

A new encrusting interstitial marine fauna from Brazil

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Abstract. This paper reports the second occurrence of a sand-grain encrusting interstitial epifauna dominated by bryozoans and polychaetes at a site thousands of kilometers from the first described occurrence of such a fauna 20 years ago. Such faunas seem to have gone almost unrecorded in the marine ecological literature, but they are potentially geographically widespread and ecologically significant, deserving recognition and further study by benthic ecologists. Although rooted-erect and free-living lunulitiform bryozoans can be abundant in soft-bottom habitats, the presence of encrusting forms was, until recently, considered to be limited to patches of hard substrata. In 1985 and 1988, a new and seemingly unique habitat for encrusting bryozoans and other organisms on single grains of shell or sand was reported from the coastal waters of Florida, USA. Here we report a second discovery of an interstitial encrusting fauna from the continental shelf off the state of São Paulo, Brazil. In addition to the cupuladriid *Discoporella umbellata*, several species of bryozoans (9 cheilostomes, 3 ctenostomes, and 1 cyclostome) were found encrusting on or boring into sand grains from the 4 stations examined. Four species were found exclusively on sand to gravel size grains. The most abundant colonies, with ~1300–1500 colonies m⁻², belonged to a new species of *Cleidochasma*. New species of *Trypostega* and *Reginella*, each with up to 200–300 colonies m⁻², were also discovered. The grain-encrusting bryozoans were characterized by their small size, and by the fact that sexual reproduction was initiated very early in colony growth; brood chambers (for the development of embryos into larvae) occurred in colonies having only a few zooids. Colonies of boring ctenostome and cheilostome bryozoans were even more abundant than those of grain encrusting forms, being present in almost every piece of shell (~5000–5500 colonies m⁻²). The fauna also included representatives of other groups of encrusting organisms, especially tubeworms (11,000–13,000 tubes m⁻²). Planned work on samples from additional stations on the São Paulo shelf will no doubt yield a larger number of species from various taxa and perhaps show some overlap in sand fauna species between the Brazilian and Floridian sites. In addition to the unique species of single grain encrusters, colonies of bryozoan species characteristic of larger subtidal hard substrata were also found on sand or gravel size grains, indicating that an interstitial refuge may be available to some epifaunal taxa and suggesting that this interstitial refuge, which remains almost completely unknown to benthic ecologists, may play a large role in determining distributions of those taxa.

Additional key words: Bryozoa, epifauna, soft-bottom benthos, São Paulo

Marine ecologists who study soft-bottom benthic ecosystems have acquired considerable knowledge concerning the factors controlling the fauna of these habitats. Sediment type, grain size, primary productivity, physical and chemical factors, and biotic interactions all play a role in determining distributions, while the resident organisms themselves also act to

change their environment through bioturbation or by creating structures that bind and stabilize sediments or in some way affect water flow patterns (Alongi 1990; Watling 1991; Lenihan & Micheli 2001). The sandy sediments that make up a large part of the continental shelves undoubtedly appear much more homogeneous to their infaunal and motile inhabitants than to any encrusting epifauna that occupy this type of habitat. Optimal habitats for epifaunal organisms are characterized by an abundance of

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different types of hard substrata (shells, rocks, pilings, algae, etc.), often with many three-dimensional microhabitats. Until fairly recently, specialists in bryozoan ecology, like other benthic ecologists, would have considered soft-bottom habitats extremely patchy habitats for epifauna, the expanses of sediment unusable, and only limited benthic “islands,” i.e., small patches of hard substrata, dead shells, rocks, sunken wood, or trash, on which epifaunal organisms could settle and establish a population. For example, Gray (1971) considered the Bryozoa to constitute a “relatively insignificant part of the meiobenthos,” being represented only by the rare, truly interstitial genus *Monobryozoon*, and the widespread, rooted-erect, and free-living lunulitiform species. Although lunulitiform bryozoans can be abundant in soft-bottom habitats (e.g., Marcus & Marcus 1962; Maturó 1968; Gray 1971; Dick et al. 2003), the presence of encrusting forms was considered to be limited to whatever patches of hard substrata might exist. However, from 1983 to 1985, a study of the population biology of two species of free-living bryozoans inhabiting Capron Shoal, a high-energy shoal off the east coast of Florida, led to the discovery of a new and apparently unique habitat for encrusting bryozoans on single grains of shell or sand. During this study, 33 species of interstitial encrusting bryozoans were identified, 9 of which were new to science and exclusively interstitial (Håkansson & Winston 1985; Winston & Håkansson 1986; Winston 1988). Statistical analyses showed that different species settled preferentially on sand and shell grains of a particular size. Colonies of sand grain-encrusting species became sexually reproductive at much smaller sizes than colonies of species occupying larger substrata, and were thus able to live out their lives on a single grain. Living colonies of these bryozoans, found in cores to 16-cm deep in the sediment, were able to feed, grow, and reproduce completely interstitially.

