The macrofauna associated with the bryozoan *Schizoporella errata* (Walters) in southeastern Brazil*

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SUMMARY: The invertebrate fauna associated with colonies of the bryozoan *Schizoporella errata* was studied at two sites differing in hydrodynamism in southeastern Brazil. Patterns of species distribution, abundance, and diversity were similar at both sites. Polychaetes dominated the assemblages, both in number of individuals and species, with 70 species distributed in 20 families. Decapod crustaceans were also abundant, mainly anomuran crabs and caridean shrimps. Cluster analysis separated the samples from each site, and further analysis indicated that an interaction between water movement and trophic structure could explain these differences. At the site with low water movement, more muddy sediments were found inside the colonies, and a greater proportion of deposit-feeders was found. At the other site, higher hydrodynamism resulted in less sediments within the colonies, and favoured the occurrence of more filter-feeders. The trophic structure of faunal assemblages can help understand the structure of assemblages associated with biogenic substrata, as already demonstrated for benthic communities.

Key words: *Schizoporella*, bryozoan, faunal association, macrofauna, trophic groups, Brazil.

INTRODUCTION

The presence of biogenic substrata in benthic systems can contribute to local species diversity, increasing the range of microhabitats and resources that can be used by the organisms, through additional habitat heterogeneity and structural complexity (Sebens, 1991; Thompson *et al*., 1996). The assemblages associated with these substrata generally have high species diversity, and adjust to common species abundance models characterized by many rare species and few dominant ones, as a result of recruitment patterns and interspecific interactions (Hughes, 1984). Increasing introduction of exotic species can also influence local community dynamics, through

additional habitat alteration (Crooks and Khim, 1999). The added complexity provided both by rocky or biogenic substrata can influence benthic communities by reducing abiotic variation, or providing more refuges to escape predation and competition, and more suitable sites to forage (reviewed in Sebens, 1991). Disturbance intensity (e.g., wave action and desiccation) can be reduced within the living 'hosts', but may still influence assemblage structure (Safriel and Ben-Eliahu, 1991).

The effect of water movement can influence the structure of assemblages associated with biogenic substrata due to differential sedimentation rates, as the fraction of silt and finer sands in sediments trapped within or nearby the substrate can determine the occurrence of deposit-feeding organisms (Gallagher *et al*., 1983; Dittman, 1990; Porras *et al*.,

1996). The interaction between water movement and the distribution of deposit- and suspension-feeding organisms is recognized in macrobenthic communities (Sanders, 1958; Snelgrove and Butman, 1994). Deposit-feeders generally dominate in calm waters with muddy bottoms, while suspension-feeders dominate in sandy bottoms subject to faster currents (Sanders, 1958; Wildish and Kristmanson, 1979; Roth and Wilson, 1998). However, the influence of water movement on the trophic structure of assemblages associated with either biogenic or artificial substrata has received less attention (e.g., Dittman, 1990; Whorff et al., 1995).

Colonial organisms such as corals, bryozoans, and some polychaetes and molluscs can develop rigid three-dimensional colonies, increasing the available secondary substrata in sublittoral systems (Gore et al., 1978; Bradstock and Gordon, 1983; Lewis and Snelgrove, 1990; Safriel and Ben-Eliahu, 1991; Nalesso et al., 1995; Cocito et al., 2000). These colonies are used by boring or dwelling species such as polychaetes, molluscs, crustaceans, and echinoderms, which make small galleries or use the available internal space both to hide from predators and to forage on debris and small invertebrates (McCloskey, 1970; Gordon, 1972; Safriel and Ben-Eliahu, 1991; Porras et al., 1996). The invertebrate assemblages in these systems have importance in sublittoral food webs, being food sources for predators, consuming macro- and microlgae, and recycling detritus and organic material (Klumpp et al. 1988; Christian and Luczkovich, 1999).

