Polychaete Distribution and Abundance in Intertidal Flats of Paranaguá Bay (SE Brazil)

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POLYCHAETE DISTRIBUTION AND ABUNDANCE IN INTERTIDAL FLATS OF PARANAGUÁ BAY (SE BRAZIL)

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ABSTRACT

The effects of plant zonation on polychaete distribution and abundance were studied along an environmental gradient in intertidal flats of Paranaguá Bay (SE Brazil). Two polychaete stocks with marked preference for specific haline regimes were recognized with a low degree of spatial overlap in species distribution. Species richness and abundance were lower in the mesohaline sector, characterized by fine sediments and high organic carbon content, than in the high-energy euhaline sector, dominated by moderately sorted fine sands low in organic carbon content. Faunal differences were primarily defined by salinity and environmental energy gradients and only secondarily by the ability of polychaetes to discriminate among unvegetated, salt marsh or mangrove swamp habitats.

Zonation patterns in the form of continuous or discontinuous changes in floristic structure are a well-known feature of salt marshes and mangrove swamps both in temperate and tropical latitudes (Pennings and Callaway, 1992; Seeliger, 1992). Zonation in itself is the product of a number of different factors, such as plant succession, shoreline changes or species-specific physiological responses to environmental gradients. Sediment texture, stability, transport and chemistry vary along intertidal sites and are heavily influenced by tidal elevation and the presence of distinct plant cover (Patterson and Mendelssohn, 1991).

Although biological processes, such as predation, adult-larval interactions and interspecific competition, have been shown to regulate intertidal invertebrate assemblages, the importance of physical factors expressed through habitat-preferences can not be underestimated. Different species have preferred optima and tolerance limits along environmental gradients and one should expect that benthic fauna responds to sediment variation across tidal flats colonized by salt marshes or mangroves. A number of works attempting to relate species richness or abundance to plant zones along the intertidal in tropical or subtropical ecosystems have yielded controversial results, either correlating faunal patterns with plant zonation or failing completely to do so. In general, studies dealing with hydroids (Calder, 1991), mollusks (Plaziat, 1984; Morgan and Hailstone, 1986), polychaetes (Ibarzabal, 1985) or overall fauna (Frith et al., 1976; Wu et al., 1992) have suggested that the composition and distribution of macrobenthos are in close relationship with plant zonation. Conversely, Alongi (1987, 1989) and He (1991) showed that temperature, salinity or sediment texture were the most important factors regulating faunal distribution in mangrove estuaries of Australia and China, respectively.

In this paper we determine the species composition and abundance of polychaetes in vegetated intertidal flats of Paranaguá Bay (SE Brazil) and assess the effect of different habitat types across tidal and vegetational gradients on species richness, species composition, total abundance and density of numerically dominant species.

MATERIAL AND METHODS

Paranaguá Bay is a semi-enclosed estuarine system bounded by mangroves, salt marshes, and extensive unvegetated tidal flats, located in the State of Paraná, southeastern Brazil (Fig. 1). There are

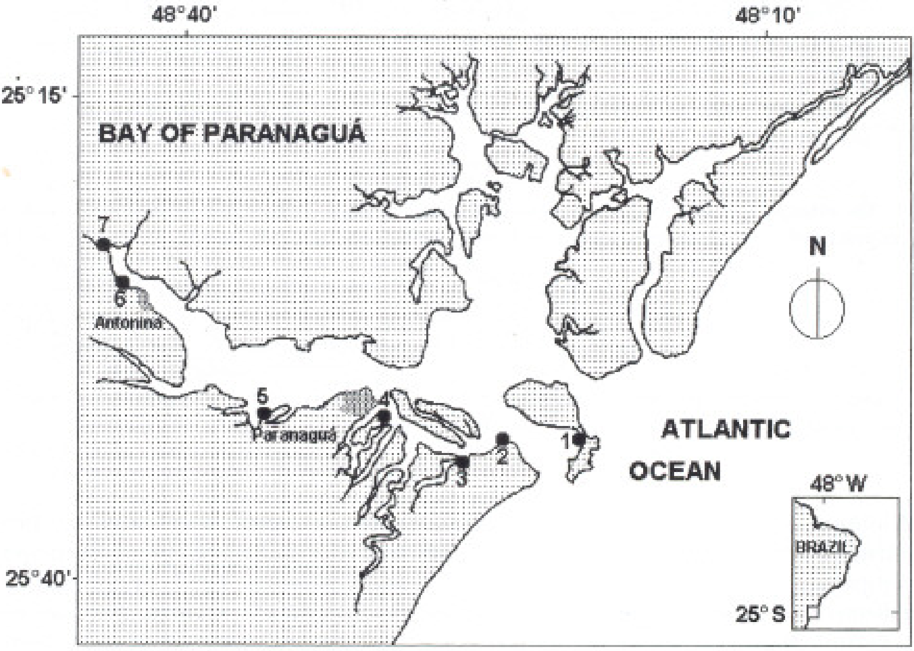

Figure 1. Location of sampling stations (•) in Paranaguá Bay, Paraná State, southeastern Brazil.

