COLONY SIZE-FREQUENCY DISTRIBUTIONS AMONG DIFFERENT POPULATIONS OF THE SCLERACTINAN CORAL *SIDERASTREA STELLATA* IN SOUTHWESTERN ATLANTIC: IMPLICATIONS FOR LIFE HISTORY PATTERNS*

*Monica Moraes Lins de Barros** & Débora de Oliveira Pires*

Museu Nacional - Universidade Federal do Rio de Janeiro
Departamento de Invertebrados, Setor de Celenterologia
(Quinta da Boa Vista, s/n, 20.940-040 Rio de Janeiro, RJ, Brasil)
**E-mail: mlbarros@acd.ufrj.br

ABSTRACT

Colony size-frequency distributions of reef corals may be used to infer growth potential and population responses upon environmental changes. The present paper compares the size structure of colonies of *Siderastrea stellata* Verrill, 1868, among 11 sites, six of them distributed along a gradient of sediment deposition in Abrolhos, Bahia, Brazil (18º S). Results indicated that the population structure is likely to be influenced by local conditions, rather than large scale factors, such as latitude. The 11 distributions, however, showed higher frequencies of small size classes. Class 1 (up to 2.5 cm diameter) was always present and the frequency of colonies from size class 3 (10 cm diameter) tended to decrease in all sites. Comparison among the six Abrolhos sites showed that *S. stellata* has advantages at sites with intermediate sedimentation, where colonies attain larger sizes, probably, reflecting a higher survivorship over time. The present study showed that, despite the influence of environmental conditions on parameters of the populations such as size of colony, the life history strategy of *S. stellata* reflects a local adaptation that allows its development and survivorship in shallow waters and horizontal substrates, sites characterized by high mortality rates.

RESUMO

Distribuições de freqüências de classes de tamanho de colônias de corais recifais, associadas a dados de fecundidade e crescimento, podem ser utilizadas para inferir o potencial de crescimento e respostas da população frente às variações ambientais. Apresentamos análise da estrutura de tamanho de colônias do coral *Siderastrea stellata* Verrill, 1868, em 11 locais, seis desses distribuídos ao longo de um gradiente de sedimentação em Abrolhos, Bahia, Brasil (18ºS). Os resultados demonstraram ausência de um padrão latitudinal, indicando maior influência de fatores locais. Em Abrolhos, locais com taxas de deposição de sedimento intermediárias apresentaram os maiores coeficientes de variação e tamanhos médios, indicando condições mais propícias para o desenvolvimento de populações desse coral na região. As 11 distribuições, porém, apresentaram maior freqüência de classes pequenas. A classe 1 (colônias com diâmetro médio de até 2,5cm) ocorreu em todos os locais. A partir da classe 3 (10 cm em diâmetro) as freqüências diminuíram consideravelmente. Esses dados, associados ao fato da espécie se reproduzir cedo e incubar larva, refletem uma estratégia de sobrevivência, em águas rasas e substratos horizontais, caracterizada por alta taxa de mortalidade e tempo de vida curto.

Descriptors: Frequency distribution, Colony size, Reef coral, *Siderastrea stellata*, Sedimentation, Life history, Brazil.
Descritores: Distribuição de freqüências, Tamanho de colônia, Coral recifal, *Siderastrea stellata*, Sedimentação, História de vida, Brasil.

INTRODUCTION

Different coral life history strategies derive from a balance among growth, survival and reproduction (Bak & Engel, 1979; Santangelo *et al*., 2003). These strategies are associated with population parameters, such as recovery and turn-over capacity, mortality, survivorship and intrinsic growth rates

(Harvell & Grosberg, 1988; Goffredo & Chadwick-Furman, 2003). Coral life-history processes are strongly related to size, and size-frequency distribution of corals may be used as a simple and non-destructive method to analyze life history and dynamics of coral populations (Bak & Meesters, 1998; Meesters *et al.,* 2001).

The inference of a dynamic process from a size-frequency distribution is made possible when other aspects of the species biology, such as the relationship between size, growth and reproduction, are known. In the case of a modular organism, such as

_____

a colonial scleractinian coral, partial mortality, fragmentation and fusion of colonies may disrupt the relationship between life processes and size. However, in massive corals, most partial mortality occurs as very small lesions that are regenerated within a few days (Bak & Meesters, 1998), and careful observation *in situ* to detect fusion and/or fragmentation, using knowledge of growth patterns and coral surface structures, can overcome the problem.

During the present study, size structure of the massive scleractinian coral *Siderastrea stellata* Verrill, 1868, was analyzed for 11 populations, along a latitudinal gradient of 20° in the Southwestern Tropical Atlantic Ocean, comprising areas throughout almost the whole geographical distribution of the species. Growth rate and fecundity data of different size classes of colonies of *S. stellata* were used to discuss life history strategies based on size-frequency distributions. Six of the populations studied were distributed along a gradient of sediment deposition in the Abrolhos Reef Complex, Bahia (18^oS). The present study presents an analysis of the potential impact of this factor upon *S. stellata* populations based on size-frequency distributions obtained for each site.

MATERIALS AND METHODS

The Species

Siderastrea stellata is an endemic and a common scleractinian coral species from Brazil (Laborel, 1970; Castro & Pires, 2001). It is a zooxanthellate, colonial and massive coral, occurring in all the Brazilian reef regions and in coral communities from Maranhão (00°53'S, 044°16'W) to Rio de Janeiro State (23°S, 042°W) (Castro & Pires, 2001) (Fig. 1). In some reef areas, such as in the Atol das Rocas (03°52`S, 033°49`W), it is the main reef building organism (Echeverría *et al*., 1997). It usually occurs in shallow waters (up to 10 m depth) and often occupies horizontal substrates (Segal & Castro, 2000). This species is considered relatively resistant to sedimentation, temperature and salinity variations and strong wave action (Hartt in Laborel, 1970; Chevalier, 1987). *Siderastrea stellata* is a gonochoric brooder, with a high female to male sex ratio and an annual reproductive cycle. Planulation occurs during January/February (Lins de Barros *et al.,* 2003).

