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Benthic assemblages of a temperate estuarine system in South America: Transition from a freshwater to an estuarine zone

Agustina Cortelezzi a,*, Alberto Rodrigues Capítulo a, Lucía Boccardi b, Rafael Arocena b

^a Instituto de Limnología "Dr. Raúl A. Ringuelet", CC 712 (1900) La Plata, Argentina ^b Sección Limnología, Facultad de Ciencias, Montevideo, Uruguay

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Abstract

The objectives of the present study were to describe the species composition, diversity and distribution of the zoobenthic assemblages, to estimate the abundance and biomass of the dominant species, and to identify the main environmental factors determining the distribution patterns of the invertebrates from a freshwater to an estuarine zone in a temperate estuary of South America. The Río de la Plata estuary is a microtidal system characterized by a high concentration of suspended solids. Fifty-three taxa of meso- and macro-invertebrates were identified in the samples collected during November and December 2001. Molluscs, annelids, crustaceans and nematodes were found at 90% of the sampling sites. Molluscs comprised up to about 90% of the total zoobenthos biomass: the remaining percentage corresponded mainly to annelids and less to nematodes and crustaceans. An ecocline along the salinity gradient could be observed for the benthic assemblages from the freshwater to the estuarine zone in Rio de la Plata. A Canonical Correspondence Analysis shows that results from sampling sites in the outer zone were strongly related to salinity, depth and pH and less to oxygen and percentage of clay. The results from stations in the inner zone, and part of the middle zone, were mainly related to the occurrence of sand and contents of NH₄⁺-N, NO₃⁻-N, and PO₄³-P.

Keywords: Estuarine systems; Zoobenthos; Diversity; Biomass; Distribution; Río de la Plata

1. Introduction

The Río de la Plata (34°–36°30′S; 55°–58°30′W) is a temperate microtidal system located on the southeastern Atlantic coast of South America, between Argentina and Uruguay. It has an average discharge of 20,000–25,000 m³ s⁻¹ (Urien, 1972; CARP–SIHN–SOHMA, 1989) much of which is supplied by the Paraná River, while the rest comes mainly via the Uruguay River, with a minor fraction from smaller affluents. This system is

* Corresponding author. E-mail address: agus@ilpla.edu.ar (A. Cortelezzi). one of the most important South American estuarine environments, and first in terms of economic importance and human population (15 million inhabitants). The estuarine system has a surface area greater than 13,000 km², and is characterized by a high concentration of suspended sediment. Low water transparency, due to a high content of suspended solids brought down by the rivers, may limit primary production despite the high nutrient supply from the basin and the oxygen availability (Pizarro and Orlando, 1984).

The estuary is characterized by marked horizontal and vertical salinity gradients (Acha et al., 2003) with a zone of maximum turbidity among the average surface

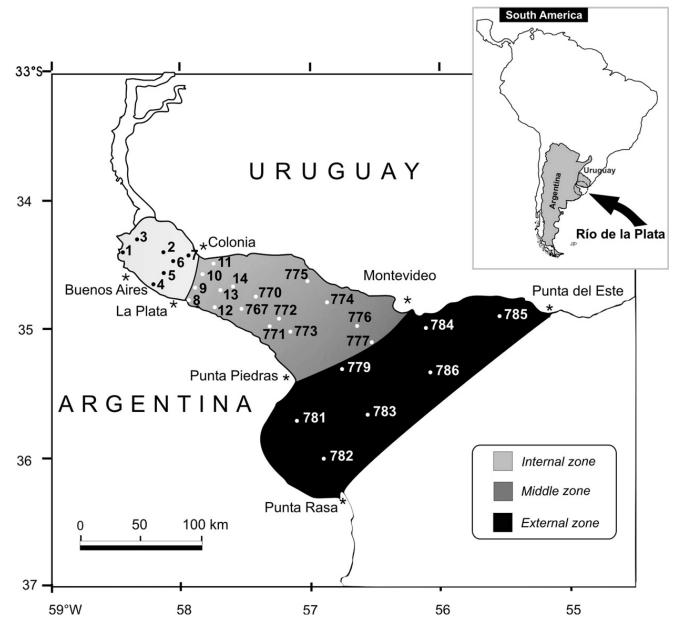


Fig. 1. Map of the study area and location of sampling sites.

salinity isoclines of 0.5 and 5 PSU (Bazan and Arraga, 1993). This zone of maximum turbidity forms a physical boundary between the fresh and estuarine waters. Wind and river discharge control the salinity and turbidity levels in the upper layer, while diluted shelf waters occupy the bottom layer (Guerrero et al., 1997).