The role of bryozoan colonies as habitats was described mainly in temperate systems (Stebbing, 1971; Gordon, 1972; Bradstock and Gordon, 1983; Maluquer, 1985; Conradi and Cervera, 1995; Ferdeghini and Cocito, 1999; Cocito et al., 2000), with fewer work on tropical or subtropical regions (Lindberg and Stanton, 1988; Mantelatto and Souza-Carey, 1998). The bryozoan *Schizoporella errata* (Walters) generally forms massive colonies with variously shaped branches, determined from interactions with other organisms and hydrodynamic conditions (Cocito et al., 2000; Ferdeghini et al., 2000). Colonies may dominate the sublittoral, covering 5-100% of the substratum in Mediterranean sites, depending on water movement (Cocito et al., 2000). Other *Schizoporella* species can also construct large buildups and contribute effectively as secondary substratum for local fauna (Ferdeghini et al., 2000). In southeastern Brazil, colonies of *Schizoporella errata* may reach 25 cm in height, growing in shallow waters (0-10 m) attached to rocks or pier columns. The presence of *Schizoporella* colonies and other biogenic substrates can enhance habitat heterogeneity and influence patterns of species diversity, supplying a diverse range of secondary substrata that can be used by the cryptic fauna (Nalesso et al., 1995; Duarte and Nalesso, 1996). However, these patterns are being lost due to a fast degradation of the habitats (Nipper, 1990). The objective of this study was to examine the structure of the macrofaunal assemblage associated with colonies of *Schizoporella errata* at two sites differing in water movement in SE Brazil, comparing the distribution of species abundances and trophic groups at both sites.

MATERIALS AND METHODS

Sampling was carried out in four shores from two major sites, Codó and Lamberto within Flamengo Bay at Ubatuba district, Araçá and Segredo in São Sebastião's Channel, São Sebastião district (Fig. 1), during 1974-1976.

Ubatuba sites are sheltered from wave action, with predominantly muddy sand bottoms (Mahiques et al., 1998). *Schizoporella* colonies were fixed to rocks at about 1 m below MLWS, together with other sessile organisms such as the macroalgae *Acanthophora spicifera*, *Laurencia papillosa* and *Sargassum filipendula*, the sponges *Zygomycale parishii*, *Tedania ignis*, *Haliclona erina*, *Halichondria magniconulosa*, and colonies of cnidarians and tunicates. Among these shores, *S. errata* colonies had partially fused tubular
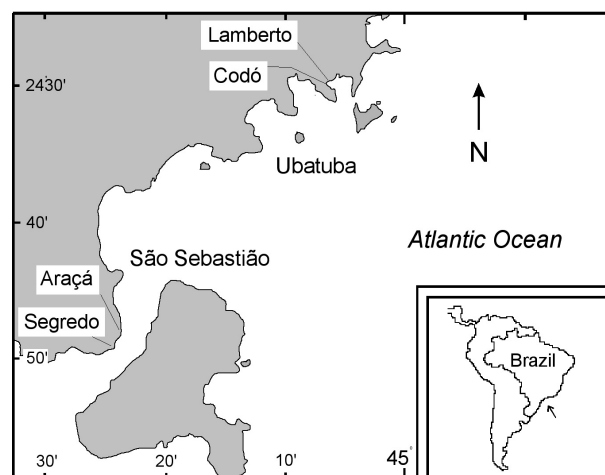

Fig. 1. – Location of São Paulo State in Brazil (detail), and the sites studied along its northern coast. Codó and Lamberto are in Ubatuba district, Araçá and Segredo in São Sebastião (see text).

branches with free extremities that extended from the base. The extremities were colonized by macroalgae such as *Laurencia*, *Acanthophora* and *Dictyota*. The colony base and tubes were filled with sediments, basically composed by fine sand and silt. Five samples were collected in Codó and 13 samples in Lamberto (Fig. 1).

In São Sebastião, the shores are subject to greater wave action. Although Araçá is a sheltered beach, it is more exposed in its southern area, where two colonies of *S. errata* were collected from small boulders located 0.3 m below the water mark. Segredo presents coarse sand (Amaral *et al.*, 1990), and is more exposed to wave action; six colonies were sampled at a depth of about 5 m. Other sessile organisms in the area included the algae *Galaxaura stupocaulon*, *Caulerpa racemosa*, *Sargassum* spp. and *Dictyopteris* spp., gorgonians, corals and other colonial anthozoans. In these sites, *Schizoporella* colonies were globular, with highly fused branches and extremely compact growth forms. The upper parts of the colonies did not present free extremities, but holes irregularly distributed on the colony surface. They also contained less mud than the colonies from Ubatuba and more cavities within the colony.

