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Abundance and distribution of sessile invertebrates under intertidal boulders (São Paulo, Brazil)

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• *Abstract:* The encrusting communities under two boulder fields (Praia Grande and Ponta do Baleeiro) were monitored monthly during 1990 and 1991, in São Sebastião, on the northern coast of São Paulo State, Brazil. Two sizes of boulders were chosen: small (20-30 cm^2 underside area) and larger ones (160-220 cm^2) located on the middle and lower levels of the intertidal. The community's components were mainly sessile animals either compound ones such as Bryozoa, Ascidiacea, Porifera and Cnidaria, in this order of abundance, or simple ones such as Polychaeta and Bivalvia, also in this order of abundance. All groups, except by serpulids (Polychaeta), had higher percent cover in the low intertidal region and under large boulders. Diversity was higher at Ponta do Baleeiro, and in the low intertidal region and on large boulders for both shores.

• *Resumo:* Em São Sebastião, litoral norte do Estado de São Paulo, Brasil, foram monitorados mensalmente dois ambientes de matações em costões rochosos, Praia Grande e Ponta do Baleeiro, ao longo de 1990 e 1991. As condições ambientais avaliadas foram: temperatura e salinidade da água, hidrodinâmica, capacidade de abrasão da areia acumulada, heterogeneidade ambiental e porosidade das pedras. Foi estudada a comunidade incrustante na superfície inferior de pedras pequenas (20-30 cm^2 de área na face inferior) e maiores (160-220 cm^2) dispostas nos estratos médio e inferior da zona entremarés. Esta comunidade era constituída principalmente por organismos sésseis coloniais (Bryozoa, Ascidiacea, Porifera e Cnidaria, nesta ordem de abundância) ou solitários (Polychaeta e Bivalvia, nesta ordem de abundância). Todos os grupos, com exceção dos serpulídeos (Polychaeta), apresentaram maior porcentagem de cobertura nos estratos inferiores e nas pedras grandes. A composiçao específica foi similar nos dois costões estudados, mas várias espécies ocorreram exclusivamente em um determinado nível de maré, ou tamanho de pedra, indicando que estes fatores têm maior influência na distribuição das espécies. A diversidade foi maior na Ponta do Baleeiro, nos estratos inferiores e em pedras grandes, nos dois costões, não havendo nenhum tipo de padrão sazonal de variação.

• *Descriptors:* Encrusting community, Boulders, Diversity, Intertidal, Bryozoa, Ascidiacea, Porifera, Serpulidae, São Sebastião Channel, São Paulo, Brazil.

• *Descritores:* Comunidade incrustante, Matações, Região Entremarés, Diversidade, Bryozoa, Ascidiacea, Porifera, Serpulidae, Canal de São Sebastião, São Paulo, Brasil.

Introduction

Most work describing the distribution of encrusting communities in the intertidal region deal with stabilized hard substrate, such as vertical walls or large boulders. Small boulders, on the other hand, are non-stabilized substrata as they suffer displacement and overturning, therefore subjecting encrusting organisms to abrasion, smothering or over-exposition to sunlight and predators.

The exposed upper surfaces of small boulders are usually covered by algae (Sousa, 1979a, b; Littler & Litter, 1981, 1984; McGuinness & Underwood, 1986) while the

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undersurfaces are covered by sessile or sedentary animals (Osman, 1977; McGuinness, 1987a, b).

The distribution of the fauna on stabilized substrata is fairly known for many shores in São Paulo State, and we find reports on both the vertical distribution (Nonato & Pérès, 1961; Oliveira- Filho & Mayal, 1976; Petersen *et al.*, 1986; Kadekaru *et al.*, 1987; Paula, 1987; Rosso, 1990) and on the horizontal one (Guerazzi, 1987; Nalesso, 1988; Johnscher-Fornasaro *et al.*, 1990; Traldi & Schlenz, 1990). On the other hand, the encrusting fauna on non-stabilized substrata is poorly known in Brazil, and there is no report on the species composition, abundance, vertical distribution or geographic variation. The only study on this kind of habitat was done by Rodrigues & Shimizu (1988) and Shimizu & Rodrigues (1988) who investigated the vagile fauna that uses the undersurface of boulders as a refuge against desiccation during low tides.

The main goal of this paper is to describe the encrusting fauna on boulder fields in two different shores, comparing the faunal distribution and diversity between the shores, tide levels and boulder sizes. Description of some new records of ascidian species from this habitat will be found elsewhere (Rocha & Monniot, 1993, Rocha & Monniot, in press).

Study site

The northern coast of São Paulo State has many sand beaches bordered by more or less extensive rocky shores. Boulders of various sizes are frequent beside rocky walls, from the intertidal region to the subtidal region .

This work was done on the northern coast of São Paulo State, at two shores situated in the São Sebastiao Channel (between 23°43'S and 23°53'S, 45°0'W and 45°27'W): Praia Grande and Ponta do Baleeiro (Fig. 1).

Ponta do Baleeiro is located in a environmental protected area (Centro de Biologia Marinha - CEBIMar, USP), therefore less subjected to antropic interference. It is also less exposed to the waves than Praia Grande. The boulder field is 18 m long (parallel axis to the shore) and 7 m wide. The boulders are usually round or oval, with different levels of flatness. Among boulders we can find medium sized granules of sand.

Praia Grande is very appreciated by tourists, who easily reach the study site during low tides. The boulder field is approximately 10 m long in the high intertidal region to 20 m long in the subtidal region (parallel axis to the shore), and is 10 m wide. Boulders are either round, oval, or angulate with flattened faces. Among them we can find large size granules of sand.

No difference in boulders porosity was detected between the shores. The abrasion power of the sand was neither significantly different between shores.

Hydrodynamics (see methods) was greater at Praia Grande for six times in a total of twelve which were evaluated; and it was greater at Ponta do Baleeiro only once. There was no perceptible seasonal pattern. Great storms, longer than two days, were rare and occured in April, May, June and September in 1990, and between September and October in 1991.

Superficial water temperature, measured daily next to the laboratory at CEBIMar, varied from 20°C in the end of winter (September or October) to 26,5°C in fall (April or May) during the study period. Salinity kept values between 33 and 35‰.

Materials and methods

Characterization of environmental conditions was done according to the following parameters: water temperature and salinity, hydrodynamics, abrasion power of the sand and habitat heterogeneity. The boulder features studied were: undersurface area (small: 20-30 cm^2 and large: 160-220 cm^2), location: medium (MI) or low (LI) intertidal level, porosity and the intensity of disturbance caused by waves (displacement and overturning). Results on recruitment experiments are found in Rocha (1994), and those on disturbance, and transposition of boulders in Rocha (1993).

Hydrodynamics between the shores was compared using the difference of weight before and after the submersion of plaster half-spheres (6 cm diameter). Ten of them were placed in each shore, for 24 hours. The shores were compared with one-factor covariance analyses (ANCOVA), considering initial weight as the co-variable and the two shores as the levels of the treatment.

