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Coexistence of reef organisms in the Abrolhos Archipelago, Brazil

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Abstract: The first study on coexistence of reef benthic organisms in Brazilian coral reefs was done in three localities of the Abrolhos Archipelago. Organisms were recorded in concentric circle samples (10 and 20 cm in diameter) randomly laid on transects. Type and frequency of "coexistence events" between pairs of organisms were determined. Most frequent organisms (massive and branched coralline algae, *Favia gravida*, and *Agaricia agaricites*) also had many significant positive coexistence events. These results might be related to the abundances of these organisms. The most frequent coral (*Siderastrea stellata*), however, exhibited only a few significant coexistence events (9% of 32 tests). Since the great majority of events were positive, and since there was high variation in the species/groups involved in significant events in different localities, benthic communities of Abrolhos Archipelago may well be structured primarily by abiotic rather than biotic factors.

Key-words: Brazil, community, reef benthic fauna, coexistence, biotic factor, abiotic factor.

Different factors have been related to the distribution and abundance of sessile organisms of coral reefs. Sedimentation, light, temperature, salinity, hydrodynamics and exposure are among the physical factors that influence coral populations (Sheppard 1982, Carleton and Sammarco 1987, Sorokin 1995). Species interactions, especially competition, was the first ecological process considered to be an important biological factor controlling coral community structure (Lang 1973, Bak *et al.* 1982). Different coral species may react differently to disturbances, competing with their neighbors for vital resources, including space (Sorokin 1995). Modes of reproduction and early life strategies influence succession and also the final community structure (Sheppard 1982, Carlon and Olson 1993). Studies of factors influencing coral community structure have shifted from competition to other factors, extrinsic to the community, such as physical, historical and geological phenomena (Souza 1979, Cornell and Karlson 1996). Disturbances associated with such phenomena may generate a decrease of population size of more abundant species, and free space for others which are less favored by direct competition (Souza 1979, Bak *et al.* 1982, Cornell and Karlson 1996).

Bradbury and Young (1981a) devised a method to examine neighbor events among coral species to analyze the ecological significance of forces structuring reef communities. If competition was a major structuring force in reef communities, we should see the effects of interactions reflected in the distributions of the species involved. We adapted this basic method here.

In this report, we present the first study of coexistence of reef organisms in Brazilian coral reefs. Physical and/or biotic parameters that may be influencing their distribution are discussed.

MATERIALS AND METHODS

This study was conducted on the fringing reefs of the Abrolhos Archipelago, from October 26th to 31st, 1997. Three localities were sampled: the northern (17°57.70’ S, 038°41.90’ W) and the southern (17°57.84’ S, 038°41.99’ W) shores of Santa Bárbara Island (NSB and SSB, respectively) and the northern shore of Siriba Island (17°58.16’ S, 038°42.54’ W) (SIR).

A tape measure was placed perpendicular to the coast in each area. At each meter of the tape measure, a 20 m long weighted rope (transects) was extended perpendicularly to it; 20 randomly selected points were marked on each transect. Each point received a system of concentric circles of 10 and 20 cm in diameter, selected based on the average colony sizes of main coral species occurring in the area (B. Segal, unpublished). The occurrence of different species or functional groups was recorded for each circle and frequency tables for each locality were prepared.

Association tests were performed on organisms occurring in at least 10% of the samples. This was done in order to avoid errors due to dealing with rare species or insufficient sampling. The data were analyzed using 2x2 contingency tables, and chi-square statistics ($p< 0.05$). Significant results were interpreted as “positive associations” when the observed co-occurrence frequency of tested organisms was larger than their expected frequency; “negative associations” would occur when the former was smaller than the latter. Further analyses included all organisms observed, including a multi-dimensional scaling analysis (MDS) on the species/circle tables, using the Bray-Curtis similarity coefficient (Clarke and Warwick 1994), with the aid of “Plymouth Routines in Multivariate Ecological Research” software (PRIMER).

