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Environmental factors structuring fish communities of the Río de la Plata estuary

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Abstract

We examined the changes in composition of fish assemblages for all seasons in the Río de la Plata estuary (36°S, 56°W), and identified the parameters that control the main structuring of the estuarine community. Multivariate analysis (DCCA), performed on species biomass (t nm^{-2}), indicated a spatial structuring of the estuarine community in three areas: inner, central and outer. Bottom salinity was the main factor associated with the significant differences in species composition. Examination of the estuary as a whole indicated a persistent spatial pattern, and suggested that temperature has the strongest influence on seasonal structure of fish assemblages. Both seasonal migrations (for example, of *Trichiurus lepturus* and *Discopyge tschudii*) and reproductive movements (for example, of *Micropogonias furnieri*, *Mustelus schmitti* and *Cynoscion guatucupa*), appear as important factors affecting the temporal structure of the estuarine community.
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Keywords: Fish assemblages; Temporal and spatial patterns; Estuarine community; Environmental factor; Río de la Plata

1. Introduction

Communities of fish inhabiting estuaries are a combination of freshwater and marine species including many juveniles (Claridge et al., 1986). A relatively low diversity but high abundance of some species characterizes these communities. Most species exhibit wide tolerance to fluctuating environmental conditions typical of these systems (Whitfield, 1999).

The main parameters known to affect the spatial organization of estuarine communities are salinity (Loneragan et al., 1987; Cyrus and Blaber, 1992; Bulger et al., 1993; Thiel et al., 1995; Marshall and Elliott, 1998; Whitfield, 1999) and depth (Wantiez et al., 1996; Hyndes et al., 1999). Other factors such as temperature (Peterson and Ross, 1991), turbidity (Blaber and Blaber, 1980; Cyrus and Blaber, 1992) and some components of the habitat, such as benthic community composition and substrate type (Wantiez et al., 1996) further influence this organization.

Nearshore marine waters and estuaries act as important nursery areas for several marine teleost species in temperate regions, before they migrate out to deeper water as they mature (Blaber and Blaber, 1980). Seasonal migrations of young fish from the

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coast to adjacent waters, and adults moving to spawning areas produce temporal changes in community structure (Claridge et al., 1986).

Spatial heterogeneity of species assemblages makes it possible to identify broad geographic areas characterized by relatively homogeneous fish assemblages (Menni and Gosztonyi, 1982; Tyler et al., 1982) and identify the main environmental characteristic of these areas as a first step toward understanding the structure of fish communities.

The fish community of the Río de la Plata estuary supports one of the traditional fisheries activities of the Argentinean and Uruguayan coastal region (Lasta and Acha, 1996). Several aspects of the estuarine fish community have been described (Anganuzzi, 1983; Cousseau, 1985; Boschi, 1988; Prenski and Sánchez, 1988; Lasta et al., 1998; Díaz de Astarloa et al., 1999). However, little is known about the manner in which environmental factors determine the spatial organiza-tion and the seasonal variation of the estuarine community. This study represents the first attempt to estimate the influence of environmental factors on the spatial distribution and the seasonal variations of fish assemblages within the Río de la Plata estuary.

2. Material and methods

2.1. Study area

The Río de la Plata is an extensive shallow coastal plain estuary in the western South Atlantic coast (36°S–56°W; Fig. 1). The freshwater input, which mainly comes from the Paraná and Uruguay rivers, averages 20,000–25,000 m^3 s^{-1} (CARP, 1989). The Barra del Indio, a shallow bar across the river, divides the estuary into inner and outer regions (CARP, 1989). The inner region has a pluvial regime and it is entirely
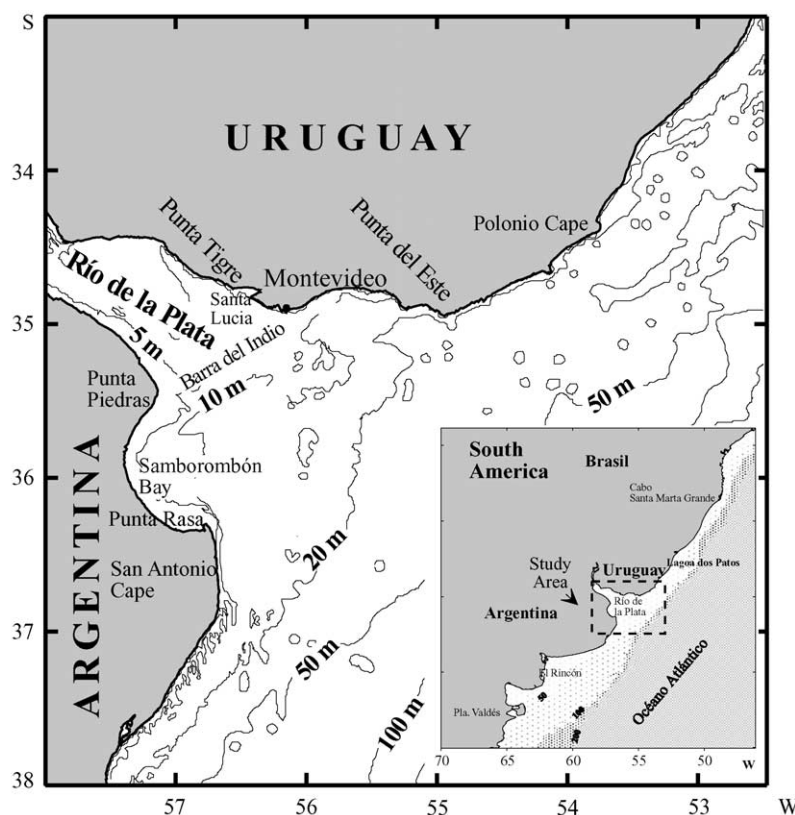

