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Scale-dependent patterns of macrofaunal distribution in soft-sediment intertidal habitats along a large-scale estuarine gradient

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Abstract We investigated the pattern of distribution of intertidal soft-bottom fauna in streams and lagoons of the Uruguayan coast at three spatial scales. The Río de la Plata and the Atlantic Ocean produce on this coast a large-scale gradient in salinity, defining a freshwater (west), an estuarine (central) and a marine (east) region. Within each region, there are several streams and coastal lagoons (sites) that define a second scale of variability. A third scale is given by intertidal gradients within each site. Species richness and total abundance was low in the freshwater west region and high in the central and east regions. The community in the west region was characterized by the clam *Curbicula fluminea*; in the other regions, it was dominated mainly by the polychaete *Heteromastus similis*. The polychaete *Nephtys fluviatilis* was more abundant in the east region, while another polychaete, *Laeonereis acuta*, characterized the central region. Sediment fractions did not vary significantly at this scale. At the scale of the sites, species richness and total macrofaunal abundance were higher in coastal lagoons than in streams. Coarse sands were more common in coastal lagoons, while medium and fine sand characterized the sediment in streams. Within each site, species richness and total abundance increased towards the lower intertidal level; the macrofauna of the upper levels were a subsample of the fauna occurring at the lower

levels. There was also a significantly lower proportion of fine sand at the upper level. At regional scales, the observed patterns may be indirectly or directly related to the gradient in salinity, through differential physiological tolerance to osmotic stress. At the scale of the sites, variability may be explained mainly by geomorphological and sedimentological differences between lagoons and streams. Variation among levels may be related to gradients in desiccation, colonization and predation.

Keywords Biodiversity · Macrobenthos · Estuarine fauna · Scale dependence

Introduction

Most ecological theories rely on the study of small-scale patterns of distribution of animals and plants; however, the patterns of distribution change with the temporal and spatial scale of observation (Wiens 1989; Schneider 1994). Scale-dependent patterns of distribution have been increasingly evidenced in studies of benthic fauna (Thrush et al. 1997, 2003; Giménez and Yannicelli 2000; Ysebaert and Herman 2002). An evaluation of these patterns is the first step to understand the set of processes that structures the communities and thus to formulate predictive models (Underwood et al. 2000).

Scale-dependent patterns of distribution may be particularly important in coastal areas since they are characterized by a high spatial and temporal variability in abiotic conditions. For benthic fauna, the patterns of distribution are related to depth, salinity (Remane and Schlieper 1971; Wolff 1983; Holland et al. 1987; Mannino and Montagna 1997; Ysebaert et al. 1998, 2003; Attrill 2002; Attrill and Rundle 2002), sediment characteristics (Gray 1981; Day et al. 1989; Teske and Wooldridge 2001, 2003; Anderson et al. 2004) among others. For instance, low salinity and/or variability in salinity are responsible for a consistently low number of species occurring in estuarine waters as compared with

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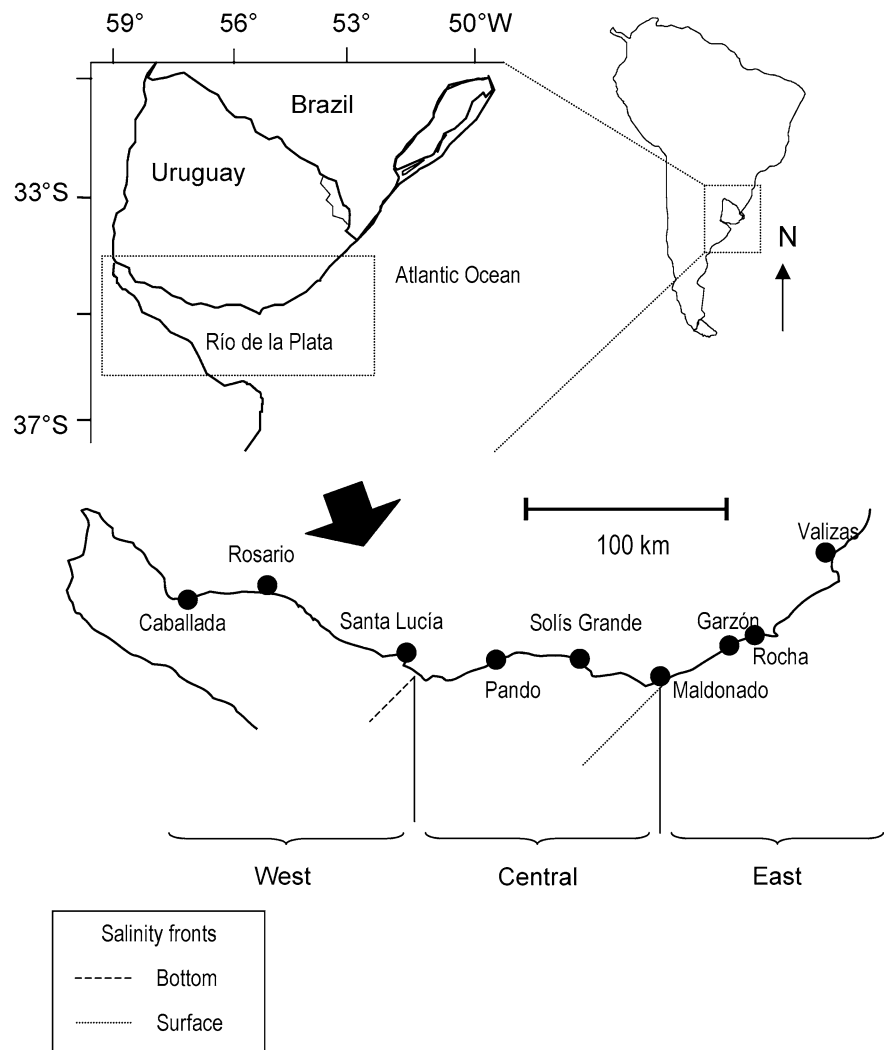
freshwater- or ocean-influenced habitats. However, the patterns may be more complex due to spatial heterogeneity in the distribution of substrate types. Apart from any effect produced by a gradient in intertidal height, a higher level of complexity may arise in intertidal zones if they are located directly on the coast or on streams, rivers, or lagoons that are open to the oceanic coast or to an estuarine zone.

Therefore, for the case of large estuarine areas such as the Río de la Plata in South America, studies on patterns of distribution in relation to physical gradients involve consideration of various spatial scales of variability. No study about the benthic fauna has covered a spatial scale large enough to include the whole environmental gradient of the estuary. The Río de la Plata estuary (Fig. 1) is one of the largest estuaries of South America, with a river funnel of 280 km in extent and 80–230 km in cross-section (Guerrero et al. 1997; Mianzan et al. 2001). At the northeast side, the Uruguayan coast, with a tidal range of less than 0.3 m, is characterized by a large-scale gradient caused by the estuary flowing into the Atlantic Ocean. The gradient defines an upper region of highly turbid waters with salinity < 1 ppt, and a lower region

of less-turbid waters with salinity varying between 1 ppt and 30 ppt (Calliari et al. 2003; Mianzan et al. 2001). This pattern is related to the position of the bottom salinity front of Río de la Plata, located off Montevideo and defines, at the Uruguayan coast, a west region of about 200 km of extension experiencing mostly freshwater. The surface salinity front varies temporally but at the Uruguayan coast, it is located near Punta del Este and separates a central mixohaline region of ca. 150 km from an east oceanic region. Thus, there is a west region influenced by freshwater (< 1 ppt), a central region that is influenced by water of variable salinity (1–30 ppt) and an east region open to ocean waters (> 30 ppt). Within each region, there are several streams and coastal lagoons discharging their waters to the Río de la Plata or the Atlantic Ocean. They constitute small estuarine areas, shallower and more protected than the main body of the Río de la Plata. The intertidal zone of these habitats is dominated by narrow (< 50 m width) unvegetated sandflats and salt marshes.