The bryozoan was initially identified as *Schizoporella unicornis* following Marcus (1937). However, according to Hayward and Ryland (1979), *S. unicornis* sensu Marcus (1937) is in fact *S. errata*, a widespread species in warm-temperate to tropical waters frequently misidentified as *S. unicornis*. *Schizoporella errata* occurs mainly in calm waters, and is a strong competitor in fouling communities (Sutherland, 1978; Maluquer, 1985). Growth forms vary with hydrodynamism: in exposed sites, colonies form a densely packed mass with no branching, while in calmer waters colonies are erect, highly branched and have thicker bases (Cocito *et al.*, 2000; Ferdeghini *et al.*, 2000). Branching may be a result of overgrowth of sessile organisms by *S. errata*, as those with hard skeletons stay enclosed within the bryozoan layers, while soft-bodied organisms leave no remnants but a hollow cavity (Cocito *et al.*, 2000).

Samples of *S. errata* were manually collected by enclosing each colony in a plastic bag and detaching it from the substrate. In the laboratory, colonies were transferred to receptacles containing seawater, where they were broken with a hammer. All the macrofauna was carefully collected and the organisms fixed using standard techniques. Dry weight of each colony was measured after drying the frag-

ments first in the sun and later in oven for 24 hours at 50°C.

The colonies from different shores located in Ubatuba and São Sebastião were pooled to compare the two regions, as the few samples collected on each shore prevented a more detailed analysis. To verify if the number of samples was adequate, we fitted species recruitment curves to the model $y = a + b\ln x$ (where y = cumulative number of species, x = cumulative dry weight of the colonies, a and b are constants) (Krebs, 1989). Patterns of species abundance were analysed by adjusting a log series model, which is appropriate when there are many rare species (Magurran, 1988). We compared the community structure among and within regions with cluster analysis using UPGMA (unweighted pair group) on the Bray-Curtis dissimilarity matrix, that was calculated from square-root transformed densities (i.e., number of individuals/g of colony dry weight) (Clarke, 1993).

Trophic groups were determined following McCloskey (1970), Gore *et al.* (1978), Fauchauld and Jumars (1979), Cruz-Abrego *et al.* (1994), Conradi and Cervera (1995) and Sheridan (1997). Five groups were considered: carnivores, herbivores, omnivores, deposit- and suspension-feeders. Most suspension-feeders can also ingest deposited matter in some situations (Snelgrove and Butman, 1994), and actual diets of animals in any category can include more than one trophic level (Christian and Luczkovich, 1999). Although the knowledge of diets in the field is still poor for several groups, broad patterns of assemblage structure can be explained using this approach (e.g., Wildish and Kristmanson, 1979; Roth and Wilson, 1998). We compared the trophic structure between Ubatuba and São Sebastião with a contingency table, using a *G*-test on total abundances.

RESULTS

Colonies of *Schizoporella errata* sheltered a rich macrofauna in both sites: total number of species collected was 88 in São Sebastião and 115 in Ubatuba. According to the species recruitment curves, the number of samples was adequate for a description of the fauna associated with *S. errata* (Ubatuba: $y = -70.4 + 21.8 \ln x$, $r^2 = 0.99$, $p < 0.0001$; São Sebastião: $y = -87.6 + 23.1 \ln x$, $r^2 = 0.99$, $p < 0.0001$). Thus, if twice the dry weight of colonies had been collected, about 15% more species would have been recorded.
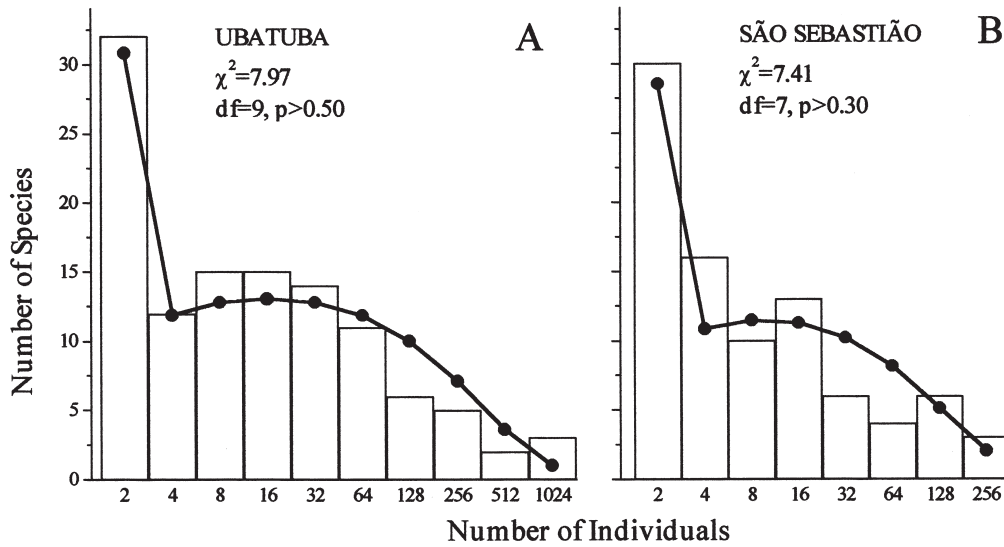
Fig. 2. – Species distribution of the fauna associated with *Schizoporella* at (A) Ubatuba and (B) São Sebastião: observed (bars) and expected (lines) abundance of species following a log series distribution.