Fig. 1. Location and bathymetry of the study area.

occupied by freshwater, with a depth range between 1 and 5 m. The outer region is mainly mixohaline, with an area about 38,000 km^2 (Mianzan et al., 2001) and a depth range of 5 to 15–25 m. The boundary with shelf waters is defined by the extension of the 27–30 ups isohaline, its location depending on the dynamics of estuarine waters (Guerrero et al., 1997a).

Because of the low depth, the structure of the entire water column is highly influenced by atmospheric conditions that determine the spatial and temporal distribution of temperature and salinity. In the estuarine waters there is a warm period (December–March, 21–22 °C) and a cold period (June–September, 10–12 °C). In both periods, the waters are almost thermally homogeneous both vertically and horizontally. The penetration of marine water as a bottom layer into the riverine systems occurs as a salt wedge, defining an area of strong vertical stratification. Winds and discharge force patterns of surface salinity, while bottom salinity is controlled by bathymetry (Guerrero et al., 1997a). Two periods with different estuarine discharge pattern are defined for this estuary. From April to August there is a main NNE drift of estuarine water along the Uruguayan coast. From October to February freshwaters show a southern extension along the Argentine coast while shelf waters penetrate up to Punta del Este (Uruguay), constraining the NNE drift (Guerrero et al., 1997a). The same seasonal circulation pattern has been deduced to occur off southern Brazil and Uruguay (Pereira, 1989; Lima et al., 1996).

2.2. Sampling and data analysis

Biological and oceanographic data were collected during four fishery evaluation cruises on board R/V "Eduardo L. Holmberg" from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). The cruises were conducted in winter (08/1993), spring (10/1995), summer (02/1996) and autumn (06/1996) (Fig. 1).

Fish were sampled from 178 bottom trawl sets (38 in winter, 41 in spring, 56 in summer and 43 in autumn), with an Engel type trawl (200 mm stretched mesh in the wings and 120 mm stretched mesh in the cod ends, 4 m vertical opening and 15 m horizontal aperture) towed at 4 knots for 15 min per set.

Temperature and salinity at each sampling station were obtained using a Seabird series SBE19 and SBE9

conductivity–temperature–depth (CTD) profiler, with a sampling rate of 2 scans and 24 per second and a lowering speed of 0.5 m s^{-1}. Data were reduced to 1 m vertical resolution, with a precision of ±0.03 °C for temperature and ±0.05 psu for salinity.

Fish, identified to species level, were ordered according to Nelson (1994). Biomass (t nm^{-2}) of each species by sampling station was used to obtain a grouping of stations based on species composition for each season (spatial ordination) and between seasons (seasonal ordination).

At the seasonal analysis, the spring (10/1995), summer (02/1996) and autumn (06/1996) sampling are consecutive, but winter (08/1993) sampling is not consecutive with the other three seasons. A one-way ANOSIM test revealed no significant difference on the Río de la Plata fish community between mid and late 1990s during spring season ($P > 0.05$). Based on presence–absence data, a two-way analysis of variance (ANOVA) showed a seasonal significant difference between spring, summer and autumn (Jaureguizar, personal communication). These results indicate that the seasonal changes of the estuarine community are stronger than the temporal changes, thus the seasonal comparison including winter across mid to late 1990s may be valid.