In this paper, we investigated if the macrofauna of the intertidal sandflats varied among regions, among sites within regions and among intertidal levels within sites. At

Fig. 1 Geographic location of regions and sites sampled along the Uruguayan coast of the Río de la Plata and the Atlantic Ocean. The position of the salinity fronts on the coast is also indicated



the scale of regions, we investigated the variability of macroinfauna in relation to the above-described large-scale salinity gradient. As a potential source of among-site variability, we explored if there were differences between coastal lagoons and streams. We also explored potential relationships between sediment characteristics and macroinfauna at all scales of variability.

Methods

Sampling design

We sampled three sites at random in each of the above-defined regions (Fig. 1) in the spring of 2002, at low tide. Each site consisted of a stream or a coastal lagoon open to coastal waters. The sites were from west to east, La Caballada, Rosario, Santa Lucía (for the west region); Pando, Solís Grande, Maldonado (central region); Garzón, Rocha and Valizas (east region). The sites Garzón and Rocha are coastal lagoons; the other sites are streams. The most common habitats at these sites are narrow (< 50 m) unvegetated intertidal sandflats limited by saltmarshes at the upper level. Saltmarshes are more common in the upper intertidal and supratidal zone.

At each site, four replicate transects were defined within the first 1,000 m of the mouths. In most cases, two transects were located at each side of the lagoons or streams. The exceptions were La Caballada, Santa Lucía and Rosario where one of the shorelines was covered by vegetation or by rocky outcrops. For each transect, three intertidal levels were sampled: the upper level of the sandflat limited by the saltmarsh (0.3–1 m above the waterline), the middle (depth = 0.20 m) and the lower (depth = 0.50 m). The distances among stations varied from 2 m to 10 m depending on the shore profile. At each level per transect, one sample of macroinfauna was taken with a PVC tube of 16 cm in diameter, buried 20 cm. Thus, we had, at each site, four samples per level. The sediment was sieved through a 1-mm sieve and all macrofauna retained was fixed in 5% formalin and taken to the laboratory to be identified.

At the middle and lower level, we also took one sample per transect using a drop-trap of 0.50 m² surface as described in Pihl and Rosenberg (1982). This sampling was aimed to capture epifaunal organisms, although infaunal organisms were also collected. The trap consisted of an aluminium cage of 0.7×0.7 cm which was suspended by two lines from the middle of a 4-m-long wooden stick. The wooden stick was moved carefully in the water and the trap was dropped down. Correct sampling was ensured by allowing the lower border of the traps to be buried in the sediment while the upper one protruded above the water surface by at least 10 cm. Animals were sampled by scraping the sediment surface with a hand net of 1 mm mesh size. After several trials, we found out that scraping the surface for 30 times was enough to remove most of the epibenthos in the trap. We also removed infauna since it was not possible to

avoid burying the hand net in the sediment at least 1–2 cm. On the other hand, this was also necessary to disturb crabs or other epibenthic organisms that are partially buried. Sampled organisms were fixed in 5% formalin and transferred to the laboratory, where they were classified and counted.

At all defined levels, samples of sediments were taken for granulometric analyses from two of the four transects for macrofauna, selected randomly. They were taken with a small tube of 4 cm in diameter, buried 10 cm. Sediments were dried and weighed, and wet-sieved through a mesh of 0.063 mm to separate the mud fraction. The mud fraction was not further analysed and is expressed as percentage of the total sediment. The sand fraction was dried, weighed again and mechanically passed through a series of sieves ranging from 4 mm to 0.63 µm (interval = 1φ). The median of the sediment distribution and the classification of sediments were done using the Wentworth scale (Buchanan 1984). At all sites, salinity was measured with a Horiba U-10 Multi-parameter sensor.

Data analyses

We evaluated the effect of region, site and level on the proportion of each granulometric fraction and on the distribution and abundance of macroinfauna. For granulometric fractions, we first performed a principal component analysis (PCA: Legendre and Legendre 1998) to obtain the fractions that explained the highest percentage of variability in the data. The effect of region and site was evaluated with a permutational multivariate analysis of variance (PERMANOVA: Anderson 2001, 2005) on all granulometric fractions as variables, and Canonical analysis of principal coordinates (CAP: Anderson and Willis 2003; Anderson 2003) to visualise significant effects obtained by the previous analysis. Each term in the analysis was tested using 499 permutations of the appropriate units; if there were not enough units, the test was done using the Monte Carlo method (Anderson 2003, 2005). For these analyses, we used untransformed data and Euclidean distance. The main granulometric fractions obtained from PCA and CAP were also tested for effects of region and site using two-way nested ANOVA (Zar 1996), with the factor Site nested within the factor Region. To evaluate the effect of levels within sites, we used repeated-measures ANOVA on the main granulometric fractions obtained from PCA and CAP.

Data collected from core samples was treated separately from drop-trap samples. We used two-way nested ANOVA as described above to test the hypothesis that species richness and total abundance per replicate transect varied among regions and sites. We further tested if species richness and total abundance was different in coastal lagoons (Garzon and Rocha) from streams using planned comparisons. The effect of region and site on species composition was evaluated with PERMANOVA

and CAP. For these multivariate analyses, data was log ($X+1$) transformed; the similarity matrix was built with the Bray–Curtis index. Then, we performed univariate two-way nested ANOVAs with the most important species to test for effects of regions and sites, and planned comparisons to test for differences between lagoons and streams. We used log ($X+1$)-transformed data since, unlike untransformed data, they were homogeneous and normally distributed. For core samples, we tested if species richness and total abundance varied among intertidal levels with repeated-measures ANOVA. In these tests, we excluded Caballada and Rosario since almost no macroinfauna was found at these sites (see Results).

Relationships between species richness and salinity were analysed with single and multiple Pearson correlation and regression. Relationships between granulometric data and fauna were investigated by correlating granulometric fractions and the two main axis of principal coordinate analysis (PCO) done on the species matrix and by multiple Pearson correlation of abundance of each species and the proportion of the main granulometric fractions.

Results

Salinity and granulometric fractions

Salinities were lower than 1 ppt at the freshwater extreme (La Caballada, Rosario and Santa Lucía); at the sites open to estuarine waters it ranged from 1 ppt (Pando stream) to 15 ppt (Maldonado stream) while at those open to oceanic waters it ranged from <1 ppt (Valizas stream) to 14 ppt (Rocha lagoon).

Sediments were dominated by sands and gravels (Fig. 2a). At La Caballada, Pando and Maldonado, the dominating type was medium sand while Rosario, Solís, and Valizas were dominated by fine to medium sands. Santa Lucía was dominated by gravels and the coastal lagoons were dominated by coarse sand and gravels.

Principal component analysis of sediment fractions based on variance–covariance matrix showed that medium and fine sands were the most important variables contributing to the formation of the first principal axis (Table 1): medium sand was positively correlated to the first factor ($r = 0.98$) while fine sand was negatively correlated to the second factor ($r = -0.94$). PERMANOVA showed that sand fractions varied significantly among sites ($F_{6,9} = 6.02$, $P = 0.002$) but not among regions ($F_{6,9} = 0.85$, $P = 0.54$). CAP analysis based on Euclidean distance to test for differences among sites clearly differentiated the coastal lagoons and Santa Lucía river from other sites (Fig. 2b): the main sediment fractions contributing to such differences were the gravels and medium sand.

Medium and coarse sands did not vary with intertidal level (Table 2); fine sands had a lower percentage at the

upper intertidal level. With respect to gravel, there was not a consistent pattern among sites where gravel was important (Santa Lucía river and the coastal lagoons): At Santa Lucía, the percentage of gravel was lower at the upper level, at Garzón, it was higher at the middle level, compared to the other respective levels.

Macrobenthos

We identified 22 taxonomic groups from the core samples and 29 from the drop-trap. Species richness from core samples varied significantly among regions and sites (Table 3). Species richness increased from the west to the east region (Fig. 3). Within the west region, the sites with lowest species richness were La Caballada (one species) and Rosario (no macrofauna). At all other sites, the species richness was higher, but within the east region total species richness was significantly higher at the coastal lagoons ($F_{1,9} = 5.40$, $P < 0.05$). Total abundance varied significantly among regions, with the west region showing a significantly lower abundance than the other two (Table 3). There was only a marginally significant effect of Site on total abundance. Data from the central and east regions showed that total abundance was significantly higher at the coastal lagoons than at streams ($F_{1,18} = 5.19$, $P < 0.05$). Species richness and total abundance of drop-trap samples varied among sites but not among regions (Table 3). The lowest values were recorded at Rosario (no macrofauna) and the highest at Garzón and Rocha lagoons (Fig. 3). The coastal lagoons had a significant higher species richness ($F_{1,18} = 12.72$, $P < 0.01$) and abundance ($F_{1,18} = 17.37$, $P < 0.001$) than streams and rivers. Among site variability in species richness or total abundance was not explained by salinity ($P > 0.05$).