marked salinity and environmental energy gradients from the meso- and polyhaline upper estuarine reaches to the high-energy euhaline section near the bay outlet (Knoppers et al., 1987). Netto (1993) divided the bay into different sectors according to sediment characteristics of tidal flats. Inner sectors, with meso- and polyhaline features, are characterized by poorly sorted fluid sediments, with the predominance of medium silt, and high organic and water contents. Deposits in the high-energy euhaline sector, close to the bay outlet, tend to be dominated by well-sorted fine sands, with low organic content.

Aerial surveys indicate that the tidal flats of Paraná State cover an area of 310 km^2 (Angulo and Muller, 1990). In Paranaguá Bay, tidal flats can reach a width of 2 km and are mainly colonized by mangrove woodland and salt marshes, though extensive areas remain unvegetated. Pure stands of the cord grass *Spartina alterniflora*, ranging from high creekside to short discontinuous mangrove-fringing belts, form the bulk of saltmarsh vegetation all around the bay. Local mangroves trees are *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana*. Mangrove vegetation shows different aspects along the bay, from almost monospecific *L. racemosa* in high-energy euhaline areas to well-developed mixed formations in sheltered sectors (Martin, 1993). *Rhizophora mangle* usually forms the outer margin of local mangroves, followed landward by more or less conspicuous belts of *L. racemosa* and *A. schaueriana*. Vegetation patterns can vary depending upon the distance of the mangroves from the bay outlets and zonation patterns are not always well defined. However, even when there is overlap between species and only a slight pattern of zonation with respect to shore level, it is still possible to recognize spots or patches of a same plant species.

In order to assess the effect of environmental gradients and different habitat types upon the composition and distribution of polychaete species, seven sampling stations were established along the east-west axis of the bay, from the high-energy euhaline sector (St. 1 at Mel Island, St. 2 at Baguaçu tidal creek, St. 3 at the mouth of Maciel River), through the polyhaline sector (St. 4 at Valadares Island and St 5 at the mouth of Embocuí River, near the city of Paranaguá) to the low-energy mesohaline sector (St. 6 at Graciosa Point and St. 7 at Figueira Island, near the city of Antonina), in September and October 1989 (Fig. 1). At each station, five distinct habitats were sampled along transects running landward: 1) unvegetated flats; 2) salt marshes made up of the cord grass *Spartina alterniflora*; 3) zone of *Rizophora mangle*; 4) zone of *Laguncularia racemosa*, and 5) zone of *Avicennia schaueriana*. This design allowed for the sampling of 35 different sites along the bay (5 different habitats per 7 different stations). Replicates of five faunal samples were randomly taken with a 15-cm-diameter core tube to a depth of 15 cm from similar tidal levels at each site. Sediment parameters (mean grain diameter, sorting, sand, silt, and clay contents, together with organic and inorganic car-

Table 1. Mean values (standard deviation in brackets) of total polychaete density (ind.·0.018 m^{-2}), species number (per 0.018 m^2), grain size (phi), sorting, sand (%), silt (%), clay (%), organic carbon (%) and inorganic carbon (%) contents among habitat-types and from Station 1 to Station 7.

