CORAL COMMUNITY STRUCTURE AND SEDIMENTATION AT DIFFERENT DISTANCES FROM THE COAST OF THE ABROLHOS BANK, BRAZIL

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ABSTRACT

Sedimentation has previously been considered an important source of impact in coral reefs. We compared 3 sites on the Abrolhos Bank, Brazil, regarding sedimentation rates, carbonate sediment composition, coral cover, and colony size for the commonest local coral species (Mussismilia braziliensis, Siderastrea stellata, and Favia gravida). The sites are located at different distances from the mainland: Pedra de Leste (14 km), Pontas Sul (26 km), and Parcel dos Abrolhos (58 km). Sedimentation was higher in winter (p <0.05), but no difference among sites was noted. Sites differed in sediment type (P <0.05), with Parcel dos Abrolhos showing nearly 90% of carbonate in sediment composition, Pontas Sul nearly 65%, and Pedra de Leste only nearly 50%. The farther from the mainland, where the zoanthid cover was smaller, the higher was the coral cover (p <0.01). Differences in colony sizes were found only for M. braziliensis, with smaller colonies occurring at Pedra de Leste (p <0.05). It is suggested that terrigenous sediment distribution and turbidity may be the main factors controlling reef development at the Abrolhos Reefs.

Resumo

A sedimentação tem sido considerada uma importante fonte de impacto nos recifes de coral. Uma comparação entre as taxas de sedimentação, teor de carbonatos nos sedimentos, cobertura coralínea e tamanho de colônias de corais para as espécies mais comuns (*Mussismilia braziliensis, Siderastrea stellata*, e *Favia gravida*) foi realizada em 3 locais no Banco dos Abrolhos. Os locais representam um gradiente de distância da costa: Pedra de Leste (14 km), Pontas Sul (26 km) e Parcel dos Abrolhos (58 km). A sedimentação foi maior no inverno (p <0,05), mas não foi observada diferença entre os locais. O tipo de sedimento diferiu entre locais (P <0,05), sendo que Parcel dos Abrolhos apresentou 90% de carbonatos, Pontas Sul 65% e Pedra de Leste 50%. A cobertura coralínea foi maior no local mais afastado de terra (p <0,01), onde a cobertura de zoantídeos foi menor. Diferenças de tamanho de colônias foram encontradas apenas para *M. braziliensis*, com menores colônias em Pedra de Leste (p <0,05). A distribuição dos sedimentos terrígenos e a turbidez devem ser os principais fatores controladores do desenvolvimento dos recifes de Abrolhos.

Descriptors: Coral community, Sedimentation, Point intercept transect, Sediment trap, Abrolhos, Brazil

Descritores: Comunidade coralínea, Sedimentação, Transecto de interseção de pontos, Armadilha de sedimento. Abrolhos. Brasil.

Introduction

Several kinds of disturbances to coral reefs have been described, including several anthropogenic impacts, such as destructive fishing practices, oil spills, sewage discharge, eutrophication, and sedimentation (RICHMOND, 1993; HUGHES, 1994; BROWN, 1997; NYSTRÖM et al., 2000). A common and well-documented source of impact is sedimentation (LOYA, 1976; DODGE; VAISNYS, 1977; CORTÉS; RISK, 1985; VAN KATWIJK et al.,

1993; BROWN et al., 2002). High sedimentation rates on coral reefs can lead to smothering, abrasion, shading, and/or coral settlement inhibition (HUBBARD, 1997). Furthermore, studies have related sedimentation to coral recruitment (GILMOUR, 1999), skeleton morphology (FOSTER, 1980), growth (DODGE et al., 1974; DODGE; VAISNYS, 1977), and community structure (LOYA, 1976; CORTÉS; RISK, 1985; TOMASCIK; SANDER, 1987).

The Abrolhos region, the reefs of which are the most diverse and richest of the South Atlantic,

covers an area of approximately 6,000 km². LABOREL (1969) reported the occurrence of fifteen scleractinian coral species, five of which are Brazilian endemics, on these reefs. However, there are new records of scleractinian species in other Brazilian reef communities (see Neves et al.; 2008), which probably also appear on the Abrolhos. These findings suggest that Abrolhos coral diversity may be even higher. Leão (1995) mentioned that activities such as deforestation in coastal areas in southern Bahia might be responsible for an increase in sediment deposition at reef sites. However, there is almost no quantitative data on sedimentation rates to which Brazilian coral communities are subject (but see Dutra et al., 2006). The relationship between sedimentation and recent coral communities in Brazil remains poorly understood (but see Dutra et al., 2006). Hence, this study aims to quantify sediment deposition rates, sediment type, coral cover, and size of coral colonies at different sites, in order to investigate the relationships between these parameters. Furthermore, since it has been suggested that coral communities on the Abrolhos Bank vary according to their distance from the mainland (LABOREL, 1970; DUTRA et al., 2006), this hypothesis is reviewed in the light of new quantitative data.

An assessment was designed, therefore, to quantify several parameters and compare sites at different distances from the mainland. Size of individual reef pinnacles, depth at the top of reefs, and wave exposure varied comparatively little between the

reefs studied, while more conspicuous differences were expected in turbidity, since extremely turbid waters are more common on the inner reefs (personal observation). Such a scenario would then lead to a turbidity gradient inversely proportional to distance from the mainland. Sedimentation would, therefore, probably vary in accordance with increasing distance from the shoreline, and this may be a process that contributes to variations in reef composition or structure.

MATERIAL AND METHODS

The three sites sampled were Pedra de Leste, at Parcel das Paredes (17°47.261'S; 039°02.795'W); Pontas Sul, at Parcel das Paredes (17°53.025'S; 038°59.265'W); and Parcel dos Abrolhos (17°58.203'S; 038°40.230'W) (Fig. 1). These sites were selected because they stand near the commonest route from the mainland to the reefs most distant from the shore. Although we tried to sample the same depths at each location, depth differed among reefs due to the lack of shallower areas on the outer reefs. As a result, the Pedra de Leste (PL) site was approximately 3.4 to 3.7 m deep, whereas that at Pontas Sul (PS) was 3 to 6.5 m deep, and that at Parcel dos Abrolhos (PA) from 5.2 to 7.7 m deep. The depths indicated were corrected in accordance with the lowest levels of spring tides. Maximum tide amplitude in the area is approximately 1.7 m.