Until now, the few studies carried out on the ecology of this system have been focused on those coastal zones connected to the great harbours and production centres of the two capital cities (Buenos Aires and Montevideo), where pollution is highest (Rodrigues Capítulo et al., 1998; Venturini et al., 1999). Previous studies on the benthic fauna of Río de la Plata mainly refer to the mollusc fauna (Ituarte, 1981, 1985; Darrigran and Maroñas,

1989; Darrigran, 1992a,b; Pastorino et al., 1993; Ituarte, 1994; Scarabino, 1999), in particular, to the coastal molluscs. More comprehensive studies have been made on some of the affluents (Chalar, 1994; Arocena, 1996; Tangorra et al., 1998; Rodrigues Capítulo et al., 2001). Boschi (1988) gave an ecological description of the environment and an up-to-date bibliographic synthesis about the dominant faunal groups, while Rodrigues Capítulo et al. (1997) and Cesar et al. (2000) have studied the distribution and diversity of benthic invertebrates in the southern coastal strip of Río de la Plata. Nevertheless, information about the benthic fauna of Río de la Plata is still fragmented. Except for the studies of Balay (1961) about the river dynamics and those of Urien (1966, 1967,

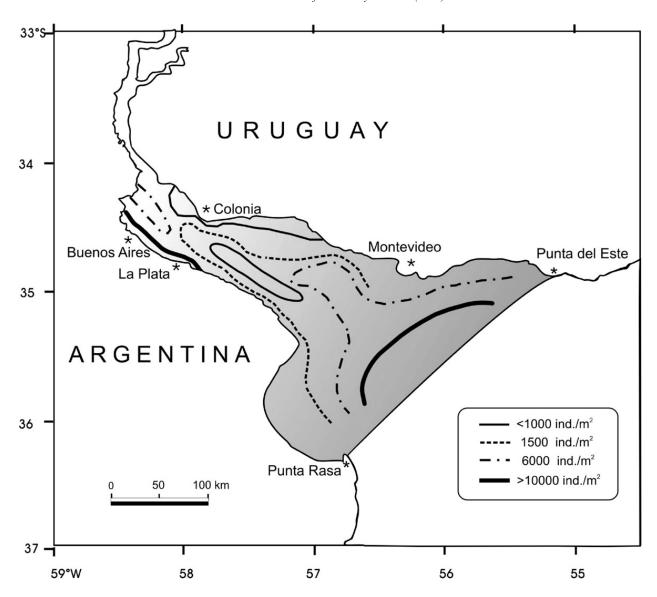


Fig. 2. Distribution of zoobenthic density.

1972) about hydrography and sediments, the Rio de la Plata has not been studied properly and perhaps it is one of the least known regions. There are not even complete faunistic and floristic lists, although there is some information scattered in different publications.

Studies of benthic communities are essential for monitoring biodiversity and the environment, not only in order to preserve them, but also for the species of commercial interest that they support (Desroy et al., 2002). Such monitoring should be a long-term program in order to identify trends of environmental degradation, but the high cost of sampling leads to a compromise between its spatial and temporal extent and frequency (Currie and Small, 2005).

This study presents integrated information about the subtidal benthic fauna from a sampling of the whole area (freshwater and estuarine zones) of the Río de la Plata estuary system. In order to obtain baseline data for future comparisons which can be used in monitoring programs or impact studies in temperate estuaries, the objectives of this study were: (i) to describe the species composition, diversity and distribution of zoobenthic assemblages, (ii) to estimate the abundance and biomass of the dominant species and (iii) to identify the main environmental factors determining the distribution patterns of the invertebrates from a freshwater to an estuarine zone in Río de la Plata.