Habitat local	Total density	Species number	Grain size	Sorting	Sand	Silt	Clay	Organic carbon	Inorganic carbon	Salinity
FLAT	44.2	7.8	2.5	0.9	92.0	7.5	0.4	7.5	1.0	23.8
	(23.4)	(3.8)	(0.4)	(0.5)	(11.2)	(10.1)	(1.1)	(7.3)	(0.8)	(6.8)
MARSH	90.3	8.7	2.5	1.0	91.3	8.1	0.4	9.5	1.1	22.8
	(68.6)	(3.4)	(0.3)	(0.6)	(10.7)	(9.7)	(1.1)	(7.8)	(1.0)	(9.5)
RHIZO	58.3	7.4	2.6	1.1	88.8	10.5	0.6	8.7	1.1	24.4
	(65.2)	(3.0)	(0.5)	(0.6)	(14.7)	(13.1)	(1.7)	(7.3)	(1.0)	(7.1)
LAGUN	46.3	6.0	2.4	1.0	93.3	6.4	0.0	8.4	0.9	23.7
	(29.8)	(2.4)	(0.4)	(0.4)	(3.7)	(3.8)		(6.8)	(0.8)	(8.9)
AVIC	32.4	5.6	2.5	1.0	92.2	6.9	0.8	11.2	1.4	24.7
	(17.4)	(1.7)	(0.3)	(0.5)	(6.3)	(5.3)	(2.3)	(8.3)	(1.3)	(7.7)
St 1	103.6	9.0	2.8	0.7	95.7	4.2	0.0	4.6	.5	27.2
	(59.6)	(2.0)	(0.1)	(0.1)	(2.4)	(2.4)		(1.7)	(0.1)	(1.6)
St 2	81.2	8.6	2.5	0.8	94.5	5.3	0.0	7.2	1.0	31.8
	(42.8)	(2.3)	(1.1)	(0.2)	(2.9)	(2.8)		(5.8)	(0.7)	(0.4)
St 3	37.8	6.6	2.7	0.8	93.7	5.8	0.0	7.9	0.7	30.2
	(24,0)	(0.5)	(0.2)	(0.2)	(2.6)	(2.4)		(6.1)	(0.6)	(1.3)
St 4	61.2	9.0	2.7	0.5	97.7	2.3	0.0	3.8	0.4	27.0
	(68.9)	(2.9)	(0.2)	(0.1)	(0.8)	(0.8)		(0.8)	(0.1)	(0.0)
St 5	52.8	9.0	2.4	0.6	98.2	1.8	0.0	2.6	.3	25.8
	(37.4)	(3.8)	(0.1)	(0.1)	(1.1)	(1.1)		(1.4)	(0.3)	(0.8)
St 6	14.0	3.6	1.9	1.3	87.7	12.3	0.0	16.7	2.2	11.8
	(1.4)	(0.5)	(0.2)	(0.1)	(2.8)	(2.8)		(0.9)	(0.3)	(3.4)
St 7	29.6	4.0	2.5	2.1	73.3	23.4	3.3	20.6	2.5	13.6
	(15.4)	(1.0)	(0.7)	(0.3)	(13.3)	(12.7)	(2.2)	(2.2)	(0.8)	(1.7)

bon), and salinity of ponded water were measured from adjacent sediment samples. Organic carbon was estimated from dried sediment subsamples combusted at 550°C for 60 min, and inorganic carbon from an additional 60-min combustion at 1,000°C. Faunal samples were sieved through 500- and 1,000-μm mesh sieves, fixed in 10% formalin and preserved in 70% alcohol. All polychaete specimens were identified at the lowest practical taxonomic level and counted under a dissecting microscope.

The number of species, total density and the density of numerically dominant species were computed for each replicate to evaluate and compare faunal changes among sites. The basic biological matrix comprised, in addition to total density and species number, density values of the 13 top-ranked polychaete species, defined by absolute abundance (more than 30 individuals) and constancy (present in at least 5 replicates) criteria. All subsequent analyses were applied on log (x + 0.001) transformed biological and physicochemical data.

One-way MANOVAs (multivariate analysis of variance) were used to test for significant differences ($P < 0.05$) in means of faunal (species number and total density) and physicochemical parameters, with stations and habitats considered as fixed factors. Whenever significant effects were detected, Least Significant Difference post hoc tests were performed to compare between-habitat or between-station means.

To represent site or species similarities in the form of dendrograms, cluster analyses of species and sites were applied to a frequency matrix of the numerically dominant species, using 1-Pearson's r coefficient (R-mode), City-block or Manhattan distance (Q-mode), and the unweighted arithmetic average sorting strategy (UPGMA).

Multi-dimensional scaling ordination analysis (MDS) was applied to a distance matrix (City-block distance) of the 35 sampling sites. MDS arranges sites in a space with a particular number of dimensions so as to reproduce the observed distances. To examine the degree to which distribution of sampling sites could be related to environmental factors, multiple regression analysis was used to regress physicochemical variables on the coordinates for the two first dimensions of MDS.

