-180 μm long and 300-500 μm in diameter, somewhat prominent with a sunken center (Fig. 2D). The tetrasporangial pore measures 10-18 μm in diameter, and is surrounded by 6-8 rosette cells. Tetrasporangial conceptacle roof formed by 4-6 cells high; pore canal measuring 30-40 μm long and 10-15 μm in diameter (Fig. 2E). Gametangial samples were not observed.

Lithothamnion superpositum was found at all depths with lumpy to encrusting growth form, thallus pseudoparenchymatous 130-300 μm thick, presenting nodular protuberances (Fig. 3A). The internal organization is monomerous in the crustose portions and radial and monomerous in the protuberances (Fig. 3C). Cells of adjacent filaments are connected laterally by cell fusions (Fig. 3B). Flared epithallial cells, 2.5-4 μm long and 5-8 μm in diameter are arranged in a single layer (Fig. 3B). Tetrasporangial conceptacles multiporate, 110-225 μm long and 220-450 μm in diameter are raised in relation to the surrounding vegetative thallus surface (Fig. 4A). Tetraspores measure 100-145 μm long and 35-60 μm in diameter. Roofs of mature conceptacles, 3-5 cells high, pitted with depressions (Fig. 4A-D) resulting from disintegration of uppermost cells in filaments surrounding pore canal (HARVEY et al., 2003). Pore canal measure 20-27 μm long and 8-12 μm in diameter. Tetrasporangial pore, 10-16 μm in diameter surrounded by 5-6 rosette cells (Fig. 4C). Gametangial samples were not observed. Main taxonomic characteristics of *L. brasiliense* and *L. superpositum* are summarized in Table 1.

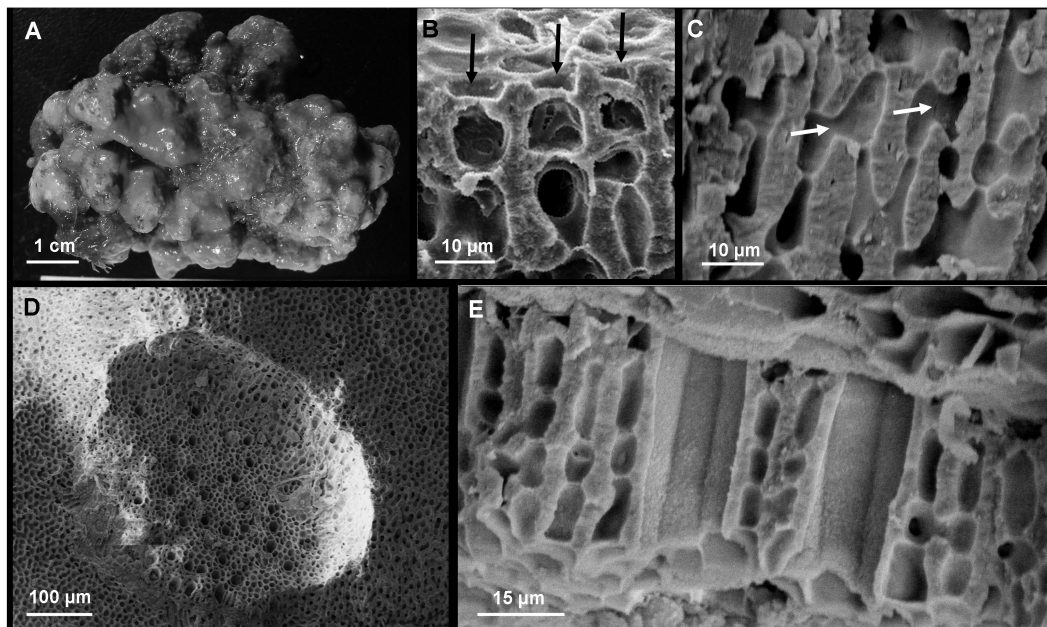


Fig. 2A-D. *Lithothamnion brasiliense*: vegetative and reproductive features. (A) General view of the growth form. (B) Flared epithallial cells (arrows). (C) Cell fusions (arrows). (D) Surface view of a sunken multiporate conceptacle. (E) Detail of tetrasporangial conceptacle roof and pore canal.

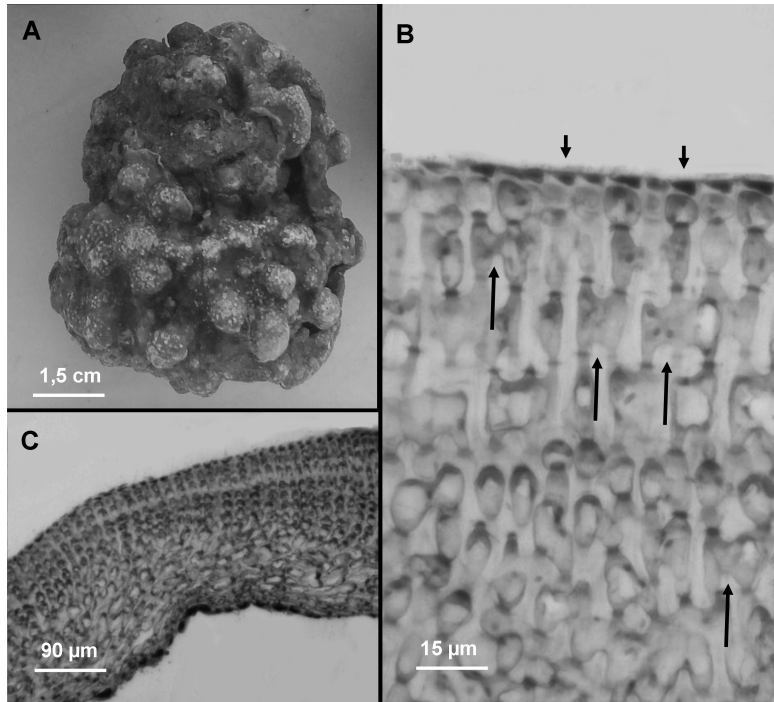


Fig. 3A-D. *Lithothamnion superpositum*: vegetative features. (A) General view of the growth form. (B) Flared epithelial cells (small arrows) and cell fusions (large arrows) (C) Vertical section showing the thallus monomerous construction.