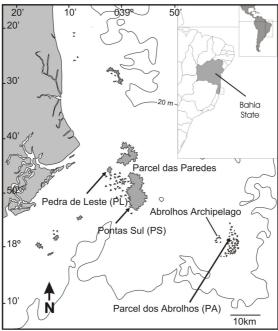


Fig.1. Location of the study sites at Abrolhos Bank, Brazil.

Sediment deposition was measured using sediment traps with a height/diameter ratio >3 (BLOMQVIST; KOFOED, 1981). Traps were built with PVC tubes (7 cm in diameter and 25 cm in height) closed at the bottom and tied to metal pins fixed to the reef. Trap bottoms were located circa 20 cm above the seafloor. Ten traps were placed and kept for approximately 2 months at each sample site in the summer of 2000 (November/1999-January/2000) and the winter of 2000 (May/July) and 2001 (July/August). In two instances, some traps were not retrieved (Pontas Sul, summer and winter/2000 – see Table 1) due to the loss of a trap or to its coming loose and its bottom's resting on the seafloor. All the winter/2000 traps from Pedra de Leste were lost in the field (see Table 1). Sediments collected by the traps were taken to the laboratory for analysis. The sediment was composed mainly of very fine particles, making the use of filtering processes for sediment quantification impossible (ROGERS, 1983). The mollusk shells and crab carapaces that were occasionally found inside the traps were removed before the analysis. Samples were diluted and washed (to diminish the contribution of salt to the dry weight), dried at approximately 50°C and weighed. Data were log-transformed for statistical analysis of sedimentation rates, owing to the nonnormality of raw data. Comparisons of sedimentation rates between localities and seasons were performed using two-way analysis of variance (ANOVA), with SYSTAT 7.0.1 for Windows (SPSS Inc. 1997).

Table 1. Mean sedimentation rates, with standard deviation, at the Abrolhos Bank, Brazil. Number of samples are shown between parenthesis. # = data not collected.

	Sedimentation rates (mg cm ⁻² day ⁻¹)						
Site	Summer/2000	Winter/2000	Winter/2001				
Parcel dos	$5.2 \pm 1.6 (10)$	$10.7 \pm 2.0 (10)$	9.5 ± 2.6 (10)				
Abrolhos							
Pontas Sul	3.3 ± 1.9 (6)	10.2 ± 4.5 (8)	$9.8 \pm 4.1 (10)$				
Pedra de Leste	5.6 ± 2.3 (10)	#	$10.1 \pm 6.5 (10)$				

For sediment type analysis, 6 pre-weighed sub-samples from 3 samples of each site in each season were treated with a solution of formic acid (10%) and formalin (5%) to remove the carbonate fraction (CALLIS 2008; see Westphal et al. 2008 for the removal of the carbonate fraction with formic acid). Each sub-sample was dried and re-weighed, and the carbonate percentage was calculated by weight loss.

Benthic coverage data were collected in November, 1999 at each site. We sampled 5 point intercept transects at each of the 3 stations on each site, to a total of 15 transects per site, in accordance with a method described in Segal and Castro (2001). Ten-meter-long transect lines were previously tagged with 250 random points. Each organism (alga, coral or other invertebrate) positioned below each point was

recorded. One-way ANOVA was used to compare *Palythoa caribaeorum*, total coral, and other benthic group coverage between sites, with arcsin transformed data, using SYSTAT 7.0.1 (SPSS Inc., 1997). Species composition and abundance were compared between sites and within stations with multi-dimensional scaling (MDS) and cluster analysis, using the Bray-Curtis similarity coefficient. After these procedures, SIMPER analysis was performed to identify the species/categories that best explained similarities within groups and differences between groups. All these analyses were performed with the aid of PRIMER 4.0 (CLARKE; WARWICK, 1994; CARR, 1997).

When assessing colony size structuring, large and irregular colonies are difficult to measure, mainly due to parallax. Therefore, the use of linear tissue length, instead of colony diameter, was tested. Initially, 36 colonies of *Mussismilia braziliensis* were randomly selected. Their largest and smallest diameters (straight lines – one dimension) between opposite sides, and equivalent linear lengths of the living tissue (length of arcs – two dimensions) were taken. The correlation between the two measurements was assessed by Pearson's coefficient, using Statistica 4.3 for Windows (STATSOFT Inc., 1993), resulting in r = 0.97 (p < 0.05) for higher diameter x higher linear tissue length and r = 0.96 (p < 0.05) for smaller diameter x smaller linear tissue length.

Subsequently, average linear tissue length measurements ((largest+smallest)/2) were taken from up to 40 colonies of *M. braziliensis*, *Favia gravida*, and *Siderastrea stellata* at each site. A 50 m tape measure marked at 4 m intervals (points) was placed at the bottom. The size of the colony nearest to the points on both sides of the tape was recorded. To compare colony sizes among sites ANOVA, with SYSTAT 7.0.1 (SPSS Inc., 1997), was used.

RESULTS

The highest sediment deposition was observed during winter 2000 at Parcel dos Abrolhos (10.7 \pm 2.0 mg cm⁻² day⁻¹), and the lowest during the summer at Pontas Sul (3.3 \pm 1.9 mg cm⁻² day⁻¹) (Table 1). Sedimentation rates did not differ significantly among sites, but rather between seasons (n = 56, df 16, f = 31.85, p<0.01), with higher rates occurring in winter.

Sediment composition was different between sites (Fig. 2), with Parcel dos Abrolhos presenting a calcium carbonate composition of 91.7% \pm 0.4 (SD) in winter and 92.1% \pm 2.4 (SD) in summer, Pontas Sul presenting 65.9% \pm 0.3 (SD) in winter and 66.4% \pm 1.3 (SD) in summer, and Pedra de Leste, with the smallest contribution of carbonate to sediment composition, presenting 54.6% \pm 4.4 (SD) in winter

and $51.0\% \pm 1.7$ (SD) in summer. There was no difference in carbonate contribution between seasons.

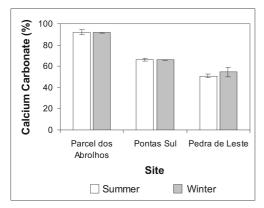


Fig. 2. Carbonate contribution (in percentage of sediment composition) during summer (2000) and winter (2001) in sediment samples from three sites at the Abrolhos Bank, Brazil.