Table 1. – Relative contribution of the main taxa to the fauna associated with colonies of *Schizoporella errata*.

	Number of species (%)		Number of individuals (%)	
	Ubatuba	São Sebastião	Ubatuba	São Sebastião
Polychaeta	53.9	61.4	59.5	61.6
Crustacea	23.5	14.8	18.5	21.9
Mollusca	16.5	18.2	4.2	3.4
Echinodermata	3.5	4.5	16.7	13.0
Other	2.6	1.1	1.1	0.1

Although colonies in both sites were morphologically distinct, mean colony dry weight was similar in Ubatuba (244.0g ± 39.1; mean ± SE) and São Sebastião (245.1g ± 56.9), and sheltered a similar number of individuals (Ubatuba: 299.7 ± 27.2, São Sebastião: 228.0 ± 48.3). Diversity patterns of the associated fauna were also similar, when comparing the mean number of species (Ubatuba: 38.9 ± 1.5, São Sebastião: 35.4 ± 4.5), Shannon's diversity index (Ubatuba: 2.8 ± 0.1, São Sebastião: 2.7 ± 0.2) and rarefacted species richness (Ubatuba: 78.1, São Sebastião: 75.7; calculated for 1,000 individuals).

Relatively few species dominated the associated fauna, with 90% of all individuals corresponding to 27.8% of the species in Ubatuba and 31.1% in São Sebastião. Patterns of species abundance in both sites did not differ from those predicted by the log series model (Fig. 2), with many rare species occurring in the samples.

Polychaetes dominated the associated fauna, both in numbers of species and individuals (Table 1). In São Sebastião there was a larger proportion of polychaete species (61.4%) than in Ubatuba

(53.9%), where more crustaceans were found; molluscs occurred in similar proportions at both sites (Table 1). The five most abundant species in Ubatuba contributed with 52.0% of all individuals, including the ophiuroid *Ophiactis savignyi* (12.4%), the polychaetes *Ophiodromus pugettensis* (10.7%), *Cirriformia filigera* (10.4%) and *Lumbrineris albifrons* (9.0%), and the isopod *Excorallana quadricornis* (9.5%) (Table 2). In São Sebastião, the five most abundant species were the polychaetes *Syllis gracilis* (12.9%), *L. albifrons* (11.8%), and *C. filigera* (5.7%), the anomuran decapod *Pachycheles maginanus* (11.8%), and the ophiuroid *O. savignyi* (6.5%); together, they represented 48.7% of all individuals.

There was a strong variation of the assemblage structure within regions, as reflected in the cluster analysis (Fig. 3). However, differences among shores within the same area were smaller than differences between areas, resulting in a separation of samples from Ubatuba and São Sebastião in two large groups. The detected differences were mainly due to the relative abundance of some species in Ubatuba and São Sebastião. For example, the polychaetes *C. filigera*, *O. pugettensis*, *Dorvillea sociabilis* and the ophiuroids *Ophiactis savignyi* and O. *lymani* were much more abundant in Ubatuba than in São Sebastião, whereas the anomuran *P. maginanus* and the polychaete *S. gracilis* followed the reverse pattern (Table 2). Abundant species such as the polychaetes *L. albifrons* and *Eunice cariboea* occurred with different densities in the two areas, contributing to a greater dissimilarity.