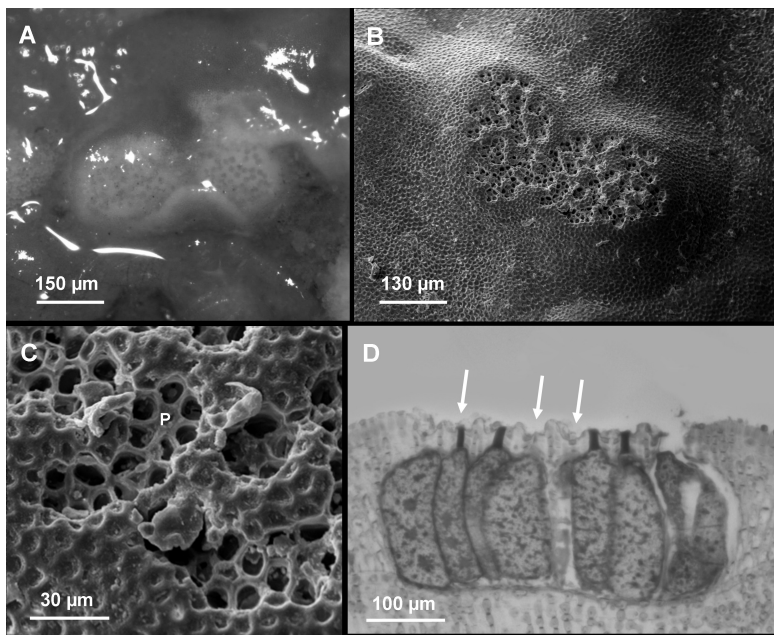


Fig. 4A-D. *Lithothamnion superpositum*: reproductive features. (A) Surface view of conceptacles in stereomicroscopy. (B) SEM surface view of two fused conceptacles. (C) SEM surface view of conceptacle showing pores (p) within a depression, surrounded by 5-6 rosette cells. (D) Conceptacle section showing the tetraspores and depressions (arrows).

Table 1. Data on characters of the two *Lithothamnion* species in study area.

Character	<i>L. brasiliense</i>	<i>L. superpositum</i>
Thallus thickness	1000-2000 μm	130-300 μm
Protuberance length	2-30 mm	3-13 mm
Protuberance diameter	2-5 mm	2-10 mm
Sunken tetrasporangial conceptacles	Present	Absent
Tetrasporangial conceptacle chamber height	100-180 μm	110-225 μm
Tetrasporangial conceptacle chamber diameter	300-500 μm	220-450 μm
Number of cells in filaments of tetrasporangial conceptacle roof	4-6	3-5
Pore canal length	30-40 μm	20-27 μm
Pore canal diameter	10-15 μm	8-12 μm
Tetrasporangial pore diameter	10-18 μm	10-16 μm
Conceptacles roof pitted with depressions	No	Yes

Mesophyllum erubescens was only found at 15 m depth, forming rhodoliths with fruticose to warty growth form. Specimens have coaxial monomerous thallus, cell fusions, rounded epithallial cells, and subepithallial initials longer than the cell immediately below them. Tetrasporangial conceptacles multiporate, 130-200 μm long and 400-500 μm in diameter, flat-topped, and raised in relation to surrounding vegetative thallus surface. Tetrasporangial conceptacle pore canals bordered by cells that are more elongated, especially near the base of the pore, than other roof cells. Gametangial samples were not seen.

Sporolithon episporum was only found at 15 m depth, forming rhodoliths with growth form predominantly encrusting (see Woelkerling et al., 1993). Specimens present monomerous thallus, flared epithallial cells, and both secondary pit connections and cell fusions (4-5:1 ratio, respectively). Tetrasporangial chambers, 70-100 μm long and 40-65 μm in diameter, grouped into *sori* which are raised in relation to surrounding vegetative thallus surface and formed on a basal layer of elongated cells. No preserved sporangial compartments were found in the deeper parts of the thallus.

Lithophyllum sp. was only found at 25 m depth, forming rhodoliths with encrusting growth form. Specimens have dimerous thallus, rounded to flattened epithallial cells, secondary pit connections, and uniporate tetrasporangial conceptacles. Not enough fertile specimens were found for identification at species level.

Vitality, Dimensions and Density

The percentage cover of living coralline algae on rhodoliths decreases from $87\% \pm 7\%$ at 5 m, to $57\% \pm 9\%$ at 15 m, and to $17\% \pm 3\%$ at 25 m. The ANOVA indicates differences between depths ($p < 0.05$) (Fig. 5). The rhodoliths' mean diameter varied with depth (ANOVA, $p < 0.05$), decreasing from 2.78

± 0.15 cm at 5 m, to 2.32 ± 0.21 cm at 15 m, and to 0.87 ± 0.03 cm at 25 m (Fig. 5). The volume occupied by the rhodolith ranged from 13 ± 1.13 ml at 5 m, to 14 ± 1.8 ml at 15 m, and to 0.3 ± 0.02 ml at 25 m depth.

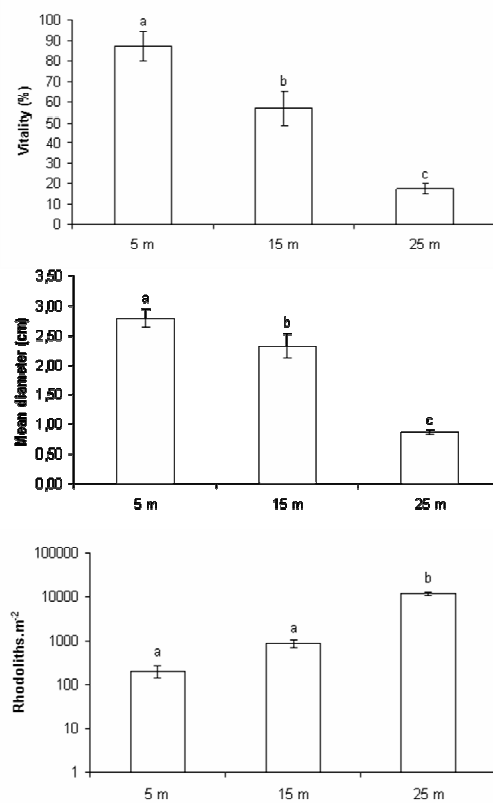


Fig. 5. Mean (\pm 95% confidence interval) for rhodoliths' mean diameter, density, and vitality at three sampling depths. The letters indicate differences detected by Tukey test. The density graphic is presented on logarithmic scale.

The rhodoliths density increased from 207 ± 67 rhodoliths.m⁻² at 5 m, to 882 ± 170 rhodoliths.m⁻² at 15 m, and to $11,775 \pm 1,102$ rhodoliths.m⁻² at 25 m. The results varied with depth (ANOVA, $p < 0.05$) (Fig. 5).

Morphology

Four predominant rhodolith coralline algae growth forms were identified in the Salvador bed: warty, lumpy, fruticose and encrusting. The encrusting growth form frequency was prevalent at all depths

(Table 2, Fig. 6), ranging from $61 \pm 2\%$ at 15 m to $66 \pm 3\%$ at 25 m. An increase in the fruticose growth form was seen toward 25 m depths ($8 \pm 5\%$, $10 \pm 1\%$ and $29 \pm 2\%$, respectively at 5, 15 and 25 m) (Table 3).

The spheroidal shape frequency was prevalent (Table 2) at all depths with the minimum of $78 \pm 0.8\%$ at 25 m and maximum $92 \pm 1\%$ at 15 m (Fig. 7). An increase in the ellipsoidal shape and a concomitant reduction in the spheroidal shape were observed towards 25 m (Table 3 and Figure 7).

Table 2. Results of Analysis of Variance (ANOVA) and Tukey test comparing rhodolith growth forms and rhodolith shapes at each depth sampled. Growth forms: E=Encrusting, W=Warty, L=Lumpy and F=Fruticose. Rhodolith Shapes: S=Spheroidal, D=Discoidal and EL= Ellipsoidal.

