BENTHIC MACROFAUNA OF *SPARTINA ALTERNIFLORA* MARSHES AND NEARBY UNVEGETATED TIDAL FLATS OF PARANAGUÁ BAY (SE BRAZIL)

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INTRODUCTION

The presence of plants in intertidal coastal areas can affect the composition and distribution of benthic associations. Plant structures increase environmental heterogeneity and food availability, besides providing additional substrata and protection from predation. Plants can also modify the hydrodynamic conditions, oxygen distribution and the stability of sediment (Kneib, 1984; Caperhart & Hackney, 1989; Lin, 1989). The extent of plant effects on invertebrate populations will depend, however, on the different shape, length and density of above- and below-ground structures, such as roots and rhizomes.

Spartina alterniflora marshes are typical features of estuarine systems along the Brazilian southeastern coast. The presence of mangrove woodlands restricts local *S. alterniflora* marshes to narrow pioneer formations at the seaward edge of tidal plains (Lana & Guiss, 1991; Angulo 1992; Costa & Davy 1992). Although the composition and distribution of salt marsh invertebrates from temperate areas of the northern hemisphere have been extensively investigated (Nichol, 1936; Kneib, 1984; Adam, 1990), studies of tropical and subtropical marsh fauna in Brazil are comparatively recent (Tararam & Wakabara, 1987; Takeda, 1988; Flynn, 1993; Netto, 1993; Bonnet *et al.*, 1994; Cunha, 1994).

Lana & Guiss (1991, 1992) stated that the presence of above- and below-ground biomass of *S. alterniflora* marshes exerts a strong influence on the composition and

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abundance of benthic macrofauna in the euhaline sector of Paranaguá Bay. They suggested that physical and chemical parameters may have a secondary role in determining local macrobenthic diversity and abundance. These studies, however, did not attempt to quantify the spatial variability of plant cover along the bay. It is known that the biomass and production of *S. alterniflora* is negatively correlated with the salinity (Gross *et al.*, 1990). Therefore, the presence of a distinct gradient of salinity and the degree of exposure along the bay, as shown by Lana (1986) for the sublittoral benthic macrofauna and by Knoppers *et al.*, (1987) for physical and chemical variables, could also modify salt marsh structure, affecting below- and above-ground plant biomass as well as associated benthic fauna.

In this paper, we investigate if the composition and distribution of the benthic macrofauna of *S. alterniflora* marshes and nearby unvegetated flats of Paranaguá Bay are affected along this salinity and environmental energy gradient.

MATERIALS AND METHODS

Study site

Paranaguá Bay (2520S - 2535S / 4820W - 4845W) is an estuarine system bounded by mangroves and salt marshes, extending for almost 50 km inland from Mel Island to the city of Antonina (Fig. 1). The regional climate is subtropical humid mesothermic with hot summers. Air temperature ranges from 16° C in winter to 34° C in summer. The annual precipitation averaged 2,248 mm between 1975 and 1984 (IPARDES, 1991). Although few studies have been carried out on the hydrodynamic conditions (Knoppers et al., 1987; Marone & Camargo, 1993), Paranaguá Bay has semidiurnal tides, characterized by diurnal inequalities with maximum amplitudes of ca. 2 m. According to Bigarella *et al.* (1978) and Knoppers *et al.* (1987), the bay can be divided into two sectors based on sediment nature and hydrographic characteristics. The first sector, including the area from Antonina to Paranaguá, is estuarine with silt-clay sediments. The second, from Paranaguá to Mel Island, presents both poly- and euhaline high energy characteristics and well sorted fine sand bottoms.

Sampling

In order to describe the specific composition and analyze the spatial distribution patterns of benthic invertebrates of the salt marshes and adjacent unvegetated tidal flats, 20 sites were sampled along a salinity and environmental energy gradient during July and August of 1991 (Fig. 1). At each site, faunal and sedimentological samples were taken in vegetated (1v to 20v) and nearby unvegetated (1nv to 20nv) areas.