Studied Sites

Siderastrea stellata colony size data were obtained in January 2001, in two sites at the Fernando de Noronha Archipelago ("Sancho" - 03°512`S, 032°267`W; and "Inferno" - 03°493`S, 032°231`W), in two sites at Tamandaré ("Barra" - 08°45,673`S, 035° 05,869`W; and "Meio" - 08°45,724`S, 035°05,465`W), and in Canudos reef (16°53,816' S, 039°04,965'W). Data for another six reefs of the Abrolhos Reef Complex ("Guaratibas" - 17°26,204`S, 039° 08,038`W; "Lixa" - 17°41,535`S, 038°56,608`W; "Leste" - 17°47,169`S, 039°02,979`W; "Sebastião Gomes" – 17°54,158`S, 039°07,568`W; "Coroa Vermelha" -17°58,004`S, 039°11,889`W; and "Viçosa" - 17°58,873`S, 039°15,338`W) were collected in June/2003 (Fig. 1).

METHOD

At each site, the closest colony, from 0.5 m to 0.5 m or 1 m to 1 m, of two to three belt transects of 20 m each were measured, depending on the number of colonies in the area and the reef morphology. For each colony we measured the largest and the smallest diameters, and total surface area (size) was calculated using the formula for an halve spherical segment (A = 2 X [(D/2 X d/2) X π], where: A = area (cm^2), D = largest diameter (cm), d = smallest diameter (cm), π = 3.1419). Up to 80 colonies were measured at each site; however, in some sites, the total number of colonies in the area was less than 80. In "Guaratibas" and "Coroa Vermelha" only 73 and 58 colonies were measured, respectively. In the six Abrolhos Reef Complex sites, the presence of bioeroders, identified by holes on colonies surfaces, was quantified as present or absent for each measured colony.

Analyses of Data

The size structure of *S. stellata* populations was analyzed for each of the 11 sites by calculating the size-frequency distribution parameters: mean colony size and standard deviation, coefficient of variation (=standard deviation/mean), the largest colony size, maximum colony size (95th percentile), commonest colony size and skewness (g_1).

Colony size data were log transformed to become approximately normal, tested by Kruskal-Wallis test. Also, we followed Bak & Meesters (1998) and Meesters *et al*. (2001), who argued that "living coral colony surface, which can be modelled as e.g. semi-spheres, increases as a power function in size" and that "population dynamic are first order processes, i.e. modelled by exponential functions". Transformed data also reduced heteroscedasticity, tested by Cochran test. Mean colony sizes were analyzed by ANOVA and Student-Newman-Keuls for a posteriori comparison.

Colonies were grouped into 21 size classes of 1.40 cm^2 each, with the exception of class 1, which included colonies with up to 0.70 cm^2, unfertile or with an extremely low fecundity (Lins-de-Barros & Pires, *in press*). Size-frequency distributions were compared to each other using a 2-sample Kolmogorov-Smirnov test. For statistical analyses we used the program "Statistica 6.0", with *p* < 0.05.
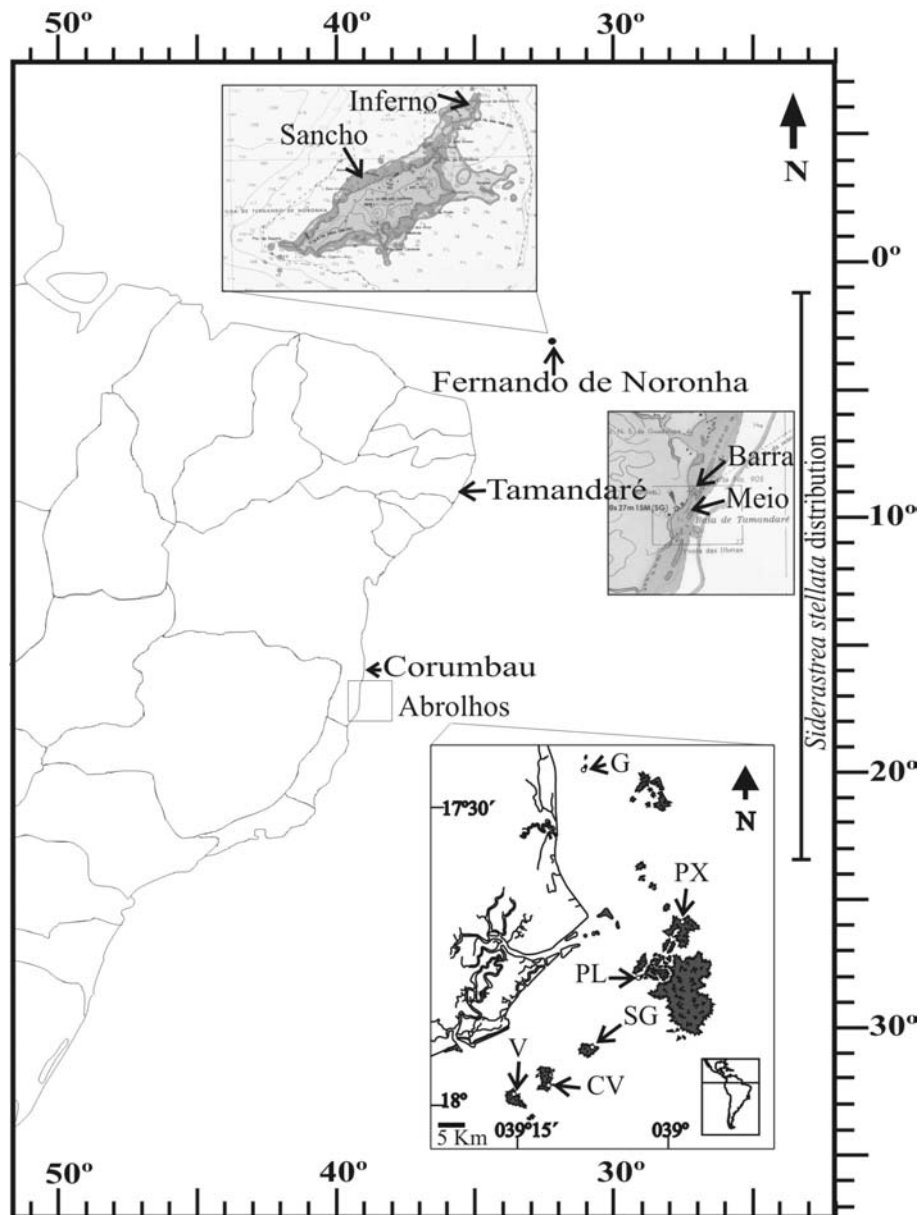
Fig. 1. Map of the studied sites and the geographical distribution of the Brazilian reef coral *Siderastrea stellata* (vertical bar). Nautical charts of Fernando de Noronha and Tamandaré (source: DHN – Diretoria de Hidrografia e Navegação). Reef names: G = Guaratibas; PX = Pedra Lixa; PL = Pedra de Leste; CV = Coroa Vermelha; S = Sebastião Gomes; V = Viçosa.

