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

ELOÍSA H. MORGADO¹ and MARCEL O. TANAKA²

¹ Depto. de Zoologia, IB, Universidade Estadual de Campinas, Campinas, Brazil. E-mail: morgamar@bestway.com.br
² Depto. de Biologia, Setor Ecologia, CCBS, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil.

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., *)
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 microalgae, 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; Ferdgehini 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; Ferdgehini 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 (Ferdgehini 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...
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 Lomberto (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. Segrerdo 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 algea *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 fragments 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 (Snellgrove 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: \(y = -7.04 + 21.8 \ln x, r^2 = 0.99, p < 0.0001\); 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.
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%), Circriformia 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 magi

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, Dormillea sociabilis and the ophiuroids Ophiactis savignyi and O. lymani were much more abundant in Ubatuba than in São Sebastião, whereas the anomuran P. magi

| Taxa              | 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               |

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 2. – Species collected in 26 colonies of *Schizoparella 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                 | Thalassessa sp.                              | 1  | 1   | 0  |
| ECHINODERMATA – Ophiuroidea | Amphiporidae: *Axinopus squamatus* (Delle Chiaje) | 2  | 5   | 2  |
|                         | Ophiactis lymani Lijungman                   | 20 | 185 | 92 |
|                         | Ophiactis saviynyi (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: Sellia adamsi (Lea)          | 1  | 0   | 3  |
|                         | Columbellidae: Costoananchis sertulariariam Orbigny | 1 | 0 | 1 |
|                         | Costoananchis 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  |
|                         | Nassaridae: Nassarius sp.                    | 1  | 0   | 1  |
|                         | Phasianellidae: Tricollia affinis (Adams)    | 2  | 4   | 0  |
|                         | Thaïdidae: Morula nodulosa (Adams)           | 3  | 0   | 3  |
|                         | Trochidae: Solariella sp.                    | 4  | 7   | 7  |
| MOLLUSCA - Bivalvia      | Anomiidae: Anomia ephippium L.               | 4  | 5   | 0  |
|                         | Arcidae: Arca imbricata Bruguère             | 1  | 0   | 1  |
|                         | Gastrochaenidae: Gastrochaena hians (Gmelin) | 7  | 2   | 0  |
|                         | Hiatellidae: Hiatella arctica (L.)           | 18 | 23  | 30 |
|                         | Lyonsiidae: Lyonsia (Entodesma) beana (Orbigny) | 12 | 104 | 9  |
|                         | Mytilidae: Lithophaga bisalculata (Orbigny)  | 4  | 1   | 5  |
|                         | Modiolus carvalho (Klappebach)               | 7  | 7   | 13 |
|                         | Musculus lateralis (Say)                     | 3  | 3   | 0  |
|                         | Petricolidae: Ruppalaria (Petricola) typica (Jonas) | 7  | 5   | 4  |
|                         | Pholadidae: Martesia cuneiformis (Say)       | 2  | 1   | 2  |
|                         | Veneridae: Chione papha (L.)                 | 1  | 1   | 0  |
|                         | Gouldia cerina (Adams)                       | 1  | 1   | 0  |
| ARTHROPODA - Pycnogonida| Achelida sawayai (Marcus)                    | 5  | 5   | 0  |
|                         | Anomothella sp.                              | 5  | 9   | 0  |
| ARTHROPODA - Isopoda    | Excorallanidae: Excoralliana 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 apicurus Coutiere                 | 18 | 69  | 4  |
|                         | Synalpheus brevicarpus (Herrick)             | 17 | 15  | 28 |
|                         | Synalpheus fritzmuelleri Coutiere            | 19 | 25  | 78 |
|                         | Hyppolytidae: Hippolite curacaoae 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: Hexapanaeus paulensis Rathbun | 1  | 1   | 0  |
|                         | Hexapanaeus schmitti Rathbun                 | 16 | 106 | 0  |
|                         | Menippus nodifrons Stimpson                  | 8  | 17  | 0  |
|                         | Pilumnus dasypodus Kingsley                  | 12 | 7   | 18 |
|                         | Pilumnus floridanus Stimpson                 | 5  | 9   | 0  |
|                         | Majidae: Epius brasilienis Dana              | 2  | 1   | 1  |
|                         | Mithracus forceps (Milne Edwards)            | 7  | 4   | 9  |
|                         | Microphys bicornutus (Latreille)             | 4  | 6   | 0  |
|                         | Podochela risiel Stimpson                   | 3  | 1   | 2  |
|                         | Grapsidae: Pachygrapsus transversus Gibbes  | 3  | 7   | 0  |
| ARTHROPODA - Decapoda: Anomura | Porcellanidae: Megalograchium soriatus Haig | 10 | 15  | 10 |