Total coral cover showed significant differences among localities (n = 45, df. 42, f = 50.28, p <0.01). The highest coral cover was found at Parcel dos Abrolhos, and the lowest at Pedra de Leste, which is closer to the mainland (Table 2 and Fig. 3). Palythoa caribaeorum cover also showed significant differences among localities (n = 45, df. 42, f = 112.4, p <0.05), but with a strong increase towards reefs closer to shore (Table 2, see zoanthid cover on Fig. 3). abundance of Mussismilia braziliensis, Siderastrea stellata, and Agaricia humilis was also higher on the outer reefs of Parcel dos Abrolhos (Table 2 and Fig. 4). A marked difference in composition was observed in relation to scleractinian corals versus milleporids: the outer reefs of Parcel dos Abrolhos showed a higher contribution of scleractinians and the inner reefs of Pedra de Leste, showed a higher contribution of milleporids (Table 2 and Fig. 4).

Table 2. Mean percent cover and standard deviation of benthic organisms at the 3 sampled sites at the Abrolhos Bank, Brazil. PL = Pedra de Leste; PS = Pontas Sul; PA = Parcel dos Abrolhos.

Benthic organisms	PL1	PL2	PL3	PS1	PS2	PS3	PA1	PA2	PA3
Agaricia humilis	0.79 ±0.78	0.89 ± 0.86	0.99 ± 0.82	0.39 ± 0.56	0.49 ± 0.73	0.34 ± 0.54	7.64 ± 1.59	7.83 ± 3.36	5.86 ± 2.70
Crustose coralline algae	13.39 ± 6.67	12.77 ± 3.27	9.16 ± 1.82	8.34 ± 2.49	8.39 ± 2.32	7.41 ± 1.77	11.22 5.77	17.18 ± 4.96	12.94 ± 5.02
Turf algae	10.62 ± 4.01	13.95 ± 4.79	16.05 ± 5.43	39.97 ± 7.22	32.38 ± 3.63	30.52 ± 5.97	38.99 ± 7.92	33.99 ± 7.83	44.47 ± 4.20
Foliose algae	0.00	0.16 ± 0.36	0.08 ± 0.18	0.00	0.26 ± 0.57	2.86 ± 1.92	0.00	0.49 ± 0.88	0.86 ± 1.92
Favia gravida	0.16 ± 0.36	0.49 ± 0.51	0.00	0.40 ± 0.40	0.67 ± 0.49	0.96 ± 0.81	0.99 ± 0.63	0.73 ± 0.33	0.87 ± 0.76
Favia leptophylla	0.00	0.00	0.00	0.00	0.00	0.00	0.50 ± 1.12	0.00	0.00
Millepora alcicornis	2.03 ± 1.86	3.49 ± 1.42	2.31 ± 2.29	0.95 ± 1.33	1.58 ± 1.86	1.04 ± 1.29	0.90 ± 1.33	0.16 0.36	1.10 ± 2.04
Millepora braziliensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.48 ± 0.72
Millepora nitida	0.08 ± 0.17	0.91 ± 0.69	0.00	0.00	0.00	0.32 ± 0.72	0.00	0.00	0.00
Montastrea cavernosa	0.00	0.00	0.16 ± 0.35	6.48 ± 4.39	2.94 ± 3.09	3.58 ± 2.65	0.16 ± 0.36	1.30 ± 1.97	1.76 ± 2.20
Mussismilia braziliensis	0.00	0.00	0.16 ± 0.35	0.40 ± 0.89	0.00	0.17 ± 0.37	7.41 ± 4.47	2.67 ± 3.13	7.67 ± 4.20
Mussismilia harttii	1.80 ± 3.00	0.41 ± 0.69	0.08 ± 0.18	2.64 ± 3.50	2.26 ± 1.80	0.68 ± 1.07	0.41 ± 0.91	0.00	0.72 ± 0.87
Mussismilia hispida	0.24 ± 0.54	0.16 ± 0.22	0.00	1.64 ± 1.03	0.42 ± 0.42	2.44 ± 1.14	0.08 ± 0.19	0.40 ± 0.49	0.73 ± 1.01
Palythoa caribaeorum	67.33 ± 6.45	65.08 ± 8.00	67.61 ± 4.95	30.13 ± 10.62	46.12 ± 9.19	42.61 ± 4.47	13.05 ± 5.74	26.51 ± 9.05	1.20 ± 0.94
Porites astreoides	0.24 ± 0.54	0.00	0.00	0.08 ± 0.19	0.25 ± 0.37	0.00	2.36 ± 4.82	0.16 ± 0.37	0.00
Porites branneri	0.08 ± 0.17	0.00	0.08 ± 0.18	0.40 ± 0.30	0.09 ± 0.19	0.17 ± 0.23	0.00	0.00	1.80 ± 4.02
Siderastrea stellata	0.32 ± 0.72	0.24 ± 0.54	0.08 ± 0.18	2.72 ± 2.59	0.00	1.14 ± 1.46	9.04 ± 2.82	7.05 ± 4.79	16.73 ± 1.19
Zoanthus spp.	1.74 ± 1.07	0.78 ± 0.72	1.72 ± 0.58	2.35 ± 0.74	2.67 ± 1.14	0.48 ± 0.51	3.14 ± 1.69	0.81 ± 0.64	2.19 ± 1.79
Milleporidae	2.10 ± 1.83	4.40 ± 1.78	2.31 ± 2.29	0.95 ± 1.33	1.58 ± 1.86	1.37 ± 1.72	0.90 ± 1.33	0.16 ± 0.36	1.58 ± 2.28
Zoanthids	69.07 ± 6.68	65.86 ± 7.45	69.34 ± 5.20	32.48 ± 10.83	48.78 ± 8.93	43.09 ± 4.34	16.19 ± 6.76	27.32 ± 9.12	3.39 ± 2.18
Scleractinians	3.62 ± 2.08	2.20 ± 1.28	1.55 ± 0.52	15.14 ± 6.80	7.11 ± 4.94	9.46 ± 3.51	28.59 ± 7.95	20.14 ± 6.96	36.14 ± 4.79

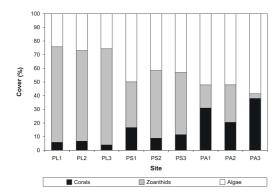


Fig. 3. Mean percent cover of corals, zoanthids, and algae at each station sampled at the Abrolhos Bank, Brazil. PL = Pedra de Leste; PS = Pontas Sul; PA = Parcel dos Abrolhos.