Identification of sampling station groupings, assemblage areas, and their relationship with depth, temperature and salinity of surface and bottom waters were analyzed using detrended canonical correspondence analysis (DCCA). DCCA is a direct analysis performed by the computer program CANOCO (version 4.02), that selects the linear combination of environmental variables that maximizes the dispersion of the species scores. The species scores are restricted to be a linear combination of measured environmental variables, and the correlation of the environmental variables with the first two axes is termed intra-set correlation. The ordination output shows patterns that are directly related to the environmental conditions being examined. The significance test was based on Monte Carlo permutation test (10^3 permutations) for the sum of all eigenvalue and the significance of relationship between gradients and the individual environment variables were evaluated by t-test (CANOCO version 4.02).

Only species that occurred in >0.1% of catches in each season were included in the analysis. Species

biomass data were $\log_{10}(x+1)$ transformed to reduce the dominance effect of some species.

To determine whether or not major shifts in community structure have occurred between groups of stations identified by DCCA we used a non-parametric analysis, permutation-based one-way analysis of similarity (ANOSIM, Clarke, 1993). Where appropriate, R-statistic values for pair-wise comparisons provide by ANOSIM were used to determine the dissimilarity between groups. Values close to 1 indicate very different composition, while values near zero show little difference. It was used to test the null hypothesis that within seasons no changes in community structure were observed between assemblages, and secondly to test that within assemblages, no changes in community structure were observed between seasons.

The fish biomass was used to compare similarity between assemblages within a season, and for an assemblage between seasons. Through the similarity percentage (SIMPER) procedure, species that on average contribute strongly to assemblages were quantified and ranked (Clarke, 1993). This procedure uses the standard deviation of the Bray–Curtis dissimilarity matrix, attributed to a species, for all species pairs and compares that with the average contribution of a species to the dissimilarity. Also, it allowed us to quantify the average contribution, by species, to the measure of dissimilarity between assemblages and for an assemblage between seasons.

3. Results

3.1. Faunal composition

During the four seasons 60 species belonging to 33 families were caught, including 24 teleost and 9 elasmobranch families. Thirty-four species contributed >0.1% to total biomass in at least one season (Table 1). *Micropogonias furnieri* (White croaker, 25.8%) was the most abundant, followed by *Cynoscion guatucupa* (Stripped weakfish, 13.9%), *Mustelus schmitti* (Patagonian smoothhound, 10.11%), *Brevoortia aurea* (Brazilian menhaden, 9.8%) and *Macrodon ancylodon* (King weakfish, 6.05%). Dominant species changed seasonally. The most abundant species were *M. furnieri* (55.23 and 27.43%) during winter and

summer, *C. guatucupa* (49.66%) during the autumn and *M. schmitti* (27.92%) during spring.

3.2. Environmental conditions

Throughout this study, surface salinity showed larger seasonal variation than bottom water salinity. Mean salinity at the surface ranged from 10.44 psu (winter) to 16.63 psu (spring). Bottom salinity had a minimum in summer (20.84 psu) and a maximum during spring (24.64 psu). Water temperature showed stronger seasonal variability than salinity. Both surface and bottom water temperatures reached minimum values during autumn and winter, and maximum values during summer (Table 2).

3.3. Fish assemblages and environmental variables

Each one of the four canonical axes obtained from DCCA analysis represents a linear combination of environmental data calculated from the oceanographic data. The four axes together explained between 18.1 and 26.5% of species variation in biomass. The first two axes together explained between 69 and 78% of the total variation explained by environmental factors over the four seasons. Eigenvalues and variances explained by the first two axes are given in Table 3. The variance explained by the whole ordination, as well as the first axis, was significant ($P = 0.01$). The permutation Monte Carlo test was also significant ($n = 199$, $P = 0.01$ for both tests).

For each season, the two first axes of DCCA ordination diagram (Fig. 2) separate sampling stations into discrete groupings. Values for the first canonical axis show that bottom salinity and depth are the most important factors in the spatial distributions of species composition. The influence of salinity was larger during summer, winter and spring, while depth was more important during autumn. This axis, which explained from 57.93 to 80.0% of total variation, ordered sampling stations in three groups (Fig. 2A) corresponding to inner, central and outer portions of the estuary (Fig. 2B). These areas differed significantly in their species composition in all seasons (ANOSIM, Table 4), because each consistently contained unique diagnostic species (SIMPER, Table 5).