TABLE 2. – Species collected in 26 colonies of *Schizoporella errata*, including the number of colonies where each species occurred (NS), and its abundance in 18 colonies from Ubatuba (U) and 8 colonies from São Sebastião (SS).

Family	Species	NS	U	SS
SIPUNCULA				
Golfingiidae	*Golfingia confusa* (Sluiter)	15	55	2
	Themiste alutacea (Grube)	1	1	0
ECHIURA	*Thalassema* sp.	1	1	0
ECHINODERMATA – Ophiuroidea				
Amphiuridae	*Axiognathus squamatus* (Delle Chiaje)	2	5	2
	Ophiactis lymani Ljungman	20	185	92
	Ophiactis savignyi (Müller and Trschel)	24	670	118
	Ophiothrix angulata (Say)	18	37	22
MOLLUSCA - Gastropoda				
Calyptraeidae	*Crepidula aculeata* (Gmelin)	9	33	1
	Crepidula plana Say	2	0	2
Cerithiopsidae	*Seila adamsi* (Lea)	1	0	3
Columbellidae	*Costoanachis sertulariarum* Orbigny	1	0	1
	Costoanachis sparsa (Reeve)	10	32	1
	Mitrella argus (Orbigny)	4	3	1
	Mitrella lunata (Say)	5	9	0
Fissurellidae	*Fissurella* sp.	1	1	0
Fossaridae	*Fossarus* sp.	1	1	0
Nassariidae	*Nassarius* sp.	1	0	1
Phasianellidae	*Tricolia affinis* (Adams)	2	4	0
Thaididae	*Morula nodulosa* (Adams)	3	0	3
Trochidae	*Solariella* sp.	4	7	7
MOLLUSCA - Bivalvia				
Anomiidae	*Anomia ephippium* L.	4	5	0
Arcidae	*Arca imbricata* Brugiuère	1	0	1
Gastrochaenidae	*Gastrochaena hians* (Gmelin)	2	2	0
Hiatellidae	*Hiatella arctica* (L.)	18	23	30
Lyonsiidae	*Lyonsia (Entodesma) beana* (Orbigny)	12	104	9
Mytilidae	*Lithophaga bisulcata* (Orbigny)	4	1	5
	Modiolus carvalhoi (Klappenbach)	7	7	13
	Musculus lateralis (Say)	3	3	0
Petricolidae	*Ruppelaria (Petricola) typica* (Jonas)	7	5	4
Pholadidae	*Martesia cuneiformis* (Say)	2	1	2
Veneridae	*Chione paphia* (L.)	1	1	0
	Gouldia cerina (Adams)	1	1	0
ARTHROPODA - Pycnogonida				
	Achelia sawayai (Marcus)	5	5	0
	Ammothella sp.	5	9	0
ARTHROPODA - Isopoda				
Excorallanidae	*Excorallana quadricornis* Hansen	15	510	1
ARTHROPODA - Decapoda: Caridea				
Alphaeidae	*Alpheus formosus* Gibbes	2	3	0
	Alpheus thomasi Hendrix and Gore	2	3	0
	Alpheus sp.	1	1	0
	Synalpheus apiocerus Coutière	18	69	4
	Synalpheus brevicarpus (Herrick)	17	15	28
	Synalpheus fritzmuelleri Coutière	19	23	78
Hyppolytidae	*Hippolite curacaoensis* Schmitt	1	2	0
	Lysmata sp.	1	1	0
	Thor manningi Chace	7	20	10
Palaemonidae	*Typton gnathophylloides* Holthuis	2	4	0
ARTHROPODA - Decapoda: Brachyura				
Xanthidae	*Hexapanopeus paulensis* Rathbun	1	1	0
	Hexapanopeus schmitti Rathbun	16	106	0
	Menippe nodifrons Stimpson	8	17	0
	Pilumnus dasypodus Kingsley	12	7	18
	Pilumnus floridanus Stimpson	5	9	0
Majidae	*Epialtus brasiliensis* Dana	2	1	1
	Mithraculus forceps (Milne Edwards)	7	4	9
	Microphrys bicornutus (Latreille)	4	6	0
	Podochela riisei Stimpson	3	1	2
Grapsidae	*Pachygrapsus transversus* Gibbes	3	7	0
ARTHROPODA - Decapoda: Anomura				
Porcellanidae	*Megalobrachium soriatum* Haig	10	15	10
	Pachycheles maginanus Milne Edwards	22	71	215
	Petrolisthes galatinus Bosc	11	29	5
	Porcellanidae sp.	16	56	13

TABLE 2. (Cont.)– Species collected in 26 colonies of *Schizoporella errata*, including the number of colonies where each species occurred (NS), and its abundance in 18 colonies from Ubatuba (U) and 8 colonies from São Sebastião (SS).

