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Macrobenthic Recolonization Processes in Mangroves of Southern Brazil

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ABSTRACT

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Sediment characteristics are important in determining distribution and abundance patterns of benthic invertebrates, but it is still not clear if these patterns reflect an active selection of settlement sites by the organisms or a mutual response of sediments and animals to physical forces. Patterns of benthic macrofaunal recolonization were investigated using a reciprocal transplant experiment, conducted in two adjacent sites, in order to investigate the effects of different sediment types on this process. Recolonization of defaunated sediments, by a suite of 51 invertebrate taxa, with predominance of polychaetes, oligochaetes and crabs, was followed up for ca. 3 months. Defaunated areas were quickly occupied, initially by oligochaetes, in both sites. After 95 days, total abundance and species composition were very similar in defaunated and control samples. Despite a high level of variation, commonly observed in natural invertebrate assemblages in local mangroves, some definite patterns were identified for a few more common species. For most species, recolonization followed a random pattern and was independent of sediment type and location of samples, being probably affected by larvae supplied from other estuarine environments. Whereas most species occurred in low densities, occupying new habitats in a random way, *Isolda pulchella* and oligochaete species, which showed high natural densities, numerically dominating the macrobenthic fauna, were able to quickly colonize new habitats. This implies that recovery of local mangrove fauna after physical disturbance, caused by sources such as storms or human interference, may depend primarily on the reproductive success of local populations, and only secondarily on external larval supply.

ADDITIONAL INDEX WORDS: *Reciprocal transplant, analysis of similarity (ANOSIM), defaunated*

INTRODUCTION

Increasing human occupation of coastal areas makes it ever more urgent for scientists and policy-makers to develop appropriate management tools. Macrobenthic organisms are considered appropriate indicators for impact assessment and monitoring studies in coastal areas and are used both in descriptive and experimental approaches. For these studies to be meaningful it is necessary to better understand the dynamics of benthic communities, specially the mechanisms and rates of occupation by new organisms in areas subjected to natural or anthropogenic disturbance (SMITH and SIMPSON, 1998).

Distribution of species and density of organisms in a given place are the result of a number of different and complex physical and chemical factors, such as the hydrological regime, the patterns of transport and deposition of sediments, the organic matter content and the occurrence of stochastic events. Intertidal soft-bottoms, including those covered with mangrove forests, suffer constant physical, chemical and biological disturbances, both from natural (e.g. wave action, currents, predator feeding activities) and anthropogenic sources (e.g. eutrophication, spilling of chemical substances) (GÜNTHER, 1992). The occurrence of these disturbances, their irregular distribution in space and time and factors such as the scale, type, frequency and intensity of the disturbance are some of the causes of the patchy arrangement that characterizes these communities (HALL, 1994).

Colonization of a site occurs mainly through recruitment of larvae and migration of juveniles and adults (SMITH and BRUMSICKLE, 1989). The dispersal ability of plancktotrophic larvae, which occur in about 70% of marine species with known life-cycles (GIANGRANDE *et al.*, 1994), makes them potential colonizers of numerous habitats over large geographical areas. According to ÓLAFSSON *et al.* (1994), events affecting post-establishment phases of the organisms are the main cause of variation in overall abundance, contributing significantly to the creation of infaunal distribution patterns. Temporal variation in recruitment would play only a minor role in explaining variability in adult populations in a scenario of defaunation followed by recolonization.

While larval supply may or may not be limiting, the success in species establishment in a specific site depends on the nature of the existing assemblage together with substrate attributes, such as, for example, its stability (CONSTABLE, 1999). Although the arrival of larvae to a specific location is mainly a result of physical processes, habitat selection seems to play an important role in determining initial patterns of establishment and distribution (SNELGROVE *et al.*, 1999).

According to HALL (1994), the hydrodynamic regime (specially tidal currents) is the main determinant of the sediment characteristics in an area, and could be considered as the main source of large scale patterns in the species distribution from marine soft-bottom communities. Sediment characteristics, specially granulometry and organic matter content, are important pattern determinants in benthic invertebrate associations, but it is not clear if this results from active sediment selection by the organisms (larvae, post-larvae or migrating juveniles and adults) or from a mutual response of sediments and animals to physical forces (ÓLAFSSON *et al.*, 1994).