The mixed terrigenous carbonate sand of Capron Shoal also supported a number of other kinds of encrusting organisms, including foraminiferans, serpulid and spirorbid tube worms, hydroids, and entoprocts, as well as the more familiar motile meiofaunal taxa, including flatworms, gastrotrichs, nematodes, and copepods. In addition to the new bryozoan species found on single sand-size grains, other encrusting bryozoan species were found on larger shell fragment grains and on whole dead shells in the vicinity of the shoal. One possible ecological significance of such an interstitial refuge is to provide a means by which encrusting organisms with short-lived non-feeding larvae (like most bryozoans) maintain remarkably broad distributions. It remained to

be seen, however, whether such habitats occurred anywhere but this one shoal.

Here we report a second location and provide a description of an interstitial encrusting fauna—this time from the continental shelf off the state of São Paulo, Brazil.

Methods

Study site

The samples analyzed were part of a long-term study of the marine fauna of the state of São Paulo (BIOTA/FAPESP/Bentos Marinho Project). The sampled area was located in the Caraguatatuba bight and vicinity, on the inner shelf of the northeast coast of the state of São Paulo, Brazil (Fig. 1, Table 1); the samples studied from stations 205, 208, 209, and 211 were obtained during November, 2002. The Caraguatatuba bight lies approximately in the middle of the South Brazil Bight, just south of the Tropic of Capricorn, within the Paulista Province, a transitional zoogeographical zone, located between the tropical and subtropical domains, but with a prevailing Caribbean fauna (Palacio 1982; Boltovskoy et al. 1999).



Fig. 1. Location of sampling stations.

Table 1. Environmental and sampling information for the 4 stations studied in the coast of the state of São Paulo, Brazil.

Station	Depth (m)	Latitude (S)	Longitude (W)	T (°C)		Salinity (ppm)		Granulometry					CaCO ₃ (%)	OM (%)
				surf	bot	surf	bot	MG (mm)	Sa (%)	S+A (%)	Sed	SC		
205	9	23°35.654'	45°16.780'	27.5	24.0	35	35	0.65	97.11	1.29	CSa	MS	31.6	0.14
208	11	23°43.442'	45°18.914'	26.1	21.2	35	35	0.94	96.84	0.16	CSa	MS	48.5	0.45
209	12	23°46.731'	45°13.790'	28.9	22.4	32	33	2.59	99.58	0.42	FSa	WS	55.4	0.09
211	36	23°48.507'	45°06.749'	29.0	21.5	34	35	2.26	98.52	1.27	FSa	WS	82.5	0.26

bot, bottom; CaCO₃, calcium carbonate content; CSa, coarse sand; FSa, fine sand; MG, mean grain size; MS, moderately sorted; OM, Organic matter; S+A, silt plus clay; Sa, sand; SC, sorting coefficient; Sed, sediment; surf, surface; WS, well-sorted.

The water mass that is dominated by coastal water, with intrusions from the warm Brazil Current and the relatively cooler South Atlantic Central Water (Campos et al. 1995), is warm (>20°C) and saline (33–36 ppt). The Caraguatatuba bight is protected from the dominant winds (S-SW) by the Island of São Sebastião (Ilhabela). The bottom of the bay is relatively flat and homogeneous, with sediments ranging from clay to coarse gravels, usually with high contents of biotrital carbonates (fragments of corals, shells of brachiopods, bryozoans, molluscs and echinoderms, spines of echinoids, etc.), except on the northern side of Caraguatatuba bight where the carbonate contents are relatively low (<10%) (Barros et al. 1997). The sand constituents are quaternary deposits, while the clay and silt sediments were deposited more recently (Barros et al. 1997).

Collection and examination of samples

Benthic samples were taken with a Van Veen grab sampler (volume 0.25 m³) at various depths (5–45 m). At each station, a Nansen bottle sampler with a reversing thermometer was used to measure water temperature and to sample water for determining salinity from the surface and bottom depths. Salinity was measured using an optical refractometer, and granulometry was determined by the Suguio method (Suguio 1973).

Portions of live samples from these stations were initially examined in seawater after they were brought into the laboratory at the Centro de Biologia Marinha (CEBIMar) of the University of São Paulo. Once the presence of a new interstitial fauna was detected, some encrusting bryozoan colonies were photographed (stereomicroscope Zeiss SV-11 equipped with a Nikon Coolpix 995 digital camera). Since systematics of calcified bryozoans rely largely on ultrastructural characters of zooid skeletons as seen using scanning electron microscopy (SEM), subsamples (~200 ml) were rinsed in freshwater and dried for later sorting using a dissecting microscope and preparation for SEM. To obtain preliminary identification, subsamples were sorted 1–2 cm³ at a time at a magnification of ×12 or higher using a dissecting microscope. Ten cm² samples from each station were also sorted and the number of bryozoan colonies and tube worm tubes counted. These numbers were used to obtain an estimated density of those groups in an area 1-m² and 1-cm deep at each station. The specimens for SEM were rinsed in freshwater again, dried, and examined uncoated or sputter coated with gold before examination in either a JEOL 6400 Vision 6 or an ASPEX PCSEM.