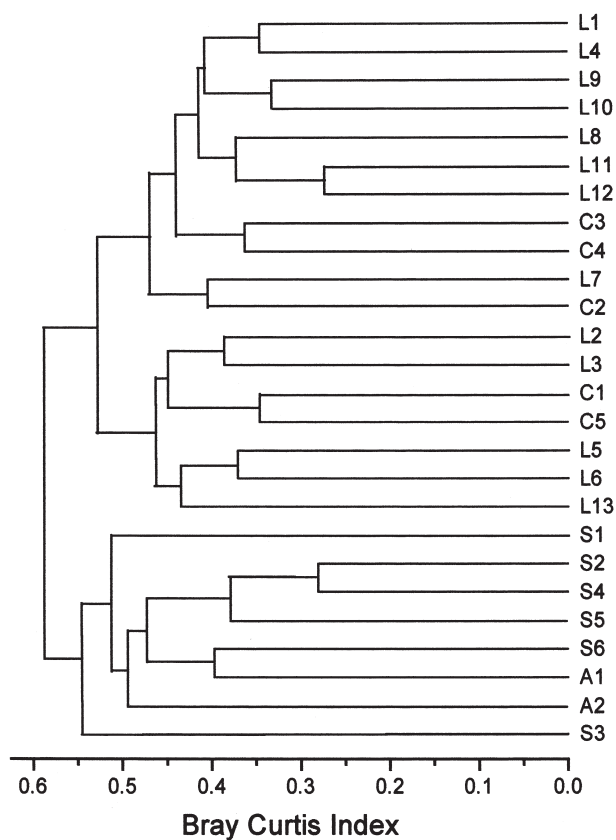| Family	Species	NS	U	SS
ANNELIDA - Polychaeta				
Amphinomidae	*Amphinome* sp	1	0	1
Capitellidae	*Notomastus* sp.	1	0	1
	Capitellidae sp. A	1	1	0
	Capitellidae sp. B	1	0	1
	Capitellidae sp. C	1	2	0
	Capitellidae sp. D	1	1	0
Chrysopetallidae	*Bhawania brunnea* Morgado and Amaral	5	6	5
	Chrysopetalum occidentale Johnson	21	37	33
Cirratulidae	*Dodecaceria concharum* Oersted	6	12	2
	Cirriformia filigera (Delle Chiaje)	23	559	104
Dorvilleidae	*Dorvillea rudolphi* (Delle Chiaje)	6	9	0
	Dorvillea sociabilis (Webster)	24	189	17
Eunicidae	*Eunice binominata* Quatrefages	12	20	10
	Eunice cariboea Grube	21	176	52
	Eunice filamentosa Grube	2	4	0
	Eunice rubra Grube	17	55	6
	Eunice cf. *tenuis* Treadwell	7	41	1
	Lysidice ninetta Audouin and Milne Edwards	5	7	3
	Marphysa angelensis Fauchauld	1	0	1
	Marphysa sanguinea (Montagu)	1	0	2
	Nematonereis hebes Verrill	20	12	4
	Palola esbelta Morgado and Amaral	3	2	4
Hesionidae	*Hesione picta* Müller	1	1	0
	Ophiodromus pugettensis (Johnston)	26	578	78
Lumbrineridae	*Lumbrineris albifrons* Crossland	26	487	216
	Oenone diphyllidia Schmarda	13	19	6
Nereidae	*Neanthes succinea* (Frey and Leuckart)	17	63	23
	Nereis riisei Grube	21	84	12
	Pseudonereis sp.	10	20	13
Ophellidae	*Armandia maculata* (Webster)	8	11	1
Paraonidae	*Paradoneis* cf. *lyra* (Southern)	17	60	3
Phyllodocidae	*Eulalia myriacyclum* (Schmarda)	5	13	0
	Eulalia viridis (L.)	13	16	12
	Eumida sanguinea (Oersted)	6	7	1
Polynoidae	*Halosydna glabra* Hartman	11	17	1
	Harmothoë macginitiei Pettibone	13	22	2
	Harmothoë sp.	1	1	0
	Lepidonotus caeruleus Kinberg	26	204	42
	Scalisetosus gracilis Morgado and Amaral	9	11	3
Sabellidae	*Branchiomma nigromaculata* (Baird)	3	8	0
	Hypsicomus elegans (Webster)	18	38	66
	Potamilla reniformis (Leuckart)	2	0	7
	Sabellidae sp.	2	1	1
Sabellariidae	*Phragmatopoma* sp.	1	1	0
	Sabellaria floridensis Hartman	6	5	9
Serpulidae	*Hydroides brachyacantha* Rioja	8	9	3
	Hydroides dirampha Mörch	3	2	8
	Pomatocerus minutus Rioja	2	2	1
Sigalionidae	Sigalionidae sp. A	1	1	0
Spionidae	*Boccardia redeki* (Horst)	5	2	4
	Polydora websteri Hartman	18	36	16
Syllidae	*Autolytus* sp.	2	1	2
	Exogone occidentalis Westheide	3	1	3
	Haplosyllis spongicola (Grube)	7	13	5
	Opistosyllis corallicola Hartman-Scröder	1	0	4
	Syllis gracilis Grube	21	130	236
	Trypanosyllis taeniaformis (Haswell)	13	28	11
	Typosyllis variegata (Grube)	23	96	52
	Typosyllis maculata Imajima	4	7	1
	Syllidae sp. A	1	1	0
	Syllidae sp. B	1	1	0
	Syllidae sp. C	1	1	0
	Syllidae sp. D	2	4	0
	Syllidae sp. E	8	23	1
	Syllidae sp. F	2	3	0
Terebellidae	*Loimia medusa* (Savigny)	1	0	2
	Pista herpini Fauvel	8	12	3
	Polycirrus hamiltoni Benham	12	24	3
	Streblosoma bairdi (Malmgren)	3	3	8
	Terebella cf. *pterochaeta* Schmarda	6	3	4