The boulders were found over other boulders, directly over sand, buried, or even immobilized by other boulders, creating at least four different microhabitat conditions for the undersurface community. To quantify this kind of environmental heterogeneity, the percentage of boulders in each of these four situations was calculated for every month. A standard deviation (SD) of the percentage values of 50 would correspond to low heterogeneity (all boulders in the same situation) and a SD of zero, to high heterogeneity (all boulders equally distributed among the four situations).

The community was monitored monthly during 1990 and 1991. Initially, ten boulders of each size, from each tide level, were permanently marked with commercial epoxi cement with a low relief number written on it. Due to the difficulty in locating all the marked boulders in each visit, more boulders were marked to increase the probability of finding at least eight.

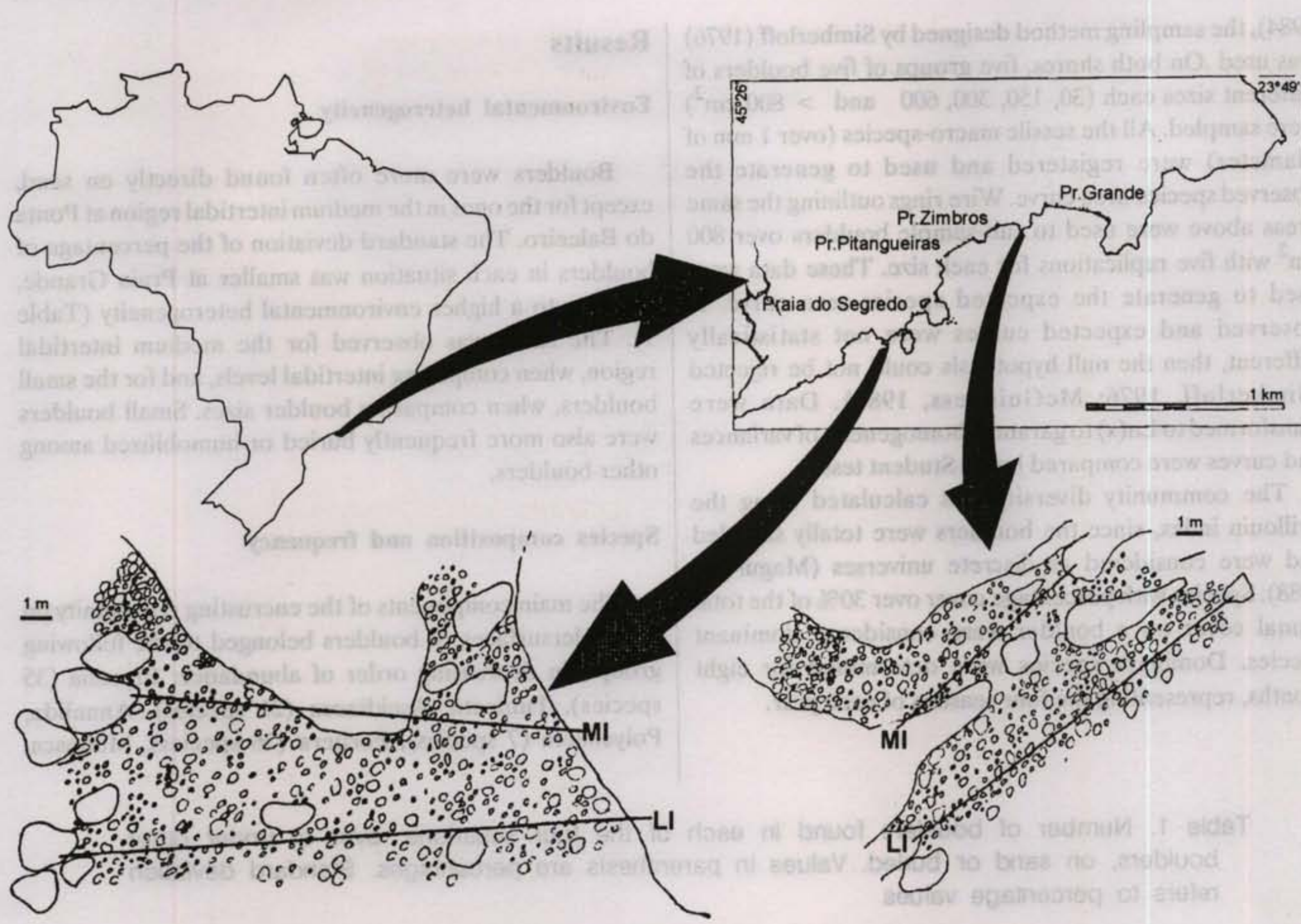

Fig. 1. Map of the region studied at São Sebastião Channel with the detailed map of the boulder fields studied (A = Ponta do Baleeiro, B = Praia Grande, MI = medium intertidal zone, LI = low intertidal zone).

To observe the community, I placed each boulder upside down in a bowl filled with sea water. A quadrat with PVC frame and nylon mesh (holes of 1 cm^2) was placed over the undersurface of the boulder and the area covered by each organism was measured counting the number of squares occupied. This method was used both for compound and solitary organisms since they were often fixed side by side (otherwise I calculated the cover surface as if they were fixed side by side). The percentage cover of the species was the result of the fraction between the number of squares occupied by each species by the total undersurface area (cm^2) of each boulder.

Some species were grouped together for the data analysis because of the difficulty to set them appart during field work. The Bryozoa Calloporidae and Membraniporidae were grouped and called "net Bryozoa", the species *Stylopoma spongites, Schizoporella unicornis* and *Hipodiplosia americana* were grouped as Schizoporellidae, all the arborescent bryozoa were also grouped together. Among ascidians, *Didemnum speciosum* and *Lissoclinum fragile* were grouped under Didemnidae. Among sponges, species 13, 15 and 16 from Suberetidae family were put together under species 16; *Reniera* sp, *Amphimedon viridis, Callyspongia* sp, *Myxilla mucronata*, *Clathria* sp and *Chondrilla nucula* were observed in the study site but did not enter the analysis because they were not found on the marked boulders. Among polychaetes, the two species of *Spirorbis* were considered together, and two species were not identified, called here serpulid 1 and 2. Empty shells of bivalves were considered for the analysis of total percent cover of bivalves. Cnidarians species did not entered the analysis because of their little abundance and difficulty of identification during field work.

Since boulders are discrete substrates with limited area, it was possible to study the effect of available space on the number of species. To verify whether the number of species was a consequence of random sampling (null hypothesis), that is, smaller areas would receive fewer colonists and, therefore, fewer species (Connor & McCoy, 1979; Coleman *et al.*, 1982) or whether there were other factors influencing species-area curve (McGuinness, 1984), the sampling method designed by Simberloff (1976) was used .On both shores, five groups of five boulders of different sizes each (30, 150, 300, 600 and > 800 cm^2) were sampled. All the sessile macro-species (over 1 mm of diameter) were registered and used to generate the observed species-area curve. Wire rings outlining the same areas above were used to sub-sample boulders over 800 cm^2 with five replications for each size. These data were used to generate the expected species-area curve. If observed and expected curves were not statistically different, then the null hypothesis could not be rejected (Simberloff, 1976; McGuinness, 1984). Data were transformed to Ln(x) to garantee homogeneity of variances and curves were compared by a t-Student test.