Results

Several species of bryozoans were found encrusting on or boring into sand grains from the 4 stations examined: 9 cheilostomes, 3 ctenostomes, and 1 cyclostome (Table 2). Four species were found exclusively on sand to gravel size grains. We also recognized the possible presence of additional species of bryozoans, but do not yet have sufficient unabraded material to

enable their specific characterization. Two stations (205 and 211) shared the same bryozoan and encrusting calcareous tube worm fauna despite differences in water depth (9 vs. 36 m) and granulometry (moderately sorted coarse vs. well-sorted fine sand) (Tables 1 and 2). Most calcareous grains at these stations were either unaltered or were polished in appearance, their edges often rounded, but the shell grains retained their coloration. The inorganic component consisted

Table 2. Species of interstitial encrusting bryozoans from the coasts of São Paulo, Brazil, and Capron Shoal, Florida, USA.

Species of interstitial encrusting bryozoans	
São Paulo, Brazil	Capron Shoal, Florida, USA ^a
Stations 205 and 211	Cyclostomata
Cyclostomata	<i>Disporella plumosa</i> WINSTON & HÅKANSSON 1986
<i>Disporella</i> sp.	Ctenostomata
Ctenostomata	<i>Alcyonidium capronae</i> WINSTON & HÅKANSSON 1986
<i>Spathipora ditrupae</i> NORMAN 1907	<i>Spathipora brevicauda</i> POHOWSKY 1978
<i>Spathipora sertum</i> FISCHER 1866	Cheilostomata
<i>Terebripora</i> sp.	<i>Aimulosia pusilla</i> (SMITT 1873)
Cheilostomata	<i>Aimulosia uvulifera</i> (OSBURN 1914)
<i>Cleidochasma</i> sp. ^b	<i>Alderina smitti</i> OSBURN 1950
<i>Escharina</i> sp.	<i>Antropora leucocypha</i> (MARCUS 1937)
<i>Floridina</i> sp.	<i>Beania klugei</i> (COOK 1968)
<i>Hippoporella</i> sp.	<i>Bellulopora bellula</i> (OSBURN 1950)
<i>Membranipora paulensis</i> (MARCUS 1937)	<i>Cleidochasma angustum</i> WINSTON & HÅKANSSON 1986
<i>Puellina</i> sp.	<i>Cleidochasma porcellanum</i> (BUSK 1860)
<i>Reginella</i> sp. ^b	<i>Cribrilaria parva</i> WINSTON & HÅKANSSON 1986
<i>Trypostega</i> sp. ^b	<i>Cribrilaria innominata</i> (COUCH 1844)
Station 208	<i>Cupuladria doma</i> (D'ORBIGNY 1851)
Ctenostomata	<i>Cymulopora uniserialis</i> WINSTON & HÅKANSSON 1986
<i>Spathipora</i> spp.	<i>Discoporella umbellata</i> subsp. <i>depressa</i> (CONRAD 1841)
<i>Terebripora</i> sp.	<i>Drepanophora torquata</i> WINSTON & HÅKANSSON 1986
Cheilostomata	<i>Escharina pesanseris</i> (SMITT 1873)
<i>Cleidochasma</i> sp. ^b	<i>Floridina parvicella</i> CANU & BASSLER 1923
<i>Discoporella umbellata</i> (DEFRANCE 1823)	<i>Hippothoa balanophila</i> WINSTON & HÅKANSSON 1986
<i>Hippoporella</i> sp.	<i>Membranipora arborescens</i> (CANU & BASSLER 1928)
Station 209	<i>Membranipora savartii</i> (AUDOUIN 1826)
Cyclostomata	<i>Membranipora triangularis</i> WINSTON & HÅKANSSON 1986
<i>Disporella</i> sp.	<i>Microporella umbracula</i> (AUDOUIN 1826)
Cheilostomata	<i>Parasmittina nitida</i> morphotype B MATURO & SCHOPF 1968
<i>Discoporella umbellata</i> (DEFRANCE 1823)	<i>Parasmittina signata</i> (WATERS 1889)
<i>Membranipora paulensis</i> (MARCUS 1937)	<i>Phylactella ais</i> WINSTON & HÅKANSSON 1986
<i>Trypostega</i> sp. ^b	<i>Reginella repangulata</i> WINSTON & HÅKANSSON 1986
	<i>Retevirgula caribbea</i> (OSBURN 1947)
	<i>Schizoporella rugosa</i> (OSBURN 1940)
	<i>Trematoecia psammophila</i> WINSTON & HÅKANSSON 1986
	<i>Trypostega venusta</i> (NORMAN 1864)
	<i>Vibracellina laxibasis</i> CANU & BASSLER 1928

^a Data from Winston & Håkansson (1986).