1.1. Study area

The Río de la Plata is generally partitioned into three main zones (Fig. 1) on the basis of its physical features (CARP-SIHN-SOHMA, 1989) as well as its faunistic and floristic components (Boschi, 1988). The inner zone

extends from the confluence of the Paraná and Uruguay rivers to a line between the cities of Colonia in Uruguay and La Plata in Argentina. It has a substrate mainly of fine sand (modal diameter=0.25-0.12 mm) on the Uruguayan shore, and abundant mud (modal diameter=0.062-0.004 mm) and sand on the Argentine shore. The water depth does not exceed 4 m and the salinity 0.4 PSU. The middle zone, down to a line between Montevideo and Punta Piedras, is characterized as a transitional zone with depths between 3 and 10 m and salinity up to 5.0 PSU. The oceanic influence is noticeable and there are mud and clay (modal diameter=0.004-0.0002 mm) sediments. The outer or estuarine zone includes brackish waters of varied salinity (7–18PSU) according to the extent of marine intrusion. Depth varies between 7 and 15.5 m (PNUD/ GEF RLA/99/G31 database, 2002) and in this zone the sediment is variable with a prevalence of mud at its junction with the middle zone, and sand nearer the oceanic front.

2. Materials and methods

The area sampled stretches from the Paraná Delta to the marine boundary of the Río de la Plata. The sampling program consisted of 30 sites distributed along transverse transects between both banks of the river, as shown in Fig. 1. Such a design represents the best compromise achievable between available resources and the quality of data needed to get a first overview of the distribution of benthos.

Sampling was carried out in November and December 2001. A van Veen dredge of 470 cm² and a Dietz–Lafond sampler of 173 cm² were used to take three replicate samples at each station. The material was fixed *in situ* with 5% formaldehyde and the sorting of biological material took place in the laboratory under a stereomicroscope, after cleaning out the sediment over a sieve of 250 µm mesh size.

Individuals were determined to the lowest taxonomic level whenever it was possible and regional keys were available (Brinkhurst and Marchese, 1991; Lopretto and Tell, 1995). Chironomids were identified according to Merrit and Cummins (1996) and Paggi (2001). Nematoda and minor groups were not identified further. The zoobenthos was expressed in number of individuals m⁻² for each sampling site using the average of the three replicates. The program Statistica was used to plot the densities of the main taxonomic groups for the 3 zones (STATISTICA for Windows 4.5 Soft, Inc., 1993).

Species diversity was estimated using the Shannon Weiner Index (H') (Shannon and Wiener, 1949).

For grouping the sampling stations the technique of unweighted pair-group average (UPGMA) was used from a matrix of r Pearson among densities (Crisci and López Armengol, 1983). Biomass of the main benthic organisms was estimated as dry weight (48 h at 60 °C).

A Canonical Correspondence Analysis (CCA) (ter Braak, 1986) was applied in order to examine relationships between the abundances of zoobenthic organisms and environmental variables from the oceanographic survey: dissolved oxygen, salinity, depth, pH, nitrites, nitrates, phosphate, ammonium, % sand and % clay. These data were taken from the PNUD/GEF RLA/99/G31 database (2002). The biological and physico-chemical data were $\ln(x+1)$ transformed to reduce the effects of heterogeneity of variance and the scale variation.

For the final data arrangement, the program "CANOCO for Windows" was used (ter Braak and Smilauer, 1998), for estimating the reliable statistical limits with a Monte Carlo permutation test (p<0.01).

3. Results

During the study, 53 taxa of meso- and macro-invertebrates were identified in the samples collected in Río de la Plata. These included the following main phyla: molluscs, annelids, crustaceans and nematodes, which were found at most (90%) of the sampling sites.

3.1. Density

The lowest values of total invertebrate density (<1000 ind m⁻²) were confined to two sectors (Fig. 2): one in front of the Uruguayan shore, in the inner and middle zones, and the other offshore about 20 km from Buenos Aires province, in the middle zone. The highest densities (>10,000 ind m⁻²) were located on the Argentine coast of the inner zone, and in the outer zone near the oceanic front. The high density of benthic organisms in the inner Argentine zone is mainly the result of young bivalve molluscs and micro-crustaceans, both with wide variations among stations. Oligochaetes and nematodes were also abundant in this zone. However, in the outer zone of Río de la Plata, nematodes dominated, despite their wide variation. The middle zone presented more homogeneous densities of the four main phyla (Fig. 3).