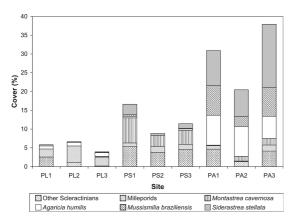


Fig. 4. Mean percent cover of scleractinian and milleporid corals at each station sampled at the Abrolhos Bank, Brazil. Milleporids include *Millepora alcicornis*, *M. nitida*, and *M. braziliensis*. Other scleractinians include species with less than 3% cover: *Favia gravida*, *F. leptophylla*, *Mussismilia harttii*, *M. hispida*, *Porites astreoides*, and *P. branneri*. PL = Pedra de Leste; PS = Pontas Sul; PA = Parcel dos Abrolhos.

The cluster analysis for the complete data set (all species/categories) revealed 2 groups at 60% of similarity, the first comprising all PA stations, and the other linking PS and PL, which are further distinguished at the 70% level of similarity (Fig. 5). These groups were easily identified in the MDS plot (stress value = 0.10) (Fig. 6). Sites were separated mainly on the x-axis. There is also some differentiation in benthic communities among stations of PA on this same axis (see rectangles in Fig. 6). The MDS plot showed a continuous distribution of sites according to their distance from the mainland on the xaxis. A first group comprised all the Parcel dos Abrolhos stations (SIMPER average similarity = 75.90%), and was characterized mainly by turf algae cover (SIMPER explaining 30.65% of similarity), crustose coralline algae (SIMPER = 15.79% of similarity), and Siderastrea stellata (SIMPER = 13.33%). These three categories accounted for 59.76% of the overall similarity within this group. A second group included Pedra de Leste and Pontas Sul stations (SIMPER average similarity = 73.68%) and was characterized mainly by P. caribaeorum dominance (SIMPER = 42.41%), and secondly by turf algae (SIMPER = 23.68%) and crustose coralline algae (SIMPER = 16.47%). These three categories accounted for 82.57% of the group's overall similarity. These two groups were fairly distinct (SIMPER average dissimilarity = 42.66%), with differences explained mainly by the higher P. caribaeorum cover in the second group (SIMPER dissimilarity = 22.93%), and secondly by the higher cover of several corals in the first group (S. stellata SIMPER = 13.10%; Mussismilia braziliensis SIMPER = 9.95; Agaricia humilis SIMPER = 9.68). These four categories accounted for 55.66% of the overall dissimilarity. The second group could be further clustered in two subgroups at 70% similarity, which distinguished the transects of Pedra de Leste (SIMPER average similarity = 83.32%) from those of Pontas Sul (SIMPER average similarity = 77.61%). Although less than those cited above, these subgroups differed (SIMPER average dissimilarity = 32.33%) mainly by the extremely high cover of P. caribaeorum at Pedra de Leste (SIMPER dissimilarity = 18.25%), as opposed to a higher cover of turf algae (SIMPER = 16.55%), *M. cavernosa* (SIMPER = 11.38%) and other scleractinian corals at Pontas Sul.

P. caribaeorum and/or turf algae showed an overwhelming dominance in most samples (Table 2). Therefore, in order to better evaluate the distribution of corals, crustose coralline and foliose algae, we performed another set of analyses after removing zoanthids and turf algae from the matrix (Figs 7 and 8). The cluster showed three main groups near 60% similarity (Fig. 7). The transects from Parcel dos Abrolhos (PA) clustered again in a distinct group (SIMPER average similarity = 71.44%), characterized by a higher cover of crustose coralline algae (SIMPER explaining 29.18% of the similarity), and scleractinian corals (Siderastrea stellata SIMPER = 24.42%; Agaricia humilis SIMPER = 21.42%; Mussismilia braziliensis SIMPER = 14.01%). A second group included exclusively transects from Pontas Sul (PS) (SIMPER average similarity = 64.47%), being characterized by a lower (but mostly uniform) cover of crustose coralline algae (SIMPER explaining 34.28% of the similarity) and a higher cover of other coral species (Montastrea cavernosa SIMPER = 18.55%; Mussismilia hispida SIMPER = 13.12; M. harttii SIMPER = 9.28). A third group comprised almost all the transects from Pedra de Leste and a few of those from Pontas Sul (PL-PS) (SIMPER average similarity = 64.03%). This group is characterized by crustose

coralline algae (SIMPER = 64.25%), Millepora alcicornis (SIMPER = 17.85%), and A. humilis (SIMPER = 10.73%). PA differed from PS (SIMPER average dissimilarity = 54.63%) mostly by a higher abundance of several corals in PA (A. humilis SIMPER = 15.90%; S. stellata SIMPER = 15.40%; Mussismilia braziliensis SIMPER = 13.71%) and a higher abundance of Montastrea cavernosa (SIMPER = 10.87%) and Mussismilia harttii (SIMPER = 7.37%) in PS. PA differed from PL-PS (SIMPER average dissimilarity = 57.24%) by a higher abundance of the same scleractinian corals in PA (S. stellata SIMPER = 24.29%; Mussismilia braziliensis SIMPER = 16.60%; A. humilis SIMPER = 14.42%) and a higher abundance of Millepora alcicornis in PL-PS (SIMPER = 8.73%). The most abundant species on PS or PL-PS, when compared with PA, also accounted for the differences between these groups (SIMPER average dissimilarity = 50.84%, M. cavernosa SIMPER = 18.57%, Mussismilia harttii SIMPER = 10.93%, Millepora alcicornis SIMPER = 10.04%). Mussismilia hispida (SIMPER = 11.25%) was also important to explain the differences between PS and PL-PS.

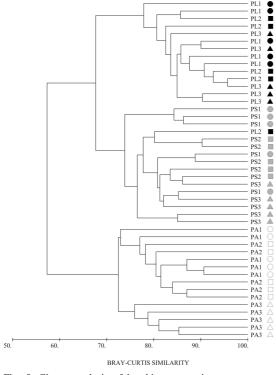


Fig. 5. Cluster analysis of benthic community coverage at three sample sites at the Abrolhos Bank, Brazil. Black symbols represent Pedra de Leste (PL) site, gray represent Pontas Sul (PS), and white corresponds to Parcel dos Abrolhos (PA). Different symbols (circles, triangles, and squares) represent distinct sampled stations.

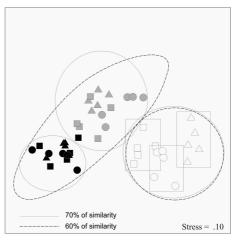


Fig. 6. MDS plot of benthic community coverage at three sample sites at the Abrolhos Bank, Brazil. Black symbols represent Pedra de Leste (PL) site, gray represent Pontas Sul (PS), and white corresponds to Parcel dos Abrolhos (PA). Different symbols (circles, triangles, and squares) represent distinct sampled stations.