The community diversity was calculated using the Brillouin index, since the boulders were totally sampled and were considered as discrete universes (Magurran, 1988). Species with percentage cover over 30% of the total faunal cover on a boulder were considered dominant species. Dominant species were determined for eight months, representing the four seasons of each year.

Results

Environmental heterogeneity

Boulders were more often found directly on sand, except for the ones in the medium intertidal region at Ponta do Baleeiro. The standard deviation of the percentage of boulders in each situation was smaller at Praia Grande, pointing to a higher environmental heterogeneity (Table 1). The same was observed for the medium intertidal region, when comparing intertidal levels, and for the small boulders, when comparing boulder sizes. Small boulders were also more frequently buried or immobilized among other boulders.

Species composition and frequency

The main components of the encrusting community on the undersurfaces of boulders belonged to the following groups, in decreasing order of abundance: Bryozoa (35 species), Tunicata, Ascidiacea (21 species), Annelida, Polychaeta (7 species), Porifera (26 species), Mollusca,

Table 1. Number of boulders found in each of the four situations: over or under other boulders, on sand or buried. Values in parenthesis are percentages. Standard deviation refers to percentage values

		N	Over Boulders	Under Boulders	Over Sand	Buried	Standard deviation
SHORE	Ponta do Baleeiro	650	350 (53.8)	7 (1.1)	270 (41.5)	30 (4.6)	26.39
	Praia Grande	50	134 (26.6)	19 (3.8)	294 (58.4)	74 (14.7)	23.60
TIDE LEVEL	Medium intertide	619	360 (58.2)	20 (3.2)	204 (33.0)	55 (8.9)	25.15
	Low intertide	534	124 (23.2)	6 (1.1)	360 (67.4)	49 (9.2)	29.56
SIZE	Small boulders	456	175 (38.4)	22 (4.8)	219 (48.0)	61 (13.4)	20.38
	Large boulders	697	309 (44.3)	4 (0.6)	345 (49.5)	43 (6.2)	25.31

Bivalvia (2 species), Cnidaria, Hydrozoa (5 species), and Crustacea (Cirripedia and Amphipoda tubes - not identified) (see Appendix I for a complete list of species).

Most species occured more frequently at Ponta do Baleeiro, in the low intertidal region and on large boulders (Appendix I). Few species occured exclusively in one of the shores (14 at Ponta do Baleeiro and 2 at Praia Grande) showing a similarity between their faunas. Quite more species occured exclusively in a tide level (37 species in the low intertidal region) or boulder size (25 species on large boulders), indicating that those are more important features of the environment for the encrusting community.

Main groups abundance

The fauna had higher percentage cover values on large boulders in the low intertidal region, and minimal values in the medium intertidal region, specially for small boulders (Fig. 2). The flora had high percentage cover values on small boulders in the medium intertidal region. Empty substrate was abundant in all situations, mainly on small boulders and in the medium intertidal region.

Appendix I

	BAL[3]	PG	MI	LI	L	S
BRYOZOA						
Order CHEILOSTOMIDA						
Family Aeteidae						
Aetea anguinea (Linné, 1758)						
Family Calloporidae						
?[1] *Antropora minus* (Hincks, 1880)						
*[2] *Crassimarginatella tuberosa* (Canu & Bassler, 1928)						
Family Membraniporidae						
Acanthodesia savartii (Audouin, 1826)						
Acanthodesia tenuis (Desor, 1848)						
Conopeum reticulum (Linné, 1767)						
? *Conopeum commensale* Kirkpatrick & Metzelaar, 1922						
Family Steginoporellidae						
Steginoporella buskii Harmer, 1900	**	**	0	***	***	*
* *Labioporella sinuosa* Osburn, 1940	***	**	*	***	***	*
Family Beanidae						
Beania australis Busk, 1852						
Beania hirtissima (Heller, 1867)	**	**	0	**	**	*
Beania intermedia (Hincks, 1881)						
Family Cabereidae						
? *Scrupocellaria cornigera* (Smitt, 1872)						
Family Bicellariellidae						
Bicellariella ciliata (Linné, 1758)						
Family Exechonellidae						
Exechonella antillea (Osburn, 1927)	**	0	0	**	**	0
Family Schizoporellidae						
Stylopoma spongites (Pallas, 1766)	**	*	*	**	**	*
Schizoporella unicornis (Johnston, 1847)						
? *Dakaria vaginata* (Canu & Bassler, 1928)	**	*	0	**	**	*
Arthropoma cecilii (Audouin, 1826)	**	*	0	**	**	0
Hippodiplosia americana (Verrill, 1875)						
Family Hippoporinidae						
Calyptotheca sp						
Family Watersiporidae						
Watersipora subtorquata (d'Orbigny, 1852)						

Appendix I - Cont.

	BAL[3]	PG	MI	LI	L	S
Family Smittinidae						
Parasmittina trispinosa Johnston, 1838	*	*	0	*	*	0
Family Sertellidae						
Cleidochasma porcellanum (Busk, 1860)	*	0	0	*	*	0
Family Catenicellidae						
Catenicella contei (Audouin, 1826)						
Family Savignyellidae						
Savignyella lafontii (Audouin, 1826)						
Family Celleporariidae						
Celleporaria mordax (Marcus, 1937)	**	*	*	**	**	*
Celleporaria atlantica (Busk, 1884)	**	0	0	**	**	0
Family Phidoloporidae						
Rhynchozoon verruculatum (Smitt, 1873)	**	0	0	**	**	*
Order CTENOSTOMIDA						
Family Arachnidiidae						
Nolella gigantea (Busk, 1856)	**	*	0	**	**	*
Family Vesicularridae						
* *Amathia vidovici* (Heller, 1867)						
Order CYCLOSTOMIDA						
Family Crisiidae						
Crisia ficulnea Buge, 1979						
arborescent bryozoans	0	*	0	*	*	0
net bryozoans	***	**	**	***	***	**
ASCIDIACEA						
Order APLOUSOBRANCHIA						
Family Polyclinidae						
Polyclinum constellatum Savigny, 1816	*	*	0	*	*	0
Aplidium sp	*	**	0	**	**	0
Family Didemnidae						
* *Didemnum ahu* Monniot, 1987	**	0	0	**	**	0
* *Didemnum granulatum* Tokioka, 1954						
* *Didemnum lutarium* Van Name, 1924	**	**	0	**	**	*
* *Didemnum perlucidum* Monniot, 1983	**	**	0	**	**	*
Didemnum psammathodes (Sluiter, 1895)	**	**	**	**	**	*
Didemnum speciosum (Herdman, 1886)	**	**	0	**	**	*
Didemnum vanderhorsti Van Name, 1924	**	**	0	**	**	0
Trididemnum orbiculatum (Van Name, 1902)	**	*	0	**	**	*
Diplosoma listerianum (Milne-Edwards, 1841)	**	**	**	**	**	*
Lissoclinum fragile (Van Name, 1902)						
Polysyncraton amethysteum (Van Name, 1902)	*	*	0	*	*	0
Family Polycitoridae						
Clavelina oblonga Herdman, 1880	*	0	0	*	*	0
Distaplia bermudensis Van Name, 1902	*	*	0	*	*	0
Order PHLEBOBRANCHIA						
Family Cionidae						
Ciona intestinalis (Linnaeus, 1767)						
Family Ascidiidae						
Phallusia nigra Savigny, 1816	*	*	0	*	*	0

Appendix I - Cont.