Faunal samples were taken with a 25 cm in diameter and 30 cm height core tube (area of 0.05 m^2). Samples were fixed with 10 % formalin and sieved through 0.5 and 1 mm meshes. All specimens were identified to the lowest possible taxonomic level

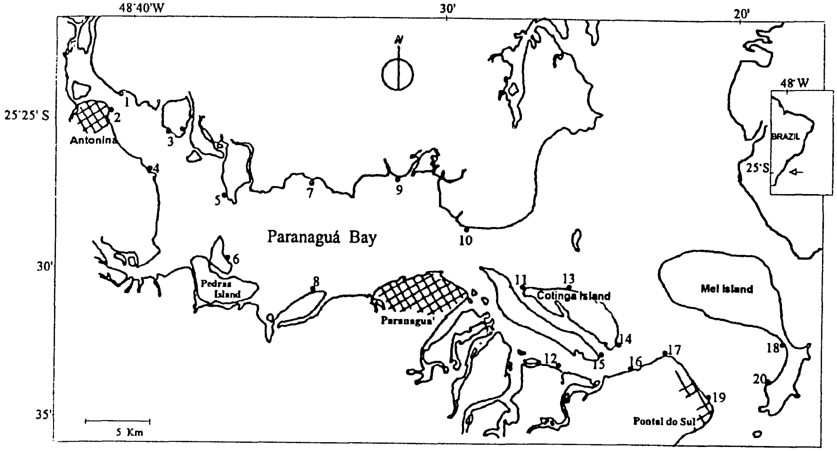

Fig. 1
Location of sampling sites along Paranaguá Bay, SE Brazil.

and counted under a dissecting microscope. The maximum height of *S. alterniflora* and density of stems (counted inside the core tube) were recorded.

Sediment samples were taken with a 50 mm in diameter and 100 mm height core adjacent to each faunal sample. Water content was estimated through water loss after the sediment was dried for 24 h at 70°C. Dried subsamples were combusted at 550° C for 60 min in order to determine organic content (Dean, 1974). Granulometric data was obtained by sieving and pipette analyses. Samples from the inner area of the bay were first treated with 30 % H_2O_2 due to the high percentages of silt-clay and organic content (Carver, 1972). Salinity of interstitial water (temperature-compensating refractometer, ±1ppt) and sediment temperature (±1° C) were also recorded.

Data analysis

Cluster analyses were conducted in order to verify the degree of association between stations (Q mode) and species (R mode) of benthic macrofauna. Analyses were performed using log (x+1) transformed data. Clustering was carried out with the Bray-Curtis measure of similarity and the unweighted arithmetic average sorting strategy (Romesburg, 1984).

Statistical parameters of Folk & Ward (1957) were initially determined for sediment samples. Sample clustering (Q mode) was also performed using the Bray-Curtis index of similarity and the group-average linking of normalised data. Principal component analyses (Q and R mode) were used to characterise plant cover (*S. alterniflora* height and stem density) and its relationship with physical and chemical parameters of salt marshes (Hair *et al.*, 1979).

On the basis of the classification and ordination analyses, the bay was divided into sectors. Differences between faunal and sedimentological parameters, comparing vegetated and unvegetated areas of each sector, were tested with one-way ANOVA. Data was log (x+1) transformed to increase the normality distribution. The Barttlet test was used to check for the homogeneity of variances. The Least Significance Difference (LSD) multiple comparison test was used whenever significant differences were detected (Hair *et al.*, 1979).