Canonical analysis of principal coordinates (CAP) done on core and drop-trap samples separated the three regions (Fig. 4). PERMANOVA was performed only from core samples from the central and east regions due to lack of a balanced design: it showed significant variability among sites ($F_{4,18} = 2.20$, $P < 0.001$) but only marginally significant effect of regions ($F_{1,4} = 2.06$, $P = 0.08$). Core samples were dominated mostly by the polychaetes *Heteromastus similis*, *Laeonereis acuta* and *Nephtys fluviatilis* comprising 67% of the total number of animals collected (Table 4). Abundance of *H. similis* was higher at the central and east regions (Table 5; Fig. 5) with maximal values at Solís stream and Garzón lagoon, contributing to separate the west region from the others in the CAP (Fig. 4). Abundance of *L. acuta* was significantly higher at the central region, while that of *N. fluviatilis* was higher at the east region (Table 5; Fig. 5), contributing to separate the central and the east regions in the CAP (Fig. 4). *Nephtys fluviatilis* was significantly more abundant in the coastal lagoons than in Valizas stream ($F_{1,9} = 34.69$, $P < 0.001$). Other species including molluscs and crustaceans comprised the rest of the macrobenthos (Table 4). The tanaidacean *Kalli-*

Fig. 2 Variation of the main granulometric fractions of unvegetated sandflats along the Uruguayan coast of the Río de la Plata and the Atlantic Ocean (a); biplot of Canonical analysis of principal coordinates to look for variation in sediment fractions among sites (b). Abbreviations of sites are *Ca* Caballada, *Ro* Rosario; *Sa* Santa Lucía, *Pa* Pando, *So* Solís Grande, *Ma* Maldonado, *Ga* Garzón lagoon, *Ra* Rocha lagoon, *Va* Valizas

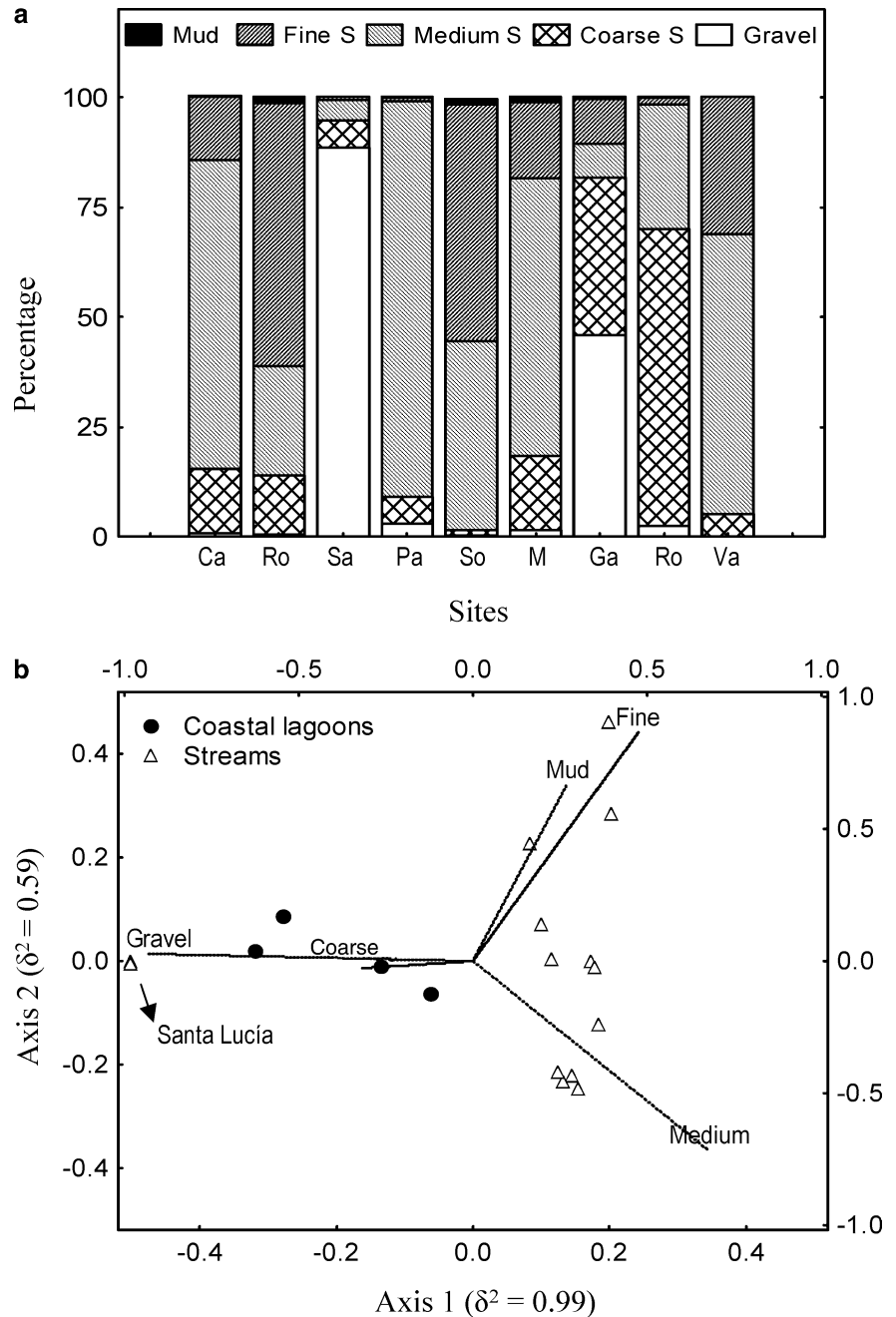


Table 1 Contribution of each granulometric fraction to the formation of the two principal factors obtained from a principal component analysis

	Factor I (47.23%)	Factor II (33.58%)
Gravel	0.235	0.249
Coarse sand	0.011	0.066
Medium sand	0.698	0.007
Fine sand	0.058	0.678
Mud	<0.001	<0.001

The percentage of variance explained by each axis is given in parenthesis

opseudes schubarti was found only at Solís stream. Other species were seldom sampled: the deep burrowing razor clam *Tagehus plebeius* was found in only one site, but it may not be well sampled by the corer used here; the polychaete *Neanthes succinea* and mussels *Brachidontes* spp were found very seldom, but they are more common on rocky shores (Giménez et al. in preparation); the same occurred with the isopod *Excirolana armata*, a characteristic species of sandy beaches (Giménez and Yannicelli 1997).