|                         | Pachycheles maginatus Milne Edwards          | 22 | 71  | 215|
|                         | Petrolisthes gulaconus 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    |
|                       | **Chrysopetalidae**               |    |     |      |
|                       | *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 rudolphii* (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 angelenesis* Fauchaud    | 1  | 0   | 1    |
|                       | *Marphysa sanguinea* (Montagu)    | 1  | 0   | 2    |
|                       | *Nematonereis hebes* Verrill      | 20 | 12  | 4    |
|                       | *Palola esbeta* Morgado and Amaral | 3  | 2  | 4    |
|                       | **Hesionidae**                    |    |     |      |
|                       | *Hesione picta* Müller            | 1  | 1   | 0    |
|                       | *Ophiodromus pugettensis* (Johnston) | 26 | 578| 78   |
|                       | **Lumbrineridae**                 |    |     |      |
|                       | *Lumbrineris albindons* Crossland | 26 | 487 | 216  |
|                       | *Oenone diphylidida* Schmarda      | 13 | 19  | 6    |
|                       | **Nereidae**                      |    |     |      |
|                       | *Neanthes succinea* (Frey and Leuckart) | 17 | 63 | 23   |
|                       | *Nereis riset* Grube              | 21 | 84  | 12   |
|                       | *Pseudonereis* sp.                | 10 | 20  | 13   |
|                       | **Ophellidae**                    |    |     |      |
|                       | *Armandia maculata* (Webster)     | 8  | 11  | 1    |
|                       | **Paraonidae**                    |    |     |      |
|                       | *Paradoneis* cf. *lyra* (Southern) | 17 | 60 | 3    |
|                       | **Phyllocodidae**                 |    |     |      |
|                       | *Eulalia myriacyclum* (Schmarda)  | 5  | 13  | 0    |
|                       | *Eulalia viridis* (L.)            | 13 | 16  | 12   |
|                       | *Eumida sanguinea* (Oersted)      | 6  | 7   | 1    |
|                       | **Polynoidae**                    |    |     |      |
|                       | *Halosynida glabra* Hartman       | 11 | 17  | 1    |
|                       | *Harmothoe macginieiti* Pettibone  | 13 | 22  | 2    |
|                       | *Harmothoe* sp.                   | 1  | 1   | 0    |
|                       | *Lepadonotus caeruleus* Kinberg    | 26 | 204 | 42   |
|                       | *Scalsetosus gracilis* Morgado and Amaral | 9  | 11 | 3    |
|                       | **Sabellidae**                    |    |     |      |
|                       | *Branchiomma nigromaculata* (Baird) | 3  | 8   | 0    |
|                       | *Hypsicoma elegans* (Webster)     | 18 | 38  | 66   |
|                       | *Potamilla reniformis* (Leuckart) | 2  | 0   | 7    |
|                       | **Sabellariidae**                 |    |     |      |
|                       | *Phragmatopoma* sp.               | 1  | 1   | 0    |
|                       | *Sabellaria floridensis* Hartman   | 6  | 5   | 9    |
|                       | **Serpulidae**                    |    |     |      |
|                       | *Hydroids brachycantha* Rioja     | 8  | 9   | 3    |
|                       | *Hydroids diramphä* Mörch        | 3  | 2   | 8    |
|                       | *Pomatoeres minutus* Rioja        | 2  | 2   | 1    |
|                       | **Sigalionidae**                  |    |     |      |
|                       | *Sigalionidae* sp. A              | 1  | 1   | 0    |
|                       | **Spionidae**                     |    |     |      |
|                       | *Boccardia redeki* (Horst)         | 5  | 2   | 4    |
|                       | **Syllidae**                      |    |     |      |
|                       | *Polydora websteri* Hartman       | 18 | 36  | 16   |
|                       | *Syllidae* sp.                    | 2  | 1   | 2    |
|                       | *Exogone occidentalis* Westheide   | 3  | 1   | 3    |
|                       | *Haplosyllis spongicola* (Grube)  | 7  | 13  | 5    |
|                       | *Opiostylis corallicola* Hartman-Scröder | 1  | 0  | 4    |
|                       | *Syllis gracilis* Grube           | 21 | 130 | 236  |
|                       | *Trypanosyllis tenuiformis* (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 bairdii* (Malmgren)  | 3  | 3   | 8    |
|                       | *Terebellia* cf. *pterochaeta* Schmarda | 6  | 3  | 4    |
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).

DISCUSSION

The fauna associated with colonies of *Schizoporella* 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 (Nalessio et al., 1995; Duarte and Nalessio, 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-

| Trophic Group | 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 magianus 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 constitute 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 hydrodynamism 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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REFERENCES

Amaral, A.C.Z., E.H. Morgado, P.P. Lopes, L.F. Beládio, F.P.P. Leite and C.P. Ferreira. – 1990. Composition and distribution of the intertidal macrofuna of sandy beaches on São Paulo coast. Anais II Simpósio de ecossistemas da costa sul e sudeste brasileira, 3: 258-279.