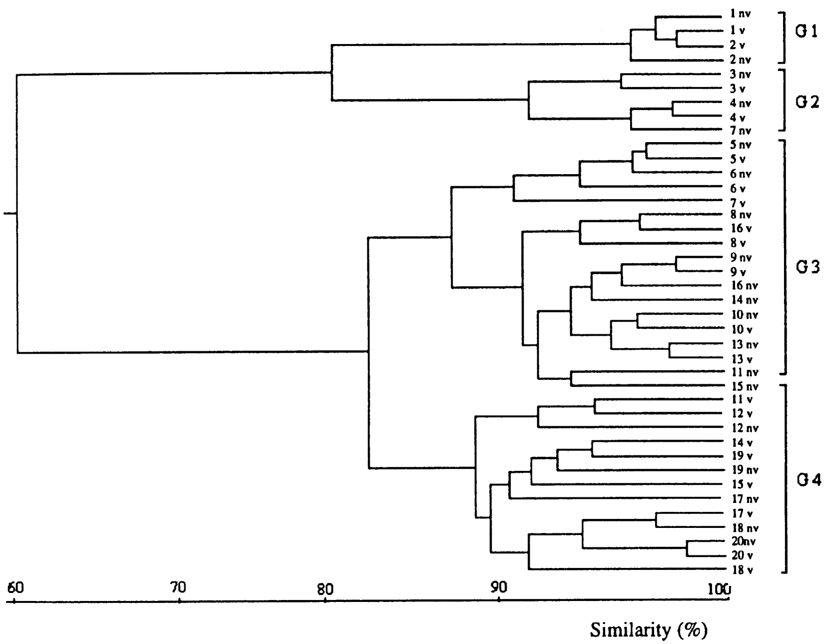

Fig. 2
Dendrogram (Q mode) of sedimentological parameters. v - vegetated sites; nv - nearby unvegetated sites.

RESULTS

Physical and chemical parameters

Classification analyses of sedimentological parameters yielded 4 station groups at 80 % similarity level (Fig. 2): - group 1, inner stations (1nv, 1v and 2v); - group 2, stations around Antonina (3v, 3nv, 4v, 4nv and 7nv); - group 3, intermediate bay stations

(8nv, 16v, 8v, 9nv, 9v, 16nv, 14nv, 10nv, 10v, 13nv, 13v, 11nv, 15nv); - group 4, outer bay stations (11v, 12v, 12nv, 14v, 19v, 19nv, 15v, 17nv, 17v, 18nv, 20nv, 20v and 18v).

Interstitial water salinity ranged from 17 - 21 in inner stations to 35 in outer stations. The salinity of salt marshes and unvegetated flats did not differ significantly (Table 1). Sediment temperatures varied between 17°C to 20°C with similar values in vegetated and unvegetated areas.

Water content was higher in stations next to Antonina (69.3 to 82.3 %) than those close to Mel Island (22.4 to 35.6 %). Water content of marshes and unvegetated flats did not differ significantly (Table 1).

Table 1. Results of one-way ANOVA evaluating the effects os sampling sites (vegetated vs unvegetated) on physical and chemical parameters after the division of the bay into sectors. NS-no significant difference.

	Inner bay	**Intermediate portion**	**Outer bay**
Salinity (ppt)	0,2 NS	0,4 NS	0,2 NS
Mean grain size (PHI)	0,1 NS	0,3 NS	0,7 NS
Standart deviation	0,6 NS	0,6 NS	0,4 NS
Sorting	0,8 NS	0,4 NS	0,4 NS
Skewness	0,5 NS	0,2 NS	0,1 NS
Sand (%)	0,8 NS	0,3 NS	0,6 NS
Silt (%)	0,3 NS	0,1 NS	0,8 NS
Clay(%)	0,4 NS	0,8 NS	0,4 NS
Water content (%)	1,2 NS	1,3 NS	1,1 NS
Organic content (%)	1,4 NS	1,4 NS	0,7 NS

Organic content ranged from 20 - 25 % next to Antonina, decreasing towards the outer stations (0.5 - 2.7 %). Although salt marshes showed higher sediment organic content, the difference was not significant (Table 1).

Sediment parameters were variable along the bay with mean grain size ranging from 2.4 - 5.4 . Sediments were medium silt around Antonina, very fine sand in the intermediate zone, and fine sand near Mel Island. Sorting values varied between 2.1 and 0.3. The sediments were poorly sorted with exception of the outer bay stations. A distribution towards fine sediments in most of the stations was indicated by negative skewness, with most sediment samples being leptokurtic. Analyses of variance between sediment parameters of marshes and unvegetated sites (divided into sectors according to classification analyses) did not show any significant differences (Table 1).

Salt marsh characterisation

Stem densities in salt marshes ranged from 120 to 560 m^{-2} and did not shown any gradient along the bay (Fig. 3). The maximum height of *S. alterniflora* was significantly greater in the inner bay (average of 110 cm) than in the outer bay (average of 50 cm, Fig. 3).

Principal component analyses relating plant cover and sediment variables are shown in Figure 4. On the R mode, the first and second axes were responsible for 89.9 % of total variance. In the first component, which accounted for 76.5 % of the total variability, the greatest positive value was sand percentage, and the greatest negative value was silt percentage. The second component (13.4 % of total variance) was related to sand content and *S. alterniflora* height. *S. alterniflora* height was shown to be primarily related to the sediment gradient. Higher marshes in the inner bay were associated with higher silt percentage and organic content, whilst the lower marshes, in the outer bay, were related to higher sand percentages.