	BAL[3]	PG	MI	LI	L	S
Order STOLIDOBRANCHIA						
Family Styelidae						
Botryllus niger (Herdman, 1886)	*	**	*	**	**	*
Botryllus giganteus Aron & Sole Cava, 1991	*	0	0	*	*	0
Botryllus tabori Rodrigues, 1962	**	**	*	**	**	*
Eusynstyela tincta (Van Name, 1902)	**	**	0	**	**	*
Symplegma brakenhielmi (Michaelsen, 1904)	**	**	*	**	**	*
PORIFERA						
Order DICTYOCERATIDA						
Family Spongiidae						
species 1 (rose)	**	0	0	**	**	*
species 2 (half-sphere, beige)	*	0	0	*	*	0
Order HAPLOSCLERIDA						
Family Haliclonidae						
Adocia carbonara Lamarck, 1814						
Adocia sp (linear, beige)	*	**	*	**	**	*
Reniera sp						
Haliclona group:species 4 (crust, beige)	**	*	0	**	**	0
species 5 (brown or dark grey)	*	0	0	*	*	0
species 6 (thick, yellow)	*	0	0	*	*	0
Family Niphatidae						
Amphimedon viridis Duchassaing & Michelotti, 1864						
Family Callyspongiidae						
Callyspongia sp						
Order POECILOSCLERIDA						
Family Mycalidae						
Mycale (Aegogropila) americana Van Soest, 1984	**	*	0	**	**	*
Mycale (Carmia) microsigmatosa Arndt, 1927	**	*	0	**	**	0
species 10 (brown or violet)						
Family Myxillidae						
Myxilla sp						
Myxilla mucronata Pulitzer-Finali, 1986						
Family Clathriidae						
Clathria sp						
aff. Fam. Desmacellidae						
species 11 (thin and smooth crust, red)	**	0	0	**	**	0
aff. Fam. Microcionidae						
species 12 (brownish red)	**	0	0	**	**	0
Family Ophlitaspongiidae						
Artemisina aff. melana						
Order HADROMERIDA						
Family Suberitidae						
species 13 (yellow, oscules and channels well defined)						
species 14 (smooth black crust)	**	0	0	**	**	*
species 15 (thin smooth orange crust)						
species 16 (very thin and smooth crust, yellow or orange)	**	*	0	**	**	*
Order CHONDROSIDA						
Family Chondrosiidae						
Chondrilla nucula Schmidt, 1870						
Classe CALCAREA						

Appendix I - Cont.

	BAL[3]	PG	MI	LI	L	S
Order SYCETIIDA						
Family Sycettidae						
? Sycon sp	*	*	0	*	*	0
POLYCHAETA						
Família Serpulidae						
Spirorbis moerchi Levinsen, 1383						
Spirorbis (Paralaeospira) calypso Zibrowius, 1969						
*Spirorbis*s spp	***	***	***	***	****	**
Hydroides brachyacantha Rioja, 1941	**	**	*	**	**	*
Pomatoceros minutos Rioja, 1942	***	**	**	***	***	**
serpulid 1	**	**	**	**	***	**
serpulid 2	**	**	*	**	**	*
Family Sabellariidae						
Phragmatopoma lapidosa Kinberg, 1867	**	**	**	**	**	*
Family Terebellidae						
Polycirrus sp	**	**	*	**	**	*
Family Eunicidae						
Eunice tubifex Crossland, 1904	**	*	0	**	**	*
Family Cirratulidae	*	*	**	*	**	0
Family Sabellidae	0	*	*	*	*	0
MOLLUSCA						
Classe Bivalvia						
Family Ostreidae						
Ostrea puelchana Orb., 1841	**	**	**	**	**	*
Family Chamidae						
Chama congregata Conrad, 1833	**	**	0	**	**	*
CNIDARIA						
Classe Hydrozoa						
Subclasse Athecatae						
Family Eudendriidae						
Eudendrium sp						
Subclasse Thecatae						
Family Halopteriidae						
Halopteris diaphana (Heller, 1868)						
Family Kirchenpaueriidae						
Kirchenpaueria halecioides (Alder, 1859)						
Family Campanulariidae						
Clytia sp						
Obelia dichotoma (Linnaeus, 1758)						

[1] ? = uncertain identification

[2] * = new report for Brazil

[3] Frequency is relative to all boulders observed during the study period: 0 = absence of the species, * = less then 1%, ** = 1 - 10%, *** = 10 - 20%, **** = more than 20% of boulders with the species. BAL = Ponta do Baleeiro, PG = Praia Grande, MI = medium intertidal zone, LI = low intertidal zone, L = large boulders, S = small boulders.

Species without frequency indicated were grouped with other species, or could not be identified in the field, or were present in the study site but not on marked boulders (see text).