3.2. Distribution

Cluster analysis of species abundance allowed us to distinguish four main groups of sampling sites (Fig. 4). The first grouped 7 sites in the outer zone of Río de la Plata with one from the middle zone. They shared a

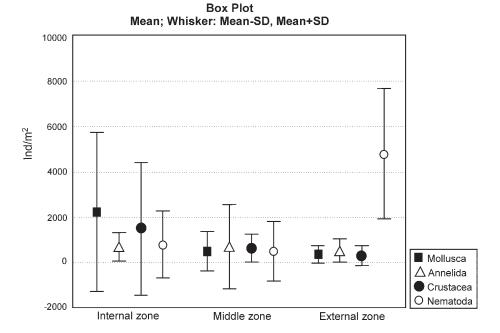


Fig. 3. Mean density and standard deviation of main phyla in the internal (ZI), middle (ZM) and external (ZE) zones of the Rio de la Plata.

dominance of Nematoda and Foraminifera. Stations along the oceanic front also share the exclusive presence of *Mactra isabelleana* and Orbiinidae.

The second group clusters the sites located near the Uruguayan shore of the inner zone with abundant Nephtyidae and the presence of *Heleobia* spp. The third group comprises sites covering the greater part of the middle zone, excluding some points that form the fourth group with sites in the inner zone. A few sites near the coast west of Montevideo share Tubificidae and Nephtyidae, whereas the points located between the Argentine coast and the centre of the estuary share Nephtyidae and a few micro-crustacean taxa. The fourth

group, which is dominated by molluscs, is different from the rest and very heterogeneous. Stations 10 and 5, in the centre of the river, share *Corbicula fluminea*, Nematoda, *Heleobia* spp. and Dugesidae, whereas stations 12 and 8, along the right bank, share Naididae and Harpacticoida. Stations between Buenos Aires and the Parana Delta have many *Narapa bonettoi*, *Heleobia* spp., Nematoda and micro-crustaceans.

3.3. Diversity and richness

The overall diversity of taxa estimated by the Shannon Weiner Index varied between 0.18 and 2.36 bits for the

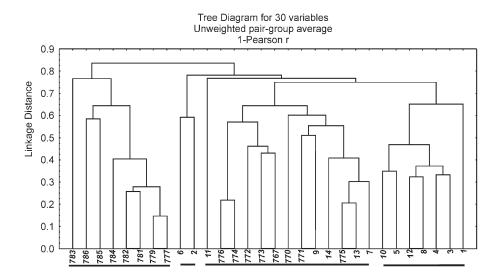


Fig. 4. Grouping of sampling stations by species abundance through the Pearson correlation index and the UPGMA method.

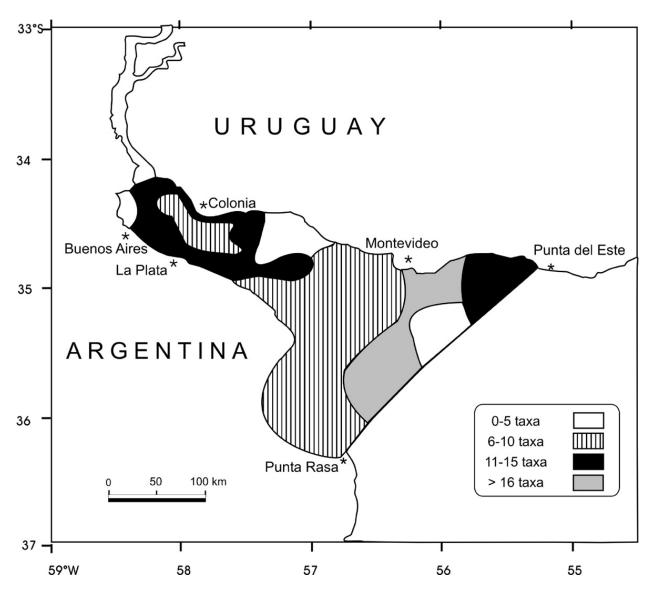


Fig. 5. Distribution of zoobenthic taxa richness of the Río de la Plata.

whole study area, with means and standard deviations of 1.53 ± 0.66 , 1.71 ± 0.41 and 1.01 ± 0.47 for the inner, middle and outer zones respectively. The highest values are concentrated between the inner and middle zones, from Buenos Aires and Colonia towards the east of the Río de la Plata.