Results

Mean values and standard deviations of faunal and physicochemical variables at stations 1 to 7 and among habitat-types are shown in Table 1. Spatial varia-

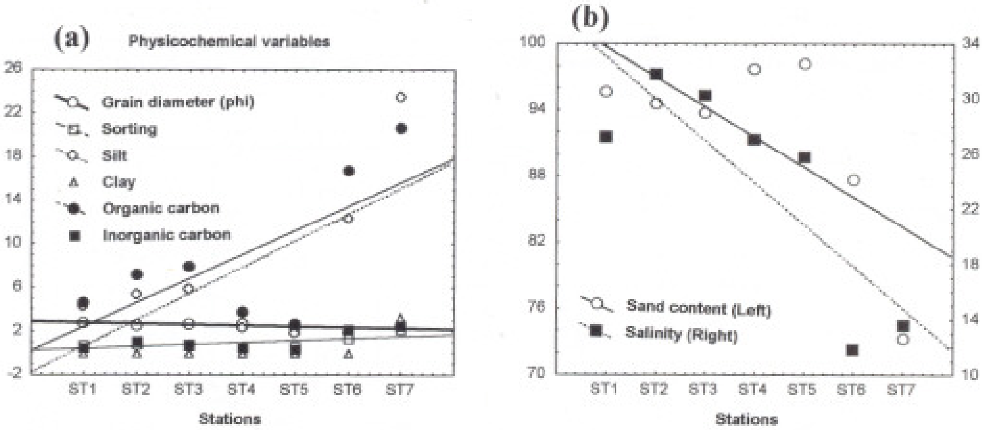

Figure 2. (a) Mean sediment grain size (∅), sorting coefficient, silt (%), clay (%), organic and inorganic carbon (%) contents at stations 1 to 7 in Paranaguá Bay, with fitted functions. (b) Sand content (%) and salinity (‰) at stations 1 to 7 in Paranaguá Bay, with fitted functions.

tions in temperature, salinity and sediment parameters are shown in Figure 2 a,b. Salinity of interstitial water showed a marked gradient from stations in the mesohaline sector, ranging from 11.8 to 13.6‰, to the high-energy euhaline sector, with values higher than 30.0‰. Gradients of sand, organic carbon and silt contents were also evident, with inner stations characterized by less than 85% sand and with silt contents higher than 20%; organic carbon percentages were less than 10% in poly- and euhaline stations, but higher than 15% in the mesohaline sector. A less marked gradient was evident for inorganic carbon content, lower in poly- and euhaline than in mesohaline sectors. Clay fraction was absent throughout the bay, with the exception of the innermost station, with a 3.3% value. Sediment grain size ranged from 1.93 to 2.77 ∅ and was significantly lower in St. 6. Most deposits were dominated by fine sands, moderately sorted in the eu- and polyhaline sites, but poorly sorted in the inner stations.

Significant differences ($P < 0.05$) among stations were evident for all sediment variables, with stations 6 and 7 of the mesohaline sector clearly separated from the others (Table 2). However, no significant differences were evident among habitats (Table 2). Average values of salinity and sediment parameters were rather constant along transects running landward, with a non-significant tendency of an increase in organic carbon content and a decrease in silt content towards *Avicennia* zones.

Twenty-nine polychaete species were recorded. The ampharetid *Isolda pulchella*, the nereidids *Laeonereis acuta* and *Nereis oligohalina*, the capitellids *Heteromastus similis* and *Capitella capitata*, the nephthyid *Nephthys fluviatilis* and the pilargiid *Sigambra grubii* accounted for 85% of all individuals. Species number and total polychaete abundance varied significantly along the same gradients as the environmental variables (Fig. 3a, Table 3). The polychaete fauna were less diverse at mesohaline stations 6 and 7 (averages of 3.6 and 4 species·0.018 m^{-2}), but relatively diverse in the poly- and euhaline sectors, with up to 9 species·0.018 m^{-2}. Total polychaete density was significantly higher in euhaline (up to 103.6 ind·0.018 m^{-2}) than in mesohaline sites (down to 14.0 ind·0.018 m^{-2}), with intermediate values in the polyhaline sector (61.2 ind·0.018 m^{-2}). Between-habitat variation was not evident (Fig. 3b, Table 3). Species numbers were similar across intertidal habitats, but average densities were significantly lower in *Avicennia* than

Table 2. Summary of results of 1-way MANOVA evaluating effects of station and habitat locations on sediment variables. Analysis performed on log (x + 0.001) transformed data. $P > 0.05$, no significant differences. Differences between stations determined by LSD post hoc comparisons.