^b Species exclusively interstitial.

of sharp-edged, irregularly shaped, mineral grains. The organic component was mostly fragments of bivalve mollusc shell, but also contained shells of adult gastropods in the genus *Caecum* (Fig. 3A), micro-gastropods, and sea urchin test fragments and spines.

One of most abundant bryozoans in the São Paulo shelf samples examined so far was the cupuladriid cheilostome *Discoporella umbellata* (DEFRANCE 1823). Adult colonies of this species were found in 27% of the samples so far examined. Young colonies of *D. umbellata* (Fig. 2A) also occurred in samples from stations 205 and 211.

In addition to the cupuladriids, stations 205 and 211 had a similar suite of sand grain-encrusting bryozoans (Table 2). The most abundant colonies, with ~1300–1500 colonies m^{-2} , belonged to a new species of *Cleidochasma* (Fig. 2B). New species of *Trypostega* (Fig. 2C) and *Reginella* (Fig. 2D) were also common, with up to 200–300 colonies m^{-2} of each genus at these stations. The species of *Cleidochasma* was similar to *Cleidochasma angustum* Winston & Håkansson 1986 of the Florida coast Capron Shoal interstitial fauna, but had a different pattern of orificial tubercles. The species of *Trypostega* was similar in morphology to *Trypostega venusta* (NORMAN 1864) found in the interstitial Capron Shoal fauna, but Brazilian specimens differed in ovicell and female zooid orifice characters. The species of *Reginella* somewhat resembled the Florida interstitial *Reginella repangulata* Winston & Håkansson 1986, but had a much smaller frontal shield area.

Specimens of *Trypostega* and *Reginella* formed semiderminate dot-like colonies, limited in size, and with reproductive zooids developing in the zooids budded in the series immediately following the ancestrula (metamorphosed larva and founding zooid/s of the colony) (e.g., Fig. 2C). Zooids of *Cleidochasma* formed runner-like colonies that developed along the ridges of mineral grains (Fig. 2B).

Shells of the gastropod *Caecum* (Fig. 3A) were common, but the calcified tubes of the serpulids and spirorbids were by far the most abundant encrusting organisms in the samples, with an estimated 11,000–13,000 individual tubes m^{-2} , compared with 3100–3700 colonies m^{-2} for all encrusting bryozoan species combined. Like the colonies of *Cleidochasma*, the serpulid polychaetes (Fig. 3B) often aligned their tubes along the sharp ridges of the grains. Additional as yet unidentified species of grain-encrusting bryozoans, various microgastropods, and unidentified egg cases (Fig. 3C–E) were also common.

Colonies of boring ctenostome and cheilostome bryozoans were more abundant than those of grain-

encrusting forms, being present in almost every piece of shell (~5000–5500 colonies m^{-2}). Studies by Marcus (1938) had previously shown that a diverse assemblage of these bryozoans inhabit intact dead shells in the region. Since our samples were examined after drying, nothing remained of these soft-bodied bryozoans except their borings, which, however, have species-specific patterns. The presence of uneroded borings in very small grains indicates that living colonies had occupied them at or near the time of collection and were not merely remnants of colonies that had existed before the shells were broken down into small fragments. The boring pattern of one such colony of the ctenostome *Spathipora* sp. is shown in Fig. 2E. Larger pieces of shell (> 8-mm diameter) and whole shells found in the 2 samples had encrusting bryozoans, including *Escharina* sp., *Floridina* sp., *Hippoporella* sp., *Membranipora paulensis* (MARCUS 1937), and *Puellina* sp., and serpulid species known to occur on hard substrata in the region.

Calcareous grains of station 208 sediments were brown-stained and eroded, their calcium carbonate appearing in some cases to be undergoing dissolution. Shells of molluscs, especially bivalves, were more predominant in the calcium carbonate fraction than in the samples from the previous 2 stations. Samples from Station 208 also contained gastropods of the genus *Caecum* and microgastropods, as well as barnacle plates, sea urchin spines, and foraminiferans. Fewer bryozoan borings occurred in these samples (~1200 m^{-2}). No sexually produced juveniles of *Discoporella umbellata* (which can be identified by the triad of zooids produced by a settled larva) were found, nor were there as many single-grain encrusters (~500 m^{-2}). However, 1 encrusting colony was found in the crevice of a barnacle plate grain, rather than on convex surfaces or ridges, as characteristically occurred in the samples of stations 205 and 211. Only spirorbid tube worms were found at this station, and they occurred in much lower numbers (~300 m^{-2}) than at stations 205 and 211.