Life-history patterns of *S. stellata* in each site were inferred from size-frequency distributions, using data on growth rate and fecundity in each size class, obtained for colonies from Canudos reef (Lins-de-Barros & Pires, *in press*). For the six sites at the Abrolhos Reef Complex, size-frequency distribution parameters were also compared to the frequency of colonies infested by bioeroders (collected during the present study), sediment deposition rates and species cover (extracted from Segal-Ramos, 2003) and, family recruitment rate (extracted from Alvarenga, 2004), using Pearson correlation analyses.

RESULTS

Size-Frequency Distributions

Colony size-frequency distribution of *S. stellata* varied among the 11 study sites (Figs 2 A-K). At some sites, a broader representation of size classes was observed, as at "Viçosa" and "Guaratibas" (Abrolhos), where eight and 12 classes were observed respectively, and at all other sites outside the Abrolhos Reef Complex, where more than 15 classes were observed, except at "Barra" (Tamandaré) (Fig. 2). The sites "Barra" (Tamandaré), "Leste" and "Coroa Vermelha" (Abrolhos) did not have any colony larger than size class 4 (Figs 2 C, F-K), while "Fernando de Noronha" sites and "Meio" (Tamandaré) had colonies up to class 17 (Figs 2 A, B, D). Size class 21 colony was only observed in "Canudos" (Fig. 2 E). Apart from the differences in size-frequency distributions, all sites had a higher percentage of the smaller size classes (classes 1 to 4). Size class 2 was the most frequent at almost all sites (Fig. 2), except at "Coroa Vermelha", where size class 1 was the most frequent (Fig. 2 H) and Inferno, where size class 3 was the most frequent (Fig. 2 B).

After log transformation, the 11 size-frequency distributions were statistically not significantly different from a normal distribution (K-S; $p > 0.20$). Kolmogorov-Smirnov analyses between pairs of size-frequency distributions showed that for the 54 pairs tested, 13 (24.07%) were not significantly different (K-S; $p > 0.05$). However, size-frequency distribution similarities and differences were not related to the geographic location of sites or to latitude. Distant sites showed similarities between their size-frequency distributions, while adjacent sites showed differences.

"Sebastião Gomes" and "Coroa Vermelha" (Abrolhos), sites that are close to each other, showed similar size-frequency distributions (K-S; $p > 0.05$), but they were significantly different from all other sites, including the other sites from Abrolhos ("Leste", "Lixa", "Guaratibas" and "Viçosa"). These four sites were similar to each other, but also showed similarity with the "Barra" site (08°S; 035°W), which is located 2000 km away. However, the size-frequency distribution obtained for "Barra" was significantly different from those obtained for its closest site "Meio" (08°S; 035°W), which, instead, was similar to "Canudos" (16°S; 039°W). The only geographic pattern was observed at Noronha, where both sites, "Inferno" and "Sancho", were similar to each other (K-S; $p > 0.05$) and significantly different from any other site (K-S; $p < 0.05$).

Mean Colony Size

Mean colony size varied among the sites (ANOVA; F = 49.197; d.f. = 10; $p < 0.0001$). The six sites from Abrolhos, and the site "Barra" (Tamandaré), showed mean colony sizes smaller than the sites from Noronha, "Sancho" and "Inferno" (Table 1). Mean colony area of *S. stellata* was 1.57 ($\pm$ 0.62[s.d]) (corresponding to colonies with a mean diameter of 0.8 cm), ranging from 0.95 cm^2 ($\pm$ 0.44[s.d]), in "Coroa Vermelha", to 2.17 cm^2 ($\pm$ 0.43[s.d]), in "Sancho".

Coefficient of Variation

The mean coefficient of variation range for *S. stellata*, with log transformed size data, 22 % (0.22 $\pm$ 0.10[s.d]), ranging from 0.13 (13%) at "Meio" and "Canudos" to 0.46 (46%) at "Coroa Vermelha" (Table 1).

The coefficient of variation was inversely related to mean colony size (r Pearson; r = 0.911; r^2 = 0.830; p = 9.520E-05) and directly related to skewness (r Pearson; r = 0.633; r^2 = 0.4008; p = 0.0365). This means that, in populations dominated by large colonies, the frequency of small colonies and the size variation are relatively small.

Maximum Colony Size ("95th percentile") and Largest Colony Size

Maximum log colony size of *S. stellata* colonies averaged 2.14 cm^2 ($\pm$ 0.47[s.d]), ranging from 1.52 cm^2 (or 20 cm in diameter) at "Coroa Vermelha" (Abrolhos) to 3.25cm^2 (or 44 cm in diameter) at "Canudos". Considering the growth rate defined for different size classes of colonies of *S. stellata* (0.5 cm in diameter per year) (Lins-de-Barros & Pires, *in press*), the oldest colony at "Coroa Vermelha" would be at least 10 years old, while at "Canudos" it would be approximately 88 years old.