Depths	Growth Forms			Shapes		
	F	P	Tukey	F	P	Tukey
5 m	31.9	<0.01	E>W>L=F	122.9	<0.01	S>D=EL
15 m	155.2	<0.01	E>W>L=F	937	<0.01	S>D=EL
25m	233.5	<0.01	E>F>W>L	1718.7	<0.01	S>EL>D

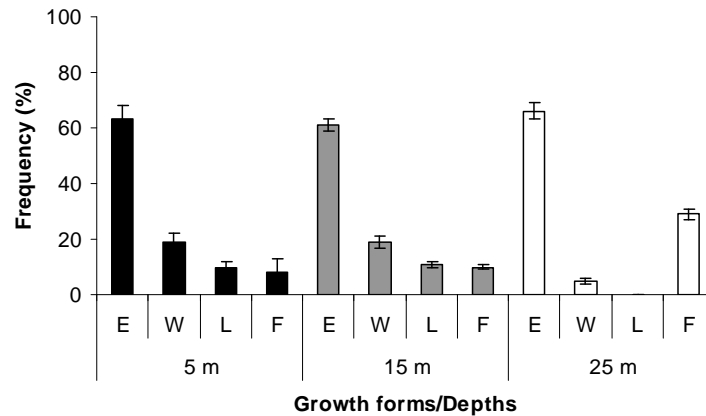


Fig. 6. Mean (\pm SD) frequency of growth forms (E = encrusting, W =warty, L = lumpy, F = fruticose) at the depths sampled.

Table 3. Results of Analysis of Variance (ANOVA) and Tukey test comparing depths (5, 15 and 25 m) in relation to rhodolith growth forms and rhodolith shapes; ns = non significant.

	F	P	Tukey
Growth form			
Encrusting	1.1	>0.05	ns
Warty	26.8	<0.001	5=15>25
Lumpy	45.0	<0.001	5=15>25
Fruticose	26.7	<0.001	25>15=5
Shape			
Spheroidal	23.0	<0.001	5=15>25
Discoidal	3.8	<0.05	25=5>15
Ellipsoidal	28.7	<0.001	25>15=5

Table 4. Associated flora mean biomass (g.m⁻²) (± S.D.) per depth sampled. (-) indicates absence of the species.

Taxa	Depth		
	5 m	15 m	25 m
Chlorophyta (8 taxa)			
<i>Bryopsis pennata</i> J. V. Lamour.	0.01 (±0.06)	-	-
<i>Caulerpa cupressoides</i> (H. West in Vahl) C. Agardh	0.54 (±2.09)	-	-
<i>Codium taylorii</i> P. C. Silva	-	5.99 (±19.50)	-
<i>Halimeda discoidea</i> Decne.	-	-	0.85 (±3.05)
<i>Halimeda gracilis</i> Harv. ex J. Agardh	-	1.60 (±3.29)	1.96 (±3.46)
<i>Udotea flabellum</i> (J. Ellis & Sol.) J. V. Lamour.	0.33 (±1.29)	-	0.02 (±0.07)
<i>Ulva fasciata</i> Delile	0.03 (±0.13)	-	-
<i>Ulva lactuca</i> L.	0.18 (±0.71)	-	-
Ochrophyta (9 taxa)			
<i>Dictyopteris delicatula</i> J. V. Lamour.	17.11 (±20.16)	0.02 (±0.06)	-
<i>Dictyopteris jamaicensis</i> W. R. Taylor	0.04 (±0.14)	6.48 (±12.65)	0.20 (±0.38)
<i>Dictyopteris justii</i> J. V. Lamour.	1.90 (±6.23)	-	10.34 (±9.63)
<i>Dictyopteris plagiogramma</i> (Mont.) Vickers	6.36 (±12.70)	-	0.61 (±1.82)
<i>Dictyopteris polyodioides</i> (DC in Lam. & DC.) J. V. Lamour.	14.68 (±23.05)	1.88 (±3.67)	0.44 (±0.80)
<i>Dictyota mertensii</i> (Mart.) Kütz.	1.24 (±2.01)	4.09 (±5.96)	0.32 (±1.05)
<i>Lobophora variegata</i> (J. V. Lamour.) Wormersley ex. E.C. Oliveira	1.58 (±2.47)	3.12 (±4.51)	0.03 (±0.11)
<i>Sargassum vulgare</i> C. Agardh	0.09 (±0.35)	0.51 (±1.38)	-
<i>Spatoglossum schroederi</i> (C. Agardh) Kütz.	0.10 (±0.39)	-	-
Rhodophyta (39 taxa)			
<i>Acrothamnion butleriae</i> (Collins) Kylin	-	-	0.01 (±0.00)
<i>Amansia multifida</i> J. V. Lamour.	88.17 (±76.33)	0.01 (±0.03)	0.14 (±0.30)
<i>Botryocladia occidentalis</i> (Børgesen) Kylin	0.20 (±0.78)	-	-
<i>Bryothamnion seaforthii</i> (Turner) Kütz.	48.60 (±46.16)	-	-
<i>Claudea elegans</i> J. V. Lamour.	-	-	1.01 (±0.84)
<i>Cryptonemia crenulata</i> (J. Agardh) J. Agardh	-	-	0.38 (±1.08)
<i>Dichotomaria marginata</i> (J. Ellis & Sol.) Lamarck	7.35 (±11.35)	-	-
<i>Dichotomaria obtusata</i> (J. Ellis & Sol.) Lamarck	1.92 (±3.12)	-	-
<i>Dictyurus occidentalis</i> J. Agardh	-	0.69 (±2.59)	5.52 (±6.09)
<i>Gelidiella acerosa</i> (Forssk.) Feldmann & Hamel	0.75 (±2.90)	-	-
<i>Gelidiopsis planicaulis</i> (W. R. Taylor) W. R. Taylor	1.31 (±5.06)	0.01 (±0.03)	-
<i>Gracilaria cervicornis</i> (Turner) J. Agardh	20.05 (±23.80)	-	-
<i>Gracilaria curtissiae</i> J. Agardh	0.71 (±2.74)	-	0.67 (±1.08)
<i>Gracilaria ornata</i> Aresch.	1.25 (±3.16)	0.02 (±0.09)	2.41 (±5.93)
<i>Gracilaria</i> sp.	0.79 (±2.57)	-	0.24 (±0.85)
<i>Hydropuntia caudata</i> (J. Agardh) Gurgel & Fredericq	0.06 (±0.24)	0.30 (±0.44)	0.23 (±0.63)
<i>Hydropuntia cornea</i> (J. Agardh) M. J. Wynne	-	-	0.04 (±0.15)
<i>Haliptilon cubense</i> (Mont. ex. Kütz.) Garbary & H.W. Johans.	-	0.98 (±1.47)	-
<i>Haliptilon subulatum</i> (J. Ellis & Sol.) H. W. Johans.	-	0.10 (±0.29)	-
<i>Haloplegma duperreyi</i> Mont.	-	0.76 (±1.39)	16.47 (±12.66)
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	-	-	0.01 (±0.02)
<i>Heterosiphonia crispella</i> (C. Agardh) M. J. Wynne	-	-	0.02 (±0.05)
<i>Heterosiphonia gibbesii</i> (Harv.) Falkenb.	-	-	0.18 (±0.48)
<i>Hypnea musciformis</i> (Wulfen in Jacquin) J. V. Lamour.	3.59 (±6.19)	-	0.01 (±0.02)
<i>Hypnea spinella</i> (C. Agardh) Kütz.	-	-	0.01 (±0.02)
<i>Jania adhaerens</i> J. V. Lamour.	0.80 (±1.46)	0.52 (±0.89)	-
<i>Leptofaucha brasiliensis</i> A. B. Joly	-	0.01 (±0.04)	-
<i>Heterodasya mucronata</i> (Harv.) M. J. Wynne comb. nov.	-	-	0.08 (±0.16)
<i>Neosiphonia ferulacea</i> (Suhr ex J. Agardh) S. M. Guim & M. T. Fujii	-	-	-
<i>Osmundaria obtusiloba</i> (C. Agardh) R. E. Norris	0.83 (±2.82)	-	-
<i>Peyssonnelia inamoena</i> Pilg.	0.18 (±0.71)	0.06 (±0.23)	-
<i>Polysiphonia denudata</i> (Dillwyn) Grev. ex Harv. in Hook	-	-	0.04 (±0.08)
<i>Rhodymenia pseudopalmeta</i> (J. V. Lamour.) P. C. Silva	-	0.01 (±0.02)	-
<i>Solieria filiformis</i> (Kütz.) P. W. Gabrielson	-	-	1.33 (±2.29)
<i>Spyridia clavata</i> Kütz.	-	-	0.04 (±0.13)
<i>Spyridia hypnoides</i> (Bory in Belanger) Papenf.	-	-	0.21 (±0.40)
<i>Tricleocarpa cylindrica</i> (J. Ellis & Sol) Huissman & Borow	5.05 (±19.57)	14.99 (±23.54)	-
<i>Wrangelia argus</i> (Mont.) Mont.	-	-	0.01 (±0.01)
<i>Wrightiella tumanowiczii</i> (Gatty ex Harv.) F. Schimitz	-	0.27 (±1.00)	3.35 (±3.59)