Station 209 sediments were not as altered in appearance as those of 208. They consisted of a larger proportion of calcium carbonate shell grains (85.5%) than the other stations, with a larger number of barnacle plates, and the grains were not as eroded. No juveniles of *Discoporella umbellata* were found, but several species of interstitial grain-encrusting bryozoans occurred (~1100 m^{-2}). In this sample some of the grain-encrusting bryozoans were settled in the crevices of the barnacle plates. A number of spirorbid tube

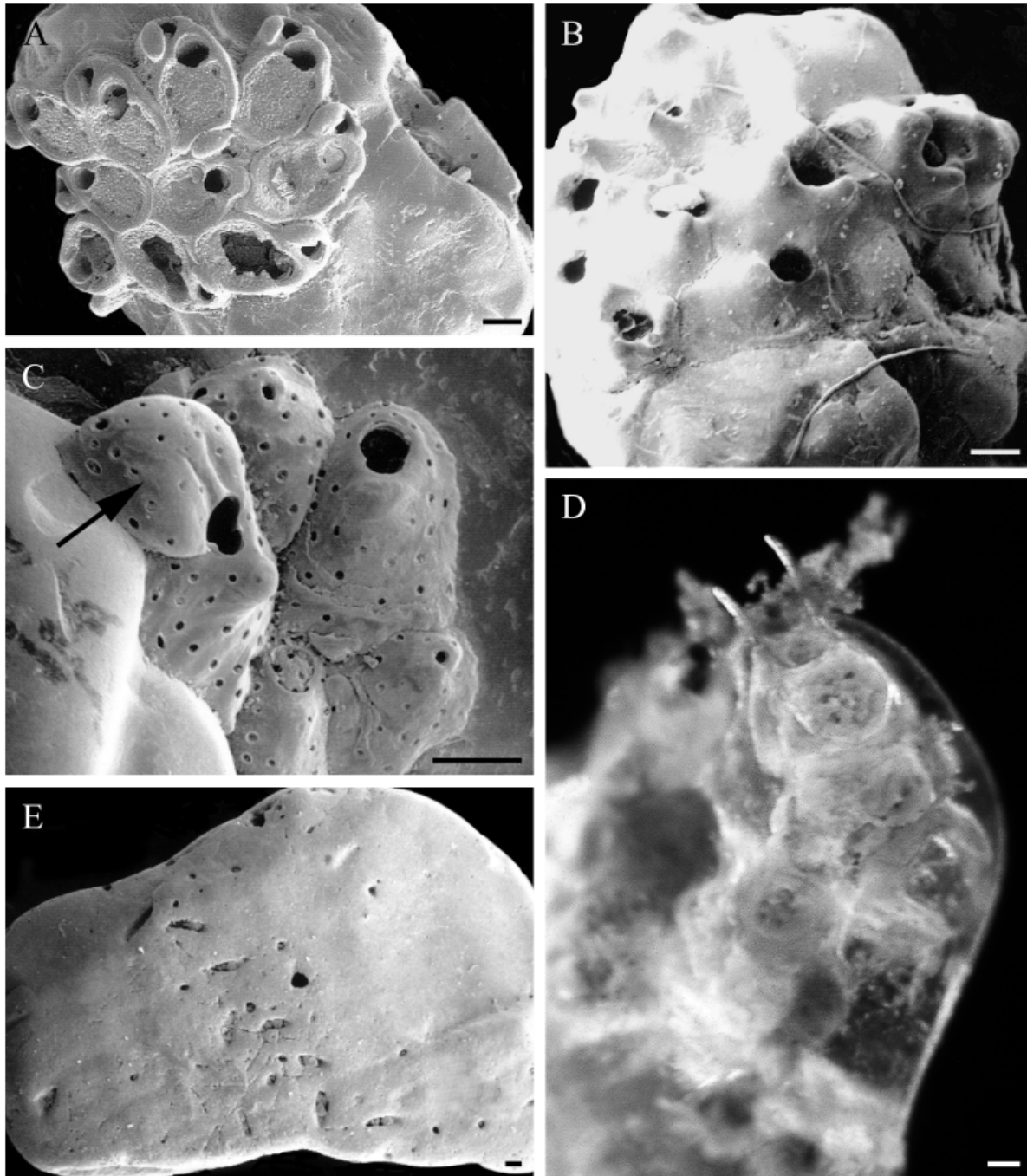


Fig. 2. Scanning electron (A–C, E) and light micrographs (D) of sand fauna bryozoans. (A) Sexually produced juvenile of *Discoporella umbellata*, the common free-living cupuludriid bryozoan of the São Paulo shelf. (B) Sand-grain-encrusting bryozoan, *Cleidochasma* sp. from station 211. (C) Specimen of *Trypostega* sp. from station 211, showing precocious sexual maturity. This colony, although composed of only five zooids, has already developed two male zooids and a female zooid with a brood chamber (arrow). (D) Living colony of *Reginella* sp. encrusting a quartz grain from station 205. (E) *Spathipora* sp., a boring ctenostome bryozoan from station 211. Scale bar, 100 μm .

worms ($\sim 700 \text{ m}^{-2}$) were present, but the long-tubed serpulids characteristic of stations 205 and 211 were absent.