Commonest Colony Size (cm^2)

The commonest size for the *S. stellata* colonies was small, corresponding to colonies of size class 2 in the six Abrolhos sites and "Barra" (Tamandaré), and size class 3 in the other sites (Table 1).
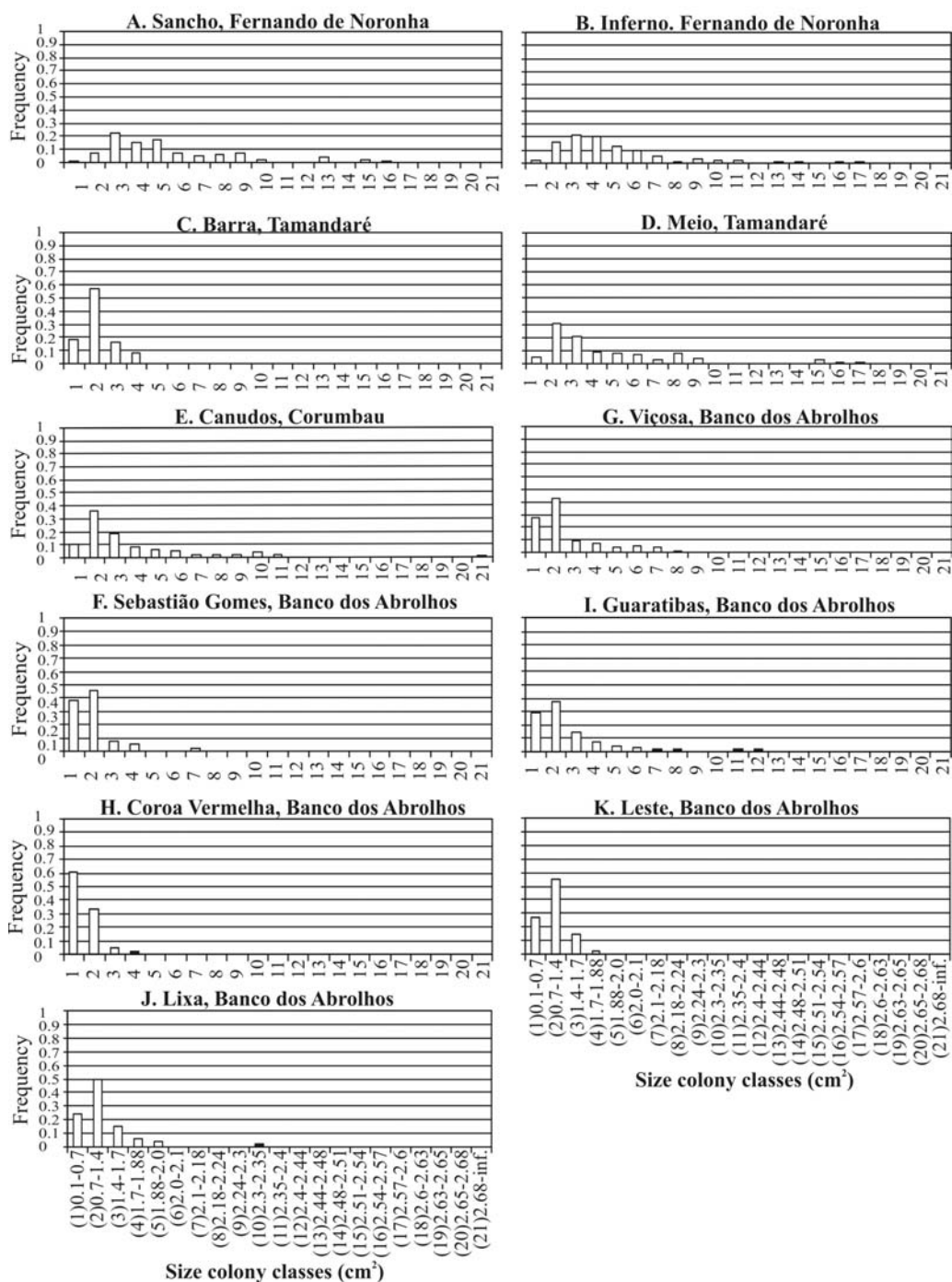
Fig. 2. Size-frequency distribution (log scale) of the Brazilian reef coral *Siderastrea stellata* at 11 sites along the species geographical distribution.

Table 1: Resume of *Siderastrea stellata* size data for 11 sites along the geographical distribution of the species and abiotic and biotic factors analyzed for the Abrolhos sites.

	Inferno	Sancho	Meio	Barra	Canudos	G	PL	PX	SG	CV	V
N	104	80	80	103	80	73	80	80	80	58	80
Smallest size	0.74	0.86	0.25	0.62	0.53	0.14	0.32	0.29	0.35	0.22	0.41
Largest size (±S.D.)	3.17	2.87	2.17	3.48	3.11	2.72	2.03	2.63	2.43	2.09	2.59
Mean size	2.07 (±0.37)	2.17 (±0.43)	1.96 (±0.25)	1.40 (±0.39)	1.80 (±0.24)	1.40(± 0.19)	1.27 (±0.40)	1.37 (±0.29)	1.16 (±0.28)	0.95 (±0.44)	1.44 (±0.24)
95th percentile	2.35	2.45	2.58	1.77	3.25	2.14	1.68	1.88	1.81	1.52	2.09
Coef. variation	0.18	0.20	0.13	0.28	0.13	0.14	0.31	0.21	0.24	0.46	0.17
Skewness (g_1)	- 0.505	- 0.616	- 0.199	- 0.239	- 0.209	- 0.388	- 0.345	- 0.345	0.224	- 0.045	- 0.019
Sediment	--	--	--	--	--	26	10	11	113	41	48
Recruits	--	--	--	--	--	1.49	0.92	0.00	1.98	14.88	10.42
% Cover	--	--	--	--	--	0.82	0.474	4.15	0.727	0.15	1.237

Legend: N = number of colonies measured; Smallest, largest, mean and 95th percentile sizes - log (cm^2); Coef. variation = coefficient of variation (S.D./mean); Sediment (mean sediment deposition rate) - mg . cm^{-2} . day^{-1}; Recruits = number of recruits/m^2; % cover – eight intersection transects of 10 meters with 250 random points (total = 2000 points); G = Guaratibas, PL = Pedra de Leste, PX = Pedra Lixa, SG = Sebastião Gomes, CV = Coroa Vermelha, V = Viçosa.

Skewness (g_1)

After log transformation, all size-frequency distributions showed a higher frequency of colonies above the mean colony size, as indicated by negative skewness values, excepting at "Viçosa" and "Sebastião Gomes" (Table 1). At "Viçosa", the skewness value was close to zero (g_1 = 0.019), indicating that most colonies present were approximately equal to or similar to the mean colony size of this population (1.44 ± 0.24[s.d]). At "Sebastião Gomes", the high positive skewness (g_1 = 0.224) indicates a high frequency of small colonies, below the mean colony size for this population (1.16 ± 0.28[s.d]).