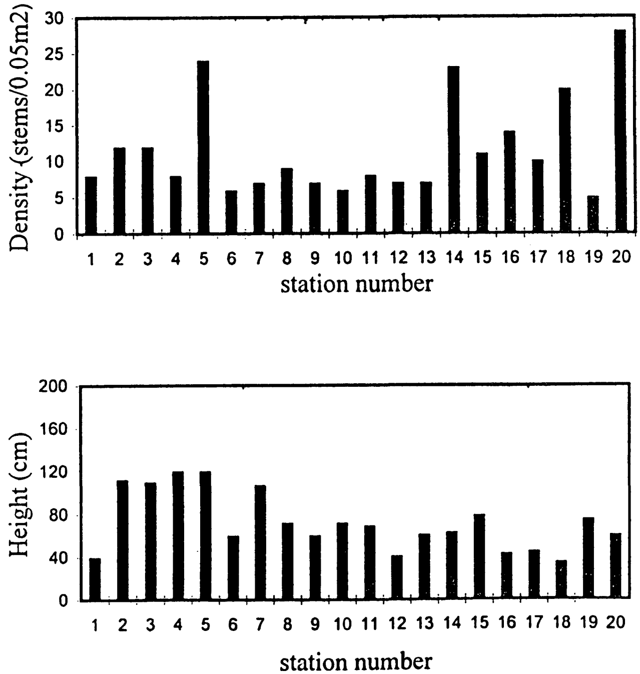

Fig. 3

Maximum height (cm) and stem density (number of stems/ 0.05 m^2) of *S. alterniflora* along Paranaguá Bay.

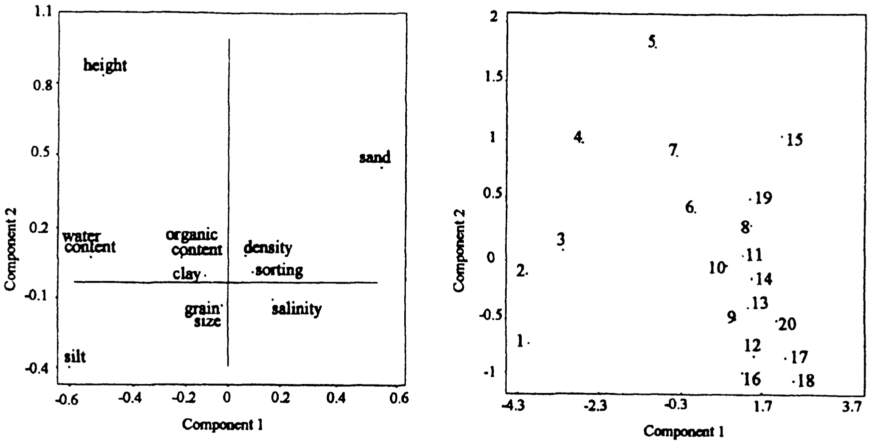

Fig. 4
Principal component analyses on R-and Q-mode, relating plant cover (*S. alterniflora* height and stems density) and sediment characteristics of marshes.

Benthic macrofauna

Faunal samples yielded 78 taxa with densities ranging from 1 to 1,038 inds.0.05 m^{-2} (Table 2). Species number increased towards the outer stations as shown in Figure 5.

A total of 72 taxa were found in unvegetated tidal flats (2,707 organisms). The bivalve *Anomalocardia brasiliana,* the deposit-feeding polychaete *Laeonereis acuta*, and the surface crawling gastropod *Heleobia australis* were the numerically dominant species, accounting for 40% of total macrofauna. The bivalve *Tellina* sp. and the polychaete *L. acuta* were the most widespread species on the unvegetated areas. Although representing less than 1 % of total fauna, *Tellina sp.* was found in 75 % of the unvegetated tidal flats samples.

In salt marshes, a total of 64 taxa were identified among 4,276 organisms. The omnivorous polychaete *Nereis oligohalina*, the tube-building deposit-feeding polychaete *Isolda pulchella* and the gastropod *Neritina virginea* accounted for 54% of total macrofauna. These species occurred in almost 80% of marshes, indicating a clear preference for the vegetated sites of the bay.