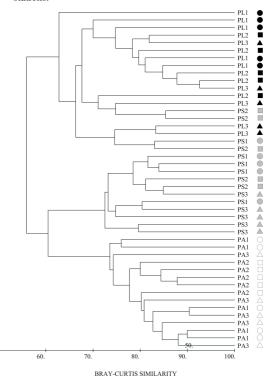


Fig. 7. Cluster analysis of benthic community coverage free from the influence of zoanthids at the three sampled sites at the Abrolhos Bank, Brazil. Black symbols represent Pedra de Leste (PL) site, gray represent Pontas Sul (PS), and white corresponds to Parcel dos Abrolhos (PA). Different symbols (circles, triangles, and squares) represent distinct sampled

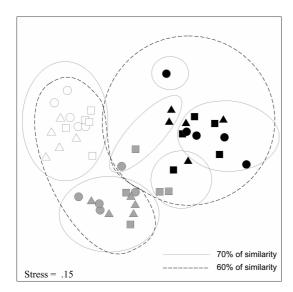


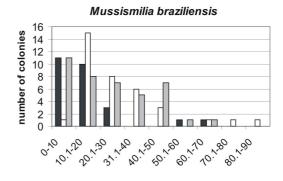
Fig. 8. MDS plot of benthic community coverage free from the influence of zoanthids at the three sampled sites at the Abrolhos Bank, Brazil. Black symbols represent Pedra de Leste (PL) site, gray represent Pontas Sul (PS), and white corresponds to Parcel dos Abrolhos (PA). Different symbols (circles, triangles, and squares) represent distinct sampled stations

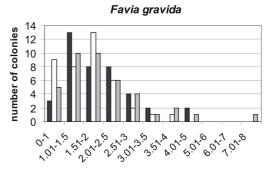
Regarding colony sizes, only *M. braziliensis* showed significant differences between the three sites (n = 102, df. 99, f = 6.81, p <0.01), with Pedra de Leste presenting smaller colonies than Pontas Sul (Tukey test, p <0.01). *S. stellata* and *F. gravida* showed no significant differences in colony size among sites. The size-frequency distribution of *M. braziliensis* at Pedra de Leste showed that the population was skewed towards small-sized colonies, which are of extensions of up to 20 cm of living tissue, while the PS and PA colonies were more evenly distributed among size classes, though also reaching larger sizes (Fig. 9). All three species presented smaller coverage on the reefs nearest to the coast.

DISCUSSION

According to Rogers (1983, 1990), normal sedimentation rates on healthy coral reefs would be of up to a maximum of around 10 mg cm⁻² day⁻¹. Values above such a rate would cause some degree of reef degradation, and above 50 mg cm⁻² day⁻¹ would lead to catastrophic situations (BROWN, 1997). Indeed, Nemeth and Sladecemeth, and Ladeck-Nowlis (2001) found a strong positive correlation between sedimentation and bleaching. However, some studies have shown that significant coral coverage (average around 40% or even higher) may occur in reef areas with sedimentation rates of above 50 mg cm⁻² day⁻¹

(CORTÉS; RISK, 1985; NZALI et al., 1998). Nevertheless, Cortés and Risk (1985) identified a significant decrease in diversity and number of species in areas with high sedimentation rates.





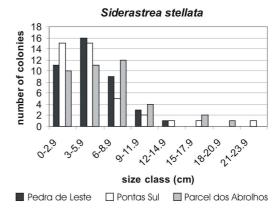


Fig. 9. Size class (average linear tissue length) distribution of the three most common reef building coral species at the three sampled sites at the Abrolhos.

Although sedimentation rates at all the sites studied on the Abrolhos Bank are within the limits expected for healthy reefs, our data have brought divergent situations to light. Our sites presented variable coral cover (from 1.5 to 36 %) under similar

sediment deposition rates. Moreover, extremely high deposition rates have been observed in other areas of the Abrolhos Bank, with mean coral cover comparable to those of Pedra de Leste and Pontas Sul (5.1 to 14.3 %) (Table 3; C. B. Castro et al., unpublished data). This scenario is further complicated by data from northern Bahia. Reefs less than 3 km offshore were considered impoverished due to excessive historical terrigenous sedimentation (LEÃO et al., 1997), with depths close to those of our stations and presenting covers of between 2.6 and 8.0%. These covers are similar to those of our site closer to shore (Pedra de Leste: 1.5-3.6%). This might imply that whatever is constraining coral cover in northern Bahia may also be acting on reefs closer to the shore in the Abrolhos area.

Sedimentation rates at all the three sites were higher during the winter than in summer. This area is affected by violent storms from the South during the winter (SEGAL et al., 2008). According to these latter authors, a higher sedimentation rate in the winter could be explained by the re-suspension of local sediments due to southerly gales during this season (SEGAL et al., 2008). This is evidenced also by the increase in sedimentation on the Parcel dos Abrolhos reef during the winter. This reef is located some 60 km offshore, and it is unlikely that it would be influenced by short-term coastal run-off, as evidenced by the distribution of soluble radioisotopes found in sediment samples (SEGAL et al., 2008). Furthermore, the carbonate fraction in the deposited sediment did not vary between seasons at all the sites. It was concluded, therefore, that the main cause of the increase in sediment deposition must be the resuspension of bottom sediments. A similar trend was observed by Torres et al. (2001), who found a high sedimentation rate (>37 mg cm⁻² day⁻¹) after the passage of Hurricane Hortense in 1996, in the Dominican Republic. In addition, Larcombe et al. (1995) observed an increase in suspended sediment concentration related to local winds on the inner-shelf shallow reefs of Australia, where fine sediments were also available. Hubbard (1997) considered that, on a micro scale, one of the main controlling factors for reef development is the light. Rogers (1979) compared experimentally the effects of both shading and sediment deposition on Acropora cerviconis colonies and found that, although growth rates were not reduced by heavy sedimentation, they were significantly reduced by the prolonged exclusion of light. Although this study used a branching coral, functionally different from all Brazilian species, it may be an important clue to the indirect effects of sedimentation upon coral communities, mainly as a result of the increase in turbidity, with the resuspension of fine sediments. Leão et al. (2006) indicated that bottom sediments near the Pedra de

Leste and Pontas Sul sites were mostly (>75%) composed of mud-sized grains.