	Station location		
Dependent variable	F-value	p-level	Post hoc comparison
Diameter	4.68	0.002	St.1=St.2=St.3=St.4=St.5=St.7>St.6
Sorting	44.09	0.000	St.1=St.2=St.3=St.4=St.5>St.6>St.7
Sand Content	12.90	0.000	St.1=St.2=St.3=St.4=St.5>St.6>St.7
Silt content	10.76	0.000	St.1=St.2=St.3=St.4=St.5>St.6>St.7
Clay content	11.00	0.000	St.1=St.2=St.3=St.4=St.5>St.6>St.7
Organic carbon	20.19	0.000	St.1=St.2=St.3=St.4=St.5>St.6=St.7
Inorganic carbon	16.81	0.000	St.1=St.2=St.3=St.4=St.5>St.6=St.7
Salinity	111.57	0.000	St.1=St.2=St.3=St.4=St.5>St.6>St.7
	Habitat location		
Dependent variable	F-value	p-level	Differences
Diameter	0.52	0.716	NS
Sorting	0.69	0.991	NS
Sand content	0.19	0.940	NS
Silt content	0.21	0.928	NS
Clay content	0.33	0.853	NS
Organic carbon	0.23	0.914	NS
Inorganic carbon	0.23	0.914	NS
Salinity	0.06	0.994	NS

in the other habitats. Differences in average densities or species numbers among replicates within a same habitat were often greater than differences among habitats along a transect.

Classification and ordination methods were not able to assign species or site groupings to specific floristic zones but rather to the different sectors along a salinity and environmental energy gradient. Three species groups could be recognized at the 0.8 level in the cluster analysis of polychaete frequency data (Fig. 4). A first group, numerically dominant in mesohaline stations 6 and 7, was made up by *Nephthys fluviatilis* and *Laeonereis acuta*. A second group was composed of widespread species, such as *Lumbrineris januarii*, *Nereis oligohalina* and *Capi-*

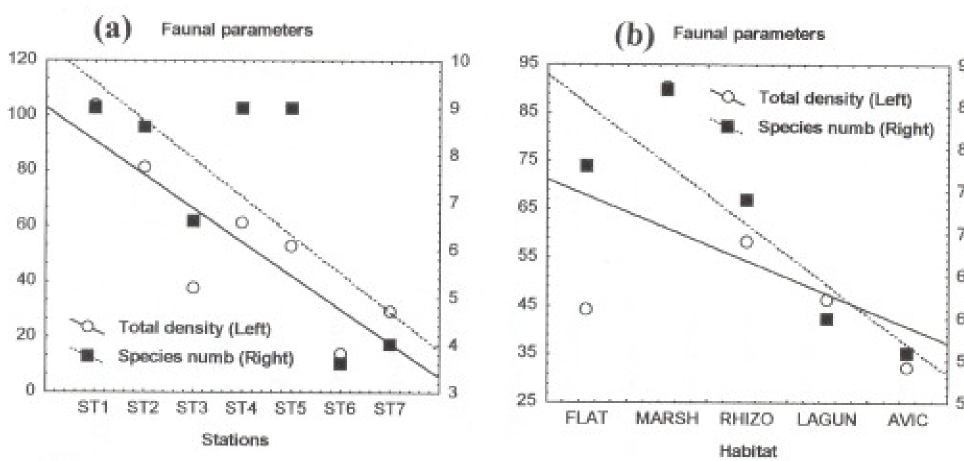

Figure 3. a) Total polychaete density and species numbers (mean values per 0.018 m^2) at stations 1 to 7 in Paranaguá Bay, with fitted functions. (b) Total polychaete density and species numbers (mean values per 0.018 m^2) in different habitat-types, with fitted functions.

Table 3. Summary of results of 1-way MANOVA evaluating effects of station and habitat locations on faunal variables (total polychaete density and species number · $0.018m^{-2}$). Analysis performed on log (x + 0.001) transformed data. $P > 0.05$, no significant differences. Differences between stations determined by LSD *post hoc* comparisons.

		Station location	
Dependent variable	F-value	p-level	Post hoc comparison
Total density	2.69	0.033	St.1=St.2=St.3=St.4=St.5>St.6=St.7
Species number	6.05	0.000	St.1=St.2=St.3=St.4=St.5>St.6=St.7
		Habitat location	
Dependent variable	F-value	p-level	Differences
Total density	0.87	0.049	FLAT=MARSH=RHIZO=LAGUN>AVIC
Species number	0.99	0.420	NS

tella capitata, which were found both in poly- and euhaline sites, though more frequent in the latter. A third group was formed by a group of species practically restricted to euhaline sites, such as *Mediomastus californiensis, Scoletoma tetraura, Isolda pulchella, Scoloplos rubra, Sigambra grubii, Heteromastus similis, Diopatra viridis*, and *Glycinde multidens*.