RESULTS

Frequency: Two hundred circles were observed on NSB and SSB, and 160 on SIR. Thirteen entities were recorded in the samples (Table 1). The two zoanthid groups were represented mostly by *Zoanthus sociatus* and *Palythoa caribaeorum*. They were nevertheless considered multispecific because of other species in the area which were sometimes hard to distinguish in the field. The crustose coralline algae were categorized into two morpho-functional groups: branched (following Steneck 1986) and massive (which includes Steneck’s thin and thick morphological states).

Five entities showed higher frequency in most stations and treatments (10 and 20 cm):

TABLE 1

Frequency (% of presence in samples) of species or groups by locality and sample (circle) size.

Locality	Nsb		Ssb		Sir	
Species	10 cm	20 cm	10 cm	20 cm	10 cm	20 cm
Agaricia agaricites	4	11	14	33	14.4	29.4
Massive coralline algae	43	51	25.5	41.5	30.6	44.4
Branched coralline algae	12.5	18	17	29.5	28.1	40.6
Favia gravida	17	35.5	10.5	23	11.9	31.3
Mussismilia braziliensis	20	30.5	3.5	7	11.3	17.5
Mussismilia harttii	0.5	0.5	0	0	1.3	1.9
Mussismilia hispida	2	5	2	4	5	6.9
Millepora alcicornis	2.5	3.5	1	1.5	0	0
Porites astreoides	0	1.5	0.5	1	0	0
Porites branneri	3	6	3.5	8.5	11.9	23.8
Palythoa spp.	5.5	12.5	3	4.5	11.3	18.1
Siderastrea stellata	41	59	10	24.5	16.3	38.8
Zoanthus spp.	6.5	8.5	1	1	6.3	14.4

Nsb = northern shore of Santa Bárbara Island; Ssb = southern shore of Santa Bárbara Island; Sir = Siriba Island. Boldface = values equal to or higher than 10%.

Siderastrea stellata, massive corallines, branched corallines, *Favia gravida*, and *Agaricia agaricites*. Other species however also had high frequencies in some locales, such as *Mussismilia braziliensis* on NSB, and *Porites branneri* and *Palythoa* spp., on SIR (Table 1).

Contingency Tables: Species frequencies differed among localities (Table 1). Accordingly, the number of association tests between pairs of species varied in each locality.

There was a single significant negative association: *S. stellata* x *M. braziliensis* in the 10 cm circles of SIR. The percentage of significant positive associations compared to the total pairs analyzed represented up to 50% of all pairs of species/groups by locality/treatment. As expected, in all localities the number of positive associations increased with the larger circle diameter. However, the associations were not necessarily the same (Fig. 1).