Cluster analyses in Q mode (Fig. 6a) of faunal data showed that the distribution of salt marshes and unvegetated areas of bay is clearly influenced by the salinity and environmental energy gradient. The analyses also separated vegetated and unvegetated areas, particularly those from Paranaguá to the outer bay (groups 3 and 4). Cluster analyses yielded four groups of stations: group 1 formed by the inner stations (1nv, 3nv, 1v, 2nv, 5nv and 3v); group 2 composed by stations 4nv, 4v, 5v, 7v, 7nv, 19v and 19nv; group 3 included the intermediate and outer marshes (8v, 9v, 10v, 14v, 15v, 16v, 17v, 18v and 20v); group 4 composed of the unvegetated flats from the same area of group 3. Stations 12nv, 12v and 13v were considered not grouped.

Table 2. Results of one-way ANOVA evaluating the effects of sampling sites (vegetated vs unvegetated) on faunal parameters after the division of the bay into sectors.

	Inner bay	**Intermediate portion**	**Outer bay**
Species number	1,9 NS	1,3 NS	0,1 NS
Total macrofauna	0,2 NS	1,5 NS	0,4 NS
Neritina virginea	5,4 NS	6,2*V>NS	6,8*V>NV
Heleobia australis	2,3 NS	0,1 NS	2,1 NS
Anomalocardia brasiliana	-	1,9 NS	2,4 NS
Nereis oligohalina	-	7,1* V>NV	11,9***V>NV
Laeonereis acuta	0,1 NS	3,2 NS	0,1 NS
Isolda pulchella	1,8 NS	4,6 NS	12,9***V>NV
Glycera americana	1,0 NS	2,7 NS	5,1**NV>V
Sphaeromopsis mourei	-	6,6*V>NV	15,1***V>NV

* *0,05<pp<0,01;**0,01<p<0,001; ***p<0,001; NS- no significant differences; V - vegetated sites; NV - nearby unvegetated.

Classification analysis of the inverse matrix discriminated 3 groups of organisms (Fig. 6b). Group I comprised species characteristic of salt marshes, such as *N. virginea* and *N. oligohalina*. Group II was divided into three subgroups: A - *Leucozonia nassa* and *Platynereis dumerilli*, widespread on the vegetated and unvegetated areas but not found in the inner bay; B - formed by species characteristic of unvegetated flats, such as *Tellina sp.* and *Sigambra grubii*; C - constituting species that occurred in both vegetated and unvegetated sites along all sectors of bay, such as *Lucina pectinata* and *Diopatra viridis*. Group III was formed by the polychaete *Nephtys fluviatilis* and the deposit-feeding gastropod *H. australis*. The gastropod *Acteocina bidentata*, the isopod *Sphaeromopsis mourei* and the tanaid *Kalliapseudes schubartii* were not grouped.

On the basis of classification and ordination analyses of sediment parameters, the bay was divided into sectors and analyses of variance were performed with the objective of testing differences between species number, total macrofaunal density, and abundance of numerically dominant species in salt marshes and unvegetated habitats (Table 2). Species number, total macrofauna and the densities of dominant organisms did not differ between marshes and unvegetated areas in the inner bay. In the intermediate area (stations 8 to 14, Table 2) *N. virginea*, *N. oligohalina* and *S. mourei* were significantly more abundant in salt marshes. Differences between vegetated and unvegetated flats were more evident in the high energy sector, where *N. virginea*, *N. oligohalina*, *I. pulchella* and *S. mourei* were significantly more abundant in salt marshes. Conversely, *Glycera americana* recorded significant higher population densities at unvegetated sites (Table 2).

DISCUSSION

Brandini *et al.* (1986) and Knoppers *et al.* (1987) reported the presence of a strong physico-chemical gradient in Paranaguá Bay, from the inner area, next to Antonina, to the outer bay, around Mel Island. The hydrographic characteristics of the inner bay are more influenced by the rainfall regime than the eastern sector, where the oceanic influence is more evident.