Mean Sediment Deposition Rate (mg. cm^{-2}. $year^{-1}$)

Segal-Ramos (2003) recorded different mean sediment deposition rates among the six Abrolhos study sites (Table 1 - data extracted from Segal-Ramos, 2003). These sites can be listed in a decreasing sediment deposition gradient as: "Sebastião Gomes" > "Viçosa" and "Coroa Vermelha" > "Guaratibas" > "Lixa" and "Leste" (Segal-Ramos, 2003).

Our results indicated that, in the six Abrolhos sites, mean sediment deposition rates were not directly related to the percentage of infested colonies (r Pearson; r = -0.076; r^2 = 0.0057; *p* = 0.887), mean *S. stellata* cover (r Pearson; r = - 0.337; r^2 = 0.114; *p* = 0.513), Siderastreidae recruitment rates (r Pearson; r = 0.127; r^2 = 0.016; *p* = 0.811) or mean colony size (r Pearson; r = 0.377; r^2 = 0.142; *p* = 0.461). However, a strong positive relationship was observed between this variable and skewness (r Pearson; r = 0.912; r^2 = 0.832; *p* = 0.011). Thus, at sites with a high sediment deposition rate, a higher frequency of colonies smaller than the mean size of the population would be expected.

Frequency of Colonies Infested by Bioeroders

A strong positive relationship between the frequency of colonies infested by bioeroders and colony size was observed (Table 2) (r Pearson; r = 0.894; r^2 = 0.799; *p* = 0.0162) in the six Abrolhos sites studied. The largest frequencies of colonies infested were observed in "Viçosa", site that had the largest mean colony sizes (Table 1).

Recruitment of Siderastreidae (Number of Recruits/m^2)

Alvarenga (2004) observed that the number of Siderastreidae recruits on recruitment plates was different among the six Abrolhos sites, ranging from 0.92recruits/m^2 in "Leste" to 14.88 recruits/m^2 in "Coroa Vermelha". No Siderastreidae recruits were observed in "Lixa" (Table 1 - data extracted from Alvarenga, 2004).

Siderastrea recruitment rate did not show a linear relationship with mean *S. stellata* cover (r Pearson; r = - 0.426; r^2 = 0.181; *p* = 0.40), mean colony size (r Pearson; r = - 0.366; r^2 = 0.134; *p* = 0.476) or the smallest colony size (r Pearson; r = 0.063; r^2 = 0.0039; *p* = 0.906). These results may be an indication that none of these factors seem to be strongly related to *S. stellata* recruitment in the Abrolhos sites studied.

Mean Cover of *S. stellata*

Segal-Ramos (2003) observed that mean cover of *S. stellata* varied among the six Abrolhos sites, ranging from 15% in "Coroa Vermelha" to 41.5% in "Lixa" (Table 1 – data extracted from Segal-Ramos, 2003). In the present study, this variable did not show any significative linear correlation with mean colony size (r Pearson; r = - 0.129; r^2 = 0.017; *p* = 0.808) or the size of the largest colony (r Pearson; r = 0.159; r^2 = 0.0236; *p* = 0.771).

Table 2: Frequency of *S. stellata* colonies infested by bioeroder organisms in six Abrolhos sites, distributed along a sediment depositional gradient (extracted from Segal-Ramos, 2003).

Size Classes	Inferior limit	Superior limit	G	PL	PX	SG	CV	V
Class 1	0.1	1	--	--	1/5	4/11	--	4/5
Class 2	1	1.78	1/20	4/35	8/28	15/32	--	14/24
Class 3	1.78	2.04	1/7	4/16	3/13	4/16	--	9/15
Class 4	2.04	2.20	--	1/10	--	2/3	--	4/5
Class 5	2.20	2.32	2/5	1/5	7/2	2/7	0	7/8
Class 6	2.32	2.41	1/5	2/3	3/5	--	--	0
Class 7	2.41	2.49	--	--	1/2	0	1/2	2/3
Class 8	2.49	2.56	--	--	0	--	0	1/3
Class 9	2.56	2.61	0	--	1/2	1/1	0	1/1
Class 10	2.61	2.66	--	--	0	0	0	--
Class 11	2.66	2.71	0	0	--	1/1	--	--
Class 12	2.71	2.75	--	0	1/3	1/1	0	0
Class 13	2.75	2.79	--	0	1/3	1/1	0	1/1
Class 14	2.79	2.82	--	0	0	0	0	1/1
Class 15	2.82	2.85	0	0	--	0	0	2/2
Class 16	2.85	2.88	--	0	0	0	0	0
Class 17	2.88	2.91	0	0	0	0	0	1/1
Class 18	2.91	2.93	--	0	0	0	0	0
Class 19	2.93	2.96	0	0	0	0	0	3/3
Class 20	2.96	2.98	0	0	0	0	0	0
Class 21	2.98	infinite	2/5	0	--	2/2	0	1/2
N			73	80	80	80	58	80
Total colonies infected			7	12	26	33	1	51
% colonies infected			9.59	15	32.5	41.25	1.7	63.75

Legend: Inferior and superior limits – smallest and largest log colony size (cm^2), comprising the size range of each size class; G = Guaratibas, PL = Pedra de Leste, PX = Pedra Lixa, SG = Sebastião Gomes, CV = Coroa Vermelha, V = Viçosa; -- = presence of colonies of the size class but none infected; 0 = absence of colonies of the size class; ratio = number of colonies infected/number of colonies measured of the size class; % colonies infected = (number of colonies infected/N) X 100.

DISCUSSION

Although the commonest size class of colonies was similar among the 11 sites (class 2), the size-frequency distributions of colonies of *S. stellata* varied among the sites (Fig. 2). However, such variation did not show any regional or latitudinal pattern. Some sites that were located near to each other had different size frequency distributions (i.e.: "Barra" and "Meio", both at Tamandaré), while similar size frequency distributions were observed between some sites (i.e.: "Meio" and "Canudos"). The same result was observed in relation to the mean size of colonies (Table 1). These results indicated that the population structure is likely to be influenced by local environmental conditions, rather than being determined by large scale factors, such as latitude.