Drop-trap samples contained mostly crustaceans and molluscs; nine species comprised more than 95% of the

Table 2 Summary of two-way ANOVA to evaluate the effect of intertidal level on the (arcsin transformed) percentage of the main sediment fractions found at nine sandflats along the Uruguayan coast

	Gravel		Medium sand		Fine sand	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Level	6.25	< 0.01	1.83	0.19	3.89	< 0.05
Site	232.31	< 10 ⁻⁴	3.97	< 0.05	3.33	0.06
Site×level	3.62	< 0.01	0.25	0.99	0.84	0.62

Fig. 3 Spatial variation in mean total number of species and abundance of macrofauna collected from core and drop-trap samples. For drop-trap samples, barnacle abundance was not included to calculate total abundance. Symbols as in Fig. 2; error bars are standard errors

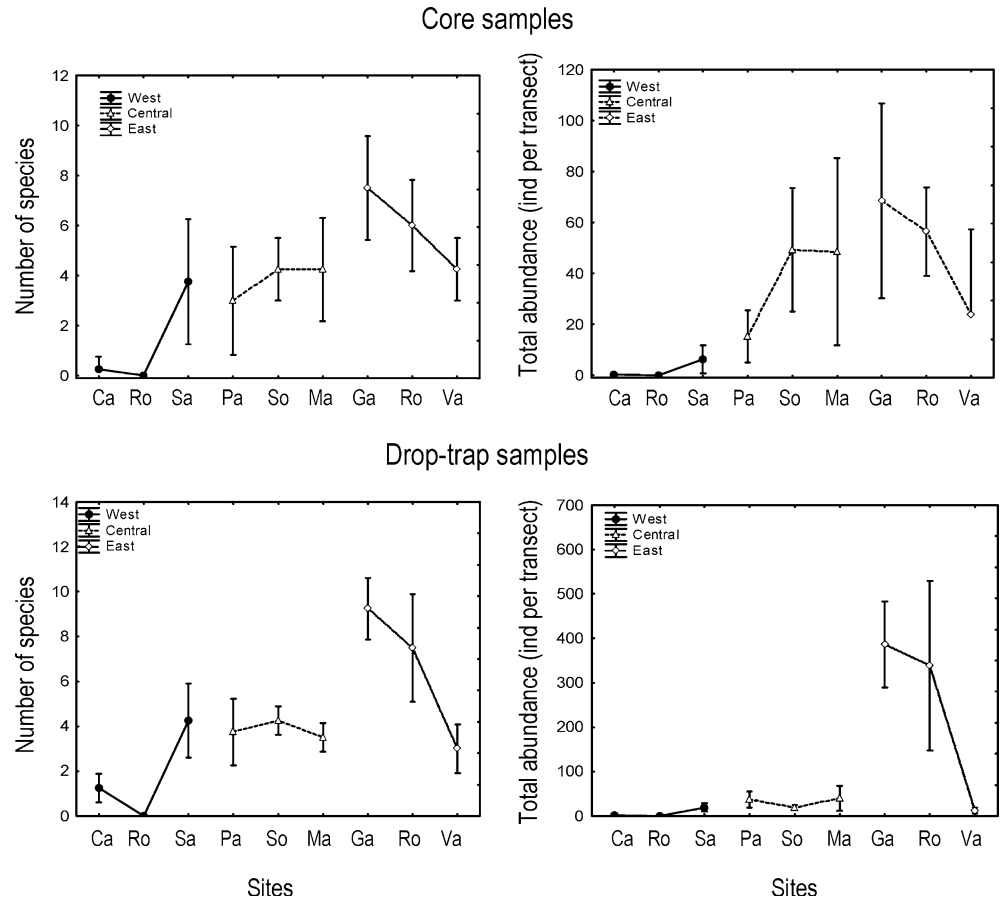


Table 3 Summary of two-way nested ANOVA to evaluate the effect of region and site (nested on region) on species richness and total abundance of macrobenthos collected with cores and drop-trap samples ($X + 1$) transformed

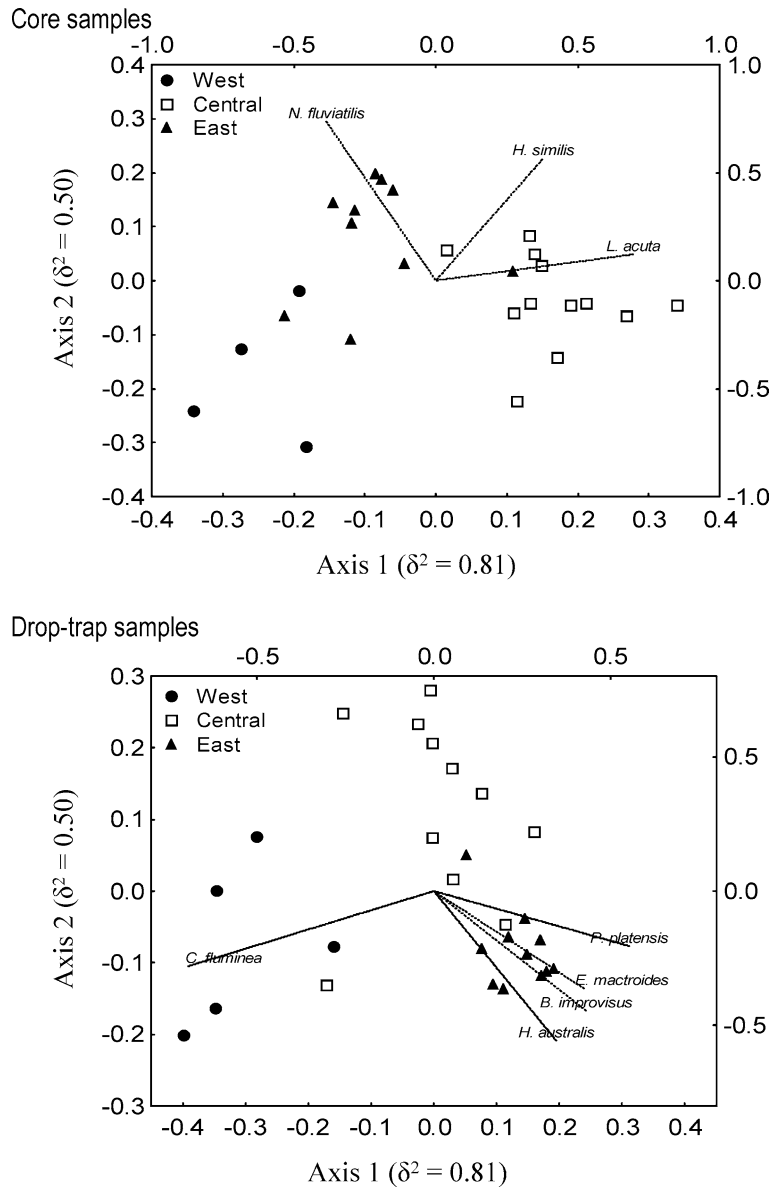
Factor	df	Richness			Total abundance		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Corers							
Region	2	65.58	6.26	0.034	7329	5.93	0.038
Site	6	10.47	3.62	0.009	1235	2.23	0.070
Error	27	2.89			552		
Drop-trap							
Region	2	68.25	3.34	0.10	29.51	3.84	0.084
Site	6	20.42	3.07	0.02	7.68	4.15	0.004
Error	27	6.66			1.85		

Data for total abundance from drop-trap were log

collected individuals (Table 4). The barnacle *Balanus improvisus*, the hydrobiid gastropod *Heleobia cf australis* and the bivalve *E. mactroides* were the most abundant and widespread species comprising more than 75% of the collected organisms and occupying more than 50% of the sampled sites. Abundance of these species varied

significantly among sites but not among regions, with peaks at the coastal lagoons (Table 5; Fig. 6). The same pattern was found for the isopod *Dies fluminensis* and the crab *Cyrtograpsus angulatus*. The abundance of the tanaid *Sinelobus stanfordi* was significantly higher in the east region, and in the coastal lagoons within that

Fig. 4 Biplot of Canonical analysis of principal coordinates to evaluate the among-site variability of macrofauna obtained from core and drop-trap samples



region. All these species contributed to separate the central from the east region in CAP analysis (Table 4; Fig. 4). Other species such as *Jassa falcata* and *Pseudosphaeroma platensis* did not vary significantly among sites or regions although they tended to increase from west to east. The bivalve *Corbicula fluminea* was only present in the west region, contributing to separate it from the other regions in CAP (Table 4; Fig. 4).

The species richness and the total abundance of macroinfauna collected from core samples were significantly lower at the upper level of the sandflats as compared with the middle and lower levels (Table 6). Among the polychaetes, *H. similis* had significantly lower abundance at the upper level, while *L. acuta* did not show any significant trend. For *N. fluviatilis*, the test for the effect of levels was possible using data from the coastal lagoons: at these sites, they were significantly less abundant at the upper level.

Relationships between environmental variables and macrofauna

Correlations between the recorded salinity and species richness were not significant. Significant correlations were found only for the total faunal abundance from core samples ($r = 0.74$, $P < 0.05$) and for the abundance of *P. platensis* from drop-trap samples ($r = 0.80$, $P < 0.01$).