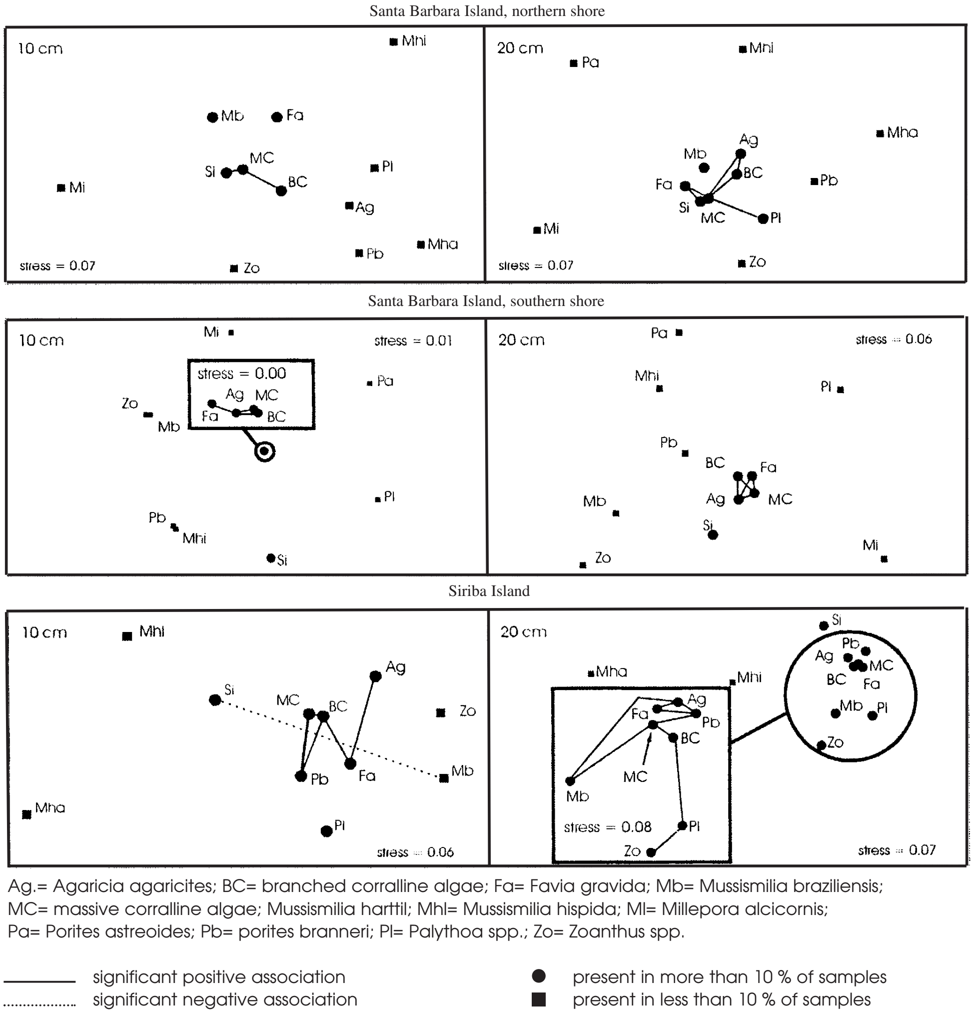

Fig. 1: Two-dimensional configurations for multi-dimensional scaling ordinations (MDS) of coexistence of studied taxa. **A** = Santa Bárbara Island, northern shore, 10 cm circles; **B** = Santa Bárbara Island, northern shore, 20 cm circles; **C** = Santa Bárbara Island, southern shore, 10 cm circles; **D** = Santa Bárbara Island, southern shore, 20 cm circles; **E** = Siriba Island, 10 cm circles; **F** = Siriba Island, 20 cm circles. Ag = *Agaricia agaricites*; BC = branched coralline algae; Fa = *Favia gravida*; Mb = *Mussismilia braziliensis*; MC = massive coralline algae; Mha = *Mussismilia hartti*; Mhi = *Mussismilia hispida*; Mi = *Millepora alcicornis*; Pa = *Porites astreoides*; Pb = *Porites branneri*; Pl = *Palythoa spp.*; Zo = *Zoanthus spp.* Circles = species/groups present in more than 10% of samples; rectangles = species/groups present in less than 10% of samples. Contingency tables tests (only species/groups marked with circles): continuous lines = significant positive association; broken lines = significant negative association.

TABLE 2

Number of contingency table tests (t) and positive significant results (n) (n/t) between pairs of species or groups, using data from three localities in the Abrolhos Archipelago and 10 and 20 cm circles.