Few studies have investigated the influence of sediment characteristics on macrobenthic recolonization processes (*e.g.* MCCALL, 1977), and this is particularly true for estuarine soft-bottom habitats, such as mangrove forests. The aim of this study was to test the influence of sediment characteristics associated with granulometry on recolonization processes of macrobenthic infaunal species occurring in two adjacent subtropical mangrove forests. The experimental design allowed us to test both the effect of sediment granulometry on the rates of recolonization by several species and the influence of local adult populations, in opposition to external larval supply, on the recolonization processes.

METHODS

Study Area

The study sites, located on opposite margins of the mouth of the Sucuriu tidal creek, in Paranaguá Bay (Figure 1), were covered by well-developed mangrove stands, with a predominance of *Rhizophora mangle* L. and *Laguncularia racemosa* Gaertn. Sediments on one margin, the site here on denominated Sandy Site, were composed of 96% sand and 4% mud-silt, while on the opposite margin, denominated Muddy Site, sediment composition was 60% sand and 40% mud-silt. To determine sediment characteristics of each site, four random sediment cores were collected in two separate dates prior to the beginning of the study. Organic matter content, mean sediment diameter, silt-clay and carbonate content were estimated through routine dry-sieving and pipetting of sediment samples.

Paranaguá Bay (25º20'S - 25º35'S / 48º20'W - 48º45'W) is a semi-enclosed estuarine system, with a total area of 612 km^2, bordered by extensive tidal plains mainly covered by mangroves and salt marshes. Physical, chemical and biological properties of this subtropical estuary were described by LANA *et al.* (2000). Mangroves in the region are formed by only three species: *R. mangle*, *L. racemosa* and *Avicennia schaueriana* STAPF and LEECHMAN. Rasa da Cotinga Island, the location of Sucuriu creek, stands on the euhaline sector of the bay, a high energy/high salinity (~ 30 p.p.m) area whose properties are largely influenced by oceanic water masses.

Sampling Design

In order to determine patterns of natural variation on species composition and abundance and to test the hypothesis that faunal composition was different between the two sites - which considers that sediment characteristics, or physical factors that regulate local sediment distribution, would influence faunal distribution - 8 random samples were taken from each site on 3 separate dates prior to the experiment (60 and 30 days before and on Day 0 of the experiment). These sampling units, as well as all the experimental units, consisted of a sediment core with Ø15 cm (0.0884 m^2 total surface) and 4 cm deep (~700 cm^3 total volume).

A reciprocal transplant experiment was conducted in order to investigate the effects of different sediment types on macrofaunal recolonization. The experimental design allowed the effects of sediment type and location to be tested simultaneously. The two main hypotheses being tested were that macrobenthic recolonization in defaunated areas would be affected by sediment type and that recolonization of defaunated areas would be different in different sites, irrespective of sediment type (effects of local populations).

The treatments consisted of sediments collected in both sites and defaunated by freezing for a minimum of 7 days. The defaunated sediments were taken back to the field on Day 0, and randomly distributed over a 450 m^2 (30 X 15 m) area on each site (Figure 2). Each of these areas had 96 previously dug crevices that were filled with the sediments of both types (48 defaunated sand - DS and 48 defaunated mud - DM), each experimental unit being placed inside a separate 1 m^2 area. Eight random samples from each treatment, plus 8 random control samples (CS = Control of Sandy Site; CM = Control of Muddy Site), were collected on each site during the following 3 months (11, 21, 32, 62 and 95 days after Day 0).

Samples were fixed in 4% formalin, preserved in 70% alcohol and washed through a 0.5 mm sieve. In the laboratory the organisms were identified and counted. Most of them were identified to the genus or species level, while taxa such as the oligochaetes were grouped at a higher taxonomical level due to uncertainties in their taxonomical status or difficulties in identification.