The shallow and freshwater inner area (Table 6) was typified by *Parapimelodus valenciennesi* and

Table 1
Mean biomass ($t\,nm^{-2}$) and percentage contributions of total catch for each species at each season and all sampling stations (Osteichthyes, Chondrichthyes)

Class	Family	Species	Summer		Autumn		Winter		Spring		Total	
Oshyes	Ariidae	*N. barbus* (Lacépède, 1803)[a]	4.0E−01	2.18%	1.7E−03	0.01%	2.8E−02	0.12%	4.0E−02	0.17%	1.4E−01	0.68%
	Atherinidae	*Odonthestes argentinensis* (Valenciennes, 1835)					1.7E−03	0.01%	6.2E−04	0.00%	5.0E−04	0.00%
	Balistidae	*Balistes capriscus* (Gmelin, 1788)	4.2E−04	0.00%	1.6E−04	0.00%					1.7E−04	0.00%
	Batrachoididae	*Porichthys porosissimus* (Valenciennes, 1837)	7.6E−04	0.00%	3.3E−03	0.02%	1.7E−02	0.08%	3.4E−03	0.01%	5.5E−03	0.03%
		Triathalassothia argentina (Berg, 1897)					2.0E−03	0.02%			4.3E−04	0.00%
	Carangidae	*P. signata* (Jenyns, 1842)[a]	5.2E−01	2.84%	1.9E−01	0.99%	3.3E−01	1.45%	4.7E−01	2.00%	3.9E−01	1.88%
		Trachinotus marginatus (Cuvier and Valenciennes, 1831)	6.8E−04	0.00%	1.1E−03	0.01%					4.8E−04	0.00%
		Trachurus lathami Nichols, 1920[a]	6.7E−04	0.00%			2.6E−01	1.14%	3.9E−01	1.65%	1.4E−01	0.70%
	Clupeidae	*B. aurea* (Agassiz, 1829)[a]	3.8E−01	2.08%	4.0E+00	20.22%	2.9E+00	13.11%	1.4E+00	6.08%	2.0E+00	9.84%
		Ramnogaster arcuata (Jenyns, 1842)	1.2E−04	0.00%	9.3E−03	0.05%	7.9E−03	0.04%			4.0E−03	0.02%
	Congridae	*C. orbignyanus* Valenciennes, 1847[a]	6.0E−02	0.33%	2.5E−01	1.25%	3.8E−01	1.68%	3.3E−02	0.14%	1.7E−01	0.80%
	Cynoglossidae	*Symphurus* sp. (Rafinesque, 1810)	3.2E−03	0.02%	4.9E−03	0.02%	1.1E−02	0.05%	4.7E−03	0.02%	5.5E−03	0.03%
	Engraulididae	*Anchoa marinii* Hildebrand, 1943	1.8E−02	0.10%	1.1E−03	0.01%	1.2E−03	0.01%	3.5E−04	0.00%	6.2E−03	0.03%
		Engraulis anchoita Hubbs and Marini, 1935[a]	9.8E−05	0.00%	5.8E−03	0.03%	4.3E−01	1.93%			9.4E−02	0.45%
		Lycengraulis grossidens (Agassiz, 1829)	1.6E−02	0.10%					1.4E−03	0.01%	5.5E−03	0.03%
	Gempylidae	*Thyrsitops lepidopodea* (Cuvier, 1830)					1.3E−03	0.01%			2.9E−04	0.00%
	Mugilidae	*Mugil* sp. (Linné,1758)[a]	1.5E+00	7.95%	2.0E−03	0.01%	4.5E−02	0.20%	1.2E−01	0.49%	4.9E−01	2.39%
	Mullidae	*Mullus argentinus* Hubbs and Marini, 1933	4.2E−03	0.02%							1.3E−03	0.01%
	Paralichthyidae	*P. orbignyanus* (Valenciennes, 1939)[a]	1.4E−01	0.76%	7.3E−02	0.37%	1.6E−01	0.72%	2.1E−01	0.92%	1.4E−01	0.70%
		P. patagonicus Jordan, 1889[a]	1.6E−01	0.85%	1.4E−01	0.70%	2.5E−01	1.10%	5.1E−01	2.20%	2.5E−01	1.22%