	Zo		Si		Pl		Pb		Mb		Fa		Bc		Mc	
Circle diameter	10	20	10	20	10	20	10	20	10	20	10	20	10	20	10	20
Agaricia agaricites (Ag)	0	0/1	0/2	0/3	0/1	0/2	0/1	1/1	0/1	1/2	2/2	2/3	1/2	2/3	1/2	2/3
Massive coralline algae (Mc)	0	0/1	1/3	1/3	0/1	1/2	1/1	1/1	0/2	0/2	0/3	2/3	3/3	3/3		
Branched coralline algae (Bc)	0	0/1	0/3	0/3	0/1	1/3	1/1	1/1	0/2	0/2	1/3	1/3				
Favia gravida (Fa)	0	0/1	0/3	1/3	0/1	0/2	0/1	1/1	0/2	0/2						
Mussismilia braziliensis (Mb)	0	0/1	0/2	0/2	0/1	0/2	0/1	0/1								
Porites branneri (Pb)	0	0/1	0/1	0/1	0/1	0/1										
Palythoa spp. (Pl)	0	1/1	0/1	0/2												
Siderastrea stellata (Si)	0	0/1														
Zoanthus spp. (Zo)	-	-														

Some associations were considered frequent, with 50% or more tests showing significant positive results (Table 2). These include mainly species-groups with high frequency. On the other hand, the most frequent coral species, *S. stellata*, presented very few significant positive associations (9% or three out of 32 tests).

MDS: Results from the MDS confirmed the results from the contingency table analysis (Fig. 1). Stress values found in these analysis (Stress<0.1) corresponds to a "good ordination with no real prospect of a misleading interpretation" (Clarke and Warwick 1994).

DISCUSSION

Results showed that 20 cm circles presented many more positive significant associations than 10 cm circles (Table 2). The expected number of species may have increased not only because the larger circles offered more area for species to settle, but because they could potentially also offer a larger number of microhabitats, as suggested by several species-area hypotheses (Begon *et al.* 1990). Underwood and Chapman (1996) suggested that intertidal invertebrates might vary in abundance at the scale of centimeters, according to the distribution of microhabitats. Biological interactions between coral species also may occur on a scale of centimeters (Bak *et al.* 1982). Here, the samplers used (circles) had a two-dimensional structure, while in many cases the bottom had a strong three-dimensional structure. Therefore, it is more likely that different microhabitats were sampled with the 20 cm circles. This factor would suggest that the associations found in smaller sample size are more reliable (in terms of biological and/or physical significance) than those found only on the larger sample size.

One concern regarding the statistical tests was the influence of each species/group frequency on obtaining a positive significant association. Even testing only species/groups that appeared in at least 10% of the samples, most significant associations still occurred among the commonest species/groups. In addition, there was a question as to whether the larger number of significant associations in the 20 cm circles was merely a result of a larger number of occurrences within the samples. For most tests it would seem so. However, *S. stellata*, the commonest coral species in the area and with a relatively high cover (Pitombo *et al.* 1988), was an exception. *S. stellata* results showed that the tests performed were valid at least for the commonest species/groups in the smaller circles. The single negative association found should be viewed with some skepticism, due to the large size of most *M. braziliensis* (*e. g.* largest distance across surface of colonies 32.9 ± 22.0 cm at SIR, B. Segal, unpublished) when compared to the circle size (10 cm) (see Greig-Smith 1983).

The commonest associations were among the two coralline morphotypes, and the corals *A. agaricites* and *F. gravida*. We considered these to be the most important positive associations found because they occurred at both scales measured (10 and 20 cm circles, Fig. 1).

The associations observed here between coralline algae and some corals could be due either to biological factors or similar habitat preferences. It was suggested that detection of suitable substrate by cnidarian planula could be controlled by cues associated with coralline algae (Sebens 1983, Morse 1991). Morse *et al.* (1996) indicated that settlement and metamorphosis of coral larvae is controlled by chemosensory recognition of a cue associated with coralline red algae and may be common in major and divergent coral families (Acroporidae, Faviidae, and Agariciidae). It has been shown that *A. agaricites*, one of the species studied here, has its larvae settlement and metamorphosis induced by coralline algae (Morse *et al.* 1988 *apud* Carlon and Olson 1993). On the other hand, Carlon and Olson (1993) found that *Favia fragum* will settle and metamorphose with equal probability on bare coral rubble, coralline algae, and rubble coated with filamentous algae. Our results with a species of this genus, *F. gravida*, could be considered similar to Carlon and Olson's (1993). *F. gravida* presented only scattered significant co-occurrence events with both algal morphotypes and mostly on 20 cm samplers (Table 2; Fig. 1).