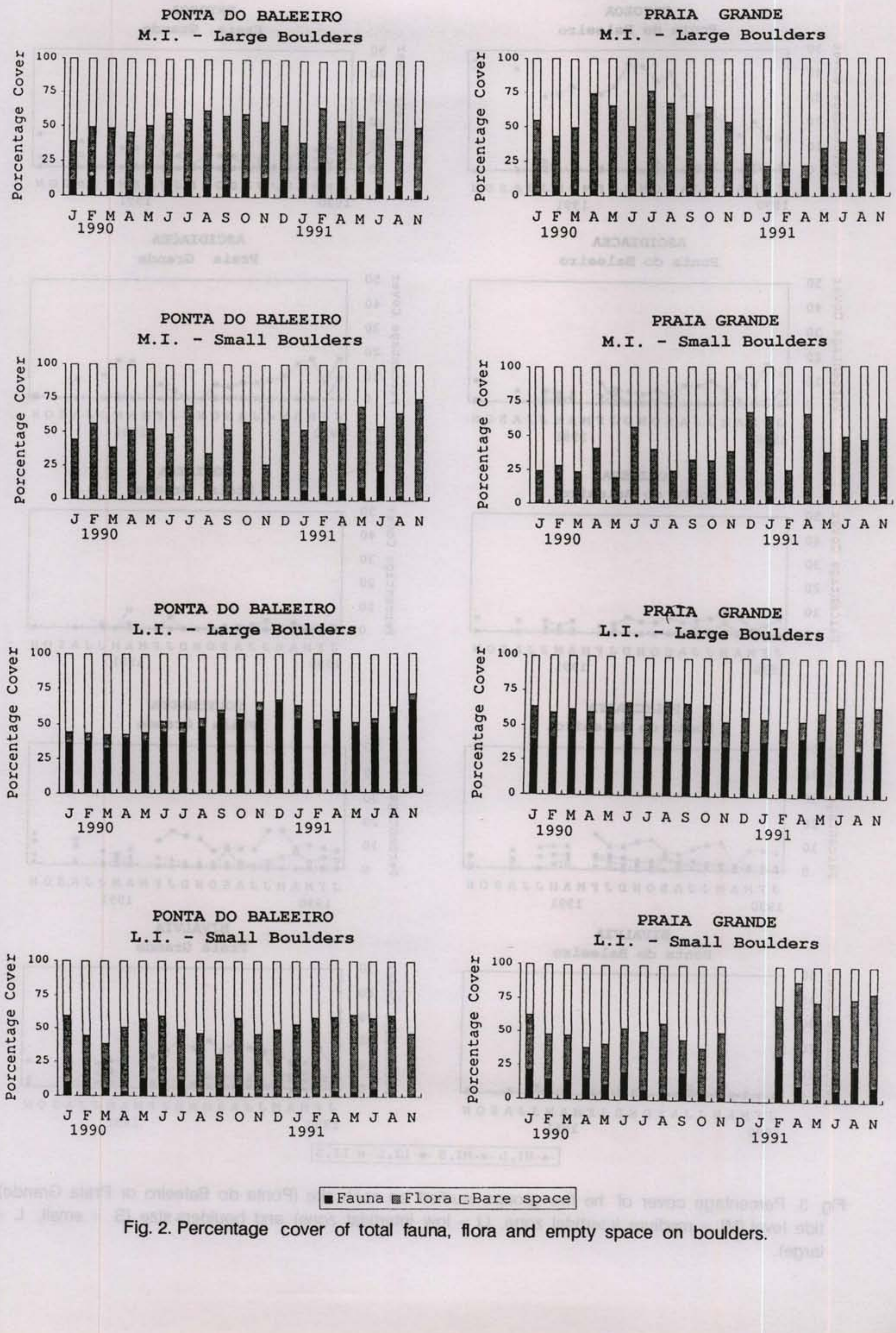

Fig. 2. Percentage cover of total fauna, flora and empty space on boulders.

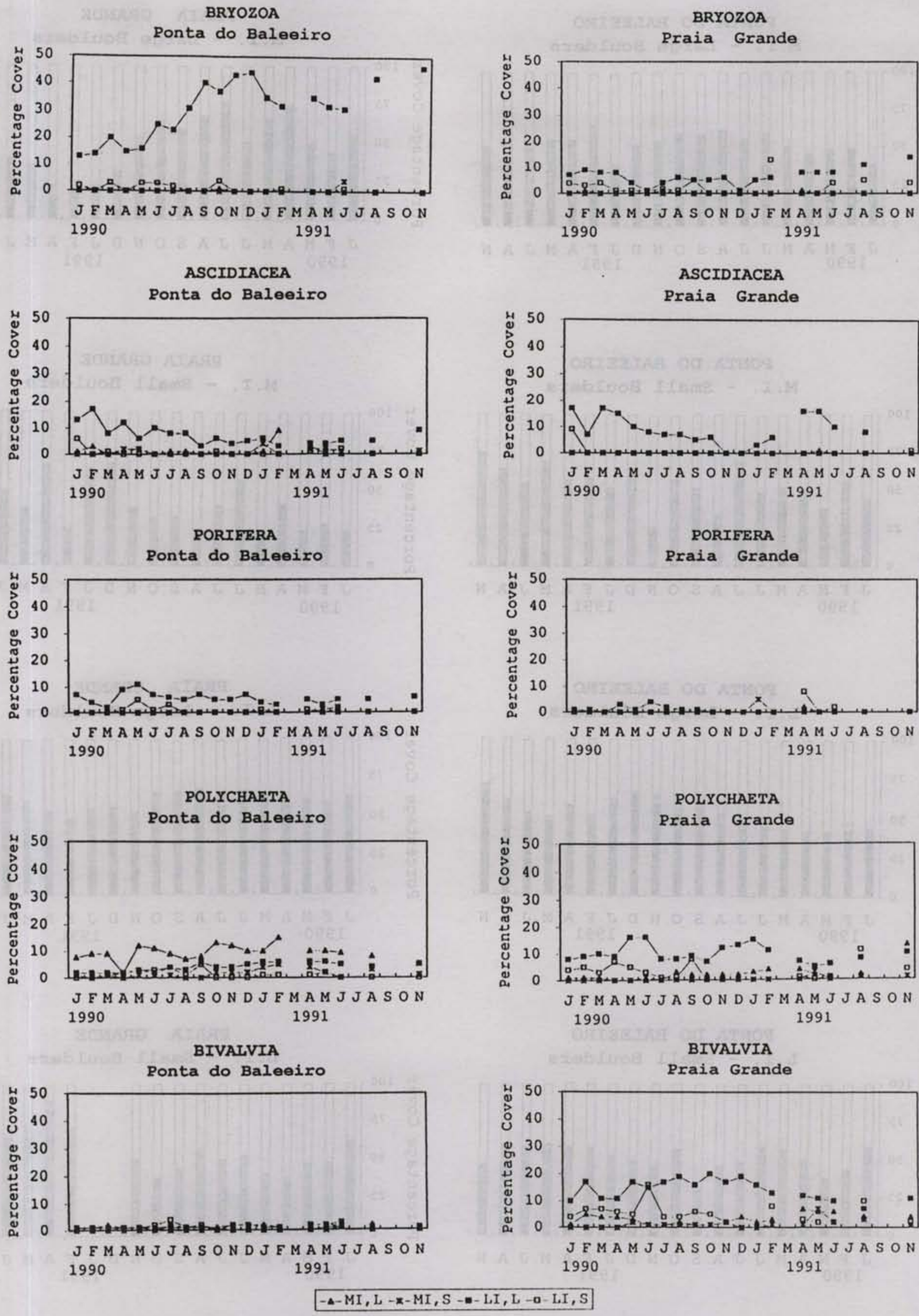

Fig. 3. Percentage cover of the five groups studied on each site (Ponta do Baleeiro or Praia Grande), tide level (MI = medium intertidal zone, LI = low intertidal zone) and boulders size (S = small, L = large).

Bryozoans had low percentage cover in the medium intertidal region in both shores (Fig. 3). In the low intertidal region, cover was higher on large boulders of Ponta do Baleeiro. The same pattern was observed for ascidians, but this group was a little more abundant at Praia Grande. Sponges had a significant cover only on large boulders in the low intertidal region at Ponta do Baleeiro. Cnidarians' percentage cover was very small in all situations, with a single peak of abundance in May, 1991. Polychaetes had the same pattern described before at Praia Grande, with high percentage cover values on large boulders in the low intertidal region. However, at Ponta do Baleeiro, higher percentage cover values occured on the large boulders from the medium intertidal region. Bivalves were rare at Ponta do Baleeiro; at Praia Grande the highest values observed were again on large boulders in the low intertidal region.

There were variations in percentage cover along the year but the pattern did not correspond to the water temperature curve of the same period neither for the total fauna nor for any single group.