Data Analysis

Differences in species composition and densities among factors (treatments, days and sites) were compared using Analysis of Similarity (ANOSIM), a multi-variate non-parametric test described in CLARKE and WARWICK (1994), and applied using the PRIMER statistical package, version 5.2.4. For these analyses, Bray-Curtis Similarity matrixes were constructed after square root transformation of raw data. The

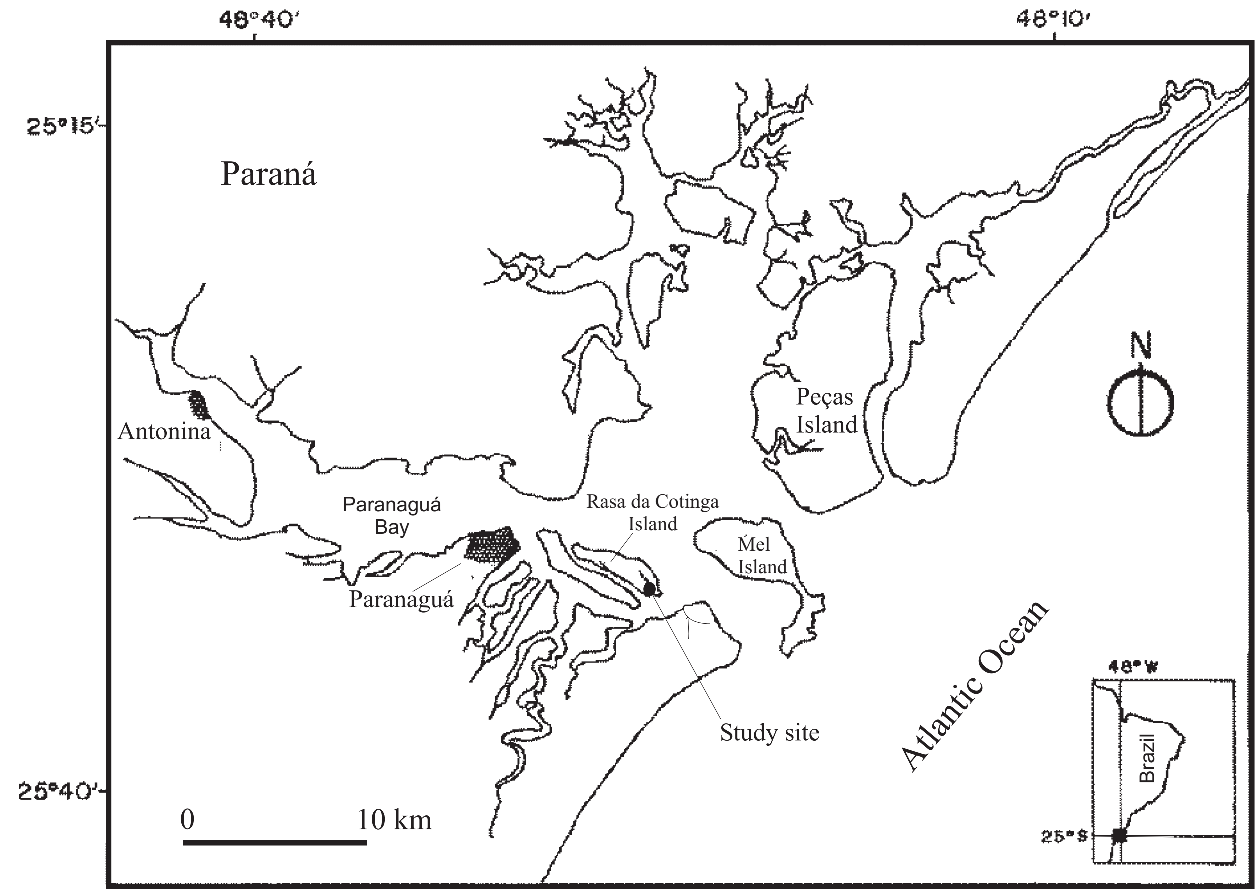

Figure 1. Location of study site on Paranaguá Bay, Brazil.