Richness ranged from 3 to 19 taxa without a clear trend. The highest richness was registered in the outer zone with more than 16 taxa (Fig. 5). Low richness was found in the central part of the middle zone on the Uruguayan coast and at the western edge of the Argentine coast.

3.4. Biomass

Molluscs comprised about 90% of the zoobenthos biomass in Río de la Plata (Fig. 6). The remaining

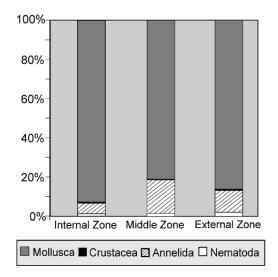


Fig. 6. Percentage of biomass of main zoobenthic groups in the Río de la Plata internal (Z1); middle (Z2) and external (Z3) zones.

Table 1
Density and biomass of most current taxa to the different zones of Río de la Plata

Taxa	Average density (ind/m ²)			Average biomass (mg/m ²)		
	Internal zone	Middle zone	External zone	Internal zone	Middle zone	External zone
Coelenterata	15.20	1.33	0.00	0.91	0.08	0.00
Dugesidae	296.35	45.21	307.75	7.41	1.13	7.69
Nematoda	789.58	500.58	4810.41	23.69	15.02	144.31
Tubificidae	166.71	122.82	10.13	711.76	524.36	43.26
Naididae	13.82	393.16	1.27	0.45	12.73	0.04
Lumbriculidae	9.57	2.74	0.00	702.35	201.40	0.00
Narapidae	263.42	0.00	1.27	26.34	0.00	0.13
Hirudinea	83.46	27.09	0.00	1168.80	379.36	0.00
Polychaeta	149.16	185.37	616.17	665.25	826.76	2748.13
Corbicula fluminea	553.86	75.97	68.90	57,048.03	7825.17	7096.20
Heleobia sp.	321.24	178.56	130.29	2394.48	1330.98	971.19
Erodona mactroides	0.00	10.49	95.24	0.00	1.05	9.52
Mactra isabelleana	0.00	0.00	48.87	0.00	0.00	14,680.52
Rapana venosa	0.00	0.00	8.90	0.00	0.00	10,680.00
Bivalvia juvenile	1372.84	225.68	482.27	82.37	13.54	28.94
Cyclopoida	242.16	35.18	51.67	2.25	0.33	0.48
Harpacticoida	671.45	48.23	3.80	4.56	0.33	0.03
Polyphemidae	0.00	0.00	60.79	0.00	0.00	2.82
Chidoridae	37.99	5.23	0.00	48.23	6.64	0.00
Bosminidae	18.57	21.44	0.00	0.38	0.44	0.00
Daphnidae	60.79	0.00	000	1.53	0.00	0.00
Ostracoda	0.00	278.51	60.54	0.00	14.20	3.09
Tanaidacea	0.00	17.73	0.00	0.00	7.09	0.00
Cumacea	7.60	1.21	0.00	0.76	0.12	0.00
Isopoda	0.00	0.00	10.49	0.00	0.00	2.10
Amphipoda	0.00	0.95	14.06	0.00	0.47	7.03
Brachyura	0.00	0.00	3.04	0.00	0.00	58.36
Acari	6.08	2.66	3.47	3.16	1.38	1.80
Chironomidae	67.97	16.18	1.45	1.76	0.42	0.04
	Average density total (ind/m ²)			Average biomass total (mg/m ²)		
	177.51	75.74	234.16	2168.77	384.93	1258.13

percentage was made up mainly of annelids and, to a lesser extent, nematodes and crustaceans in the three zones of the river, with more annelids in the middle sector.