		Xystreuris rasile (Jordan, 1890)					1.4E−02	0.06%	8.4E−03	0.04%	5.0E−03	0.02%
	Percophidae	*P. brasiliensis* Quoy and Gaimard, 1824[a]	9.6E−03	0.05%	1.7E−02	0.09%	9.7E−02	0.44%	3.6E−03	0.02%	2.9E−02	0.14%
	Phycidae	*Urophycis brasiliensis* (Kaup, 1858)[a]	4.0E−02	0.22%	2.0E−02	0.10%	2.4E−01	1.06%	1.0E−01	0.44%	9.2E−02	0.44%
	Pimelodidae	*Luciopimelodus pati* (Valenciennes, 1840)	3.1E−02	0.02%	2.0E−04	0.00%					9.6E−03	0.05%
		P. valenciennesi (Kroyer, 1874)[a]	9.0E−02	0.49%					6.2E−04	0.00%	2.8E−02	0.14%
		Pimelodus albicans (Valenciennes, 1840)[a]	7.6E−02	0.42%							2.4E−02	0.12%
	Pleuronectidae	*Oncopterus darwini* Steindachner, 1875	5.6E−04	0.00%							1.7E−04	0.00%
	Pomatomidae	*Pomatomus saltatrix* (Linné, 1758)[a]	3.0E−03	0.02%	3.0E−02	0.15%	1.2E−01	0.52%	1.8E−02	0.08%	3.7E−02	0.18%
	Scianidae	*C. guatucupa* (Cuvier, 1830)[a]	3.6E−01	1.96%	9.8E+00	49.66%	1.3E+00	5.91%	5.8E−01	2.47%	2.9E+00	13.95%
		M. ancylodon Schneider, 1801[a]	1.7E+00	9.13%	1.0E+00	5.24%	1.4E+00	6.06%	8.2E−01	3.48%	1.3E+00	6.06%
		M. americanus (Linné, 1758)[a]	2.7E−02	0.15%	2.3E−02	0.11%	8.3E−02	0.37%	8.0E−02	0.34%	5.0E−02	0.24%
		M. furnieri (Desmarrest, 1823)[a]	1.0E+01	55.23%	1.8E+00	9.23%	6.1E+00	27.43%	1.8E+00	7.58%	5.3E+00	25.83%
		P. brasiliensis (Steindachner, 1875)[a]	2.7E−01	1.47%	2.3E−01	1.18%	1.5E−01	0.68%	4.4E−01	1.89%	2.7E−01	1.33%
		Pogonias cromis (Linné, 1766)	3.2E−03	0.02%	2.4E−02	0.08%	1.6E−02	0.07%			1.0E−02	0.05%
		Umbrina canosai Berg, 1895[a]	1.4E−03	0.01%	2.0E−01	1.02%	1.5E−02	0.07%	1.8E+00	7.79%	4.7E−01	2.26%
	Serranidae	*Acanthistius brasilianus* (Valenciennes, 1828)			1.2E−02	0.06%	3.2E−02	0.08%			9.6E−03	0.05%
		Dules auriga Cuvier, 1829					7.0E−03	0.03%	2.9E−04	0.00%	1.6E−03	0.01%
	Sparidae	*Diplodus argenteus* (Valenciennes, 1830)			8.9E−03	0.05%	4.0E−02	0.18%	1.5E−02	0.06%	1.4E−02	0.07%
		Sparus pagrus (Linné, 1758)			2.5E−03	0.01%	1.2E−02	0.05%			3.1E−03	0.01%
	Stromateidae	*Peprilus paru* (Linné, 1758)[a]	2.4E−01	1.31%			5.6E−04	0.00%	9.0E−02	0.38%	9.6E−02	0.47%
		S. brasiliensis (Fowler, 1906)[a]	4.3E−02	0.23%	2.9E−01	1.50%	1.7E+00	7.39%	5.0E−01	2.12%	5.5E−01	2.67%
	Trichiuridae	*T. lepturus* Linné, 1758[a]	5.7E−01	3.12%	2.5E−03	0.01%			7.0E−02	0.30%	2.0E−01	0.95%
	Triglidae	*Prionotus nudigula* Ginsburg, 1950[a]			1.0E−01	0.51%	1.1E−01	0.51%	1.0E−01	0.44%	7.2E−02	0.35%
		P. punctatus (Cuvier 1829)[a]	2.2E−01	1.18%	6.9E−02	0.35%	5.1E−01	2.29%	1.5E+00	6.54%	5.5E−01	2.64%