Spartina alterniflora marshes of Paranaguá Bay occur from poorly sorted silt-clay sediments, in the interior region, to well sorted fine sand near Mel Island. Sediment nature appears no to be a limiting factor for the colonisation process of local *S. alterniflora* marshes. Marsh structure, mainly stem height, is influenced by the exposure degree and salinity gradient. This gradient, however, seems not to affect total stem densities, as also shown by Netto (1993). Our results suggest a close relationship between higher forms of *S. alterniflora* and high clay and water contents, as well as poorly sorted sediments, typically found at the inner sector of Paranaguá Bay.

According to water mass classification based on salinity (Venice System), the area of the bay investigated could be divided into three different sectors: mesohaline (stations 1 to 7), corresponding to the Antonina region; polyhaline (stations 8 to 14), including the area from Pedras Island to Cotinga Island; euhaline (stations 15 to 20) from the eastern end of Cotinga Island to Mel Island (Fig. 1).

In the mesohaline sector, the benthic macrofauna and sediment characteristics of stations west of Antonina clearly differ from more eastern stations. In this sector, although species richness is low, the composition and abundance of benthic invertebrates differ between unvegetated flats and *S. alterniflora* marshes. In the unvegetated sites, the surface crawling gastropod *Heleobia australis*, an eurihaline and r-strategist species (Lana, 1986), is the numerical dominant. Epibenthic forms are also the most abundant organisms in local salt marshes, though represented by *Cassidinidea tuberculata* and *Neritina virginea*. Sediments of the mesohaline sector, with high proportions of fine particles, organic and water contents are suggestive of a highly anaerobic habitat. The area, probably subjected to elevated sedimentation rates, is practically devoid of infaunal species, with the exception of some polychaetes, such as *Nephtys fluviatilis*. Conversely, shoots and stems of local *Spartina alterniflora* support a dense epifauna,

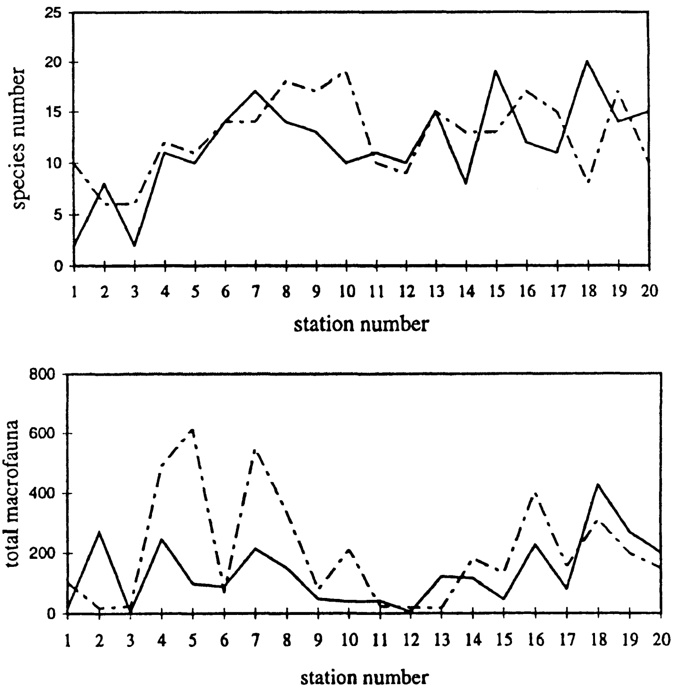

Fig. 5
Number of species and total macrofauna at salt marshes (- - -) and nearby unvegetated area (–) along Paranaguá Bay.

as also recorded in the euhaline sector by Lana & Guiss (1991, 1992). The presence of this epifauna can be attributed to an increase in substratum availability and to the development of micro- and macroalgae on the living and dead tissues of *S. alterniflora*. However, *Heleobia australis*, a typical epibenthic form that probably also feeds on the algal film associated with the sediment, was either absent or occurred only in low densities in mesohaline salt marshes. *H. australis* is a well known opportunistic species which can be found from sublittoral to intertidal areas in almost all estuarine systems from S to SE Brazil (Bemvenuti *et al.*, 1992; Lana, 1986). This unexpected pattern can not be explained by present data.