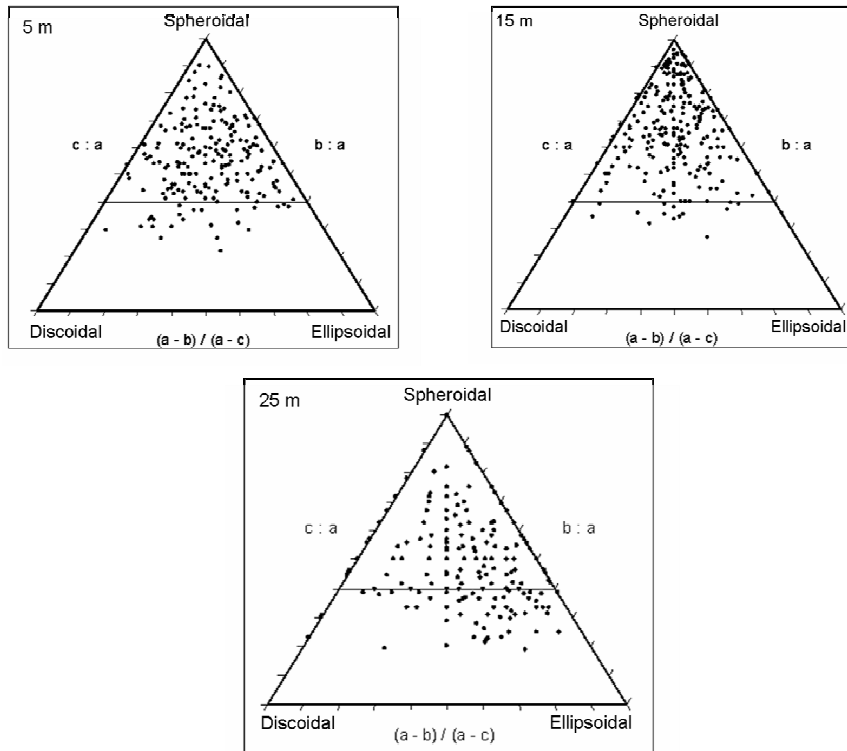


Fig. 7. Sphericity diagrams of rhodoliths from sampling depths. a, b and c correspond to long, intermediate and short rhodolith axes, respectively.

Associated Flora

A total of 56 infrageneric taxa, excluding the rhodolith-forming coralline algal species, were found to be associated with rhodoliths in the Salvador bed. Among them there were 39 Rhodophyta, 9 Ochrophyta, and 8 Chlorophyta. A total of 31 species were found at 5 m depth, 22 species at 15 m depth, and 32 species at 25 m depth. Seven taxa (12%) were present at all depths. Twelve taxa (21%) were exclusive to 5 m depth, only 5 taxa (9%) to 15 m depth, and 14 taxa (25%) to 25 m depth. The total mean biomass (dry weight) of the macroalgae varied from 42.4 g.m⁻² at 15 m to 225.8 g.m⁻² at 5 m depth.

ANOVA indicates significant differences in biomass among the depths (p<0.05) (Fig. 8). The predominant species that contributed with more than 50 % of the total mean biomass at each depth were: *Amansia multifida* and *Bryothamnion seaforthii* at 5 m depth; *Tricleocarpa cylindrica* and *Dictyopteris jamaicensis* at 15 m depth; and *Haloplegma duperreyi* and *Dictyopteris justii* at 25 m depth (Table 4). The MDS based on the Bray-Curtis similarity index shows that three groups, corresponding to the samples from each depth, were observed at the 55% level of similarity, the ANOSIM confirming the significant differences among the depths (R= 0.929; P < 0.001) (Fig. 9).

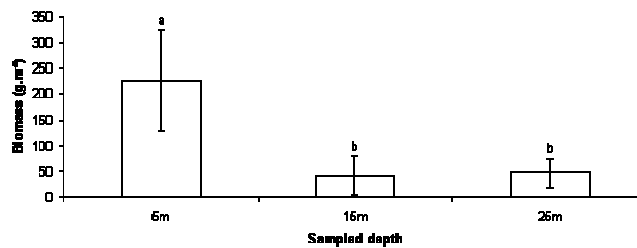


Fig. 8. Total mean biomass (g.m⁻²) at the depths sampled. The letters indicate differences detected by Tukey test.

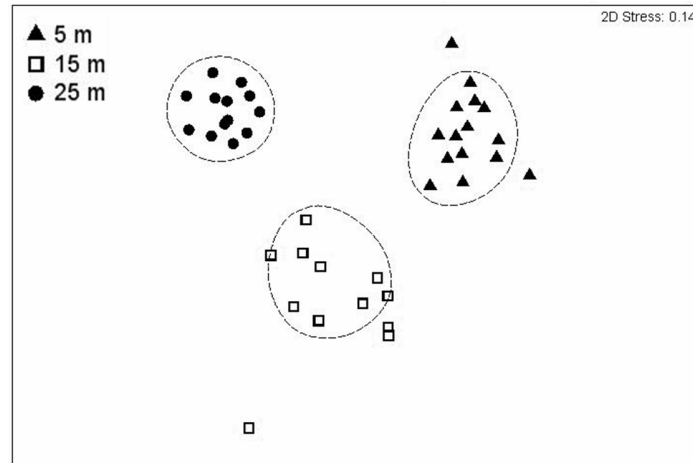


Fig. 9. Multi Dimensional Scaling (MDS) ordination of samples of associated flora at three depths based on Bray-Curtis's similarity index. The contours indicate 3 groups that show at least 55% similarity.