Table 1 (*Continued*)

Class	Family	Species	Summer		Autumn		Winter		Spring		Total	
Chyes	Dasyatidae	*Dasyatis pastinaca* (Linné, 1758)							3.1E−02	0.09%	7.1E−03	0.03%
	Hexanchidae	*Notorhynchus cepedianus* (Peron, 1807)					1.1E−02	0.05%	3.8E−03	0.02%	3.2E−03	0.02%
	Myliobatidae	*M. goodei* Garman, 1885[a]	6.2E−01	3.37%	7.0E−02	0.36%	8.6E−01	3.82%	1.6E+00	6.96%	7.7E−01	3.72%
	Rajidae	*A. castelnaui* (Miranda Ribeiro, 1907)[a]	9.0E−03	0.05%	1.1E−01	0.54%	5.4E−01	2.42%	5.9E−01	2.51%	2.8E−01	1.35%
		Atlantoraja cyclophora (Regan, 1903)			7.3E−03	0.04%	1.1E−02	0.05%	9.8E−03	0.04%	6.3E−03	0.03%
		Psammobatis bergi Marini, 1932			7.2E−03	0.04%	2.4E−03	0.01%	1.7E−02	0.07%	6.1E−03	0.03%
		Rioraja agassizi (Müller and Henle, 1841)[a]	3.0E−03	0.02%	6.8E−03	0.03%	4.9E−02	0.22%	1.1E−01	0.46%	3.8E−02	0.18%
		Sympterygia acuta Garman, 1877	7.8E−03	0.04%	9.0E−03	0.05%	2.5E−02	0.08%	8.8E−03	0.04%	1.2E−02	0.06%
		S. bonapartii Müller and Henle, 1841[a]	2.1E−01	1.15%	6.3E−01	3.21%	5.1E−01	2.28%	9.2E−01	3.91%	5.4E−01	2.60%
	Rhinobatidae	*Rhinobatos horkelii* Müller and Henle, 1841[a]	3.8E−03	0.02%	1.7E−03	0.01%	1.6E−02	0.07%	1.8E−02	0.08%	9.1E−03	0.04%
		Zapteryx brevirostris (Müller and Henle, 1841)	8.3E−03	0.05%	1.7E−02	0.08%	1.9E−02	0.08%	2.9E−02	0.06%	1.7E−02	0.06%
	Squalidae	*Squalus acanthias* Linné, 1758			1.3E−02	0.07%	1.1E−02	0.05%			5.6E−03	0.13%
	Squatinidae	*S. guggenheim* Marini, 1936[a]	2.6E−01	1.42%	5.6E−02	0.29%	4.6E−01	2.05%	1.9E+00	7.99%	6.2E−01	3.02%
	Torpedinidae	*D. tschudii* Heckel, 1846[a]			1.0E−01	0.52%	5.8E−01	2.58%	3.2E−01	1.38%	2.2E−01	1.08%
	Triakidae	*Galeorhinus galeus* Linné, 1758[a]					1.1E−01	0.49%			2.3E−02	0.11%
		M. schmitti Springer, 1939[a]	2.7E−01	1.49%	3.3E−01	1.69%	2.2E+00	9.91%	6.3E+00	27.92%	2.1E+00	10.11%

[a] Species that contributed >0.1% at any one season.

Table 2
Oceanographic (mean, S.D.) and biological data for the Río de la Plata estuary[a]

Season	St	Z (m)		SS (ups)		BS (ups)		ST (°C)		BT (°C)	
		Mean	±S.D.	Mean	±S.D.	Mean	±S.D.	Mean	±S.D.	Mean	±S.D.
Summer	56	11.50	4.060	11.95	7.620	20.84	8.070	22.25	0.890	21.57	1.080
Autumn	43	10.80	4.320	14.98	9.540	22.39	8.800	9.26	0.640	10.03	0.850
Winter	38	13.15	3.770	10.44	10.090	22.45	8.390	9.89	0.405	10.63	0.817
Spring	41	11.53	4.120	16.63	10.020	24.64	7.171	18.50	1.170	16.70	1.880

[a] St, number of sampling station; Z, depth; SS, surface salinity; BS, bottom salinity; ST, surface temperature; BT, bottom temperature.

Netuma barbus (Table 5). The central area, with intermediate depths and salinities (Table 6) consistently contained the highest densities of *M. furnieri*, *B. aurea*, *M. ancylodon*, *Paralonchurus brasiliensis*, *Paralichthys orbignyanus*, *Menticirrhus americanus* and *Mugil* sp. (Table 5). In the outer area, deeper and with the highest salinity values (Table 6), *C. guatucupa*, *M. schmitti*, *Sympterygia bonapartii*, *Stromateus brasiliensis*, *Conger orbignyanus*, *Squatina guggenheim*, *Discopyge tschudii*, *Myliobatis goodei*, *Paralichthys patagonicus*, *Percophis brasiliensis*, *Prionotus punctatus* and *Atlantoraja castelnaui* had the highest densities (Table 5).

The second canonical axis explained between 10.62 and 21.58% in the variance of relative species density. It divided the outer and central areas in two or three regions from north to south (Fig. 2). Though differences in composition were not significant (ANOSIM, $P > 0.001$), many species preferred one of these regions in most seasons. *M. ancylodon*, *P. orbignyanus*, *M. furnieri* and *M. americanus* had higher densities in the northern portion of the central area. In the southern portion of the outer area *S. guggenheim*, *D. tschudii*, *P. patagonicus* and *S. bonapartii* were constantly present. Densities of *C. guatucupa* and *M. schmitti* were higher in the northern region. The bottom temperature influenced these preferences during autumn and spring, depth during summer and surface temperature during winter (Table 3).

3.4. Seasonal changes in species composition of groups

Temporal variation of fish communities was analyzed for three areas defined by the first axis, because the areas defined by the second axis did not have significant differences in species composition.