In the stations east of Antonina, still inside the mesohaline sector, species richness increases as a direct effect of the decrease in fine sediment content. Infaunal organisms, such as *Laeonereis acuta* on the unvegetated flats and *Isolda pulchella* on salt marshes, are the dominant species. Analyses of variance did not show any significant differences between population densities at vegetated and unvegetated sites, suggesting that in the mesohaline sector, species are not characteristic of either environment. High sedimen-

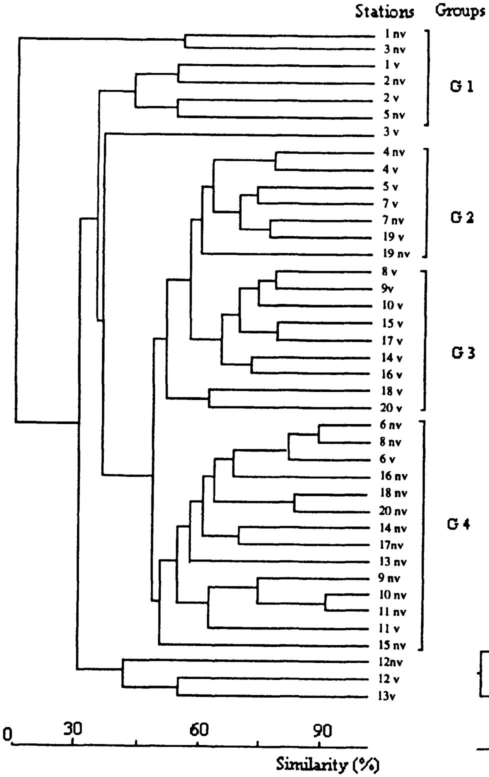

Fig. 6a

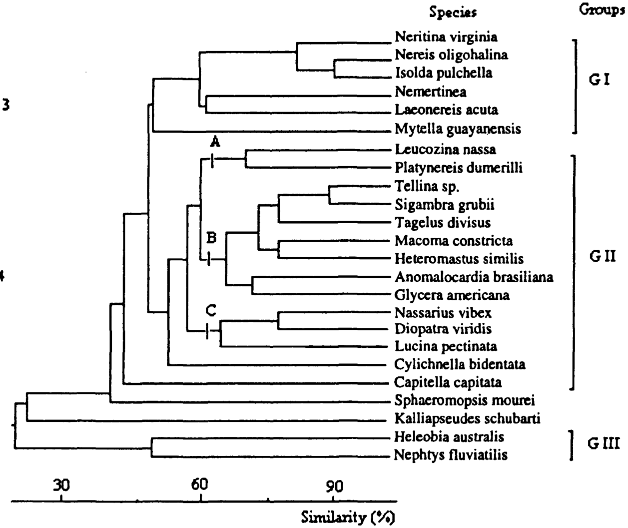

Fig. 6b

Similarity dendrogram of sampling sites (a) and macrofaunal species (b) at vegetated (v) and nearby unvegetated sites (nv).

tation rates appear to prevent the development of a more stable association when compared with other sectors.

The polyhaline sector, which covers the area from Paranaguá to Cotinga Island (Fig. 1), presents more visible differences between benthic invertebrates in *S. alterniflora* marshes and nearby unvegetated areas. The bivalve *Anomalocardia brasiliana*, absent in the mesohaline sector, is the most abundant species in the unvegetated areas together with the predatory polychaete *Glycera americana*. An increase in the abundance of species characteristic of salt marshes, such as the polychaete *N. oligohalina*, also occurs. Population density of *N. oligohalina* is positively correlated with above-ground biomass of *S. alterniflora* (Lana & Guiss 1992), and sand percentages, but negatively correlated with water content (Netto, 1993). This species is closely associated with poly- and euhaline marshes. Although these salt marshes are lower than those from mesohaline sector, the sedimentation rates are also probably low, determining an increase of epibenthic richness and abundance, as shown by the high densities of the isopod *Sphaeromopsis mourei*.