3.4.1. Annelids

Glossiphoniidae hirudineans, followed by Tubificidae and Lumbriculidae oligochaetes, and Nephtyidae and Pilargiidae polychaetes, dominated the biomass of the inner zone. In the middle zone the highest abundance was represented by polychaetes (Nephtyidae, Pilargiidae, Flabelligeridae, Scalibregmidae and Onuphidae) followed by Tubificidae and Glossiphoniidae. In the outer zone the polychaetes (Paraonidae, Onuphidae, Glyceridae, Orbiniidae, Lumbrineridae, Nephtyidae, Nereididae and Pilargiidae) mainly dominated (98%), while other annelids were poorly represented.

3.4.2. Molluscs

In the inner zone *Corbicula fluminea* was abundant, forming 96% of the biomass: the rest was made up of

Heleobia spp. and young stages of mytilids. This pattern was the same in the middle zone, even though the abundance of *C. fluminea* decreased significantly, favouring *Heleobia* spp. In the outer zone, a higher proportion of *Mactra isabelleana* was observed giving

Table 2
Mean physico-chemical parameters of Río de la Plata during
November 2001 (PNUD/GEF RLA/99/G31 database, 2002)

	Internal zone	Middle zone	External zone
Depth (m)	3.43	6.22	10.86
Salinity (PSU)	_	0.90	12.63
pН	7.39	7.62	8.19
OD (mg/l)	6.17	7.14	7.80
NO_3 (µmol N-NO ³ /l)	7.27	8.54	3.14
NO_2 (µmol N-NO ² /l)	1.26	1.36	1.25
NH ₄ (µmol N–NH ₄ /l)	3.37	4.06	2.96
PO ₄ (µmol P–PO ₄ /l)	2.72	2.20	1.57
% Clay	3.81	8.02	7.98
% Sand	73.18	34.77	48.15

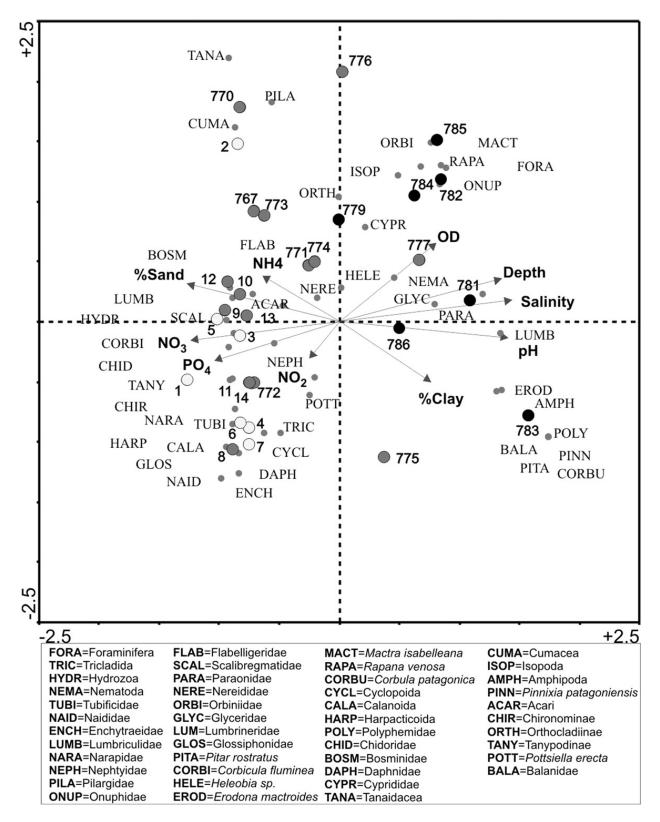


Fig. 7. Triplot of sampling sites, zoobenthic taxa and environmental variables in relation to the first two ordination axes of CCA.

further evidence for the retreat of *C. fluminea*, but with a significant increase in the number of mollusc species of marine lineage. It is important to add that the presence of

Rapana venosa, a new invading gastropoda (Pastorino et al., 2000) found in the outer zone, formed the highest benthic biomass in that zone.