The larger grains and shell fragments or whole shells in both station 208 and 209 samples also held colonies of bryozoan species known from

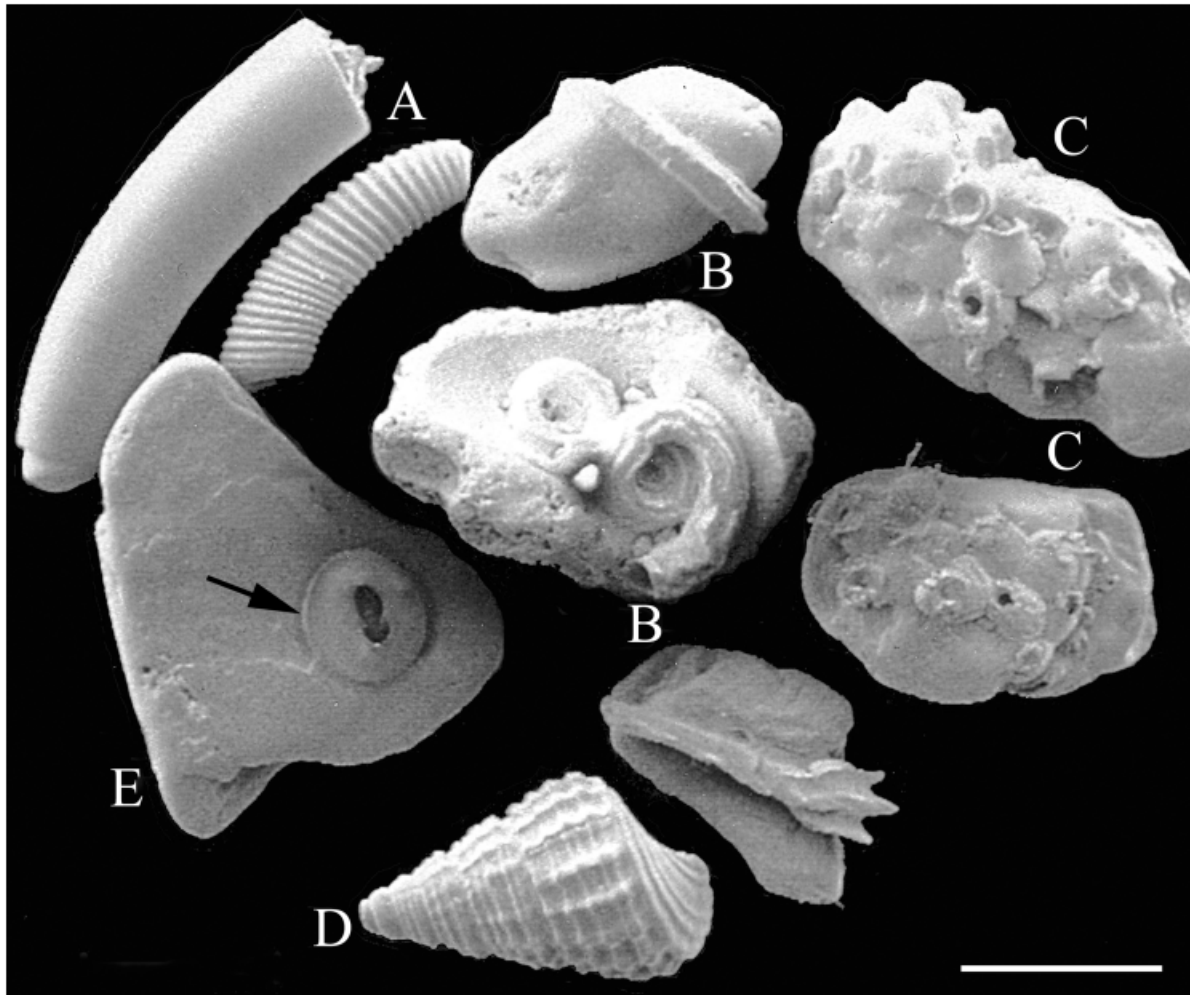


Fig. 3. A composite of SEM micrographs showing some of the most abundant hard-shelled interstitial inhabitants in the new Brazilian fauna: (A) Gastropods of the genus *Caecum*. (B) Serpulid and spirorbid tube worms. (C) Encrusting cheilostome bryozoan. (D) Microgastropod. (E) Egg-case (flatworm?, arrow). Scale bar, 1 mm.

larger substrata in the area (*Hippoporella* sp., *Membranipora paulensis*).