Site groupings were more heterogeneous, but there was a clear grouping of mesohaline sites from stations 6 and 7 together (Fig. 5). Mangrove sites from poly- and euhaline stations tended to form two mixed groups, with *Rhizophora, Avicennia* and *Laguncularia* sites clustering without a clear pattern. Marsh and flat sites from euhaline and polyhaline stations comprised a fourth group.

MDS ordination revealed a continuous distribution of sampling sites, which corresponded loosely to their geographic location along a two-dimensional space, though mesohaline sites were clearly separated from all the others (Fig. 6). Good-

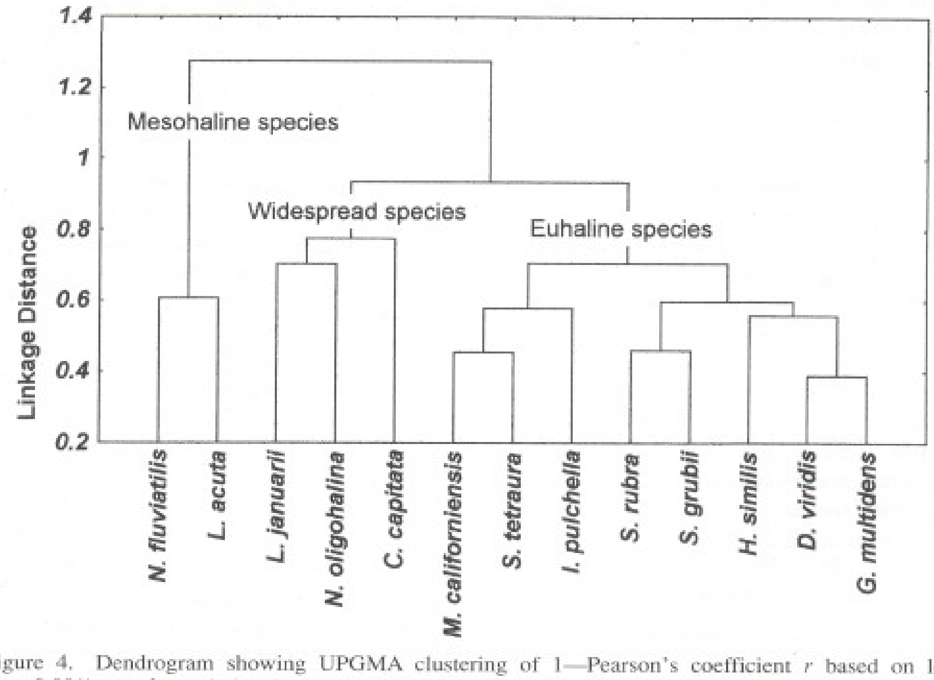

Figure 4. Dendrogram showing UPGMA clustering of 1—Pearson's coefficient *r* based on log (x + 0.001) transformed abundance of 13 top-ranked polychaete species at the 35 sampling sites from intertidal flats of Paranaguá Bay.