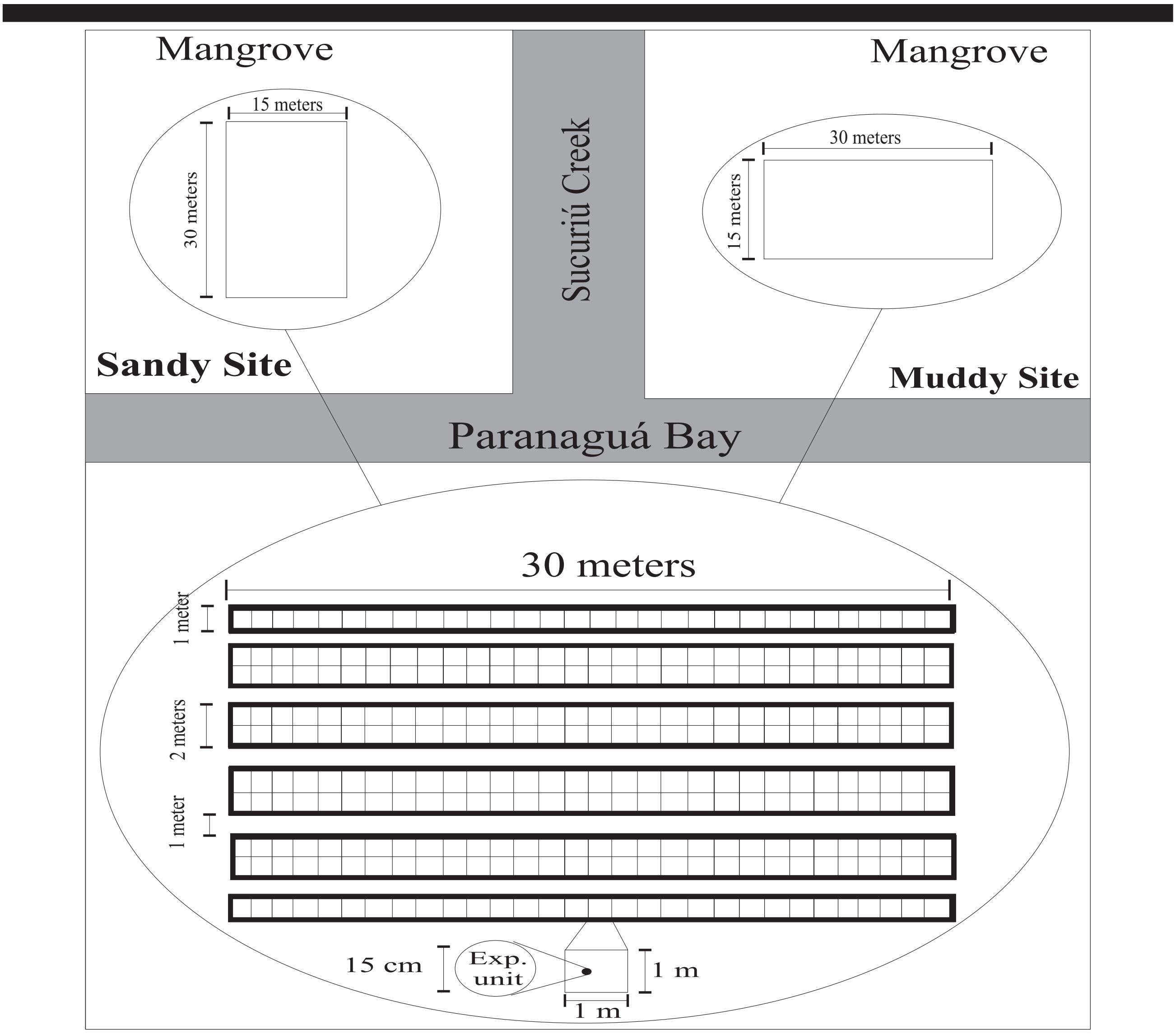

Figure 2. Schematic view of the experimental design. The one-meter alleys between the lines of 1 m^2 blocks were for locomotion to avoid trampling of the experimental units.