The largest colony sizes were observed at the two sites at Noronha, and these sites had the highest frequencies of colonies larger than the mean (g_1 Sancho = -0.616; g_1 Inferno = -0.505 (Table 1). The relationship between mean colony size and skewness (g_1) was also documented for other coral species by Bak & Meesters (1998), Meesters *et al.* (2001) and Langmead & Sheppard (2004).

At the Noronha sites, the maximum colony size ("95th percentile") was larger than in the others sites and the smallest ones were observed at the six sites at Abrolhos and at "Barra", Tamandaré (Table 1). Rinkevich & Loya (1987) and Kramasky-Winter & Loya (1998), concluded that shallow habitats would be exposed to more frequent disturbances, such as salinity and temperature variations, wave action and dessication, which are likely to decrease the life-span of organisms that inhabit such environments. Noronha

sites were the deepest, being around 7 m, while the depths of the others sites were above 4 meters. The larger colony sizes observed at the Noronha sites are probably the result of greater colony longevity and/or less partial mortality (Meesters *et al.*, 2001).

The Abrolhos Reef Complex (18°S) is considered to be the largest and most diverse reef area of the South Atlantic Ocean (Castro & Pires, 2001). However, Segal-Ramos (2003) reported extremely high sediment deposition rates at this region, considered by some authors as being catastrophic for reef development (Pastorak & Bilyard, 1985 apud Brown, 1997). More recently, other studies have registered the occurrence of rich coral communities in turbid waters around the world (Anthony & Larcombe, 2000).

Sedimentation is considered one of the main stress factors in coral environments around the world (Nughes & Roberts, 2003a), affecting coral populations by reducing the percentage cover and diversity of corals (Dodge & Vaisnys, 1977), coral growth rates (Dodge & Vaisnys, *op.cit*; Hughes & Jackson, 1985), size of colonies (Dodge & Vaisnys, *op.cit.*; Nughes & Roberts, *op.cit.*), and recruitment (Babcock & Smith, 2000).

Sedimentation affects all life phases of corals, and its influence seems to be related to colony size. Recruits and small coral colonies may be easily buried by sediment (Bak & Engel, 1979; Babcock & Smith, 2000; Miller *et al.*, 2000), and only a few corals manage to survive burial for a long time period. In contrast, large colonies less likely to be killed by sediment may be reduced in size by partial colony mortality (Bak & Meesters, 1998; Goffredo & Chadwick-Furman, 2003). By affecting the size classes differentially (Dodge & Vaisnys, 1977; Langmead & Sheppard, 2004), sedimentation changes the size structure of populations, affecting their maintenance and recovery potentials (Dodge & Vaisnys, *op.cit*; Fabricius, 2005).

Survivorship in coral populations exposed to sedimentation, depends on their capacity to become adapted to different conditions, and the intensity and duration of the stress (Anthony & Fabricius, 2000; Fabricius, 2005). Analysis of the responses of the populations of the main reef building corals among areas characterized by different sedimentation patterns provides important insights into understanding how this factor may affect reef coral population dynamics. The apparent adaptation of the Brazilian coral species to high rates of sediment deposition, as proposed by Leão *et al.* (1988), provides an interesting opportunity to study the relation between corals and long term sedimentation.

During the present study, no linear relationship was apparent between sediment deposition rate and colony size (mean and maximum),

mean cover, or number of recruits per square meter. These results are similar to those obtained by Segal-Ramos (2003), who also did not detect a direct relationship between sediment and these aspects of coral community structure. However, Segal-Ramos (2003) suggested an indirect effect of the deposition of sediment upon coral communities. In the present study we also considered the hypothesis that sedimentation may be causing some influence upon the life history of *S. stellata*, as indicated by the size structure of colonies at the six sites of Abrolhos.

The only significative linear correlation was a strong positive correlation between sediment deposition rate and skewness (g_1) (Pearson r; r = 0.912; r^2 = 0.832; p = 0.011). This result suggests that at high sedimentation conditions, a high frequency of colonies smaller than mean would be present, i.e. high and positive skewness values. Gúzman & Holst (1993) analyzed the size structure of *S. radians* populations affected by oil pollution and also found a higher frequency of small colonies. However, our results contrasted with those by Meesters *et a*l. (2001), who observed negative skewness (i.e. higher frequency of large colonies) at sites affected by sedimentation. These results indicated that different population structures may arise depending on the species and the impact factor analyzed.

The "Sebastião Gomes" site had the highest frequency of small colonies (the most positive skewness value – Table 1), which may be explained by a high recruitment rate. Considering that *S. stellata* has an annual gametogenic cycle, releasing larvae by the end of January-early February, the critical period for larvae recruitment would be February-March (Lins de Barros *et al.*, 2003). Despite the high mean sediment deposition rate observed at this site, during this critical recruitment period (February-March), sedimentation is not at its highest level (Segal-Ramos, 2003), hence it may not be a significantly limiting recruitment. However, the number of recruits per square meter observed at "Sebastião Gomes" was not particularly high (Table 1), hence recruitment alone does not explain why this site had the highest frequency of small colonies.

Reis & Leão (2000) studied *S. stellata* colonies from the North of Bahia State, and observed a growth rate similar to that estimated for this species at a Southern reef in Bahia State (Lins-de-Barros & Pires, *in press*). However, the highest sediment deposition rates registered at "Sebastião Gomes" were very high and could be causing effects on the species biology, such as reducing growth. Riegl & Branch (1995) observed that an experimental increase in sedimentation decreased the ratio of productivity/respiration and increased the mucus production of many coral species. Sedimentation can also cause the initiation of cleaning mechanisms by

ciliary action, tentacular movement and polyp expansion (Sanders & Baron-Szabo, 2005). These events represent expenditure of energy that in other conditions could be used for growth (Dodge & Vaisnys, 1977; Riegl & Branch, 1995; Babcock & Smith, 2000; Nughes & Roberts, 2003a).