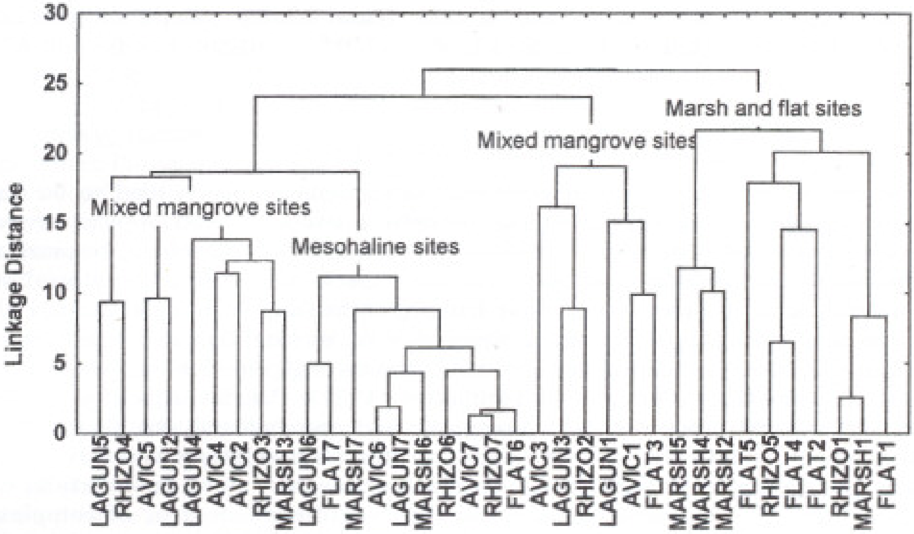

Figure 5. Dendrogram showing UPGMA clustering of City-block distance based on log (x + 0.001) transformed abundance of 13 top-ranked polychaete species at the 35 sampling sites from intertidal flats of Paranaguá Bay. Sites abbreviated as FLAT, MARSH, RHIZO, LAGUN and AVIC followed by a 1-digit number representing station location (from 1 to 7).

ness of fit given by stress value was 0.001. Once again groups of sampling sites corresponding to specific habitat types could not be discriminated. Multiple regression analysis showed that sediment diameter was the only variable significantly correlated to dimension 1 of MDS space at the 0.05 level ($P = 0.010$, con-

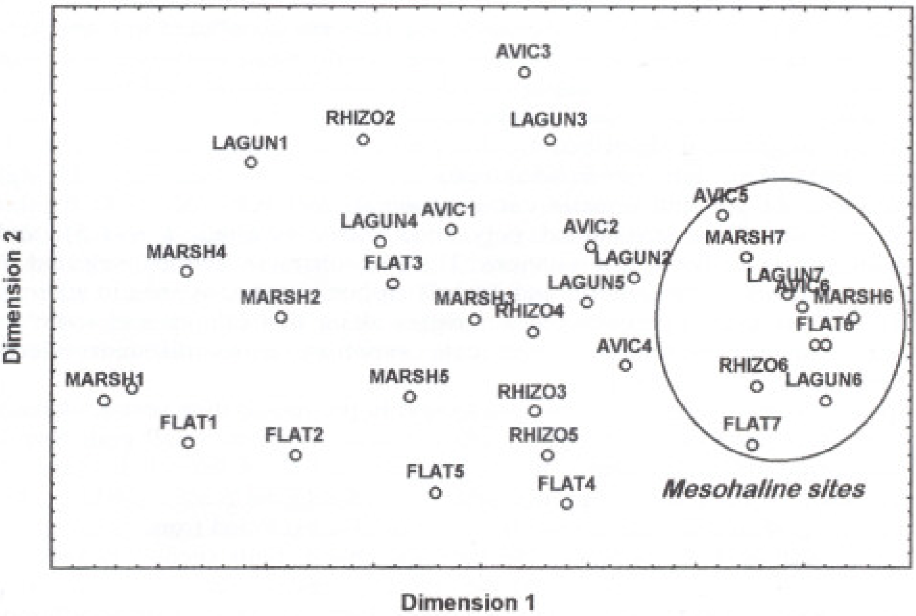

Figure 6. Non-metric multi-dimensional scaling by 35 sampling sites (with 5 replicates) of log (x + 0.001) transformed biological variables (total polychaete density, species number and density of 13 top-ranked polychaete species) from intertidal flats of Paranaguá Bay. Sites abbreviated as FLAT, MARSH, RHIZO, LAGUN and AVIC followed by a 1-digit number representing station location (from 1 to 7).

stant = −1.00 and R^2 = 0.85). On the other hand, salinity was the only variable significantly correlated to dimension 2 (P = 0.012, Constant = 0.63 and R^2 = 0.55).

Discussion

Tidal flats are low-energy depositional environments which tend to be colonized by algae or macrophyte vegetation both in temperate and tropical environments. In contrast to temperate regions in the northern hemisphere, tropical and subtropical salt marshes of the western Atlantic are poorly developed and frequently occur as pioneer mangrove-fringing formations (Costa and Davy, 1992). The presence of salt marsh or mangrove stands across tidal flats may lead to modifications in water circulation and sedimentation through the slowing down of tide-induced water flow (Pomeroy and Imberger, 1981). Besides affecting transport and depositional processes, both mangrove and marsh plants are also liable to affect faunal patterns through the presence of their trunks, stems and leaves at the surface or their roots at the subsurface. Plant architecture along the intertidal vary considerably and vegetated habitats can display different degrees of complexity even on a very small spatial scale (Rader, 1984). Probably influenced by that, many authors have correlated invertebrate distribution with plant zonation in temperate or tropical estuarine intertidal environments (Daiber, 1982; Kneib, 1984; Guelorget et al., 1990).