Correlations between axis from PCO of macrofaunal data and the main sand fractions are shown in Fig. 7. For both core and drop-trap samples, the coastal lagoons are separated from rivers and streams; that separation is correlated with an increase in the coarse sand fraction. Multiple correlations between species abundance from core samples were only significant for abundance of *Nephtys fluviatilis* and the coarse sand fraction, while for data from drop-trap samples they showed significant positive correlations of species

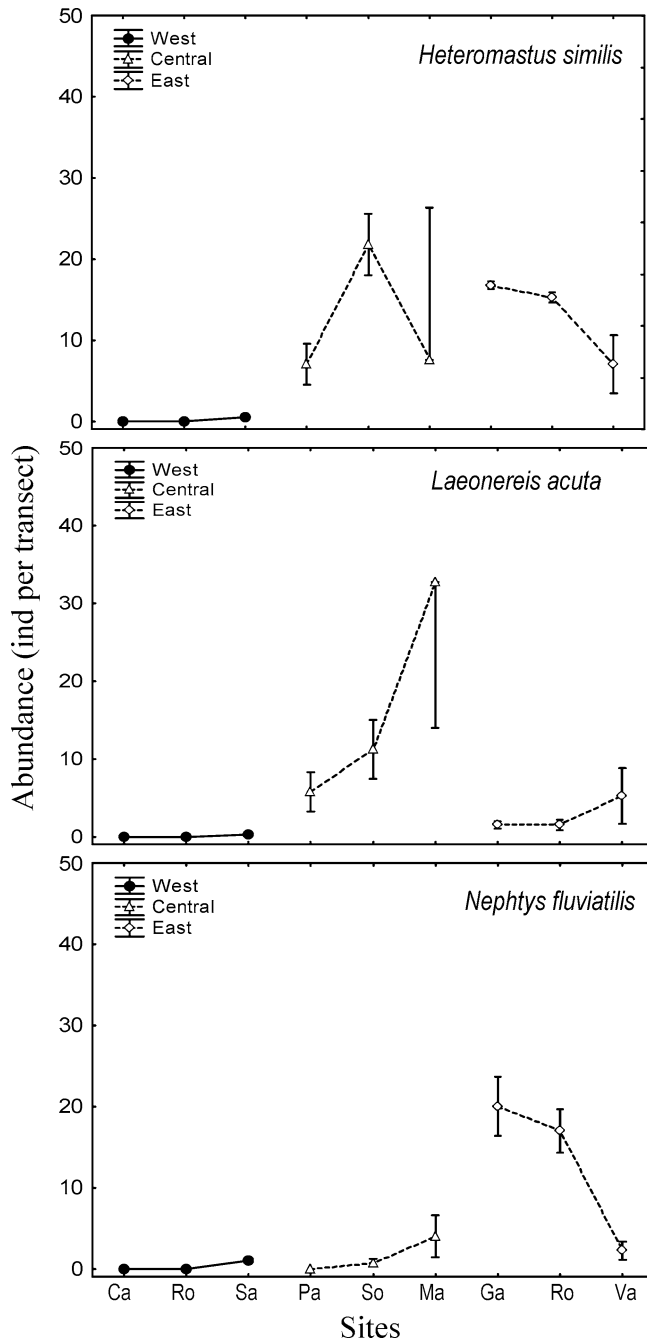


Fig. 5 Spatial variation in abundance of the main infaunal polychaetes collected with core samples. Symbols as in Fig. 2; error bars are standard errors

richness, total abundance (not including barnacles), *Erodona mactroides*, *Heleobia australis*, *Cyrtograpsus angulatus* and *Jassa falcata* (Table 7). The significant correlations were determined mainly by the high percentage of coarse sand in the coastal lagoons.

Discussion

This is one of only a few studies examining spatial variation in estuarine macrofauna at different spatial scales

(see Ysebaert and Herman 2002). We used a nested design to study variation among regions and sites. This was a requisite to examine the patterns of macrofaunal distribution in streams and coastal lagoons located along the salinity gradient produced by the Río de la Plata and the Atlantic Ocean, since several sources of variability occur at different spatial scales.

A low number of species were found in the soft-sediment estuarine sites. This is consistent with general trends in the estuarine fauna all over the world. Species composition was consistent with earlier studies on the Uruguayan coast (Muniz and Venturini 2000; Cardezo 1989; Jorcín 1999). Species composition was also similar to that of Patos lagoon (Capitoli et al. 1978; Seeliger 2001) and Samborombom bay on the Argentinean coast of the estuary (Ieno and Bastida 1998). Species composition differed from that observed in the sandy and muddy bottoms of the Río de la Plata (8–40-m deep: Mianzan et al. 2001; Giberto et al. 2004), suggesting a depth-related zonation pattern. Species richness on the Uruguayan coast seemed to be higher than the one reported by Ieno and Bastida (1998) for Samborombom bay. The fact that we used a drop-trap allowed us to estimate the abundance of several mobile epifaunal species and infaunal species with low abundance but buried within the first centimetre of sediment. The drop-trap is much better suited to collect mobile epibenthos than core sampling; this was the first time this technique was used in Uruguay.

Species richness, total abundance and species composition varied among regions, among sites within regions and among levels within sites. These patterns suggest a scale-dependent set of processes operating along the estuarine benthic communities of Uruguay, as for other estuaries (Ysebaert and Herman 2002; Thrush et al. 2003) and intertidal communities (Thrush et al. 1997; Giménez and Yannicelli 2000). The observed patterns should be related to (1) the salinity gradient produced by the Río de la Plata and the Atlantic Ocean at a regional scale, (2) morphological and/or sedimentological differences among lagoons and streams or rivers at the scale of sites and (3) the gradient in desiccation and colonization rates of sediments at the scale of intertidal levels.

Variability among regions

The influence of the Río de la Plata and the Atlantic Ocean defines three main regions on the Uruguayan coast: a west region with a salinity of < 1 ppt, a central region of variable salinity (1–30 ppt) and the east region open to the coastal ocean waters (> 30 ppt). Salinity within the estuarine areas studied by us may be co-determined by the freshwater from the basin of each stream and lagoon and from the water masses entering through the mouth. Differences in salinity between the west and central regions recorded by us were consistent with the regional pattern of salinity explained above. In

Table 4 Benthic macrofauna of unvegetated sandflats at streams and lagoons along the Uruguayan coast collected with corer and drop-trap

Taxon/species	Core samples				Drop-trap samples			
	%	N	C-1	C-2	%	N	C-1	C-2
Polychaeta								
<i>Heteromastus similis</i>	28.44	7	0.38	0.56	0.81	4		
<i>Laeonereis acuta</i>	22.01	7	0.69	0.12	0.17	4		
<i>Nephtys fluviatilis</i>	16.48	7	-0.39	0.74	3.32	5		
Crustacea								
<i>Balanus improvisus</i>	6.23	1	-0.18	0.58	50.61	5	0.43	-0.44
<i>Pseudosphaeroma platensis</i>	10.15	5	-0.08	0.37	6.43	4	0.55	-0.20
<i>Dies fluminensis</i>	1.11	2	-0.14	0.60	7.99	3	0.43	-0.44
<i>Kalliopseudes schubarti</i>	4.92	1	0.45	-0.11	0.01	1		
<i>Sinelobus stanfordii</i>	0.70	4	-0.33	0.37	1.51	2	0.42	-0.40
<i>Jassa falcata</i>	0.50	4	0.28	0.10	0.83	6	0.43	-0.11
<i>Cyrtograpsus angulatus</i>	0.10	1			1.38	6	0.25	-0.07
<i>Neomysis americana</i>	0.20	1			1.03	2	0.04	0.52
Prawn indet					0.26	2	-0.53	-0.13
Ostracoda indet					0.10	2	0.18	-0.19
Mollusca								
<i>Heleobia cf australis</i>	1.21	5	-0.38	0.04	14.54	6	0.35	-0.56
<i>Erodona mactroides</i>	5.43	5	-0.30	0.59	9.70	5	0.43	-0.36
<i>Corbicula fluminea</i>	0.10	1			0.17	2	-0.70	-0.28
<i>Planorbis</i> sp.					0.07	2	0.13	0.14
Hirudinea indet	0.20	2			0.03	1	0.20	-0.16
Lophophorata								
<i>Membranipora</i> sp.					0.17	1	0.25	-0.18
Insecta								
Insect indet					0.24	2	0.16	-0.03