Seasonal variation in fish composition of the areas increased toward the outer area of the estuary (Table 7). Fish species composition of the inner area did not change significantly through the year ($P > 0.01$). In the central area, fish composition during summer differed significantly from that in autumn and winter. Density of *M. furnieri*, *M. ancylodon* and *Mugil* sp. were higher in summer, while density of *B. aurea* increased during winter and autumn. The outer area had the largest seasonal differences in fish composition (Table 7). Densities of *M. furnieri*, *M. ancylodon*, *Trichiurus lepturus* and *Parona signata* were higher in summer, while there were large catches of *C. guatucupa* in autumn (Table 8). High densities of *D. tschudii*, *S. brasiliensis* and *M. schmitti* during winter, as well as of *M. schmitti*, *P. punctatus*, *S. guggenheim*, *M. goodei*, *A. castelnaui*, *P. patagonicus* and *P. brasiliensis* during spring, separate this community from the remaining stations (Table 8).

3.4.1. Seasonal structure and influencing environmental variables whole estuary

The first two axes of the ordination analysis accounted for 14.8% of the variance in species composition and 79.9% of environment-data variance (Table 9). When the sample station groupings determined in the seasonal analysis (Fig. 2) were superimposed on the temporal analysis (Fig. 3), the sample stations reflected the spatial pattern corresponding to each season on axis 1 and the seasonal pattern on axis 2 (Fig. 3). The first canonical axis, which explained 71.1% of the total variance, showed that bottom salinity and depth are the most important factors in the spatial distribution of stations. The second axis, which explained 21.22% of the variance, showed that surface and bottom temperature are the most influential factors determining variations in the

Table 3
Canonical coefficients ($100 \times c$) and intra-set correlation ($100 \times r$) of environmental variables with the first two axis of DCCA for each season[a]

Variable	Summer				Autumn				Spring				Winter			
	Coefficient		Correlation		Coefficient		Correlation		Coefficient		Correlation		Coefficient		Correlation	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Z	−1.95	−15.62	49.15	−35.23	−63.4	10.20	−84.47	31.10	−28.78	13.06	−78.14	−24.95	9.49	10.2	56.39	−45.33
SS	21.12	21.46	−6.24	5.64	13.87	−38.71	−28.18	47.52	0.95	24.75	51.00	−44.20	−14.00	−38.71	35.77	−65.95
ST	15.04	13.81	−32.88	−25.90	−10.52	18.24	8.30	74.19	−4.41	−27.62	75.96	30.99	31.68	18.24	−4.80	−50.30
BT	−36.90	−19.17	59.52	−3.92	43.15	6.77	−62.82	−36.08	6.50	29.78	−51.62	47.92	−33.79	6.77	69.29	−3.95
BS	44.55	−10.40	77.97	−12.30	−32.44	21.73	−64.73	22.03	−36.18	−24.4	−78.56	11.92	70.92	21.73	82.49	24.60
Spe-data	14.9	1.9	16.8		15.4	4.9	20.3		17.2	3.9	21.1		19.9	4.7	24.6	
Spe-env	63.1	9.88	72.98		47.3	21.7	69		54.6	15.22	69.82		55.1	23.06	78.16	
Eigenvalue	0.386	0.051			0.457	0.144			0.462	0.105			0.469	0.109		
Var-total	80	10.62			68.5	21.58			71.96	16			57.93	13		