Finally, the high frequency of small *S. stellata* colonies at "Sebastião Gomes" may be reflecting some limitation to growth, perhaps by competition with another organism that gains advantage in high sediment habitats. An example for the Brazilian reefs is the zoanthid *Palythoa caribaeorum*, which has the capacity to incorporate sediment into its tissue during tissue growth (Haywick & Mueller, 1997).

Segal-Ramos (2003) did not detect a linear relationship between mean sediment deposition rate and *Palythoa* cover, but observed a higher cover of this organism at "Sebastião Gomes", the site with the highest mean sediment deposition rate. This author also observed a negative correlation between *Palythoa* and Scleractinia cover. Following Bastidas & Bone (1996), in their study from Venezuela, *P. caribaeorum* presents a higher competitive capacity than the other corals, such as *S. siderea* and *Agaricia agaricites*. At the sites studied in this project, *Palythoa* occupies the same habitat as *S. stellata*, on shallow and horizontal substrates. Therefore, these organisms could be potential competitors.

"Coroa Vermelha" had a skewness value close to zero (g_1 = -0.045 – Table 1), a high frequency of size class 1 colonies (Fig. 2 C), and the smallest size of colonies (mean and maximum) (Table 1). Colony size-frequency distribution obtained for this site was similar to that obtained for "Sebastião Gomes" (K-S; $p > 0.05$), but different from the other sites. The small size of colonies at "Coroa Vermelha" could be explained by a high recruitment rate. The highest number of recruits per square meter was registered at this site (Table 1 – extracted from Alvarenga, 2003). However, despite increased recruitment, colonies at this site, apparently, did not attain large sizes. The mean sediment deposition rate documented at "Coroa Vermelha" was similar to that of "Guaratibas" and "Viçosa" (Table 1). However, Segal-Ramos (2003) registered the highest water turbidity at "Coroa Vermelha". So, the high degree of sediment in the water column could be causing the death of recruits by abrasion or displacement. It is possible that while the "Coroa Vermelha" conditions are good to recruitment, they may not be good for the adult population (see Babcock & Mundy, 1996). The low coral cover observed at "Coroa Vermelha" (Table 1) could be indicative of mortality during post-recruitment phases.

At "Coroa Vermelha", the small colony size and high frequency of size class 1 colonies could be the result of high recruitment, recruit mortality and partial mortality of large colonies. These results indicated that similar distributions, such as those from "Sebastião Gomes" and "Coroa Vermelha", could reflect different environmental conditions and selective factors acting upon the community.

From the Abrolhos sites, "Guaratibas", "Lixa" and "Leste" presented high frequency of large colonies, indicated by high and negative skewness values (Table 1). However, while "Guaratibas" showed the highest colony size, "Leste" and "Lixa" had small colonies, even when compared to those observed at "Viçosa" (Table 1). This result may indicate that at "Guaratibas" colonies grow more. Additionally, "Guaratibas" presented a well representative size-frequency distribution (Fig. 2 D), indicating that this site represents a less impacted habitat for *S. stellata* than "Lixa" and "Leste" (Figs. 2 E, F) (see Chadwick-Furman *et al.*, 2000 and Meesters *et al.*, 2001).

Sediment deposition rates varied among "Guaratibas", "Lixa" and "Leste". "Lixa" and "Leste" presented the lowest rates. The low frequency of small colonies at these sites could be the result of low recruitment rates, which were low indeed (Table 1). Despite the low recruitment rate, the recruit survivorship rate appears to be high, which can be indicated by the high *S. stellata* cover at "Lixa" (Table 1). However, if "Leste" and "Lixa" presented high frequency of large colonies, they did not present the largest colony sizes, indicating a possible effect of partial mortality events. In the present study, the frequency of colonies infested by bioeroders increased with colony size. A hypothesis could be that, at "Lixa" and "Leste", colonies did not attain large sizes because of partial mortality events caused, for example, by the borers infestation. We may conclude that the populational structure of *S. stellata* at "Lixa" and "Leste" could be the result of a balance among low recruitment, recruit survivorship and partial mortality of large colonies.

Size-frequency distribution parameters obtained for "Guaratibas" and "Viçosa" indicated that these sites present optimum environmental condition for *S. stellata* population development, being characterized, among the Abrolhos sites, by the largest mean colony sizes and the best size class representativeness (larger coefficient of variation). "Viçosa" also presented the lowest skewness (g_1 = 0.019 – Table 1), indicating similarity to a normal distribution, while at "Guaratibas" it was the most negative (g_1 = -0.388 – Table 1), indicating a high frequency of colonies larger than the mean. This size structure difference could be explained by differences in recruitment rates, since at "Viçosa" it was nine times higher than at "Guaratibas" (Table 1). However, the presence of many size classes observed at these

two sites may indicate a balance among recruitment, survivorship and mortality.

We concluded that sedimentation may be causing an indirect effect on the structure of *S. stellata* populations, acting synergistically with other factors and community parameters. In the case of the genus *Siderastrea*, its tolerance to sedimentation has already been documented for *S. stellata* (Laborel, 1970), *S. siderea* (Nughes & Robert, 2003b) and *S. radians* (Lirman *et al.*, 2002). Our results suggested that *S. stellata* has advantages at sites with intermediate sedimentation. At these sites, *S. stellata* colonies attain larger sizes, probably, reflecting a higher survivorship over time. Also, the influence of sedimentation on life history of *S. stellata* in Abrolhos reefs is probably occurring mainly during post-recruitment phases.

The present study showed that, despite of the influence of environmental conditions on parameters of the populations such as size of colony, the life history strategy of *S. stellata* reflects a local adaptation that allows its development and survivorship in shallow waters and horizontal substrates, at sites characterized by high mortality rates.

REFERENCES

Anthony, K. R. N. & Fabricius, K. E. 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J. expl., mar. Biol. Ecol., 252:221-253.

Anthony, K. R. N. & Larcombe, P. 2000. Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. Proc. 9th Int. Coral Reef Symp., 1:239-244.

Babcock, R. & Mundy, C. 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. J. expl mar. Biol. Ecol., 206:179-201.

Babcock, R. & Smith L. 2000. Effects of sedimentation on coral settlement and survivorship. In: International Coral Reef Symposium, 9. Bali, Indonesia. Proceedings. Indonesia, Indonesian Institute of Sciences, 1:245-248.