Species-area curve

On both shores there was a positive relationship between species number and area, both for boulders and for sub-samples (Fig. 4). At Ponta do Baleiro, regression curves of boulders and sub- samples were not statistically different (t-Student = -0.268, p = 0.79). At Praia Grande, however, the number of species on boulders was greater than from sub-samples (t-Student = 2.053, p = 0.047).

Diversity and dominance

In general, community diversity at Ponta do Baleeiro was greater than at Praia Grande, the higher deviations

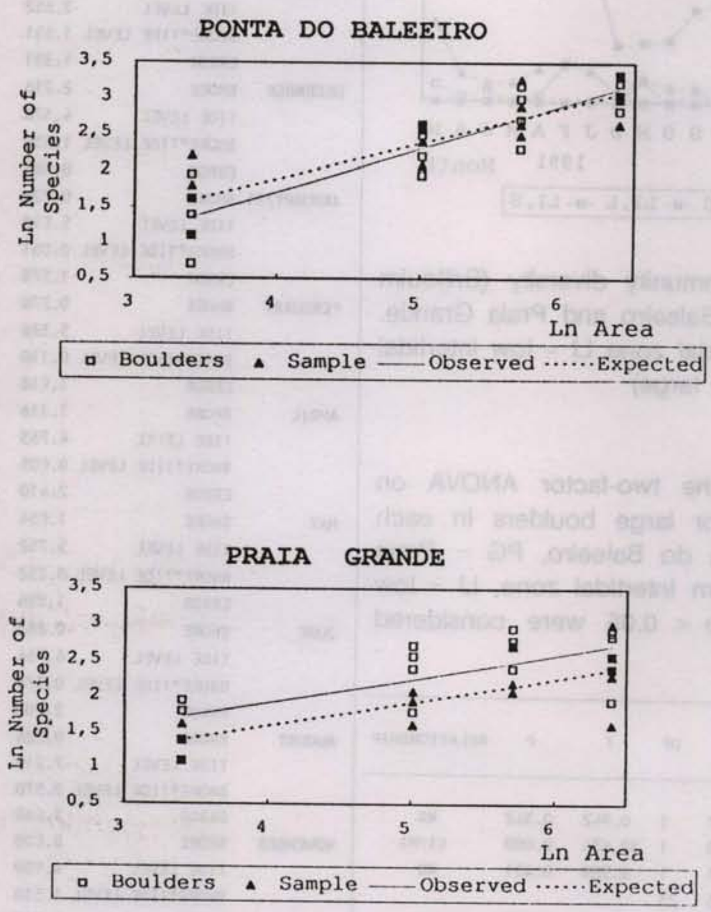

Fig. 4. Variation of the number of species on boyh boulders (observed) and sub-samples of large boulders (expected). with the undersurface area.

seen among large boulders in the low intertidal region (Fig. 5). Small boulders had low community diversity in all situations. Variation in diversity showed neither any seasonal pattern, nor correspondence to the temperature curve. Diversity on large boulders was compared through a two-factor ANOVA for each month (Tab. 2). In

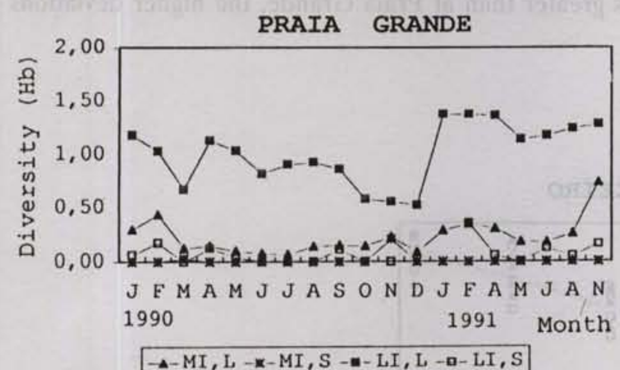

Fig. 5. Encrusting community diversity (Brillouim index) on Ponta do Baleeiro and Praia Grande. (MI = Medium intertidal zone, LI = low intertidal zone, S = small, L = large)

Table 2. Results of the two-factor ANOVA on comunity diversity for large boulders in each month. BAL = Ponta do Baleeiro, PG = Praia Grande; MI = medium intertidal zone, LI = low intertidal zone (all p < 0,05 were considered significant)

	SOURCES	SQ	DF	F	P	RELATIONSHIP
JANUARY/90	SHORE	0.177	1	0.942	0.342	NS
	TIDE LEVEL	6.138	1	32.634	0.000	LI>MI
	SHORE*TIDE LEVEL	0.111	1	0.589	0.451	NS
	ERROR	4.326	23			
FEBRUARY	SHORE	0.133	1	0.640	0.430	NS
	TIDE LEVEL	6.996	1	33.660	0.000	LI>MI
	SHORE*TIDE LEVEL	0.824	1	3.962	0.055	NS
	ERROR	6.443	31			

Table 2. Cont.

	SOURCES	SQ	DF	F	P	RELATIONSHIP
MARCH	SHORE	3.314	1	17.834	0.000	BAL>PG
	TIDE LEVEL	6.907	1	37.164	0.000	LI>MI
	SHORE*TIDE LEVEL	1.101	1	5.926	0.021	
	ERROR	5.576	30			
APRIL	SHORE	1.939	1	15.065	0.001	BAL>PG
	TIDE LEVEL	10.732	1	83.376	0.000	LI>MI
	SHORE*TIDE LEVEL	0.469	1	3.647	0.068	NS
	ERROR	3.089	24			
MAY	SHORE	2.598	1	12.539	0.001	BAL>PG
	TIDE LEVEL	8.463	1	40.847	0.000	LI>MI
	SHORE*TIDE LEVEL	0.120	1	0.581	0.452	NS
	ERROR	5.594	27			
JUNE	SHORE	2.407	1	11.952	0.002	BAL>PG
	TIDE LEVEL	6.999	1	34.746	0.000	LI>MI
	SHORE*TIDE LEVEL	0.514	1	2.551	0.123	NS
	ERROR	4.834	24			
JULY	----------					
AUGUST	----------					
SEPTEMBER	----------					
OCTOBER	SHORE	3.554	1	26.291	0.000	BAL>PG
	TIDE LEVEL	9.520	1	70.426	0.000	LI>MI
	SHORE*TIDE LEVEL	3.117	1	23.061	0.000	
	ERROR	4.461	33			
NOVEMBER	SHORE	2.111	1	19.868	0.000	BAL>PG
	TIDE LEVEL	3.652	1	34.365	0.000	LI>MI
	SHORE*TIDE LEVEL	1.551	1	14.595	0.002	
	ERROR	1.381	13			
DECEMBER	SHORE	2.216	1	23.006	0.001	BAL>PG
	TIDE LEVEL	4.176	1	43.357	0.000	LI>MI
	SHORE*TIDE LEVEL	1.555	1	16.138	0.002	
	ERROR	0.963	10			
JANUARY/91	SHORE	0.726	1	5.521	0.037	BAL>PG
	TIDE LEVEL	5.858	1	44.535	0.000	LI>MI
	SHORE*TIDE LEVEL	0.061	1	0.462	0.510	NS
	ERROR	1.578	12			
FEBRUARY	SHORE	0.276	1	1.585	0.234	NS
	TIDE LEVEL	5.326	1	30.553	0.000	LI>MI
	SHORE*TIDE LEVEL	0.110	1	0.633	0.443	NS
	ERROR	1.918	11			
APRIL	SHORE	1.116	1	5.556	0.036	BAL>PG
	TIDE LEVEL	4.763	1	23.714	0.000	LI>MI
	SHORE*TIDE LEVEL	0.005	1	0.024	0.880	NS
	ERROR	2.410	12			
MAY	SHORE	1.064	1	6.772	0.023	BAL>PG
	TIDE LEVEL	5.752	1	36.603	0.000	LI>MI
	SHORE*TIDE LEVEL	0.232	1	1.475	0.248	
	ERROR	1.886	12			
JUNE	SHORE	0.662	1	3.598	0.082	NS
	TIDE LEVEL	6.764	1	36.760	0.000	LI>MI
	SHORE*TIDE LEVEL	0.376	1	2.044	0.178	
	ERROR	2.208	12			
AUGUST	SHORE	0.324	1	2.477	0.141	NS
	TIDE LEVEL	7.219	1	55.216	0.000	LI>MI
	SHORE*TIDE LEVEL	0.570	1	4.358	0.059	
	ERROR	1.569	12			
NOVEMBER	SHORE	0.000	1	0.005	0.947	NS
	TIDE LEVEL	4.989	1	73.424	0.000	LI>MI
	SHORE*TIDE LEVEL	1.530	1	22.521	0.001	
	ERROR	0.747	11			