ANOSIM is based on comparison of rank similarities. Differences among treatments or sites are compared with differences among replicates from within a same treatment or site, the result being expressed as the variable R. Its value ranges from -1 to 1, reaching a maximum (R=1) when all the replicates within a treatment are more similar to each other than to any other replicate from different treatments. The statistical significance of the calculated variable was tested using a Monte Carlo permutation test (with the number of maximum permutations set at 999) which generates levels of significance through randomization. Parametrical t-tests were used only to test for differences in total densities of treatments in each sampling day. For all tests the significance level adopted was $p<0.05$.

RESULTS

A total of 1715 individuals, belonging to 51 invertebrate taxa, were identified, with a predominance of polychaetes, oligochaetes and crabs. Figure 3 summarizes the results, showing densities of the most abundant species in the samples collected during the 95 days of the experiment, and the 3 sampling dates prior to Day 0.

As an overall pattern, most taxa occurred in very low densities and showed great temporal and spatial variations. A few taxa occurred in higher densities and these were also the ones responsible for early colonization of defaunated patches. The 10 most abundant taxa - Oligochaeta, the polychaetes *Isolda pulchella* Mueller, 1858, *Glycinde multidens* Mueller, 1858, *Nereis oligohalina* (Rioja, 1946), *Capitella* sp. and *Sigambra grubei* Mueller, 1858, Nemertinea and the decapods *Uca* spp. and *Eurytium limosum* (Say, 1818) - represented most of the sampled organisms.

Comparison of natural invertebrate assemblages revealed that the most common taxa were found in both sites, and that statistically significant differences, observed only in the first (R= 0.31; p=0.01) and the last (R= 0.487; p=0.01) sampling days, were due mainly to a greater abundance of oligochaetes and *Capitella* sp. in the Sandy Site and the ampharetid polychaete *Isolda pulchella* in the Muddy Site. Other taxa also present in both sites and which contributed to the observed dissimilarity were the polychaetes *Aricidea* sp. and *Nereis oligohalina* (higher abundance in the Muddy Site) and Nemertinea (higher abundance in the Sandy Site).

In the Sandy Site, defaunated areas were initially colonized by oligochaetes. While on Day 5 of the experiment these were the only taxa found in defaunated sediments of this site (DS-S and DM-S), in the Muddy Site colonization started with a more diversified set of organisms, which included the polychaetes *I. pulchella*, *Aricidea* sp. and *Sigambra grubei*, besides a few oligochaetes. After 95 days all of the eight most abundant taxa were found on defaunated patches in this site (with the sole exception of *Uca* spp on DM-M), most of them still in lower densities than those observed in natural samples. The exception