Though plant zonation has traditionally been implicated in regulating animal communities inhabiting sheltered intertidal flats, differences in species composition and polychaete abundance in Paranaguá Bay suggest that faunal differences are primarily defined by salinity and environmental energy gradients and only secondarily by the ability of polychaetes to discriminate among unvegetated, salt marsh or mangrove swamp habitats.

Ordination analysis revealed that sampling sites are distributed in a continuous pattern along a bi-dimensional space correlated with mean grain size and salinity of ponded water. The distribution of salinity and sediment parameters in tidal flats along the east-west axis of Paranaguá Bay seems to follow the marked hydrological gradient described by Knoppers et al. (1987) and Netto (1993). Local tidal flats can be divided into an mesohaline sector, with higher percentages of silt and organic carbon content, that corresponds to the inner stations 6 and 7, a transitional polyhaline sector (stations 4 and 5), and a high-energy euhaline sector (stations 1 to 3), characterized by selected fine sands, practically devoid of silt and organic carbon content, as seen in stations 1, 2 and 3. Variation in edaphic characteristics along this salinity and sedimentological gradient overwhelms short-scale variation across different intertidal habitats in a same location.

Species richness and abundance are lowest in the mesohaline sector, characterized by finer sediments and higher carbon organic content. Small grain size and accumulation of organic matter, which can cause a lack of interstitial space, have been shown to limit the occurrence of benthic organisms (Gray, 1981). A diversified group of marine stenohaline species was also excluded from the inner sites, characterized by low salinities. On the other hand, both species richness and polychaete abundance increase towards the high-energy euhaline sector, dominated by well-sorted fine sands low in organic carbon content. Faunal differences along the bay are also exemplified by the low degree of spatial overlap in species distribution between meso- and euhaline sites. Two polychaete stocks with marked preference for specific haline regimes can be easily recognized and just a few species present a widespread distribution throughout the bay.

Differences in polychaete diversity and density across vegetated intertidal habitats are not so clear. Between-habitat variation is only evident in the high-energy euhaline sector, where a more abundant and diversified group of species occur in marsh sites, in opposition to a depauperate fauna in mangrove sites. Faunal differences among stations or habitats are less significant in the inner oligohaline stations, where *Laeonereis acuta* and *Nephthys fluviatilis* are the dominant species, irrespective of tidal elevation or plant cover type. In most cases, our present analyses were not able to detect significant between-habitat variation in sediment parameters. However, Netto (1993) suggests that differences between sediments of vegetated and adjacent unvegetated tidal flats are correlated with an environmental energy gradient along Paranaguá Bay. Sediment differences between marshes and unvegetated tidal flats are not evident in the inner sector but are increasingly significant towards the high-energy euhaline sector. The present results support the idea that a higher availability of silt and clay, together with a lower availability of sand, can lead to a marked sedimentological homogeneity between vegetated and unvegetated flats in the sheltered inner reaches of the bay. On the other hand, the presence of plant structures, coupled with a higher variability of grain sizes, can enhance substrate heterogeneity in the high-energy euhaline sector.

Differences in polychaete abundance, species composition and species richness between vegetated and unvegetated tidal flat habitats do not follow a linear pattern. In general, polychaete densities are significantly higher in marsh habitats than in unvegetated or mangrove habitats. This is especially true for the high-energy euhaline sector. A similar increase in the diversity and abundance of macrofauna within a salt marsh of the euhaline sector was shown by Lana and Guiss (1991, 1992). A larger polychaete diversity and abundance in salt marshes, as opposed to higher *Avicennia* sites, suggests that faunal differences among habitat types are at least partially related to tidal elevation. Blankensteyn (1995) described depauperate macrobenthic faunas in mangroves of Paranaguá Bay, as compared to adjacent habitats. This pattern has been putatively attributed to higher predation pressures, lower complexity of plant architecture or lower availability of adequate detrital food in mangrove swamps as compared to adjacent salt marshes.

In summary, overall distribution of polychaete fauna is not primarily correlated with plant zonation patterns in intertidal flats of Paranaguá Bay. Salinity and sediment texture gradients, irrespective of the nature of plant cover, seem to play a major role in controlling abundances of individual species in different intertidal habitats. Species composition and density of polychaetes vary so much along an environmental gradient that any species-specific response to plant zonation seems to be masked by this large-scale variability. Though site-groupings or species-groupings can be recognized in a small scale, suggestive of zonation patterns, such patterns probably overstate the idea of a discontinuous distribution of invertebrate fauna.

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