DISCUSSION

Coralline Algae Species

Five crustose coralline red algae species were identified revealing a multi-specific composition of rhodoliths in the study area. The genera identified were recognized as rhodolith-forming by Harvey and Woelkerling (2007).

Lithothamnion brasiliense had only been recorded for São Paulo State, a subtropical region of southeastern Brazil (FOSLIE, 1900; TAYLOR, 1930, 1960; WOELKERLING, 1993; HORTA, 2000). This is, therefore, the first record of *L. brasiliense* for a tropical region (Bahia State) which thus expands the known geographical distribution of the species. The features observed in the specimens of *L. superpositum* analyzed correspond to those details described by Wilks and Woelkerling (1995) (as *L. indicum*), by Keats et al. (2000), by Harvey et al. (2003) by Harvey and Bird (2008) and by Farias et al. (2010). The main feature to distinguish between the two species is related to the occurrence of tetrasporangial conceptacles pitted with depressions in *L. superpositum*. This feature is not observed in *L. brasiliense*. Other differences may be seen in Table 1.

Mesophyllum erubescens is the only *Mesophyllum* species recorded for Brazilian waters (TAYLOR, 1960; FIGUEIREDO; STENECK, 2002; ROCHA et al., 2006; FIGUEIREDO et al., 2007; NUNES et al. 2008) and the taxonomic characteristics observed are in agreement with the descriptions of Harvey et al. (2003) and Nunes et al. (2008).

Sporolithon episporum is a common species found in both tropical and subtropical waters. The

features observed in our specimens correspond to *S. episporum* as described by Keats and Chamberlain (1993), Verheij (1993) and Nunes et al. (2008). In Brazil, this species had previously been recorded forming rhodoliths in the states of Paraíba (RIUL et al., 2009) and Bahia (NUNES et al., 2008).

Rhodoliths

Our results show a decrease in rhodolith vitality with depth. There are few studies on the proportion of living vs. dead rhodoliths (e.g., Figueiredo et al. 2007, Harvey and Bird, 2008, Peña and Bárbara, 2008). The $17\% \pm 3\%$ live rhodoliths found in the Salvador bed at 25 m depth is similar to that observed by Figueiredo et al. (2007) in samples from a small rhodolith bed on the Abrolhos Archipelago (Bahia State, Brazil) at 7–10 m depth (~20% live rhodoliths). Just as was found at 25 m depth in this present study, this Abrolhos bed is also composed of small dense rhodoliths. The bed vitality results from the 25 m depth is also similar to that found at 1–4 m depth in a rhodolith bed located in Victoria, Australia (15–37% live rhodoliths) (HARVEY; BIRD, 2008).

Vitality is an important factor to be evaluated since it can affect the rhodolith structure as a substrate. For example, some live coralline algae can present an antifouling effect from epithelial shedding (KEATS et al., 1994; KEATS et al., 1997), others contain chemical cues that facilitate the settlement and metamorphosis of certain mollusk species (NELSON, 2009). In the southernmost Brazilian rhodolith bed, Gherardi (2004) demonstrated that a relationship existed between rhodolith vitality and epifauna abundance as it was shown that zoanthids

tend to occur in areas with a low percentage cover of living coralline algae on rhodoliths. In general, live rhodoliths may support richer communities than dead rhodoliths, gravel or sandy bottoms of equivalent grain size (CABIOCH, 1969; KEEGAN, 1974).

The non-geniculate coralline red algae are highly morphologically variable (WOELKERLING et al., 1993). The rhodolith shape and growth form may vary with environmental and biological conditions such as light, availability of nutrients, temperature, water motion, and species (FOSTER, 2001). Our results show a predominance of the encrusting growth forms for all depths. In relation to rhodolith shape, our results show a predominance of the spherical shape for all depths and a gentle increase of the ellipsoidal shape at 25 m depth as compared with the other depths. Many investigators have sought to explain the spherical morphology of rhodoliths, generally invoking some hydrological or biological mechanism for frequent turning (FOSTER, 2001). Some studies have suggested that rhodolith shape can change from spherical to discoidal associated with a decreased turning frequency caused by a reduction in water motion (BOSELLINI; GINSBURG, 1971; BOSENCE 1976, 1991; PRAGER; GINSBURG, 1989). However, some minimal water motion is required to maintain rhodolith beds and it has been suggested that they require both shelter from wave action to prevent burial of thalli but sufficient movement of the water to prevent smothering with silt (HALL-SPENCER, 1998).

A clear reduction in mean rhodolith diameter and volume was observed with increasing depth, while rhodolith density increased. The one order of magnitude increase in density at 25 m depth (total of $11,775 \pm 1,102$ rhodoliths.m⁻²) is to be explained by the small size (< 1 cm) of rhodoliths of this depth which makes a greater aggregation of individuals per unit area possible. The predominance of small rhodoliths at 25 m depth suggests that larger individuals had been fragmented by water motion thus opening the way for re-colonization and growth (SCOFFIN et al., 1985; FOSTER, 2001).

The dimensions and density pattern of the rhodoliths of the Salvador bed were the opposite of those found by Amado-Filho et al. (2007) in a rhodolith bed of Espírito Santo State (Brazil). As mentioned above, in the Salvador bed, the rhodolith dimensions decrease and the density increases with depth, while in the Espírito Santo bed, the dimensions increase and the density decreases from shallow to deeper zones. An evident difference among these beds can be attributed to the morphology of the respective coasts on which they are located. The continental shelf of the Salvador bed - about 10 km in width (Figs 10A and 10C) - slopes more steeply than the Espírito Santo bed which has a width of about 60 km (Figs 10A and

10B). In contrast with the Espírito Santo bed, at the Salvador bed depths greater than 20 m are found close (2 km) to the shore which exposes them to sedimentation from the continent and causes an increase in the turbidity of the water. These conditions are probably unsuitable for rhodolith development below 20 m depth in the study area. On the other hand, Amado-Filho et al. (2007) mention the presence of clear offshore continental shelf waters (30-60 km offshore) characterized by a low concentration of suspended particles from 35 to 120 m depth at the Espírito Santo bed. These circumstances provide more suitable light and sedimentation conditions for rhodolith growth in deep waters in contrast with those of shallow waters, which might explain the occurrence of higher rhodolith dimensions in the deeper zone in the Espírito Santo bed (AMADO-FILHO et al., 2007).

The pattern of the reduction of rhodolith dimensions with depth of the Salvador bed is similar to that observed in other rhodolith beds studied. Steller and Foster (1995) observed a decrease in rhodolith diameter from 3 to 12 m depth in Baja California (Mexico). Littler et al. (1991) also found a reduction in rhodolith dimension along a depth gradient between 67-290 m depth at San Salvador Seamount (Bahamas). Riul et al. (2009) noted a decrease in rhodolith volume from 10 to 20 m depth in Paraíba, northeastern Brazil, which also has a relatively narrow continental shelf - about 30 km in width.