The higher environmental energy of the euhaline sector, near Mel Island, is apparent from sediment characteristics, such as fine, well-sorted sand, and low water and organic contents. Benthic associations in this sector seem to be heavily influenced by the degree of exposure of local flats to waves and currents. In more exposed sites, such as stations 17 and 20, sediments are very sandy with low organic content and the number of species is low, similar to the mesohaline sector, although with a different species composition. The very compacted sands of these flats, together with occasional wave action during winter, tend to hinder the establishment of infaunal populations. The suspension-feeding *A. brasiliana* and *K. schubartii* were numerically dominant species in unvegetated areas. In the salt marshes, *Scolelepis squamata*, a common polychaete in adjacent sandy beaches (Souza & Gianuca, 1995), is the most abundant, species besides *N. oligohalina*, a typical species of sandy marshes. Conversely, in sheltered sandy areas, species richness is the highest recorded of all sectors. Besides suspension-feeding forms, a great number of infaunal species, such as the polychaete *G. americana*, were found in unvegetated tidal flats. In the salt marshes, where species number is higher, *N. oligohalina* and *I. pulchella* are numerically dominant species. Population densities of *I. pulchella* are positively correlated with above-ground biomass of *S. alterniflora* (Lana & Guiss, 1992) and negatively correlated with clay percentage (Netto, 1993). The higher population densities of *I. pulchella* in the euhaline marshes could also be attributable to the higher detritus biomass in flats of this sector of Paranaguá Bay (Netto, 1993)

In conclusion, the composition and distribution patterns of benthic associations in salt marshes and unvegetated tidal flats of Paranaguá Bay are clearly conditioned by the degree of exposure and the salinity gradient. Although sediment characteristics are very similar between salt marshes and nearby unvegetated areas, the composition and abundance of benthic invertebrates can differ, particularly in the poly- and euhaline sectors. Those differences reflect the different sedimentation patterns prevailing along the bay.

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ABSTRACT

The composition and distribution of benthic macrofauna in *Spartina alterniflora* marshes and nearby unvegetated tidal flats of Paranaguá Bay (SE, Brazil) were investigated. Samples were taken along a salinity and physical gradient, from the inner to the outer bay. The bay was divided into sectors according to its physico-chemical and faunal characteristics. Salt marshes were affected by the gradient, with the tallest formations developing in the mesohaline sector and the lowest ones in the euhaline sector. Macrobenthic associations were also affected, with the mesohaline sector presenting a low species richness of predominantly epibenthic forms. In this sector, the composition and abundance of benthic macrofauna of the salt marshes and unvegetated flats were distinct. Species richness of the polyhaline sector, particularly of the infaunal taxa, was higher than that of the mesohaline sector. Differences between the fauna of marshes and flats became increasingly evident towards the euhaline, high energy sector, characterized by the highest species richness along the bay. Benthic associations from marshes and unvegetated flats were clearly structured by the salinity and physical gradient. Although salt marsh and flats present a relative homogeneity in physico-chemical parameters, the composition and abundance of associated benthic fauna can vary widely, particularly in poly- and euhaline sectors.

Key words: Macrofauna, *Spartina alterniflora* marshes, tidal flats, Brazil

RESUMO

Macrofauna bêntica de marismas de Spartina alterniflora e baixios não vegetados da Baía de Paranaguá (Brasil). A composição e a distribuição da macrofauna bêntica em marismas de Spartina alterniflora e em baixios não vegetados adjacentes foram investigadas na Baía de Paranaguá (Paraná, Brasil). As amostras foram tomadas ao longo de um gradiente de salinidade e energia ambiental, desde a entrada até a região interior da baía, dividida em setores de acordo com suas características faunísticas e físico-químicas. As marismas foram afetadas por este gradiente, com as formações mais altas presentes no setor mesohalino e as mais baixas no euhalino. As associações macrobênticas foram igualmente afetadas, com o setor mesohalino apresentando um baixo número de espécies, predominantemente epibênticas. Neste setor, a composição e abundância da macrofauna bêntica variaram entre áreas vegetadas e não vegetadas. A riqueza de espécies, principalmente das formas infaunais, aumentou no setor polihalino. Diferenças na composição e abundância da fauna entre áreas vegetadas e não vegetadas tornaram-se progressivamente mais evidentes em direção ao setor euhalino, de alta energia, caracterizado pela maior riqueza de espécies ao longo de todo o gradiente. As associações bênticas de áreas vegetadas e não vegetadas foram claramente condicionadas pelo gradiente de salinidade e energia ambiental. Embora marismas e áreas não vegetadas adjacentes apresentem características físico-químicas similares, a composição e a abundância de suas faunas bênticas podem sofrer grandes variações, principalmente nos setores mesohalino e euhalino, devido aos diferentes padrões de sedimentação ao longo da baía.

Palavras-chave: Macrofauna, *Spartina alterniflora*, marismas, planícies de maré, Brasil.

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