3.4.3. Crustaceans

In the inner zone cladocerans predominated (87%), followed by copepods and cumaceans. In the middle zone, ostracods contributed the highest percentage biomass, followed by tanaidaceans and cladocerans. In the outer zone the brachyuran *Pinnixia patagoniensis* represented the highest percentage of the biomass. In the middle and outer zones the biomass was distributed among a large number of crustacean groups leading to a high specific diversity.

Even though the nematodes dominated numerically in the outer zone, their biomass was not important in relation to the three groups mentioned above. However, they had a higher biomass in the three zones than the minority taxa (dugesids, acari, chironomids and hydrozons) due to their high numerical density despite their small sizes (Table 1).

3.5. Relationships between organisms and environmental variables

In order to study the relationships between the organisms and their environment, we used those variables which presented significant correlation values (p < 0.05, Table 2). The correlation coefficients of the species vs. environmental variables were, for all axes of the CCA triplot (Fig. 7), greater than 0.90. The accumulated percentage of the variance was 62.6. For the first four axes the Monte Carlo Test was of *F*: 1.977 and p < 0.005. The stations located on the right of horizontal axis were strongly connected with salinity, depth and pH and less to oxygen and percentage clay. The sampling sites of the outer zone were located in that sector of the graph. Mainly marine species (Balanus improvisus, Pinnixia patagoniensis, Erodona mactroides, Corbula patagonica, Mactra isabelleana and Rapana venosa, Podon polyphemoides, Rotalia beccarii) and some families of Polychaeta (Paraonidae, Glyceridae and Lumbrineridae) were associated with these variables and stations.

The stations of the inner zone and the adjacent part of the middle zone were located at the other extreme of horizontal axis. They were mainly related to the highest percentages of sand and concentrations of NH₄⁺-N, NO₃⁻-N, and PO₄³-P. *Corbicula fluminea*, chironomids, oligochaetes and microcrustaceans are the main taxa associated with these stations.

The rest of the stations were grouped in the central sector of the horizontal canonical axis related to intermediate conditions of the environmental variables.

4. Discussion

Estuaries have the predominant characteristic of being sites of spatial and temporal continua in, for example, environmental variables such as salinity, and biological variables, such as community structure (Elliott and McLusky, 2002). In the Río de la Plata, a continuum of species can already be observed from the lower basins of the principal tributaries, the Uruguay and Paraná rivers. For example, Marchese (1996), referring to the lower section of the Paraná, recorded that Narapa bonettoi was the dominant species in the centre of the riverbed. This species disappears in the coastal area, while Limnodrilus hoffmeisteri and Corbicula fluminea abound. These observations coincide with those of the present study in the inner zone of Río de la Plata where N. bonettoi occurred at densities higher than 200 ind/m² and Tubificidae replaced it in the coastal zone.

The boundary in the species composition between the inner and middle zones of Río de la Plata is not so clear because the environmental features of both zones are more homogeneous. The major biological distinction was observed between the outer or estuarine zone and the middle zone which are separated by the turbidity front.

The spatial differences in the composition of the benthic communities along estuarine gradients have been related mainly to changes in salinity, depth, sediment grain size, and organic content (Day et al., 1989).

Giberto (2001) found in the Río de la Plata system that depth, salinity and % clay showed the strongest correlations with the observed faunal patterns, and also that beta diversity varied between dominant taxonomic groups due to changes in salinity.

Although long-term averages of environmental variables are more important than those values obtained during sampling (Ysebaert and Herman, 2002), some conclusions can be derived from the CCA performed here. Most stations of the inner zone of Río de la Plata were related to the highest contents of nutrients, typical of freshwater inputs. Bazan and Arraga (1993) determined that the Argentine area, extending between the coast and 3-5 km into the Río de la Plata, presents a high degree of contamination due to anthropogenic terrestrial inputs. Nevertheless, the very dynamics of the river produces auto-purifying processes that begin as soon as we approach the main channel. The Argentine coast, next the city of Buenos Aires, is an area particularly dense with benthic organisms. An ecological study carried out from the bank to 10 km offshore in

the southern coastal fringe (Argentina), demonstrated that Oligochaeta and Nematoda were the most abundant organisms, especially in zones with high concentrations of organic matter (Rodrigues Capítulo et al., 1998). Oligochaetes and nematodes (near the coast) and microcrustaceans and young bivalves (in the main channel) make the inner zone an area of great density of benthic organisms.