A schematic representation of the continental shelf (Fig. 10), including slope and extension, summarize the pattern of three Brazilian rhodolith bed studies that related rhodolith dimension to depth. It has been shown that rhodolith dimensions varied with depth in the three areas studied (AMADO-FILHO et al., 2007; RIUL et al., 2009 and the present study).

Associated Flora

The results obtained by MDS and ANOSIM, reveal that the associated flora composition and abundance is closely related to depth: only 12 % of the species of the local flora are common to the three depths sampled; total biomass is significantly higher at 5 m than at the 15 and 25 m depths and changes in dominant species are seen from the shallowest to the deepest sample site. The higher biomass observed at 5 m depth can be related to the proximity of a nearby reef that provides a sheltered environment for rhodoliths, and consequently stable conditions for the development of an abundant flora. The biomass found at 5 m depth is similar to that observed by Marins et al. (2008) on a sheltered subtidal reef in Todos os Santos Bay (Fig. 1). Although a higher rhodolith density provides

greater stability, increasing habitat complexity and available colonization areas (HINOJOSA-ARANGO; RIOSMENA-RODRIGUEZ, 2004), the high rhodolith density found at 25 m depth does not guarantee the bed's stability or provide a suitable substrate for a great seaweed biomass since the rhodoliths of this site are of small size which possibly makes them more susceptible to disturbance by water motion and burial. On the other hand, the higher species richness found at 25 m than at 15 m depth may be related to a greater habitat complexity promoted by the high rhodolith density.

In brief, the structure of the rhodolith bed studied is clearly influenced by depth. Rhodolith density increases while the dimensions, vitality and abundance of associated flora decrease from the shallow to the deepest zones. These results associated with other recent rhodolith bed descriptions (Amado Filho et al, 2007 and Riul et al., 2009) may indicate

that the pattern of Brazilian rhodolith bed structure along depth gradients should be related to a combination of extension and slope of the continental shelf. Descriptions of the structure of other rhodolith beds and associated organisms are needed so that these important marine communities along the Brazilian continental shelf may be better understood, managed and conserved.

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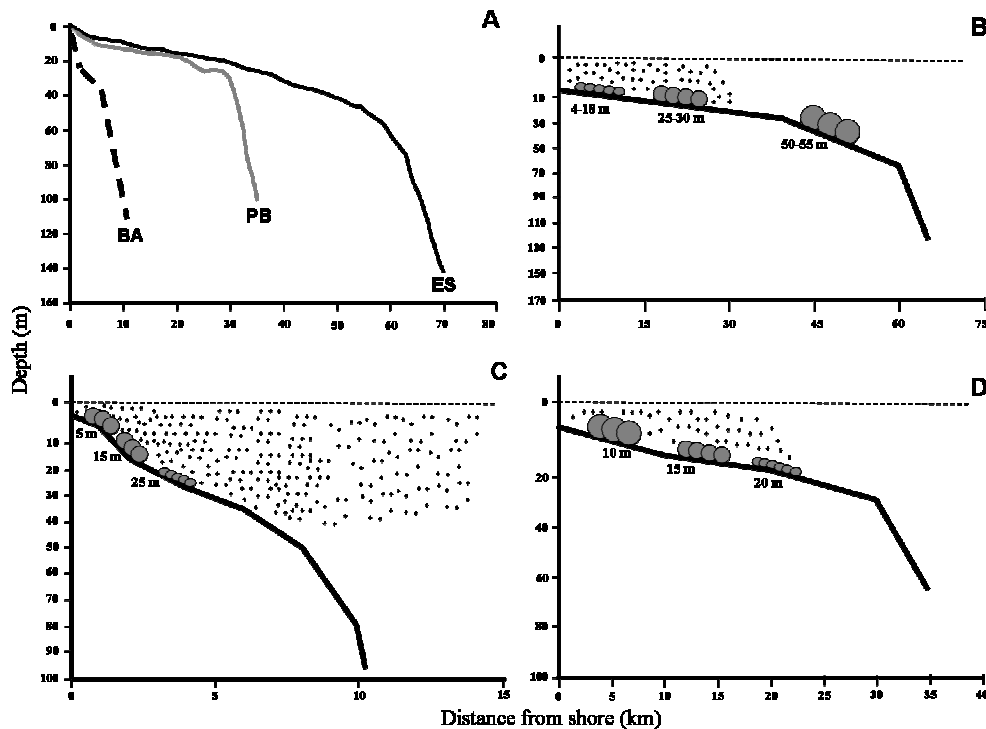


Fig. 10. Schematic representation of rhodolith dimensions distribution along depth gradients in the three Brazilian rhodolith beds studied. (A) Continental shelf profiles: BA = Salvador, Bahia (present study), PB = João Pessoa, Paraíba, and ES - south of Espírito Santo. (B-D) Specific profiles of each rhodolith bed. (B) South of Espírito Santo; (C) Present study; (D) João Pessoa. Three rhodolith size classes were used: small, medium and large; the scattered points represent an estimation of suspended particles in water column. Data from south of Espírito Santo were based on Amado-Filho et al. (2007) and those from João Pessoa were taken from Riul et al. (2009). Continental shelf extension and degree of slope were determined by using electronic nautical chart – MapSource BlueChart Americas.