On the other hand, *F. gravida* and *A. agaricites* have distinct preferences for substrata inclination. *A. agaricites* colonies were found on slightly steeper substratum than *F. gravida* (B. Segal and C. B. Castro, unpublished). Here, these two species exhibited positive significant associations (Table 2). In the studied area, these species are commonly found in crevices of the bottom, with *A. agaricites* occurring deeper in the depressions (pers. obs.). Associations were nonetheless detected because the sampling method used did not discriminate positions within the depressions. This is in accordance with Morse's (1991) observations that "in general, agariciids tend to prefer algal species that grow on the cryptic underside of piles of dead coral rubble".

The divergent results of *S. stellata* association tests was corroborated by its positions on the MDS (Fig. 1). Leão *et al.* (1988) stated that this species is very resistant to high temperature, high turbidity, and low salinity. Echeverría *et al.* (1997) believed that these features could explain the overwhelming dominance of the species in almost all areas of Atol das Rocas, Brazil. *S. stellata* occurred mostly on less steep surfaces than *A. agaricites* and *F. gravida* (B. Segal and C. B. Castro, unpublished). A higher tolerance to sedimentation could explain the species occurrence on less steep surfaces. It was hypothesized that higher coral recruitment on lower surfaces of settlement plates was mainly due to a higher sedimentation on the upper sides, grazing, hydrodinamic regime, and light levels (see Maida *et al.* 1994). The odd situation of *S. stellata* is enhanced by results showing that a larger number of coral genera grow on steeper and cryptic habitats (Carleton and Sammarco 1987). We suggest that our results are related to different habitat preferences and/or tolerances among *S. stellata* and other organisms tested.

Our results suggest that coexistence of organisms may be related to habitat factors. The three localities had different sets of associations (Fig. 1). SIR had a larger number of positive associations and the only negative association (*S. stellata* and *M. braziliensis* in 10 cm circles). Both positive associations (among six tests) between *F. gravida* and branched corallines occurred on the SIR. All positive associations of *S. stellata* (among 32 tests) occurred on the NSB.

Bradbury and Young (1981a) concluded that physical factors external to the reef community, such as wave energy, are more likely to explain community structure than biotic factors. The same authors emphasized, however, that individual responses of corals to different wave regimes are responsible to the occurrence of species and their abundance (Bradbury and Young 1981b). The three localities studied are characterized by shallow waters (less than 5 m) and very different wave regimes. SIR is the most sheltered from wave/wind influence. NSB is under the direct influence of the commonest waves/winds in the area (NE and E). The strongest waves/winds in the area (S) impinge on SSB. Our results could be related to different community structures associated with the distinct physical characteristics of our sites. These results probably could also be extended to most large reef coral communities in Brazil, as they usually occur in shallow waters (less than 10 m).

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RESUMEN

Se hizo el primer estudio de coexistencia de organismos bénticos de arrecifes brasileños en tres localidades del Archipiélago de Abrolhos, registrando la presencia de organismos en círculos de 10 y 20 cm de diametro, distribuidos al azar en transectos. La mayoría de los organismo frecuentes (algas coralinas macizas y ramificadas, *Favia gravida* y *Agaricia agaricites*) mostraron la más alta “coexistencia positiva”, tal vez por su abundancia. El coral más frecuente (*Siderastrea stellata*), sin embargo, mostró apenas algunos eventos de coexistencia significativos (9% de 32 ensayos). Debido a que la mayor parte de los eventos fue positiva, y considerando que existe una alta variabilidad en las interacciones significativas en diferentes localidades, las comunidades bénticas del Archipiélago de Abrolhos pueden haber sido estructuradas principalmente por factores abióticos, mas que por factores bióticos.

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