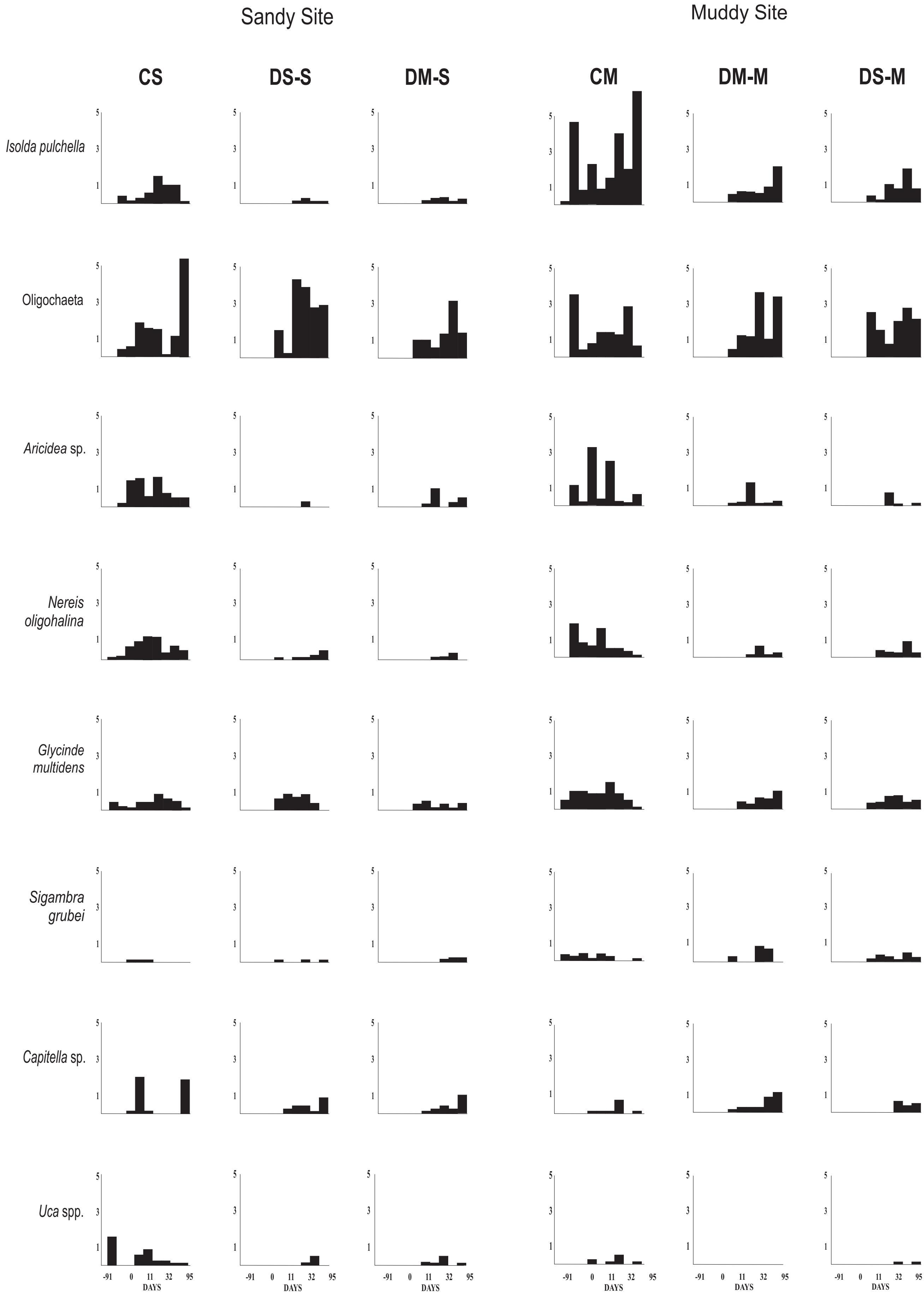

Figure 3. Mean abundances of the 8 most common taxa over time for control samples and defaunated treatments on each site. Values are given in number of individuals/experimental unit. * indicates where significant differences were observed.

was the high density of oligochaetes observed on DM-M samples on Day 95, much larger than those observed on natural samples. Analysis of total densities (considering all organisms) revealed that on Day 11 densities on defaunated treatments located in the Muddy Site were already similar to those on control samples, although differences in species composition were still evident. On Day 62 no differences in total densities among treatments were observed. In spite of densities in defaunated samples being the same as in control ones, high densities in the former were due mainly to high numbers of oligochaetes. On the last sampling day, densities on control samples from the Sandy Site were higher than those on defaunated samples (t= 2.48 for DS-S and t= 2.70 for DM-S), but species composition was already similar, with an overall predominance of oligochaetes. In the Muddy Site, densities were similar but species composition was still different mainly due to higher numbers of *I. pulchella* on control samples (R=0.392, p=0.005 for DM-M; R= 0.292, p=0.007 for DS-M).

As a general rule, recolonization was not affected by sediment composition, with different treatments located in the same site being colonized in similar ways. The sole exception was observed in samples taken from the Sandy Site on Day 21, when a higher density of oligochaetes was observed on samples containing the same type of sediment as the natural site where they were located (DS-S: defaunated sand located on the Sandy Site) and a higher colonization by *Aricidea* sp. on DM-S (R= 0.44; p= 0.006).