Less carbonate sediment was found on the inner reefs, which agrees with the analysis of Leão and Ginsburg (1997) of the bottom sediments surrounding such reefs. These latter authors found from 40 to 70% of siliciclastic particles in inner areas, from 30 to 40% in intermediate areas and less than 10% in outer areas. According to them, the lowering in sea level that occurred after 5,000 years B.P. moved the coastline closer to the reefs, and terrigenous sediments were then transported towards these reefs. Further, reefs act as trapping mechanisms for terrigenous and fine particles that are transported along the coast. Woolfe and Larcombe (1999) stated that the most prolific reef growth occurs with minimal influence of nonframework (non-biogenic) material. Coral community data from the Abrolhos Bank are in accordance with this assumption, since sediment composition shows a clear distinction between inner and outer reefs as regards their respective bottom sediments (Leão, 1982; but see Leão et al., 2006 for a less distinct trend). Just such a trend has also been perceived in the mineral composition of suspended matter by Knoppers et al. (1999), who stated that "selected surface samples clearly reflected differences between the inshore, coastal and open reef waters".

Community analysis (cluster and MDS), including the contribution of zoanthids, points to more diverse communities on the Parcel dos Abrolhos reefs, while inner reefs bear more homogeneous communities (see Figs. 5 and 6). According to Richmond (1993), "healthy" reefs present a high degree of habitat heterogeneity, which leads to a diversity of habitats for fish and invertebrates. The homogeneity of habitats seen at both sites in Parcel das Paredes (Pedra de Leste and Pontas Sul) seems to be related to the overwhelming dominance of Palythoa caribaeorum on these reefs, especially at Pedra de Leste. P. caribaeorum is a highly successful colonizer of shallow hard substrata and is known to overgrow sessile marine invertebrates. such scleractinians and soft corals (SUCHANEK; GREEN, 1981). This species seems to achieve its maximum cover (of approximately 90%) at a depth of 2 m, in the Florida Keys (HAYWICK; MUELLER, 1997). Other authors also point to a "Palythoa zone" in the first 2 meters of depth (BASTIDAS; BONE, 1996; SEGAL; CASTRO, 2002). Although there is a difference in depth between the three sites sampled (see Material and Methods), we do not believe that depth alone can explain the marked difference between sites in the cover of P. caribaeorum. The minimum depth at Pedra de Leste is approximately 3.4 meters, but P. caribaeorum at this site covers some 2/3rds of the substrate. However, shallow coral communities (from 1.9 to 4.0 m deep) around the

Abrolhos Islands (near the Parcel dos Abrolhos) showed a total coral cover of up to 31%, much higher than that at Pedra de Leste, and a low cover (less than 10%) of Palythoa spp. (SEGAL; CASTRO, 2002). A large-scale evaluation of the reefs on the Abrolhos Bank showed a widespread distribution of P. caribaeorum over the whole reef complex, but with a dominance on reefs closer inshore (CASTRO et al., 2006). Despite its importance in terms of bottom coverage in the western Atlantic, little is known about the ecology of P. caribaeorum or its interactions with other benthic organisms (but see Suchanek; Green, 1981). It is, therefore, necessary to evaluate other physical factors (such as hydrodynamics or turbidity) on the Abrolhos reefs in order to arrive at an explanation for the dominance of P. caribaeorum in some areas. Such variables could be important sources of disturbance influencing the coral-zoanthid relationship on these reefs.

Community analysis excluding zoanthids and turf algae showed somewhat diverse trends. The Parcel dos Abrolhos transects also clustered together and were totally distinct from those of other sites. However, the ordering of stations seen in the previous analysis (Fig. 6) did not appear when zoanthids and turf algae were removed from the analysis (Fig. 8). No clear distinction of the sites occurs within each reef, contrary to what occurred in the previous analysis. There is a transect group composed of transects from Pontas Sul and Pedra de Leste, which can be understood as a transition zone. We believe that these trends occur because P. caribaeorum and turf algae (hidden in this analysis) occupied most of the hard substrate that would be necessary for the development of the other benthic community. The limited space actually available would be occupied sparsely and somewhat randomly by different sets of other benthic organisms, resulting in the spreading and mixing of the transects.

Smaller colonies of Mussismilia braziliensis were found on Pedra de Leste, the reef closest inshore, than on Pontas Sul (Fig. 9). However, no statistically significant differences were found between the size of the colonies of the Parcel dos Abrolhos and those of the other two sites. We believe this was due to a flaw in the method. Although the colonies on Parcel dos Abrolhos were clearly larger than those on the other reefs, they frequently grow into very high, mushroomshaped columns. The tape-measure laid on the bottom slipped off these columnar structures. There were many smaller colonies near the base of the columns. Therefore, the colonies closer to the sampling points were most frequently these lower and smaller ones. This probably led to the underestimation of the average colony size on this reef.

The environment in the Abrolhos area is similar to that described by Potts and Jacobs (2002) for the Plio-Pleistocene period when "sediment and nutrient inputs from land and from streams incising the exposed inner shelf were probably high, and shallow sediments would have been very susceptible to re-suspension locally by tidal currents and waves". According to these authors, reef building scleractinians evolved through adaptations to this high turbidity environment. Brazilian reef corals are mostly endemic forms that can be traced back to the Tertiary (LEÃO; GINSBURG, 1997). Although we are unaware of environmental reconstructions or of any records of these species in Brazil prior to the Holocene, these species have probably been living in turbid environments for at least several thousand years (LEÃO et al., 1997).

"Turbid-zone" reefs, such as are most Brazilian ones, are likely to present coral species adapted to cope with low light levels (WOOLFE; LARCOMBE, 1999). Although some studies point to a decrease in diversity and colony growth rates related to turbidity (DODGE; VAISNYS, 1977; PINZÓN et al., 1998; TORRES, 2001 and others), others point to mechanisms of adaptation of modern scleractinian coral species to sediment and turbidity stresses (BAK; ELGERSHUIZEN, 1976; RIEGL, 1995; RIEGL et al., 1996; PINZÓN et al., 1998; GLEASON, 1998; ANTHONY; LARCOMBE, 2002; POTTS; JACOBS, 2002). Our data did not differ in sediment load across the in-shore/off-shore gradient. However, based on the high turbidity and terrigenous sediments that surround the coral communities (LEÃO, 1982; KNOPPERS et al., 1999), we agree with the suggestion that Brazilian reef corals may be included among the species adapted to low light, high sedimentation habitats (LABOREL, 1969; LEÃO; KIKUCHI, 2001).