Discussion

The interstitial encrusting bryozoan faunas of Brazil and Florida sample sites shared several genera, *Cleidochasma*, *Trypostega*, and *Reginella* among them (Table 2). The grain-encrusting bryozoans were characterized by their small colony size compared with colonies of other encrusting bryozoans, and by the fact that sexual reproduction was initiated very early in astogeny. This report is a preliminary analysis, based on sorting of a small amount of material from only 4 stations in Caraguatatuba bight and vicinity, one small stretch of the São Paulo coast. The differences in diversity between the 2 sites (Table 2)

could be explained by the more intensive collecting effort at Capron Shoal. Planned work on samples from additional stations in São Paulo coast will no doubt yield a larger number of species and perhaps show further overlap in sand fauna species between the two areas.

Larvae of cupuladriid species settle on sand grains and metamorphose into an initial group of 3 zooids. As colonies grow they eventually surround and completely engulf the grains on which the larvae settled. Larger juvenile and adult colonies become free-living in and on the surface of the sediment, moving through the sand by means of rows of bristle-like vibracula. Numbers of sexually reproduced juveniles of *D. umbellata* were lower than those found for cupuladriids in Florida samples (Winston 1988), but the paucity of sexual recruits may be related to

the enhanced ability of this Brazilian species to reproduce asexually by subcolony budding and fragmentation (Marcus & Marcus 1962).

Like those of the São Paulo shelf, the sediments in the Capron Shoal section of the East Florida shelf were mixed terrigenous and carbonate in origin. They were fine to coarse grained, moderate to well-sorted sands, with a mineral component largely quartz, and with a skeletal carbonate component of mollusc shell, barnacle, foraminiferan, bryozoan, and echinoid fragments (Winston & Håkansson 1986; Hines 1997). The biggest difference between the 2 areas was in the type of microhabitat utilized by the grain-encrusting bryozoans and serpulids. In 2 of the 4 Brazilian samples examined, both bryozoans and serpulids favored the edges and ridges of sharp mineral grains. This habitat was not utilized in Florida, possibly because the mineral grains present in Capron Shoal sediments were smaller and more rounded. The siliclastics of Capron Shoal sediments are probably pre-Miocene. Terrigenous sediments along the east coast of Florida are relict sediments, originally derived from the Appalachian and Piedmont regions of North America (Kohpina 1989; Scott 1997).

Barnacle plate grains were less abundant in the Brazilian material than in Florida samples, but, where they occurred, were utilized by encrusting bryozoans, which, as in Florida, settled in crevices.

The 2 areas also hosted similar non-bryozoan groups, particularly scaphopods, serpulids, spirorbids, gastropods of the genus *Caecum*, and microgastropods. Encrusting foraminiferans were more common in the Florida samples than in those from Brazil. Boring bryozoans were both more abundant and diverse in the Brazilian samples, and appeared to have been living even in very small grains.

Capron Shoal is located at 27°26'N, to the north of the Tropic of Cancer, and near the boundary of the temperate Carolinian and subtropical Caribbean provinces while the 4 Brazilian samples were taken at zoogeographically transitional locations near the Tropic of Capricorn. That such similar faunas occurred in these 2 areas, located at opposite ends of the Western Atlantic tropical margins, and separated from each other by more than 18,000 km, indicates that interstitial encrusting faunas may be more common and of greater significance on continental shelves than marine ecologists have realized. The occurrence of similar encrusting bryozoans, as well the presence of a suite of other taxa including free-living cupuladriid bryozoans, *Caecum*, scaphopods, serpulids, and encrusting foraminiferans, suggests that these may be communities that would be recognizable in other shelf areas.

Interstitial encrusting faunas may be found to occur in cold water areas as well. The study of cold water carbonates has so far concentrated on sedimentological and macrofaunal components, but a recent paper on heterozoan carbonates of the Norwegian shelf (Viña-Herbon et al. 2002), e.g., mentions the presence of an encrusting bryozoan colony on a grain.

The question of what controls the occurrence and distribution of such faunas still remains to be determined. Clearly, the presence of sediment with high contents of calcium carbonate is important. The large amount of pore space available in these irregularly shaped sediments may be a factor, as was noted by Winston & Håkansson (1986). Capron Shoal sediments were medium to coarse well-sorted sands with a 15–30% quartz component in water 6–10 m deep. Brazilian samples varied from fine to coarse sand and from moderately sorted to well sorted. The depth and amount of organic matter present as well as the percentage of non-biogenic mineral grains varied considerably so that no clear pattern has emerged thus far. Physical conditions similar to those at these two locations might signal potential sites to be surveyed for the presence of additional interstitial encrusting communities. The presence of adult free-living bryozoans (whose larvae must settle and survive interstitially for some period of time) might also indicate sites at which such faunas are likely to be found.

In addition to the encrusting species found on single grains, the presence of bryozoan species characteristic of larger subtidal hard substrata indicates that an interstitial refuge may be important to encrusting bryozoans and other encrusting taxa, and suggests that this interstitial soft-substratum refuge may play a significant role in determining their distributions.