Recolonization was affected by the location of samples (local population effect). On Day 21 a higher colonization of defaunated sand sediments by oligochaetes was observed on samples located in the Sandy Site, while those located in the Muddy Site showed higher densities of *I. pulchella* (R= 0.294, p= 0.004). On Day 62 the latter was observed again in DS-M samples (R= 0.241, p= 0.009). For defaunated mud samples (DM-M and DM-S) a higher colonization by *I. pulchella* was observed on the samples located on the Muddy Site (which also showed higher natural densities of this species), specially on the last day of the experiment, although no significant overall differences were observed between these samples on D95.

DISCUSSIONS

The observed pattern of patchy spatial distribution and high temporal variation of the fauna is typical of macrobenthic associations in mangroves of the region and has been observed in other studies (LANA et al., 1997; BROGIM, 2001). The 51 taxa observed in this study constitute a high level of diversity in comparison to previous descriptions of local mangroves, but the numeric dominance of polychaetes and oligochaetes, followed by crustaceans and mollusks, and the conspicuousness of a few common taxa such as *I. pulchella*, *G. multidens*, *Capitella* sp. and the genus *Uca*, is a pattern that repeats itself in these environments all over Paranaguá Bay.

With 8 of the 10 most common taxa dominating both natural assemblages and those formed by colonization of defaunated patches, it appears that organisms from the other taxa, found only occasionally, in very low densities and usually as juveniles - as was the case with the bivalves *Telina lineata* Turton, 1819 and *Lucina pectinata* (GMELIN, 1791) - do not constitute viable populations with a reproductive capacity enough to allow effective breeding and occupation of new areas inside the mangroves. Though found as adults forming large populations in other adjacent estuarine environments, these taxa apparently are unable to reproduce and persist in mangroves. This could be caused either by pre-recruitment factors, such as low larval supply, which could be due to specific hydrodynamic properties of the area, or factors acting after recruitment in mangrove soils. Several properties of these environments have been proposed as causes of low infaunal densities, such as physical forces (e.g. desiccation), competition with an abundant epifauna, predation by this epifauna and by the nekton, low food quality and availability and chemical defenses produced by mangrove trees (ROBERTSON and ALONGI, 1992).

Comparison of natural assemblages revealed few differences between sites, with the Muddy Site being characterized by higher densities of *I. pulchella*, a burrowing detritivore usually associated with fine sediment, and the Sandy Site showing higher densities of oligochaetes in some of the sampling days. Although fine sediments usually have higher organic matter contents, being in theory able to support larger densities of infaunal organisms (SACCO et al., 1994), in this study total faunal densities were similar in both sites, being significantly different (t= 2.49; $p<0.05$) only on the second sampling date prior to the experiment, when higher densities were observed at the Muddy Site due to high occurrences of *I. pulchella* and oligochaetes.

These two taxa, the most abundant in control samples, were also, together with *Capitella* sp., the major colonizers of defaunated patches. Oligochaetes and capitellids are small organisms usually found in high densities after disturbance, and some, such as *Capitella* sp., are considered indicators of organic or oil pollution. On the other hand, ampharetid polychaetes, such as *I. pulchella*, are more sedentary, building a tube and remaining inside it for most of the time, feeding on detritus from the soil and the water column. They are not usually associated with early succession stages. Nevertheless, in this study, this species was found on defaunated sediment samples, especially on those placed on the Muddy Site, suggesting, as further discussed below, colonization through migration or larval recruitment carried on mainly by populations already established on the area. The influence of these differences in the mobility of the species on recolonization can be observed by analyzing the faunal composition of defaunated samples on the last day of the experiment. While on the Sandy Site, no differences remained in density or faunal composition between control (CS) and defaunated samples (DS-S and DM-S), on the Muddy Site faunal densities were still higher on control samples. The polychaete *I. pulchella* already appeared on defaunated samples, but still in lower densities, and there was a predominance of oligochaetes and *Capitella* sp. Defaunated samples on the Sandy Site were faster on reaching a faunal composition similar to that of the control samples because on Day 95 oligochaetes and *Capitella* sp. were dominating also the natural environment. As suggested by previous studies (*e.g.* LANA *et al*., 1996), the rate of recolonization is dependent on the mobility of the species involved, and in the case of the Muddy Site, the dominant species *I. pulchella* is less mobile, and therefore appeared in defaunated samples in lower densities when compared to the natural environment.