Percentage of occurrence (%), number of sites occupied (*N*) and contribution (correlation) of main species to the first two canonical variables (C-1 and C-2) obtained from CAP maximizing differences among regions

Table 5 Univariate two-way ANOVAs to evaluate the effect of region and site (nested on region) on the three most common macrobenthic species sampled with corers and drop-trap. Data for were log ($X + 1$) transformed before analyses

Factor	df	MS	F	P	MS	F	p	MS	F	p
Corers										
		<i>H. similis</i>			<i>Nephtys fluviatilis</i>			<i>Laeonereis acuta</i>		
Region	2	16.7	10.2	0.01	14.9	6.61	0.03	13.01	23.9	<0.01
Site	6	1.63	1.75	0.15	2.26	6.80	<0.001	0.54	0.66	0.68
Error	27	0.93			0.33			0.82		
Trap										
		<i>Balanus improvisus</i>			<i>Heleobia australis</i>			<i>Erodona mactroides</i>		
Region	2	26.2	1.76	0.25	19.4	3.83	0.08	13.9	1.90	0.23
Site	6	14.8	14.5	<10 ⁻⁵	5.06	3.22	0.02	7.28	8.45	<10 ⁻⁴
Error	27	1.02			1.57			0.86		

the east region, the Valizas River had a low salinity, reflecting the influence of water discharge at the time of sampling.

The fact that the sites in the west region are open to freshwater or low-salinity brackish water explains the species composition: one of the dominant species at Caballada and Santa Lucía was the freshwater clam *Corbicula fluminea*. Communities may be differentiated if they have clear habitat boundaries, if they are characterized by dominant indicator species, if there is a strong interaction among species or if it is possible to identify an assemblage (Morin 1999). Following these criteria, the species found at La Caballada should constitute a community characterized by *C. fluminea* and differentiated from the estuarine community of other sites that are characterized by the polychaete *Heteromastus similis*. The site Santa Lucía should be part of the ecotone or ecocline (Attrill and Rundle 2002) between freshwater and estuarine communities: at this site, both

freshwater and estuarine species may be near the limit of tolerance to osmotic stress. Also for the salt marsh crab *Chasmagnathus granulata*, Santa Lucía seems to be the western limit of distribution (Giménez 2003), due to effects of osmotic stress on the survival of benthic or pelagic stages. Within the estuarine community, differences between the central and the east region involved changes in abundance of the main macrofaunal species rather than changes in species composition. While the polychaete *Laeonereis acuta* was more abundant in the central region, the polychaete *Nephtys fluviatilis* was more abundant in the east region.

According to the model of Remane and Schlieper (1971), we expected to find the highest number of species at the west region especially at the sites permanently bathed by freshwater (La Caballada and Rosario). Thus, the prediction of higher number of species at the freshwater extreme does not seem to apply for the sandflats

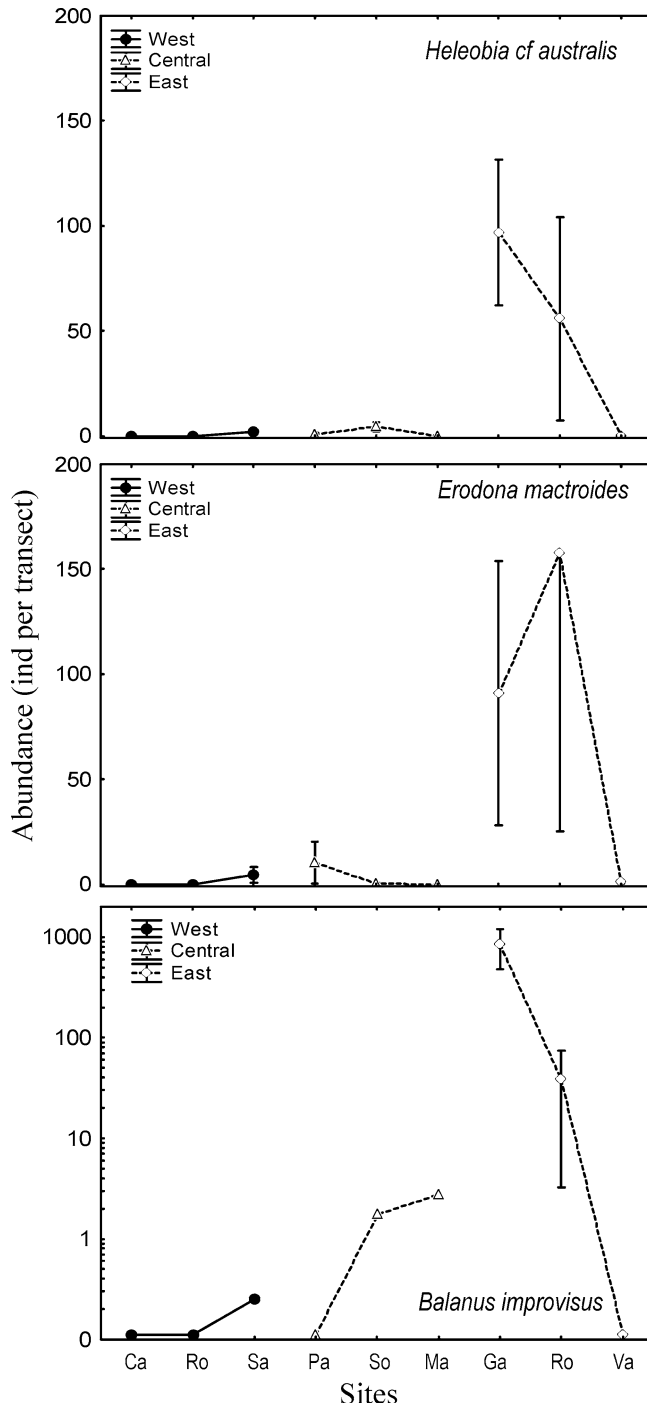


Fig. 6 Spatial variation in abundance of the main species collected with drop-trap samples. Symbols as in Fig. 2. Error bars are standard errors

located in streams and rivers along the coast of Uruguay. That model was developed for subtidal mud-dominated sediments, and it may not apply for sandy intertidal environments or for a series of small rivers and lagoons, that are subjected to their own salinity gradients. We did not find any significant variation in sediment fractions among regions.

Variability among sites

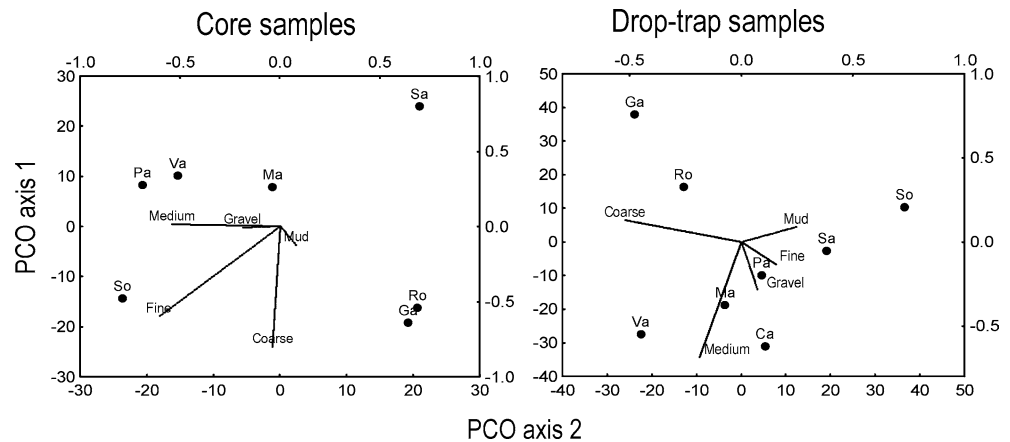
Considerable variability in macrofaunal abundance, diversity and composition occurred among sites, and was related to the differences between coastal lagoons and streams. Most epibenthic species were more abundant at Rocha and Garzón lagoon than at streams. The patterns of species composition and abundance of estuaries in South Africa were associated with differences in estuarine morphology and their open/closed regime (Teske and Woodridge 2001, 2003): permanent river-dominated open estuaries had lower densities and species richness than open/closed estuaries. On the Uruguayan coast, Jorcín (1999) found a considerable reduction in the number of species at the Valizas stream as compared with Castillos lagoon, located upriver. Coastal lagoons differ from streams and rivers in two important aspects: (1) their intermittent connection with the sea, and (2) their morphology. In addition, we found a third difference, the sediment composition: while most of the streams were dominated by fine to medium sand, coastal lagoons were dominated by coarse sand to gravel.