REFERENCES

- AMADO FILHO, G. M.; MANEVELDT, G.; MARINS, B. V.; MANSO, R. C. C.; PACHECO, M. R.; GUIMARÃES, S. P. B. Structure of rhodolith beds from 4 to 55 meters deep along the southern coast of Espírito Santo State, Brazil. **Cienc. Mar.**, v. 33, n. 4, p. 399-410, 2007.
- BASSO, D. Deep rhodolith distribution in the Pontian Islands, Italy: a model for the paleoecology of a temperate sea. **Palaeogeog. Palaeoclim. Palaeoecol.**, v. 137, p. 173-187, 1998.
- BIRKETT, D. A.; MAGGS, C.; DRING, M. J. "Maerl": An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association of Marine Science, UK Marine Special Areas of Conservation Project, 1999, 90 p.
- BOSELLINI, A.; GINSBURG, R. N. Form and internal structure of recent algal nodules (Rhodolites) from Bermuda. **J. Geol.**, v. 79, p. 669-682, 1971.
- BOSENCE, D. W. J. Ecological studies on two unattached coralline algae from western Ireland. **Paleontol.**, v. 19, n. 2, p. 365-395, 1976.
- BOSENCE, D. W. J.; PEDLEY, H. M. Sedimentology and palaeoecology of Miocene coralline algal biostrome from the Maltese Islands. **Palaeogeog. Palaeoclim. Palaeoecol.**, v. 38, p. 9-43, 1982.
- BOSENCE, D. W. J. **Coralline algae: Mineralization, taxonomy, and palaeoecology.** In: RIDING, R. (Ed.), *Calcareous Algae and Stromatolites*. Berlin: Springer-Verlag, 1991. p. 98-113.
- CABIOCH, J. Les fonds de maerls de la baie de Morlaix et leur peuplement vegetal. **Cah. Biol. Mar.**, v.10, p. 139-161, 1969.
- CLARKE, K. R.; WARWICK, R. M. **Change in marine communities: an approach to statistical analysis and interpretation.** Plymouth: Plymouth Marine Laboratory, p. 144, 1994.
- DHN. **Atlas de Cartas Pilotos.** 2.ed. Rio de Janeiro: Marinha do Brasil, Diretoria de Hidrografia e Navegação, 1993.
- DIAS, G. T. M. Marine bioclasts – calcareous algae. **Braz. J. Geophys.**, v. 18, n. 3, p. 307-318, 2000.
- FARIAS, J. N.; RIOSMENA-RODRIGUEZ, R.; BOUZON, Z.; OLIVEIRA, E. C.; HORTA, P. A. *Lithothamnion superpositum* (Corallinales; Rhodophyta): First description for the Western Atlantic or rediscovery of a species? **Phycol. Res.**, v. 58, p. 210-216, 2010.
- FIGUEIREDO, M. A. O.; STENECK, R. S. Floristic and ecological studies of crustose coralline algae on Brazil's Abrolhos reefs. In: INTERNAT. CORAL REEF SYMP., 9., 2002., Bali. v. 1, p. 493-497, 2002.
- FIGUEIREDO, M. A.O.; SANTOS DE MENEZES, K.; COSTA-PAIVA, E. M.; PAIVA, P. C.; VENTURA, C.R.R. Experimental evaluation of rhodoliths as living substrata for infauna at the Abrolhos Bank, Brazil. **Cienc. Mar.**, v. 33, p. 427-440, 2007.
- FOSLIE, M. **New or critical calcareous algae. Det K. Norske Vidensk. Selsk. Skr.**, v. 1899-5: 1-34, 1900.
- FOSTER, M. S.; RIOSMENA-RODRIGUEZ, R.; STELLER, D.; WOELKERLING, W. M. J. Living rhodolith beds in the Gulf of California and their significance for paleoenvironmental interpretation. In: JOHNSON M.; Ledesma related facies flanking the Gulf of California, Baja -Vázquez J. (Ed.). *Pliocene Carbonates and California, Mexico. Spec. Pap. Geol. Soc. Am.*, Boulder, p. 127-139, 1997.
- FOSTER, M. S. Rhodoliths: between rocks and soft places - Minireview. **J. Phycol.**, v. 37, p. 659-667, 2001.
- GHERARDI, D. F. M. Community structure and carbonate production of a temperate rhodolith bank from Arvoredo Island, southern Brazil. **Braz. J. Oceanogr.**, v. 52, p. 207-224, 2004.
- GRAHAM, D. J.; MIDGLEY, N. G. Graphical representation of particle shape using triangular diagrams: an Excel spreadsheet method. **Earth Surf. Process. Landforms**, v. 25, n. 13, p. 1473-1477, 2000.
- HALL-SPENCER, J. M. Conservation issues relating to maerl beds as habitats for molluscs. **J. Conch.** (Special Publication), v. 2, p. 271-286, 1998.
- HARVEY, A. S.; BIRD, F. L. Community structure of a rhodolith bed from cold-temperate waters (southern Australia). **Aust. J. Bot.**, v. 56, p. 437-450, 2008.
- HARVEY, A. S.; WOELKERLING, W. J.; MILLAR, A. J. K. An account of the Hapalidiaceae (Corallinales, Rhodophyta) in south-eastern Australia. **Aust. Syst. Bot.**, v. 16, p. 647-698, 2003.
- HARVEY, A. S.; WOELKERLING, W. J. A guide to nongeniculate coralline red algal (Corallinales, Rhodophyta) rhodolith identification. **Cienc. Mar.**, v. 33, n. 4, p. 411-426, 2007.
- HINOJOSA-ARANGO, G.; RIOSMENA-RODRIGUEZ, R.. Influence of rhodolith-forming species and growth-form on associated fauna of rhodolith beds in the central-west Gulf of California, Mexico. **Mar. Ecol.** v. 25, p. 109-127, 2004.
- HINOJOSA-ARANGO, G.; MAGGS, C. A.; JOHNSON, M. P. Like a rolling stone: the mobility of maerl (Corallinales) and the neutrality of the associated assemblages. **Ecology**, v. 90, n. 2, p. 517-528, 2009.
- HORTA, P. A. Macroalgas do infralitoral do sul e sudeste do Brasil: taxonomia e biogeografia. 2000. 301 p. Doctoral thesis - Instituto de Biociências, USP, São Paulo., 2000.
- HORTA P. A. Bases para a identificação das coralináceas não articuladas do litoral brasileiro – uma síntese do conhecimento. **Biotemas**, v. 15, p. 7-44, 2002.
- HORTA P. A.; AMANCIO, E.; COIMBRA, C. S.; OLIVEIRA, E. C. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras. **Hoehnea**, v. 28, n. 3, p. 243-265, 2001.
- KEATS, D. W.; CHAMBERLAIN, Y. M. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa. **J. South Afric. Bot.**, v. 59, p. 541-550, 1993.
- KEATS, D. W.; WILTON, P.; MANEVELDT, G. W. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinales, Rhodophyta) in South Africa. **J. expl mar. Biol. Ecol.**, v. 175, p. 145-154, 1994.
- KEATS, D. W.; KNIGHT, M. A.; PUESCHEL, C. M. Antifouling Effects of Epithallial Shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coastal reef. **J. expl mar. Biol. Ecol.**, v. 213, p. 281-293, 1997.