The exception to the general rule of recolonization not being affected by sediment type was the higher abundance of oligochaetes on DS-S in some of the sampling days. According to SNELGROVE *et al.* (1999), a few species (in their study capitellids and a bivalve) may colonize preferentially areas with the same type of sediment found where the adults live. This could also explain the occurrence of *Capitella* sp. on the Muddy Site where it was found on defaunated mud samples as early as Day 5, but on defaunated sand samples only after Day 32.

Testing of the third hypothesis, which considered that recolonization would be independent of sediment type but affected by other characteristics specific of each site, showed that in several moments samples located on a same site were colonized in similar ways and differed from those located on the opposite site, as previously described in the results observed for recolonization of *I. pulchella* on samples located on the Muddy Site. A higher abundance of this species was observed on the site where it naturally occurred in higher densities, indicating an active colonization by juveniles and adults coming from local populations. Reproductive characteristics of ampharetids is still little known, but all species with known life cycles have lecitotrophic larvae, with many developing inside or close to the mouth of the tube of the adult (ROUSE and PLEIJEL, 2001), which suggests a lack of a planktonic phase on development and, as a result, a low capacity for dispersal. This reproductive aspect might explain the pattern of recolonization observed for *I. pulchella* in this study. This pattern also conforms to the suggestion of SANTOS and SIMON (1980), who stated that species composition on disturbed areas tends to be more influenced by migration of post-larval stages and ends up reflecting the composition of the community immediately adjacent.

On most habitats, passive colonization by adults and juveniles tends to be an episodic event situated on a background of active colonization (SAVIDGE and TAGHON, 1988). This seems to be true for the majority of species found in mangroves. What remains unsettled is if the low observed adult abundances are a result of low recruitment rates or of high post-settlement mortality, that is, if population dynamics in these environments is controlled by external larval supply or by events acting on post-recruitment phases. Most species found in this study also conform to a concept of open populations. According to TODD (1998), a major portion of marine invertebrate populations in shallow waters are demographically open, forming systems characterized by great larval dispersal and an uncoupling between adult reproductive rates and larval establishment. For most benthic invertebrates, local production of larvae and juveniles have little or no direct role on determining the size of local populations, as the recruitment of larvae from other places provides the substantial increase of new individuals (CALEY *et al.*, 1996).

Most species found in this study occur in low abundances and fall into this model that considers the recruitment of larvae from other environments as the main controller of adult populations. This could also explain the high temporal variability observed in these populations, as establishment and recruitment are usually erratic due to the uncertainties associated with life in the plankton (WARWICK, 1993). As a result, drastic changes in species abundance may occur, leading to natural temporal changes in the structure of the community. This can make it harder to evaluate anthropogenic impacts on these communities, as the background over which these impacts should be measured is naturally unstable.

In this study, most of recolonization was performed by the few species naturally present in higher densities (oligochaetes on the Sandy Site and *I. pulchella* on the Muddy Site). For these species colonization of new areas and population dynamics are closer related to the abundance and reproductive rates of local organisms. Colonization by active migration over the substrate or the water column in local mangroves would, in this case, be important not only for highly mobile species, as proposed by CALEY *et al.* (1996) for marine environments as a whole, but also for some sedentariate and more abundant species, which are capable of establishing more stable populations, with higher reproductive rates, such as *I. pulchella*. These species, possibly better adapted to the harsh conditions of mangrove soils, were the main colonizers of new areas, which implies that recovery of local mangrove fauna after physical disturbance, caused by sources such as storms or human interference, may depend primarily on the reproductive success of local populations, and only secondarily on external larval supply.

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