Castro et al. (2006) indicate that distribution or abundance over the reef complex is species specific even among scleractinians. However, the differences in coral and Palythoa caribaeorum abundances and Mussismilia braziliensis colony sizes among sites suggest some kind of constraint to the development of at least a key builder species in reefs closer inshore on the Abrolhos Bank. Although our results do not permit a clear conclusion as to the abiotic parameters that might be responsible for this constraint, these present authors do not believe that sediment deposition on the corals per se could explain the patterns observed in the reef community. We, therefore, suggest that differences in other parameters related to sedimentation, such as turbidity or carbonatesiliciclastic composition, may be important structuring features, which deserve more attention in future studies in the area.

ACKNOWLEDGEMENTS

The authors wish to thank Debora Pires, Cláudio Ratto, Fábio Negrão, Monica Lins de Barros, Moacir Apolinário, Alexandre Borges, Emiliano Calderon, Cecília de Faria, Ernesto Viveiros de Castro, Paolo Botticelli, and Paulo Paiva for field assistance; Gustavo Nunan for his criticism and help with the English version of the manuscript; two anonymous reviewers for their valuable comments and criticism, and an anonymous English reviewer. This research project was supported by the Fundação O Boticário de Proteção à Natureza, Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro, and the Conselho Nacional de Desenvolvimento Científico e Tecnológico's grants to Bárbara Segal and Clovis Castro.

REFERENCES

- ANTHONY, K. R. N.; LARCOMBE, P. Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. In: INT. CORAL REEF SYMP., 9., 2002. **Proceedings...** v. 1, p. 239-244, 2002.
- BAK, R. P. M.; ELGERSHUIZEN, J. H. B. W. Patterns of oil-sediment rejection in corals. Mar. Biol., v. 37, p. 105-113, 1976.
- BASTIDAS, C.; BONE, D. Competitive strategies between *Palythoa caribaeorum* and *Zoanthus sociatus* (Cnidaria: Anthozoa) at a reef flat environment in Venezuela. **Bull. mar. Sci**, v. 59, n. 3, p. 543-555, 1996.
- BLOMQVIST, S.; KOFOED, C. Sediment trapping A subaquatic in situ experiment. **Limnol. Oceanogr.**, v. 26, n. 3, p. 585-590, 1981.
- BROWN, B. E. Disturbances to reefs in recent times. In: BIRKELAND, C. (Ed.). **Life and death of coral reefs**. New York: Chapman and Hall, 1997. p. 354-379.
- BROWN, B. E.; CLARKE, K. R.; WARWICK, R. M. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. **Mar. Biol.**, v. 141, p. 21-29, 2002.
- CALLIS, G. M. Bone. In: BANCROFT, J. D.; GAMBLE, M. (Ed.). Theory and practice of histological techniques. 6th ed. Philadelphia: Churchill Livingstone/Elsevier, 2008, p. 333-364.
- CARR, M. R. **PRIMER User Manual (Plymouth Routines in Multivariate Ecological Research)**. Plymouth: Plymouth Marine Laboratory, 1997.
- CASTRO, C. B.; SEGAL, B.; PIRES, D. O.; MEDEIROS, M. S. Distribution and diversity of coral communities in the Abrolhos Reef Complex, Brazil. In: ALLEN, G.; DUTRA, G. F.; WERNER, T. B.; MOURA, R. L. (Ed.). A biological assessment of Abrolhos Bank, Brazil. RAP Bull. Biol. Assess., v. 38, 2006, p. 19-39.
- CLARKE, K. R.; WARWICK, R. M. Change in marine communities: an approach to statistical analysis and

- **interpretation**. Plymouth: Plymouth Marine Laboratory, 1994. 144 p.
- CORTÉS, J.; RISK, M. J. A reef under siltation stress: Cahuita, Costa Rica. **Bull. mar. Sci**, v. 36, n. 2, p. 339-356, 1985.
- DODGE, R. E.; VAISNYS, J. R. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J. mar. Res., v. 35, p. 715-730, 1977
- DODGE, R. E.; ALLER, R. C.; THOMPSON, J. Coral growth related to resuspension of bottom sediments. **Nature**, v. 247, p. 574-576, 1974.
- DUTRA, L. X. C; KIKUCHI, R. K. P.; LEÃO, Z. M. A. N. Effects of sediment accumulation on reef corals from Abrolhos, Bahia, Brazil. **J coast. Res.**, v. 39, p. 633-638, 2006
- FOSTER, A. B. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea siderea*. **Bull. Mar. Sci.**, v. 30, n. 3, p. 678-709, 1980.
- GILMOUR, J. Experimental investigation into the effects of suspended sediment on fertilisation, larval suvival and settlement in a scleractinian coral. **Mar. Biol.**, v. 135, p. 451-462, 1999.
- GLEASON, D. F. Sedimentation and distributions of green and brown morphs of the Caribbean coral *Porites* astreoides Lamarck. J. expl mar Biol. Ecol., v. 230, p. 73-89, 1998.
- HAYWICK, D. W.; MUELLER, E. M. Sediment retention in encrusting *Palythoa* spp. – a biological twist to a geological process. **Coral Reefs**, v. 16, p. 39-46, 1997
- HUBBARD, D. K. Reefs as dynamic systems. In: BIRKELAND, C. (Ed.) **Life and death of coral reefs**. New York: Chapman and Hall, 1997. p. 43-67.
- HUGHES, T. P. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science, v. 265, p. 1547-1551, 1994.
- KNOPPERS, B.; MEYERHOFER, M.; MARONE, E.; DUTZ, J.; LOPEZ, R.; LEIPE, T.; CAMARGO, R. Compartments of the pelagic system and material exchange at the Abrolhos Bank coral reef, Brazil. **Arch. Fish mar Res**, v. 47, p. 285-306, 1999.
- LABOREL, J. L. Madréporaires et hydrocoralliaires récifaux des cotes brésiliennes: systématique, écologie, répartition verticale et géographique. Annls Inst. Océanogr., v. 47, p. 171-229, 1969.
- LABOREL, J. L. Les peuplements de Madréporaires des cotes tropicales du Brésil. Annls L'Univ. D'Abidjan, série E II, fasc. 3, p. 262, 1970.
- LARCOMBE, P.; RIDD, P. V.; PRYTZ, A.; WILSON, B. Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. Coral Reefs, v. 14, p. 163-171, 1995.
- LEÃO, Z. M. A. N. Present status of the coral reefs of Bahia and the major environmental impacts. In: SCIENTIFIC MEETING, LOICZ (Land/Ocean Interaction in the Coastal Zone). Abstracts, p. 40-42, 1995.
- LEÃO, Z. M. A. N.; GINSBURG, R. N. Living reefs surrounded by siliciclastic sediments: the Abrolhos Coastal reefs, Bahia, Brazil. In: INT. CORAL REEF SYMP., 8., 1997. Proceedings ..., v. 2, p. 1767-1772, 1997.