Sandy sediments make up a quarter to a half of the inner continental shelves in tropical and subtropical regions (Hayes 1967), a vast area of potential habitat. On a scale of kilometers or hundreds of km², the sand bottom habitat may be a more homogenous environment for encrusting epifauna than anyone would have suspected. The ability to colonize very small surfaces, to survive and reproduce on the varying sizes of grains of sand and gravel, as well as on the orders of magnitude fewer dead shell or rock benthic “islands,” may be one of the factors that has enabled encrusting organisms with short-lived larvae to distribute themselves over vast areas of the continental shelves.

A review of the methods of studying soft bottom benthic ecology is indispensable to properly estimate the distribution and ecological role of the encrusting fauna on sand grains, as the current techniques used

to collect both the macrofauna and meiofauna completely disregard them. The real challenge is to get biologists and environmentalists to take seriously the potential faunal diversity and ecological significance of what are apparently vast expanses of uninterrupted sand, a problem of perception of which the few ecologists who have conducted long-term studies on subtidal sand communities have long been aware (e.g., Morin et al. 1988).

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References

- Alongi DM 1990. The ecology of tropical soft-bottom benthic ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.* 28: 381–496.
- Barros CE, Corrêa ICS, Baitelli R, & Elias ARD 1997. Aspectos sedimentares da Enseada de Caraguatatuba, litoral do Estado de São Paulo. *An. Acad. Bras. Ci.* 69(1): 19–36.
- Boltovskoy D, Gibbons MJ, Hutchings L, & Binet D 1999. General biological features of the South Atlantic. In: *South Atlantic Zooplankton*. Boltovskoy D, ed., pp. 1–42. Backhuys Publishers, Leiden.
- Campos EJD, Gonçalves JE, & Ikeda Y 1995. Water mass characteristics and geostrophic circulation in the South Brazil Bight: summer of 1991. *J. Geophys. Res.* 100(9): 18537–18550.
- Dick MH, Herrera Cubilla A, & Jackson JBC 2003. Molecular phylogeny and phylogeography of free-living Bryozoa (Cupuladriidae) from both sides of the Isthmus of Panama. *Mol. Phylogenet. Evol.* 27: 355–371.
- Gray JS 1971. The meiobenthic Bryozoa. *Smithson. Contr. Zool.* 76: 37–39.
- Håkansson E & Winston JE 1985. Interstitial bryozoans: unexpected life forms in a high energy environment. In: *Bryozoa: Ordovician to Recent*. Nielsen C & Larwood GP, eds., pp. 125–134. Olsen & Olsen, Fredensborg.
- Hayes MO 1967. Relationship between coastal climate and bottom sediment type on the inner continental shelf. *Mar. Geol.* 5: 111–132.
- Hines AC 1997. Structural and paleoceanographic evolution of the margins of the Florida Platform. In: *The Geology of Florida*. Randazzo AF & Jones DF, eds., pp. 169–194. University Press of Florida, Gainesville.
- Kohpina P 1989. Heavy metals in sediments of the inner continental shelf, Cape Canaveral, Florida. MS thesis, Department of Geology, University of South Florida, 153 pp.
- Lenihan HS & Micheli F 2001. Soft-sediment communities. In: *Marine Community Ecology*. Bertness MD, Gaines SD, & Hay ME, eds., pp. 253–287. Sinauer Associates, Inc., Sunderland.
- Marcus E 1938. Bryozoários perfuradores de conchas. *Arq. Inst. Biol.* 9: 273–296.
- Marcus E & Marcus E 1962. On some lunulitiform Bryozoa. *Bol. Fac. Filos. Cienc. Let. Univ. São Paulo, Zool.* 261(24): 281–324.
- Maturo FJS 1968. The distributional pattern of the Bryozoa of the east coast of the United States exclusive of New England. *Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano* 108: 261–284.
- Morin JG, Kastendiek J, Harrington A, & Davis N 1988. Organisms of a subtidal sand community in Southern California. *Bull. South. Calif. Acad. Sci.* 87: 1–11.
- Palacio JP 1982. Revisión zoogeográfica marina del sur del Brasil. *Bolm. Inst. Oceanogr. S. Paulo* 31(1): 69–92.
- Scott TM 1997. Miocene to Holocene history of Florida. In: *The Geology of Florida*. Randazzo AF & Jones DF, eds., pp. 57–67. University Press of Florida, Gainesville.
- Suguio K 1973. Introdução à sedimentologia. Blücher, São Paulo. 317 pp.
- Viña-Herbon C, Murray JW, & Ottesen D 2002. Faunal distribution and composition of heterozoan carbonates of the inner shelf off southern Norway. *Sarsia* 87(4): 290–301.
- Watling L 1991. The sedimentary milieu and its consequences for resident organisms. *Am. Zool.* 31: 789–796.
- Winston JE 1988. Life histories of free-living bryozoans. *Natl. Geogr. Res.* 4(4): 528–539.
- Winston JE & Håkansson E 1986. The interstitial bryozoan fauna from Capron Shoal, Florida. *Am. Mus. Novit.* 2865: 1–50.