Trends along the middle zone stations are not clearly defined by the variables considered in this study, probably because they are located in a transitional area. Most of the stations in the outer zone of the Río de la Plata are clearly related to depth, dissolved oxygen, salinity and pH, which characterise the marine environment. In the outer zone, high densities were due mainly to the high number of nematodes beyond the turbidity front where the drifting material and small organisms are retained and concentrated.

The environmental variables restrict the range of organisms that are able to survive, with the consequence that estuaries are considered areas of low diversity and high abundance (Day et al., 1989; Atrill et al., 1996; Constable, 1999). The same has also been observed in the Río de la Plata. Mouny et al. (1998) found an impoverishment of richness (from >20 to <15 species), biomass (from 45 to 4 g m⁻²) and density (from 100 to 20 ind m⁻²) from the polyhaline to the oligonaline zones of the Seine estuary, with two different macrobenthic communities: one in the outer part of the estuary and another one in the inner part. Similarly, the Río de la Plata presented the highest density and richness of invertebrates in the outer or estuarine zone although the average biomass was higher in the inner zone where molluscs dominated in about half the stations of that zone.

According to Mianzan et al. (2001), Shannon species diversity values ranged between 1.29 and 2.44 in the estuarine area of the Río de la Plata. The values we registered in the same zone were lower, reaching on average 1.01, but increasing to an average of 1.71 in the middle zone. These results may be explained by the large extent of the middle zone that includes most of the sampling stations.

Attrill and Rundle (2002) found a continuum of assemblage types along the length of the Thames estuary rather than any definable single estuarine community. According to these authors, the estuary represents a new concept, a two-ecocline model, with an ecocline from sea to mid-estuary, overlapping with an ecocline from river to mid-estuary. The patterns of community change represent a progressive rather than an abrupt boundary (Kent et al., 1997), following the

gradual difference in one major environmental variable (salinity). In the present study, although some invertebrates were exclusive to the different zones, an ecocline along the salinity gradient could be observed for the remaining taxa. A clear example was observed for the molluses, of which Corbicula fluminea dominated in the inner and middle zones, Corbula patagonica and Erodona mactroides in the middle and outer zones and Mactra isabelleana, Pitar rostratus and Rapana venosa in the outer zone. Species distribution limits may coincide with dispersal barriers or physiological thresholds along environmental gradients, but they may also be influenced by species interactions. According to Case et al. (2005) when barriers to dispersal are weak and environmental gradients are gradual, is essential to consider co-evolved species interactions as a potential mechanism limiting species distributions. Future work could explore these possibilities in order to explain some of the observed discontinuities in the distribution patterns we observed.

Finally, it is important to pay attention to the presence of *Rapana venosa* in the outer zone of Río de la Plata. *R. venosa* is a member of the Muricidae, a family of predatory marine snails, native to the Sea of Japan. The species has all the many characteristics of a successful invader: it is fast growing; it has a high fertility and a high tolerance to lower salinities, water pollution and oxygen deficiency (Kerckhof et al., 2006). Due to its predatory impact *R. venosa* is considered to be one of the most threatening invaders worldwide. The long-term ecological impact of *R. venosa* on the American Atlantic coast could be a cause for concern.

The information gathered during this study represents a valuable increase in our knowledge about large temperate estuaries. Such data provide a baseline for monitoring changes that may occur, either in the estuary itself, in its tributaries, in the South Atlantic Ocean or in the terrestrial basin. Nevertheless, this baseline only refers to spring when the samples were taken. Seasonal changes can occur, mainly driven by hydrological and geomorphological mechanisms. An increased river discharge in winter and decreased in summer, would lead to a different salinity structure of the estuary. This in turn, would lead to the presence and dominance of freshwater or haline species at each period, respectively. These factors would help define seasonal patterns, looking forward to knowledge of the temporal as well as the spatial variation of the benthic community of Rio de la Plata and others similar systems. We hope that these preliminary findings stimulate future research to test new concepts of estuarine ecology and explore in greater depth relationships between estuary form and function.

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