ten months, Ponta do Baleeiro was more diverse than Praia Grande, and in all months, the low intertidal region was more diverse than the medium intertidal region.

Community diversity on large boulders increased with percentage cover of the fauna, especially in the low intertidal region, for both shores (Fig. 6).

Besides the low percentage cover, small boulders were also rarely dominated by one species (Table 3). Large boulders in the medium intertidal region were usually dominated by polychaetes and bivalves (dead shells mostly) in both shores. In the low intertidal region, these boulders were dominated by bryozoans at Ponta do Baleeiro and bryozoans and bivalves (dead shells) at Praia Grande. Less frequently, ascidians, sponges and polychaetes also dominated boulders in the low intertidal region.

Discussion

The species composition of the encrusting community was similar in both shores, with differences in abundance for the various groups. These differences, however, were not greater than the variation between intertidal region levels or boulder sizes, indicating that these last factors are more influential on the species distribution.

Among the features studied, no differences were detected in porosity of the boulders nor in the abrasion capacity of the sand between the shores. Hydrodynamics and environmental heterogeneity were higher at Praia Grande.

The kind of environmental heterogeneity evaluated here was not responsible for creating diversity. Small boulders, the medium intertidal region and Praia Grande

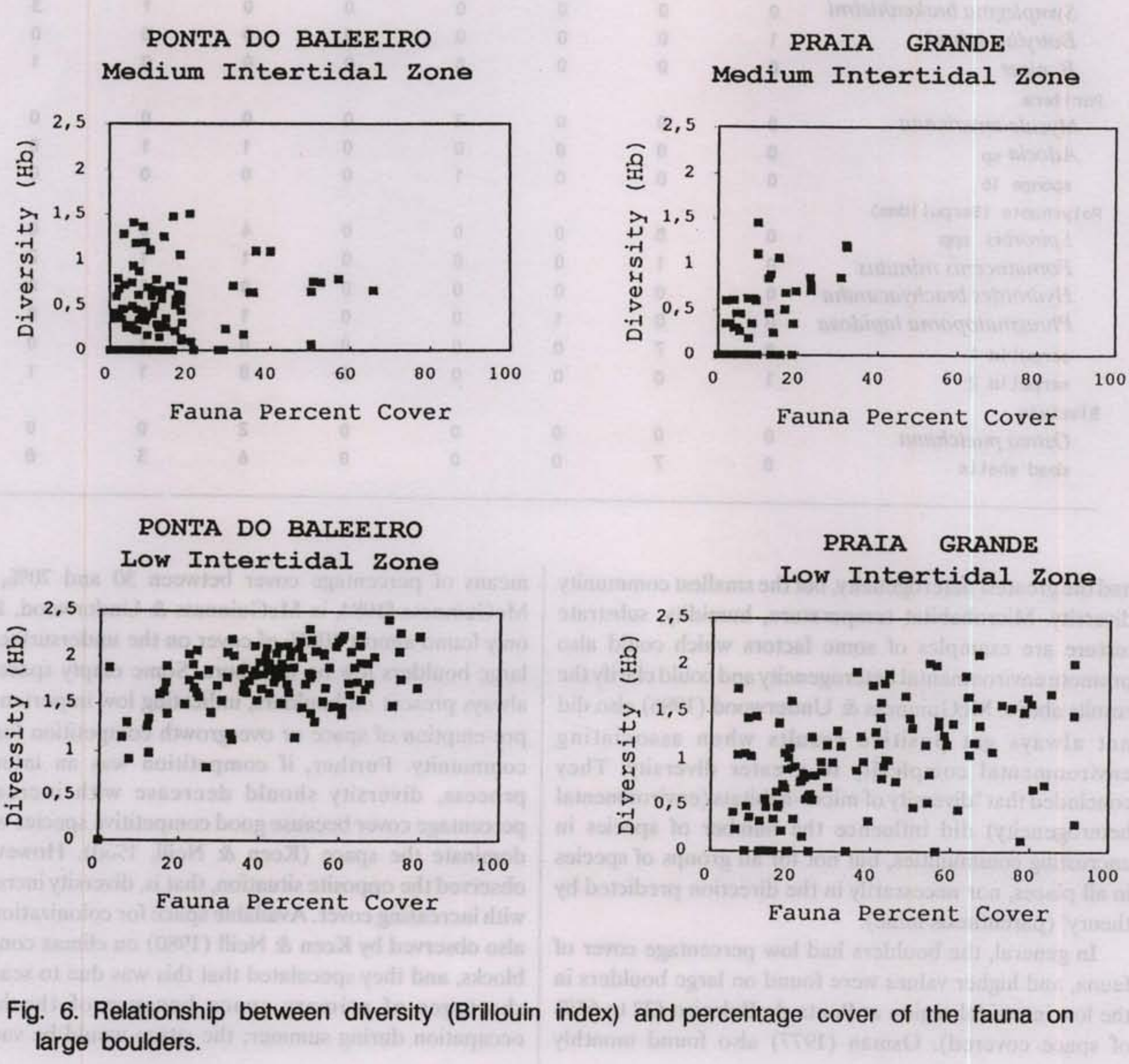

Fig. 6. Relationship between diversity (Brillouin index) and percentage cover of the fauna on large boulders.