- KEATS, D. W.; MANEVELDT, G. M.; CHAMBERLAIN, Y. M. *Lithothamnion superpositum* Foslie: a common crustose red algae (Corallinales) in South Africa. **Cryptog. Algol.**, v. 21, p. 381-400, 2000.
- KEEGAN, B. F. The macrofauna of maerl substrates on the west coast of Ireland. **Cah. Biol. Mar.**, v. 15, p. 513-530, 1974.
- KEMPF, M.; COUTINHO, P. N.; MORAIS, J. O. Plataforma continental do norte e nordeste do Brasil. Nota preliminar sobre a natureza do fundo. **Trabhs Oceanogr., Univ. Fed. Pernambuco**, n. 9/11, p. 95-110, 1967/9.
- KEMPF, M. Notes on the benthic bionomy of the N-NE Brazilian Shelf. **Mar. Biol.**, v. 5, n. 3, p. 213-224, 1970.
- KONAR, B.; RIOSMENA-RODRIGUEZ, R.; IKEN, K. Rhodolith bed: a newly discovered habitat in the North Pacific **Ocean. Bot. Mar.**, v. 49, p. 355-359, 2006.
- LITTLER, M. M.; LITTLER, D. S. Coralline algal rhodoliths form extensive benthic communities in the Gulf of Chiriquí, Pacific Panama. **Coral Reefs**, v. 27, p. 553, 2008.
- LITTLER, M. M.; LITTLER, D. S.; HANISAK, M. D. Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. **J. expl mar. Biol. Ecol.**, v. 150, p. 163-182, 1991.
- MABESOONE, J. M.; KEMPF, M.; COUTINHO, P. N. Characterization of surface sediments on the Northern and Eastern Brazilian shelf. **Trabhs. Oceanogr., Univ. Fed. Pernambuco**, v. 13, p. 41-48, 1972.
- MARINS, B. V.; BRASILEIRO, P. S.; BARROS BARRETO, M. B.; NUNES, J. M. C.; AMADO FILHO, G. M. Subtidal benthic marine algae of the Todos os Santos bay, Bahia State, Brazil. **Oecol. Bras.** v. 12, n. 2, p. 229-242. 2008.
- MILLIMAN J. D. Role of calcareous algae in Atlantic continental margin sedimentation. In: FLUGEL, E. (Ed.). **Fossil Algae**. Berlin: Springer-Verlag, 1977. p. 232-247.
- MILLIMAN, J. D.; AMARAL, C. A. B. Economic potential of Brazilian continental margin sediments. **An. Congr. Brasil. Geol.**, v. 28, p. 335-344, 1974.
- NELSON, W. A. Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: a review. **Mar. Freshwat. Res.**, v. 60, p. 787-801, 2009.
- NUNES, J. M. C. **Rodofíceas marinhas bentônicas do Estado da Bahia, Brasil**. 2005. 410 p. Tese (Doutorado), Botânica, Universidade de São Paulo, São Paulo, 2005.
- NUNES, J. M. C.; GUIMARÃES, S. M. P. B.; DONNANGELO, A.; FARIAS, J.; HORTA, P. A. Taxonomic aspects of three species of non geniculate coralline algae from Bahia State, Brazil. **Rodriguesia**, v. 59, n. 1, p. 75-86, 2008.
- PEÑA, V.; BÁRBARA, I. Biological importance of an Atlantic European maerl bed off Benencia Island (northwest Iberian Peninsula). **Bot. Mar.**, v. 51, p. 493-505, 2008.
- PERRY, C. T. Morphology and occurrence of rhodoliths in siliciclastic, intertidal environments from a high latitude reef setting, southern Mozambique. **Mar. Geol.**, v. 214, p. 143-161, 2005.
- PRAGER, E. J.; GINSBURG, R. N. Carbonate nodule growth on Florida's outer shelf and its implications for fossil interpretations. **Palaios**, v. 4, p. 310-317, 1989.
- RIOSMENA-RODRÍGUEZ, R.; WOELKERLING, W.; FOSTER, M. S. Taxonomic reassessment of rhodolith-forming species of *Lithophyllum* (Corallinales, Rhodophyta) in the Gulf of California, Mexico. **Phycol.**, v. 38, p. 401-417, 1999.
- RIUL, P.; LACOUTH, P.; PAGLIOSA, P. R.; CHRISTOFFERSEN, M. L.; HORTA, P. A. Rhodolith beds at the easternmost extreme of South America: Community structure of an endangered environment. **Aquat. Bot.**, v. 90, p. 315-320, 2009.
- ROCHA, R. M.; METRI, M.; OMURO, J. Y. Spatial distribution and abundance of ascidians in a bank of coralline algae at Porto Norte, Arvoredo Island, Santa Catarina. **J. coast. Res.**, SI 39, p. 1676 - 1679, 2006.
- SCOFFIN, T. P.; STODDART, D. R.; TUDHOPE, A. W.; WOODROFFE, C. Rhodoliths and coralloliths of Muri Lagoon, Rarotonga, Cook Islands. **Coral Reefs**, v. 4, p. 71-80, 1985.
- SNEED, E. D.; FOLK, R. L. Pebbles in the lower Colorado River, Texas, a study in particle morphogenesis. **J. Geol.**, v. 66, n. 2, p. 114-150, 1958.
- STELLER, D. L.; FOSTER, M. S. Environmental factors influencing distribution and morphology of rhodoliths in Bahía Concepcion, BCS, Mexico. **J. expl mar. Biol. Ecol.**, v. 194, p. 201-212, 1995.
- STELLER D. L.; RIOSMENA-RODRÍGUEZ R.; FOSTER, M. S.; ROBERTS, C. Rhodolith bed diversity in the Gulf of California: The importance of rhodolith structure and consequences of anthropogenic disturbances. **Aquat. Conserv. mar. Freshwat. Ecosyst.**, v. 13, p. 5-20, 2003.
- STENECK, R. S. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. **Annu. Rev. Ecol. Syst.**, v. 17, p. 273-303, 1986.
- TAYLOR, W. R. A synopsis of the marine algae of Brazil. **Rev. Algol.**, v. 5, p. 1-35, 1930.
- TAYLOR, W. R. **Marine algae of the eastern tropical and subtropical coasts of the Americas**. Michigan: University of Michigan Press, 1960.
- TESTA, V. Calcareous algae and corals in the inner shelf of Rio Grande do Norte, NE, Brazil. **Internat. Coral Reef Symp.**, 8, v. 1, p. 737-742, 1997.
- TESTA, V.; BOSENCE, D. W. Physical and biological controls on the formation of carbonate and siliciclastic bedforms on the north-east Brazilian shelf. **Sedimentol.**, v. 46, p. 279-301, 1999.
- VERHEIJ, E. The genus *Sporolithon* (Sporolithaceae, fam. Nov., Corallinales, Rhodophyta) from the Spermond Archipelago, Indonesia. **Phycol.**, v. 32, p. 184-196, 1993.
- VICALVI, M. A.; MILLIMAN, J. D. Calcium carbonate sedimentation on continental shelf off southern Brazil with special reference to benthic foraminifera In: FROST S. H.; WEISS M. P.; SAUNDERS J. B. (Ed.). **Studies in Geol.**, 4, AAPG, 1977. p. 313-328.
- VILLAS-BOAS, A. B.; RIOSMENA-RODRIGUEZ, R.; AMADO FILHO, G. M.; MANEVELDT, G.; FIGUEIREDO, M. A. O. Rhodolith-forming species of *Lithophyllum* (Corallinales; Rhodophyta) from Espírito Santo State, Brazil, including the description of *L. depressum* sp. nov. **Phycol.**, v. 48, n. 4, p. 237-248, 2009.

- WILKS, K. M.; WOELKERLING, W. J. An Account of Southern Australian Species of *Lithothamnion* (Corallinaceae, Rhodophyta). **Austr. Syst. Bot.**, v. 8, p. 549-583, 1995.
- WILSON, S.; BLAKE, C.; BERGES, J. A.; MAGGS, C. A. Environmental tolerances of free-living coralline algae (Maerl): implications for European marine conservation. **Biol. Conserv.**, v. 120, p. 279-289, 2004.
- WOELKERLING, W. J. Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). **Gunneria**, v. 67, p. 1-289, 1993.
- WOELKERLING, W. M. J.; IRVINE, L. M.; HARVEY, A. S. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). **Aust. Syst. Bot.**, v. 6, p. 277-293, 1993.
- WOMERSLEY, H. B. S. **The Marine benthic flora of Southern Australia**. Part IIIB: Australian Biological Resources Study, Canberra, 1996, p. 392, 1996.
- ZAR J. H. **Biostatistical analysis**. 4th ed. Upper Saddle River, NJ: Prentice-Hall, 1999. p. 718.

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