FIG. 3. – Cluster analysis based on species abundances (Bray-Curtis index) of macrofaunal assemblages associated with colonies of *S. errata* sampled in Ubatuba and São Sebastião. L = Lamberto, C = Codó, S = Segredo, A = Araçá.

DISCUSSION

The fauna associated with colonies of *Schizoporella errata* was dominated by a few species, and followed a log-series distribution. Theory predicts that few factors determine community structure, and species colonization at random intervals along time results in many rare species (May, 1975; Magurran, 1988). However, Hughes (1984) noted that the number of rare species in marine benthic communities may accumulate faster than predicted by the log-series distribution. Species recruiting to the substrate could eventually displace competitively inferior species, but dominance patterns should be dynamic, as mortality events, density-dependent reduction of recruitment, and variable population growth rates would prevent the same species from dominating these communities for long time intervals (Hughes, 1984). Also, resource availability must influence these patterns. The limiting resource in these communities is space, which can be used to hide from predators and as foraging sites.

The dominant faunal groups associated with *Schizoporella* colonies were polychaetes, crustaceans, and echinoderms (see Table 1), and species composition was similar to other biogenic substrata found in nearby areas (Nalesso *et al.*, 1995; Duarte and Nalesso, 1996). Polychaetes formed the largest taxonomic group, with 70 species distributed in 20 families. Although only six excavating families were found, these contributed 51% of total polychaete abundance found in the colonies. Other common boring taxa included sipunculans and bivalves of the genera *Lithophaga*, *Petricola* and *Gastrochaena* (Morton, 1983). These organisms may occur mainly in the basal parts of the colonies, where dead layers accumulate (e.g., Cocito *et al.* 2000). These results contrast with those of Hutch-

Assemblage structure also varied in relation to trophic groups ($G = 296$, df = 5, $p < 0.001$). The main differences were between the relative abundance of deposit- and suspension-feeders: 30.3 and 8.6% in Ubatuba and 20.1 and 23.3% in São Sebastião, respectively (Table 3). The other groups contributed similarly to faunal abundances in Ubatuba and São Sebastião (See Table 3).