The present data do not allow for an evaluation of which factor determined the observed differences between the lagoons and streams: they may be influenced by a large number of community and biological processes. For instance, both the intermittent connection to the sea and the morphology should affect the rate of disturbance of bottom habitats: in streams and rivers, the channel-like morphology and the permanent contact with open waters should lead to bottom water eroding the intertidal habitat more frequently. In the lagoons, the morphology ensures that an extensive portion of sandflats are located in protected bays, while the intermittent connection with the sea ensures a reduction in the frequency of disturbance and export of organisms towards the sea. The intermittent nature of the lagoons may also reduce biological disturbance by marine-fish predators if it restricts their frequency of invasion. The effect of both physical and biological disturbance should depend on life history and other adaptations. The effect of disturbance should be higher on epibenthic crustaceans and gastropod molluscs, explaining their reduced number in streams as compared to lagoons. Erosion or predation should affect also the shallow burrower *Erodona mactroides* (Capitoli et al. 1978) explaining its higher abundance in coastal lagoons. The predator polychaete *Nephtys fluviatilis*, supposed to reduce the abundance of small macroinfauna from the upper centimetres of the sediment layers (Bemvenuti 1988, 1994), should be affected in the same way. However, the infaunal worms such as *L. acuta* and *H. similis*, common in streams and lagoons bury deeper in the sediment: they should not be affected as much by erosion as the before-mentioned species. Deep burying in *H. similis* may explain the lack of relationship between its abundance and that of *N. fluviatilis* in laboratory and field experiments (Bemvenuti 1988). Limited erosion and higher abun-

Table 6 Univariate two-way ANOVA to evaluate the effect of level and site on total abundance and the distribution of the main macroinfaunal species collected with core samples. Data of total abundance and of *Heteromastus similis* and *Laeonereis acuta* were log (X + 1) transformed

	df	MS	F	p	MS	F	P
Factor		Species richness			Total abundance		
Site	6	12.58	3.43	0.016	6.56	3.11	0.024
Error	21	3.67			2.11		
Level	2	10.37	3.57	0.037	6.99	6.45	0.003
Level×Site	12	2.22	0.76	0.683	0.97	0.89	0.560
Error	42	2.90			1.08		
		<i>Heteromastus similis</i>			<i>Laeonereis acuta</i>		
Site	5	2.62	1.75	0.17	1.56	1.33	0.294
Error	18	1.50			1.17		
Level	2	10.77	18.72	< 10 ⁻⁵	0.17	0.20	0.821
Level×site	10	0.70	1.22	0.31	0.78	0.92	0.525
Error	36	0.57			0.85		

Fig. 7 Animal-sediment relationships shown by semipartial correlations between the first two axes of the principal coordinate analysis of species data and the main granulometric fractions



dance of *E. mactroides* in coastal lagoons may explain why shells of *E. mactroides* are more commonly deposited on lagoonal sandflats, while in streams, they are frequently transported to open waters. This deposition

Table 7 Forward stepwise multiple regression models to explain total abundance, species richness and abundance of selected macrobenthic species by four main sediment fractions

Variable	Variable entering the model and partial correlation coefficient	r ²
Core samples		
Total abundance	None	
Species richness	None	
<i>Heteromastus similis</i>	None	
<i>Laeonereis acuta</i>	None	
<i>Nephtys fluviatilis</i>	Coarse sand: 0.88	0.71
Drop trap samples		
Total abundance	Coarse sand: 0.88	0.73
Species richness	Coarse sand: 0.72	0.44
<i>Balanus improvisus</i>	None	
<i>Erodona mactroides</i>	Coarse sand: 0.77	0.51
<i>Heleobia australis</i>	Coarse sand: 0.96	0.92
<i>Dies fluminensis</i>	None	
<i>Jassa falcata</i>	Coarse sand: 0.82	0.54
<i>Cyrtograpsus angulatus</i>	Coarse sand: 0.76	0.56
<i>Sinelobus stanfordi</i>	None	

seems to favour the establishment of the estuarine barnacle *Balanus improvisus*.

It is well known that macrobenthic fauna respond to sediment composition, but most of the responses are related to the proportion of the mud fraction (Gray 1981; Thrush et al. 2003). In our sites, that proportion was rather low, and most of the macroinfaunal changes were associated with the proportion of coarse sand and gravel found in the coastal lagoons. Coarse sands are more penetrable than fine sands allowing perhaps epifaunal species or errant polychaetes to bury and move more easily in the sediments.

Variability among intertidal levels

In our study, we did not find any pattern of zonation, but an increase of species richness and total abundance from the upper to the lower stations. The only exception may be the barnacle *Balanus improvisus* that occurs in a very well-defined belt as a consequence of the patterns of deposition of *Erodona mactroides* shells. In some streams, *Chasmagnathus granulata* and the fiddler crab *Uca uruguayensis* occupy part of the upper level of the sandflats (LG, personal observation), but this does not occur at all places. *Chasmagnathus granulata* occurs

mostly in the salt marshes located beyond the upper levels of the sandflats. This is in contrast to the patterns of community structure of Uruguayan and other exposed oceanic microtidal sandy beaches (Defeo et al. 1992; McLachlan and Jaramillo 1995; Brazeiro and Defeo 1996; Giménez and Yannicelli 1997). Macrofauna of several tidal flats also follow a zonation pattern (Reise 1991; Dittman and Vargas 2001), but these have a wider tidal range (> 1–9 m) and extension as compared with the sandflats studied here. Our results may be the consequence of the resolution of our sampling design, which was too low to detect small-scale patterns of distribution across the sandflats. Ongoing research on Rocha lagoon using a sampling design with higher resolution did not find a consistent pattern of zonation across the sandflats (L. Giménez unpublished data; Dimitriadis et al. 2002); future publications will focus on this topic.

The sandflats of the estuarine streams and lagoons of the Uruguayan coast are narrow (< 50 m) as well as the tidal range (< 0.3 m: O'Connor 1991; Anonymous 1997; Sepúlveda et al. 2004). The variations in the water level may be mostly related to freshwater discharge and wind forcing, occurring at the scale of weeks and seasons. Thus, the gradients in the water content of the sediment across the intertidal may be maintained for relatively long times as compared with tidal- or wave-dominated sedimentary shores. Besides, the variability among levels must be related to the differential effect of disturbance, predation, food availability and recolonization rates. The effect of sediment disturbance by the crab *Chasmagnathus granulata* should reduce the abundance of the polychaetes *Laeonereis acuta* and *Heteromastus similis*, while bird predators should affect clams, as in the Argentinean coast (Botto and Iribarne 1999; Iribarne and Martínez 1999). Recolonization of the upper intertidal may be restricted to periods of high water level. Thus, high desiccation, disturbance and predation, combined with a low recolonization rate may outbalance the predatory or competition effects occurring in the lower portion of the sandflats.