- LEÃO, Z. M. A. N.; KIKUCHI, R. K. P. The Abrolhos reefs of Brazil. In SEELIGER, U.; KJERFVE, B. (Ed.). Coastal marine ecosystems of Latin America, ecological studies. v. 144. Berlin, Heidelberg: Springer-Verlag, 2001. p. 83-96.
- LEÃO, Z. M. A. N.; DUTRA, L. X. C.; SPANO, S. The characteristics of bottom sediments. In: ALLEN, G.; DUTRA, G. F.; WERNER, T. B.; MOURA, R. L. A Biological Assessment of Abrolhos Bank, Brazil. RAP Bull. Biol. Assess., v. 38, p. 75-81, 2006.
- LEÃO, Z. M. A. N.; KIKUCHI, R. K. P.; MAIA, M. P.; LAGO, R. A. L. A catastrophic coral cover decline since 3,000 years B. P., northern Bahia, Brazil. INT. CORAL REEF SYMP., 8, 1997. **Proceedings...**, v. 1, p. 583-588, 1997.
- LOYA, Y. Effects of water turbidity and sedimentation on the community structure of Puerto Rican Corals. **Bull. Mar. Sci.**, v. 26, n. 4, p. 450-466, 1976.
- NEMETH, R. S.; SLADECK-NOWLIS, J. Monitoring the effects of land development on the nearshore reef environment of St. Thomas, USVI. **Bull. Mar. Sci.**, v. 69, n. 2, p. 759-775, 2001.
- NEVES, E. G.; ANDRADE, S. C. S.; DA SILVEIRA, F. L.; SOLFERINI, V. N. Genetic variation and population structuring in two brooding coral species (*Siderastrea* stellata and *Siderastrea radians*) from Brazil. Genetica, v. 132, p. 243-254, 2008.
- NYSTRÖM, M.; FOLKE, C.; MOBERG, F. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol., v. 15, n. 10, p. 413-417, 2000.
- NZALI, L. M.; JOHNSTONE, R. W.; MGAYA, Y. D. Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. Ambio, v. 27, n. 8, p. 717-722, 1998.
- PINZÓN, J.H.; PERDOMO, A. M.; DÍAZ, J. M. Isla arena, una formacion coralina saludable en el area de influencia de la pluma del rio Magdalena, plataforma continental del Caribe colombiano. **Bol. Invest. mar cost.**, v. 27, p. 21-37, 1998.
- POTTS, D. C.; JACOBS, J. R. Evolution of reef-building scleractinian corals in turbid environments: a paleoecological hypothesis. INT. CORAL REEF SYMP., 9., 2002. **Proceedings** ... v. 1, p. 249-254, 2002.
- RICHMOND, R. H. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. Am. Zool., v. 33, p. 524-536, 1993.
- RIEGL, B. Effects of sand deposition on scleractinian and alcyonacean corals. Mar. Biol., v. 121, p. 517-526, 1995.
- RIEGL, B.; HEINE, C.; BRANCH, G. M. Function of funnel-shaped coral growth in a high-sedimentation environment. Mar. Ecol. Prog. Ser., v. 145, p. 87-93, 1996.
- ROGERS, C. S. The effect of shading on coral reef structure and function. **J expl mar. Biol Ecol**, v. 41, p. 269-288, 1979.

- ROGERS, C. S. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. **Mar. Pollut. Bull.**, v. 4, n. 3, p. 378-382, 1983.
- ROGERS, C. S. Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser., v. 62, p. 185-202, 1990.
- SEGAL, B.; CASTRO, C. B. A proposed method for coral cover assessment: a case study in Abrolhos, Brazil. **Bull. Mar. Sci.**, v. 69, n. 2, p. 487-496, 2001.
- SEGAL, B.; CASTRO, C. B. Community structure at the Abrolhos Archipelago, Brazil. INT CORAL REEF SYMP., 9, 2002. **Proceedings ...**v. 1, p. 583-588, 2002.
- SEGAL, B.; HEVANGELISTA, H.; KAMPEL, M.; GONÇALVES, A. C.; POLITO, P. S.; SANTOS, E. A. Potential impacts of polar fronts on sedimentation processes at Abrolhos Coral Reef (South-West Atlantic Ocean/Brazil). Continent. Shelf Res., v. 28, p. 533-544, 2008
- SUCHANEK, T. H.; GREEN, D. J. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St.Croix Reefs, U.S. Virgin Islands. INT. CORAL REEF SYMP, 4., 1981. **Proceedings ...,** v. 2, p. 679-684, 1981.
- TOMASCIK, T.; SANDER, F. Effects of eutrophication on reef-building corals. **Mar . Biol.**, v. 94, p. 53-75, 1987.
- TORRES, J. L. Impacts of sedimentation on the growth rates of *Montastrea annularis* in Southwest Puerto Rico. **Bull. Mar. Sci.**, v. 69, n. 2, p. 631-637, 2001.
- TORRES, J. L.; CHIAPPONE, M.; GERALDES, F.; RODRIGUEZ, Y.; VEGA, M. Sedimentation as an important environmental influence on Dominican Republic reefs. **Bull. Mar. Sci.**, v. 69, n. 2, p. 805-818, 2001.
- VAN KATWIJK, M. M.; MEIER, N. F.; VAN LOON, R.; VAN HOVE, E. M.; GIESEN, W. B. J. T.; VAN DER VELDE, G.; DEN HARTOG, C. Sabaki River sediment load and coral stress: correlation between sediments and condition of the Malindi-Watamu reefs in Kenya (Indian Ocean). Mar. Biol., v. 117, p. 675-683, 1993.
- WESTPHAL, H.; MUNNECKE, A.; BRANDANO, M. Effects of diagenesis on the astrochronological approach of defining stratigraphic boundaries in calcareous rhythmites: The Tortonian GSSP. **Lethaia**, <10.1111/j.1502-3931.2008.00101.x, 2008>.
- WOOLFE, K. J.; LARCOMBE, P. Terrigenous sedimentation and coral reef growth: a conceptual framework. Mar. Geol., v. 155, p. 331-345, 1999.

(Manuscript received 29 July 2009; revised 31 May 2010; accepted 03 August 2010)