Table 3. Dominant species (see text for definition). Cells indicate the number of months (maximum of 8) each species appeared as dominant on at least one boulders

	PONTA DO BALEEIRO				PRAIA GRANDE			
	Medium Intertidal		Low Intertidal		Medium Intertidal		Low Intertidal	
	Small Boulders	Large Boulders	Small Boulders	Large Boulders	Small Boulders	Large Boulders	Small Boulders	Large Boulders
Bryozoa								
Steginoporella buskii	0	0	0	2	0	0	0	2
Labioporella sinuosa	0	0	0	6	0	0	1	0
Net Bryozoans	0	0	0	0	0	0	0	5
Ascidiacea								
Didemnum psammathodes	1	2	1	2	0	0	1	0
D. perlucidum	0	0	0	1	0	0	1	1
Polysyncraton amethysteum	0	0	0	1	0	0	0	0
Trididemnum orbiculatum	0	0	0	1	0	0	0	1
Symplegma brakenhielmi	0	0	0	0	0	0	1	3
Botryllus tabori	1	0	0	0	0	0	0	0
B. niger	0	0	0	0	0	0	0	1
Porifera								
Mycale americana	0	0	0	2	0	0	0	0
Adocia sp	0	0	0	0	0	1	1	0
sponge 16	0	0	0	1	0	0	0	0
Polychaete (Serpulidae)								
Spirorbis spp	0	8	0	0	0	4	0	0
Pomatocerus minutus	0	1	0	0	0	1	1	2
Hydroides brachyacantha	0	0	0	0	0	0	1	0
Phragmatopoma lapidosa	0	0	1	0	0	1	0	0
serpulid 1	0	7	0	0	0	0	1	0
serpulid 2	1	0	0	0	1	0	1	1
Bivalvia								
Ostrea puelchana	0	0	0	0	0	2	0	0
dead shells	0	7	0	0	0	6	3	8

had the greatest heterogeneity, but the smallest community diversity. Microhabitat temperature, humidity, substrate texture are examples of some factors which could also promote environmental heterogeneity and could clarify the results above. McGuinness & Underwood (1986) also did not always get positive results when associating environmental complexity to greater diversity. They concluded that "diversity of micro-habitats (environmental heterogeneity) did influence the number of species in encrusting communities, but not for all groups of species in all places, nor necessarily in the direction predicted by theory" (parenthesis mine).

In general, the boulders had low percentage cover of fauna, and higher values were found on large boulders in the low intertidal region at Ponta do Baleeiro (32 to 65% of space covered). Osman (1977) also found monthly means of percentage cover between 30 and 70%, and McGuinness (1984, in McGuinness & Underwood, 1986) only found almost 100% of cover on the undersurfaces of large boulders low on the shore. Some empty space was always present on boulders, indicating low importance of pre-emption of space or overgrowth competition for this community. Further, if competition was an intensive process, diversity should decrease with increasing percentage cover because good competitive species would dominate the space (Keen & Neill, 1980). However, I observed the opposite situation, that is, diversity increased with increasing cover. Available space for colonization was also observed by Keen & Neill (1980) on climax concrete blocks, and they speculated that this was due to seasonal shortages of primary space because of the heavy occupation during summer; the space would be vacated during the other seasons. It seems that it is not the case at São Sebastião, where space was available on the undersurfaces of boulders all year long.

The size of the boulder had a great influence on the distribution of species. Fouling community studies showed that the greater the size of the substrate, the greater the number of accumulated species (Schoener, 1974; Jackson, 1977; Osman, 1977, 1982). McGuinness (1984) discuss that 4 hypothesis should be considered to explain the increment of species number with area. They are: Passive Sampling or Random Placement Hypothesis (Connor & McCoy, 1979; Coleman *et al*., 1982), the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1963, 1967), Habitat Diversity Hypothesis (Williams, 1964, in McGuinness, 1984), and the Intermediate Disturbance Hypothesis (Connell, 1978).

For the shores studied, there were two different patterns for the relation species number/boulder size. At Ponta do Baleeiro the mean number of observed species on boulders was similar to the expected number, so that the null hypothesis, that the number of species represent a sample of greater areas taken by chance, cannot be rejected. We should then conclude that no physical or biological processes is acting to create the pattern.

On the other hand, at Praia Grande the number of species observed on boulders was greater than the number expected, indicating the interference of other processes. According to McGuinness (1984), an observed curve over the expected curve indicates greater number of species on boulders of intermediate sizes, what is consistent with the Intermediate Disturbance Hypothesis (Connell, 1978). The comparison of hydrodynamics showed that Praia Grande is more exposed to water movement and, therefore, to disturbance of the boulders. Likewise, data from disturbance measurements corroborate that the boulders at Praia Grande are more subjected to displacement and overturning (to be reported elsewhere).

Boulder size can also influence dominance. Osman (1977) states that decreased substrate size increases the probability of short-term seasonal dominance of species with a seasonal peak of high growth rate, or of colonial species able to occupy a major proportion of the available space on small substrates at a much smaller size. However, Kay & Keough (1981) and Keough (1984) observed a negative correlation between colonization and competition capabilities for the great taxonomic groups, in South Australia. They found that small substrates were easily found by better colonizers (bryozoans and serpulids), which are incapable of dominating space through competition. On the other hand, large substrates had increased probability of being colonized by a good competitor species (ascidians or sponges) that eventually would dominate space.

At the shores studied, large boulders were more frequently dominated, usually by bryozoans, serpulids and bivalves, groups that are bad competitors when faced with ascidians or sponges (Kay & Keough, 1981; Russ, 1982). Keough (1984) also observed the dominance of bryozoans on boulders up to 180 cm^2, equivalent size to the large boulders at São Sebastiao. According to him, ascidians and sponges dominated only substrata over 625 cm^2. The apparent incongruence with results reported by Osman (1977) is probably because they were obtained on fouling plates that were not subjected to disturbance as were the small boulders, so that succession could proceed.

The intertidal region level was another important cause of the distribution of the fauna. The emersion and submersion of the habitat by the tides is a predictable kind of disturbance to which organisms can adapt themselves (Sousa, 1984). At São Sebastiao Channel, the medium intertidal region is emerged twice a day, usually during daytime, while the low intertidal region is not always emerged twice a day, and the lower tides occur usually at dawn or dusk times. On both shores, the most abundant organisms in the medium intertidal region had some kind of protection against desiccation such as the calcareous tubes of serpulids and the shells of bivalves. In the low intertidal region, bryozoans were also very abundant, and are relatively well protected against desiccation by the chitinous or calcareous test. The medium intertidal region had more sand than the low intertidal region on both shores, so that the abrasion of sand could have also disfavoured species without protection (ascidians and sponges).

Conclusions

Concluding, both the boulders size and the tide level influenced the distribution of the encrusting community on their undersurfaces. At Ponta do Baleeiro, species richness increased with boulders size because of random sampling, while the Intermediate Disturbance Hypothesis explains the species-area relationship at Praia Grande. Boulders in the medium intertidal region had very low values of diversity and fauna cover, which comprised mainly serpulids and bivalves. On the other hand, boulders in the low intertidal region had high values of diversity and fauna cover, mainly of bryozoans, but ascidians and sponges were also present in this level.

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