TABLE 3. – Relative abundance (%) of trophic groups associated with different biogenic substrates in sites subject to low or high water movement: the bryozoan *Schizoporella errata*, the sponge *Zygomycale parishii* (data from Duarte and Nalesso, 1996) and the scleractinian coral *Oculina arbuscula* (data from McCloskey, 1970).

	Carnivore	Deposit-feeder	Suspension-feeder	Herbivore	Omnivore
S. errata					
Ubatuba (low)	33.7	30.3	8.6	0.2	27.2
São Sebastião (high)	27.5	20.1	23.3	0.4	28.8
Z. parishii					
Ubatuba (low)	2.9	86.0	4.0	0.0	7.1
São Sebastião (high)	6.9	58.1	15.2	1.9	18.0
O. arbuscula					
Charleston, SC (low)	11.6	40.8	43.5	0.0	4.1
Cape Lookout Jetty (high)	18.8	31.5	47.7	0.0	2.1

ings (1981), who found more non-boring individuals in blocks of dead coral, where holes were mainly colonized by sipunculans. Dead corals represent an important resource for the polychaetes, but unpredictable in time; thus, opportunist species with great dispersion and colonization capacities generally occupy coral substrata (Hutchings, 1981). The resources offered by the colonies of *S. errata* are more predictable, as those colonies are stable and long-lasting, used while they are still alive. Thus, polychaetes may complete their whole life cycle and forage within these colonies, as 80% of all individuals were carnivores or deposit-feeders.

Crustaceans were dominated by decapods and the isopod *Excorallana quadricornis*, which may use the biological substrate only as a refuge. Another species of the same genus, *E. tricornis occidentalis*, has a diel migratory cycle, staying in the water column at night while hiding in corals or rocky substrata during the day (Guzman *et al*., 1988). Among the 24 decapod species associated with *S. errata*, the anomuran *Pachycheles maginanus* and the brachyuran *Hexapanopeus schmitti* were dominant (Table 2). Lindberg and Stanton (1988) found a similar number of decapod species (23) in colonies of *Schizoporella pungens* in Florida, with 90.5% of the individuals represented by 21.7% of the species in *S. pungens*, whereas 91.7% of the decapods of *S. errata* were represented by 41.7% of the species, almost a two-fold difference. These differences could be due to an active defense of *S. pungens* colonies by the dominant *Pilumnus sayi*, as they consitute the only rigid habitat in an area dominated by seagrasses (Lindberg and Frydenborg, 1980). In Brazilian shores, other biogenic substrates are available together with *S. errata*, and these resources may be less limiting for the crabs.

The colonies of *S. errata* at Ubatuba and São Sebastião sheltered assemblages with similar diversity patterns although species composition and abundance differed (Fig. 3). These results contrast with Duarte and Nalesso (1996), who found greater diversity in São Sebastião relative to Ubatuba. These authors suggested that this pattern could be due to differences in local water currents affecting recruitment or higher abundance of predatory and territorial decapods in São Sebastião, preventing dominance of *Ophiactis savignyi* (Duarte and Nalesso, 1996). Although decapods were most abundant in colonies of *S. errata* in Ubatuba, similar values of species richness and diversity were found at both sites. Also, possible differences in

water currents on species recruitment do not explain the patterns found. However, differences of local hydrodinamism can influence colony growth and form (Cocito *et al*., 2000; Ferdeghini *et al*., 2000), and sedimentation within colonies.

The accumulation of mud and silt inside the colonies found at sheltered sites in Ubatuba indicates that differences in assemblage structure could be related with water movement. At this site, more deposit-feeders were found when compared with colonies at São Sebastião shores, where more suspension-feeders were found (Tab. 3). The influence of water movement on the relative abundance of deposit- and suspension-feeders has been suggested for infaunal macrobenthos (Wildish and Kristmanson, 1979; Roth and Wilson 1998). The patterns found could be common to other biogenic substrates (Tab. 3), although Conradi and Cervera (1995) found dominance of deposit-suspension feeding amphipods associated with the bryozoan *Bugula neritina* at sites with low water movement. In their case, the greatest differences were related to the life habit of the amphipods, with more free-living organisms in exposed areas and dominance of domicolous amphipods in sheltered areas (Conradi and Cervera 1995). Thus, hydrodynamism may influence the distribution of macrofaunal assemblages associated with biogenic structures, and functional classification by trophic or life-habit characteristics may be a useful approach to predict patterns in assemblage structure.

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