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References

- Anderson M (2001) A new method for non-parametric multivariate analysis. *Aust Ecol* 26:32–46
- Anderson M (2003) CAP: a FORTRAN computer program for canonical analysis of principal coordinates. Department of Statistics, University of Auckland
- Anderson M (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland
- Anderson M, Willis T (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511–525
- Anderson M, Ford R, Feary D, Honeywill C (2004) Quantitative measures of sedimentation in an estuarine system and its relationship with intertidal soft-sediment infauna. *Mar Ecol Prog Ser* 272:33–48
- Anonymous (1997) Tablas de Marea. SOHMA, Montevideo
- Attrill M (2002). A testable linear model for diversity trends in estuaries. *J Anim Ecol* 71:262–269
- Attrill M, Rundle S (2002) Ecotone or ecocline: ecological boundaries in estuaries. *Estuar Coast Shelf Sci* 55:929–936
- Bemvenuti C (1988) Impacto da predação sobre *Heteromastus similis* Southern, 1921 e *Nephtys fluviatilis* Monro, 1937 (Annelida, Polychaeta), em Fundos Moles Estuarinos. *Atlântica* 10:85–102
- Bemvenuti C (1994) O Poliqueta *Nephtys fluviatilis* Monro, 1937, como predador da infauna na comunidade de Fundos Moles. *Atlântica* 16:87–98
- Botto F, Iribarne O (1999) Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. *J Exp Mar Biol Ecol* 241:263–284
- Brazeiro A, Defeo O (1996) Macroinfauna zonation in microtidal sandy beaches: is it possible to identify patterns in such variable environments? *Estuar Coast Shelf Sci* 42:523–536
- Buchanan J (1984) Sediment analysis. In: Holme N, McIntyre A (eds) *Methods for the study of marine benthos*. Blackwells, Oxford, pp 41–65
- Calliari D, Defeo O, Cervetto G, Gómez M, Giménez L, Scarabino F, Brazeiro A, Norbis W (2003) Marine life of Uruguay: critical update and priorities for future research. *Gayana* 67:341–370
- Capitoli R, Bemvenuti C, Gianuca N (1978) Estudios de ecología bentónica na região da Lagoa dos Patos. I. As comunidades bentónicas. *Atlântica* 3 :5–22
- Cardezo M (1989) Caracterización de la fauna macrobentónica de la laguna de Rocha (Uruguay). Thesis, Facultad de Humanidades y Ciencias, Universidad de la República, Uruguay
- Day J, Hall C, Kemp W, Yáñez-Arancibia A (1989) *Estuarine ecology*. Wiley, New York
- Defeo O, Jaramillo E, Lyonnet A (1992). Community structure and intertidal zonation of the macroinfauna in the Atlantic coast of Uruguay. *J Coastal Res* 8:830–839
- Dimitriadis C, Borthagaray A, Carranza A, Rodríguez M, Giménez L (2003) Distribution of benthic macroinfauna across sand flats of Rocha lagoon, Uruguay (Abstract in Spanish). In: First Uruguayan ecology meeting Uruguay, 15–16 October
- Dittman S, Vargas J (2001). Tropical tidal flat benthos compared between Australia and Central America. In Reise K (ed) *Ecological comparisons of sedimentary shores*. Springer, Berlin Heidelberg New York, pp 275–293
- Giberto D, Bremec C, Acha E, Mianzan H (2004) Large-scale spatial patterns of benthic assemblages in the SW Atlantic: the Río de la Plata estuary and adjacent shelf waters. *Estuar Coast Shelf Sci* 61:1–13
- Giménez L (2003) Potential effects of physiological plastic responses to salinity on population networks of the estuarine crab *Chasmagnathus granulata*. *Helgol Mar Res* 56:265–273
- Giménez L, Yannicelli B (1997) Variability of zonation patterns in temperate microtidal Uruguayan beaches with different morphodynamic types. *Mar Ecol Prog Ser* 160:197–207
- Giménez L, Yannicelli B (2000) Longshore patterns of distribution of macroinfauna on a Uruguayan sandy beach: an analysis at different spatial scales and of their potential causes. *Mar Ecol Prog Ser* 199:111–125
- Gray J (1981) *The ecology of marine sediments*. Cambridge University Press, Cambridge
- Guerrero R, Acha E, Framiñan M, Lasta C (1997) Physical oceanography of the Río de la Plata Estuary, Argentina. *Cont Shelf Res* 17:727–742
- Holland A, Shaughnessy A, Hiegel M (1987) Long-term variation in mesohaline Chesapeake Bay macrobenthos: Spatial and temporal patterns. *Estuaries* 10:227–245
- Ieno E, Bastida R (1998) Spatial and temporal patterns in coastal macrobenthos of Samborombon Bay, Argentina: a case study of very low diversity. *Estuaries* 21:690–699

- Iribarne O, Martínez M (1999). Predation on the Southwestern Atlantic fiddler crab (*Uca uruguayensis*) by migratory shorebirds (*Pluvia dominica*, *P squatarola*, *Arenaria interpres*, and *Numenius phaeopus*). *Estuaries* 22:47–54
- Jorcín A (1999) Temporal and spatial variability in the macrozoobenthic community along a salinity gradient in the Castillos Lagoon (Uruguay). *Arch Hydrobiol* 146:369–384
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Mannino A, Montagna P (1997) Small-scale spatial variation of macrobenthic community structure. *Estuaries* 20:159–173
- McLachlan A, Jaramillo E (1995) Zonation on sandy beaches. *Oceanogr Mar Biol Annu Rev* 33:305–335
- Mianzan H, Lasta C, Acha E, Guerrero R, Macchi G, Bremec C (2001) The Río de la Plata Estuary, Argentina-Uruguay. In: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America (ed). Springer, Berlin Heidelberg New York, pp 185–204
- Morin P (1999) Community ecology. Blackwell, Oxford
- Muniz P, Venturini N (2001) Spatial distribution of the macrozoobenthos in the Solís Grande stream estuary (Canelones-Maldonado, Uruguay). *Braz J Biol* 61:409–420
- O'Connor W (1991) A numerical model of tides and storm surges in the Río de la Plata Estuary. *Cont Shelf Res* 11:1491–1508
- Pihl L, Rosenberg R (1982) Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, Western Sweden. *J Exp Mar Biol Ecol* 57:273–301
- Reise K (1991). Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliot M, Ducrotoy J (eds) Estuaries and coasts: spatial and temporal intercomparisons. Macrofauna in mud and sand of tropical and temperate flats. Olsen & Olsen, Fresensborg, pp 211–216
- Remane A, Schlieper C (1971) Biology of brackish water. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart
- Schneider D (1994) Quantitative ecology: spatial and temporal scaling. Academic, New York
- Seeliger U (2001) The Patos lagoon estuary, Brazil. In: Seeliger U, Kjerfve B (eds) Coastal marine ecosystems of Latin America. Springer, Berlin Heidelberg New York, pp 167–183
- Sepúlveda H, Valle-Levinson A, Framiñan M (2004) Observations of subtidal and tidal flow in the Río de la Plata Estuary. *Cont Shelf Res* 24:509–525
- Teske P, Wooldridge T (2001) A comparison of the macrobenthic faunas of permanently open and temporarily open/closed South African estuaries. *Hydrobiologia* 464:227–243
- Teske P, Wooldridge T (2003) What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size. *Estuar Coast Shelf Sci* 57:225–238
- Thrush S, Pridmore R, Bell R, Cummings V, Dayton P, Ford R, Grant J, Green M, Hewitt J, Hines A, Hume T, Lawrie S, Legendre P, McArdle B, Morrissey D, Schneider D, Turner S, Walters R, Whitlatch R, Wilkinson M (1997) A sandflat habitat: scaling from experiments to conclusions. *J Exp Mar Biol Ecol* 216:1–9
- Thrush S, Hewitt J, Norkko A, Nicholls P, Funnell G, Ellis J (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Mar Ecol Prog Ser* 263:101–112
- Underwood A (2000) Experimental ecology of rocky intertidal habitats: what are we learning? *J Exp Mar Biol Ecol* 250:51–76
- Wiens J (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wolff W (1983) Estuarine benthos. In: Ketchum B (ed) Ecosystems of the world Vol 26: estuaries and enclosed seas. Elsevier, Amsterdam, pp 151–183
- Ysebaert T, Herman P (2002) Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. *Mar Ecol Prog Ser* 244:105–124
- Ysebaert T, Meire P, Coosen J, Essink K (1998) Zonation of intertidal macrobenthos in the estuaries of Schelde and Ems. *Aquat Ecol* 32:53–71
- Ysebaert T, Herman P, Meire P, Craeymeersch J, Verbeek H, Heip C (2003). Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. *Estuar Coast Shelf Sci* 57:335–355
- Zar J (1996) Biostatistical analysis. Prentice-Hall, London