Bak, R. P. M. & Engel, M. S. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol., 54:341-352.

Bak, R. P. M. & Meesters, E. H. 1998. Coral population structure: the hidden information of colony size-frequency distributions. Mar. Ecol.- Prog. Ser., 162:301-306.

Bastidas, C. & Bone, D. 1996. Competitive strategies between *Palythoa caribaeorum* and *Zoanthus sociatus* (Cnidaria: Anthozoa) at reef flat environment in Venezuela. Bull. mar. Sci., 59 (3):543-555.

Brown, B. E. 1997. Disturbance to reefs in recent times. In: Birkeland, C., ed. Life and death of coral reefs. New York: Chapman and Hall. p. 354-379.

Castro, C. B. & Pires, D. O. 2001. Brazilian coral reefs: what we already know and what is still missing. Bull. mar. Sci., 69(2):357-371.

Chadwick-Furman, N. E.; Goffredo, S. & Loya, Y. 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. J. expl mar. Biol. Ecol., 249:199-218.

Chevalier, J. P. 1987. Order des scléractiniaires. In: Grassé, P. P., ed. Traité de zoologie – anatomie, systématique, biologie. Cnidaires (Anthozoaires), Paris: Masson. p. 403-764.

Dodge, R. E. & Vaisnys, J. R. 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J. mar. Res., 35(4):715-730.

Echeverría C. A.; Pires D.O.; Medeiros M. S. & Castro C. B. 1997. Cnidarians of the Atol das Rocas, Brazil. Proc. 8th Int. Coral Reef Symp., 1:443-446.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull., 50(2):125-146.

Goffredo, S. & Chadwick-Furman, N. E. 2003. Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea. Mar. Biol., 142:411-418.

Gúzman, H. M. & Holst, I. 1993. Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral *Siderastrea siderea*. Mar. Pollut. Bull., 26(5): 276-282.

Harvell, C. D. & Grosberg, R. K. 1988. The timing of sexual maturity in clonal animals. Ecology, 69(6):1855-1864.

Haywick, D. W. & Mueller, E. M. 1997. Sediment retention in encrusting *Palythoa* spp. – a biological twist to a geological process. Coral Reefs, 16:39-46.

Hughes, T. P. & Jackson, J. B. C. 1985. Population dynamic and life histories of foliaceous corals. Ecol. Monogr., 55(2):141-166.

Kramarsky-Winter, E. & Loya, Y. 1998. Reproductive strategies of two fungiid corals from the northern Red Sea: environmental constraints? Mar. Ecol. - Progr. Ser., 174:175-182.

Laborel, J. 1970. Madréporaires et hydrocoralliaires récifaux des cotes brésiliennes. Systématique, écologie, répartition verticale et géographique. XXXVI Campagne de la Calypso au large des cotes Atlantiques de l'Amérique du Sud (1961-1962). Première et deuxième partie (suite):171-229.

Langmead, O. & Sheppard, C. 2004. Coral reef community dynamics and disturbance: a simulation model. Ecol. Mod., 175:271-290.

Leão, Z. M. N. A.; Araujo, T. M. F. & Nolasco, M. C. 1988. The coastal reefs of the coast of eastern Brazil. In: International Coral Reef Symposium, 6. Australia. Proceedings. Townsville, 3:339-347.

Lins de Barros M. M.; Pires D. O. & Castro, C. B. 2003. Sexual reproduction of the Brazilian reef coral *Siderastrea stellata* Verrill, 1868 (Anthozoa, Scleractinia). Bull. Mar. Sci., 73:713-724.

Lins-de-Barros, M. M. & Pires, D. O. Life history aspects of *Siderastrea stellata* in the Tropical Western Atlantic, Brazil. J. Inv. Reprod. and Develop. (*in press*).

Lirman, D.; Manzello, D. & Maciá, S. 2002. Back from the dead: the resilience of *Siderastrea radians* to severe stress. Coral Reefs, 21:291-292.

Meesters W. H.; Hilterman M.; Kardinaal, E.; Keetman M., de Vries, M. & Bak. R. P. M. 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar. Ecol. - Prog. Ser., 209:43-54.

Miller, M. W.; Weil E & Szmant A. M. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. Coral Reefs, 19:115-123.

Nughes, M. M. & Roberts, C. M. 2003a. Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. Mar. Pollut. Bull., 46:314-323.

Nughes, M. M. & Roberts, C. M. 2003b. Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs, 22(4):507-516.

Reis, M. A. C. & Leão, Z. M. A. N. 2000. Bioerosion rate of the sponge *Cliona celata* (Grant 1826) from reefs in turbid waters, north Bahia, Brazil. In: International Coral Reef Symposium, 9. Bali, Indonesia. Proceedings. Indonesia, Indonesian Institute of Sciences, 2:273-278.

Riegl, B. & Branch, G. M. 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J. expl Mar. Biol. Ecol., 186:259-275.

Rinkevich, B. & Loya, Y. 1987. Variability in the pattern of sexual reproduction of the coral *Stylophora pistillata* at Eilat, Red Sea: A long term study. Biol. Bull., 173:335-344.

Sanders, D. & Baron-Szabo, R. C. 2005. Scleractinian assemblages under sediment input: their characteristics and relation to nutrient input concept. Paleogeogr. Palaeoclimat. Palaeoecol., 216:139-181.

Santangelo, G.; Carletti, E.; Maggi, E. & Bramanti, L. 2003. Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Mar. Ecol. - Prog. Ser., 248:99-108.

Segal, B. & Castro, C. B. 2000. Slope preferences of reef corals (Cnidaria, Scleractinia) in the Abrolhos Archipelago, Brazil. Bolm Mus. Nac., n.s. Zool., 418:1-10.

Sources of Unpublished Material

Alvarenga, M. F. 2004. Recrutamento de corais recifais no Banco dos Abrolhos, Brasil. M.Sc. Thesis. Museu Nacional, Universidade Federal do Rio de Janeiro, 72p.

Segal-Ramos, B. 2003. Corais e comunidades recifais e sua relação com a sedimentação no Banco dos Abrolhos, Brasil. PhD. Thesis. Museu Nacional, Universidade Federal do Rio de Janeiro. 131p.