[a] Z, depth; ST, surface temperature; BT, bottom salinity; SS, surface salinity; BT, bottom temperature; Spe-env, percentage variance of species–environment relation; Spe-data, percentage variance of species data; Eigenvalue, measure of the importance of each of the axes; Var-total, percentage of total variance.
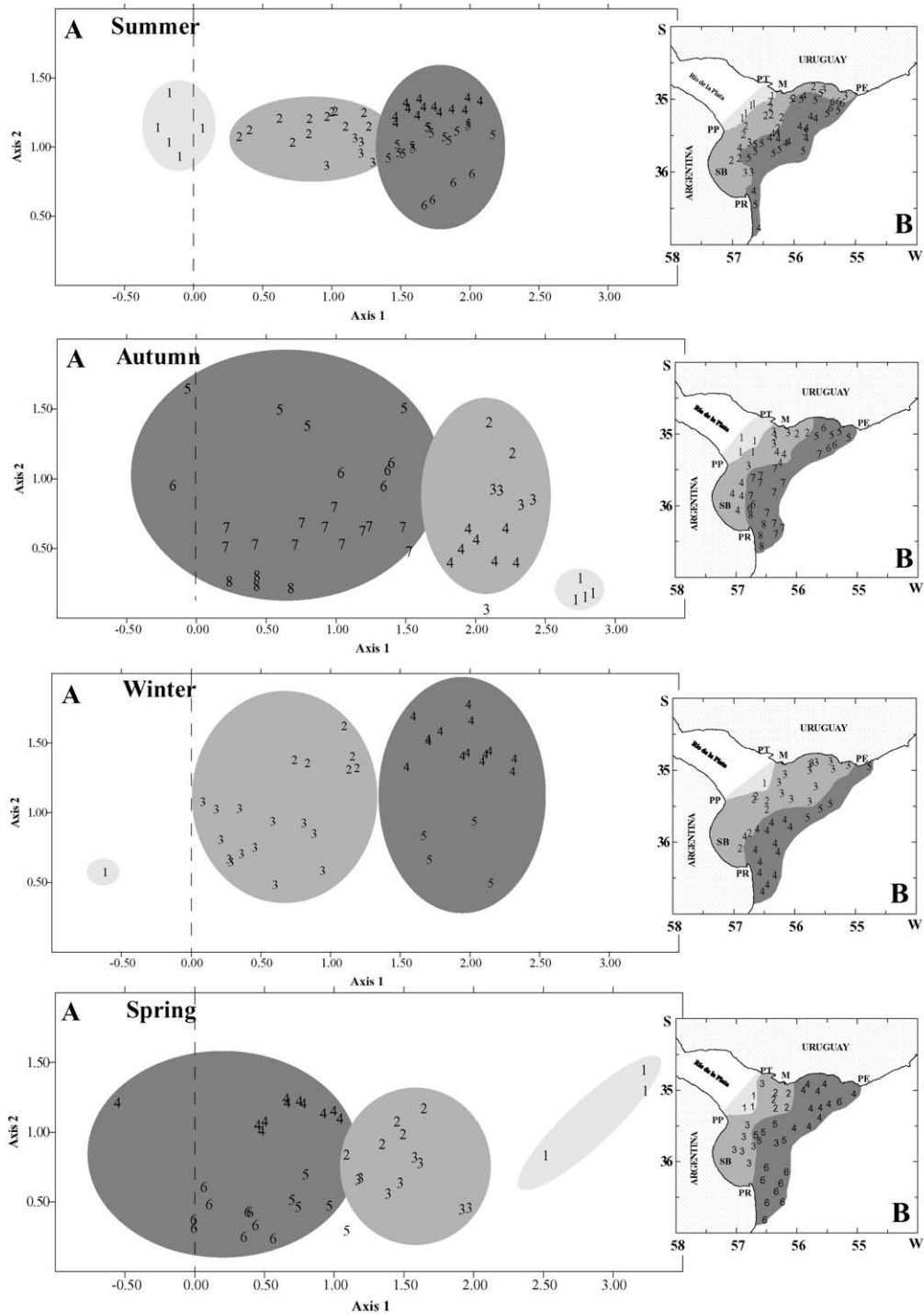
Fig. 2. (A) DCCA ordination diagram of the sampling stations for each season. (B) Area of distribution of the groups defined for axis 1 of DCCA analysis.

Table 4
R-statistic values and their significance levels for pair-wise comparisons of species composition of the areas for each season using ANOSIM ($P < 0.01$)

Area	Summer	Autumn	Winter	Spring
Inner vs. central	0.072*	0.545***	0.338	0.547*
Inner vs. outer	0.554***	0.853***	0.940	0.940***
Central vs. outer	0.385***	0.448***	0.739***	0.631***

* $P < 0.05$.
*** $P < 0.001$.

spatial distribution of communities between seasons (Table 9).

Fish composition was significantly different between seasons (ANOSIM, Table 10), and several species were identified as diagnostic species of each season (SIMPER, Table 11). For example, mean densities of *M. furnieri*, *M. ancylodon* and *T. lepturus* were higher in summer than in all other seasons, while densities of *C. guatucupa* and *B. aurea* were highest in autumn. *D. tschudii*, *S. brasiliensis* distinguish the fish composition in winter. The fish composition in spring was different because of the high densities of *M. schmitti*, *S. guggenheim*, *M. goodei*, *P. punctatus*, *P. patagonicus* and *Sympterigia bonapartii* (Table 11).

4. Discussion

This study shows that environmental factors, mainly salinity and temperature, influence the spatial and seasonal distribution of fish assemblages in the Río de la Plata estuary. Díaz de Astarloa et al. (1999) define two areas within the estuary: an inner one, with low salinity and shallow depths, and an outer one, with wide ranges of both variables. Here we demonstrated that differences in fish composition (Table 4) warrant the division of the outer area in two subareas, the central and the outer. Lasta et al. (1998) proposed three different zones within the outer area. We did not find significant differences in this area, but *C. guatucupa* appeared associated with the outer coastal Uruguayan zone (North Outer Zone) and *D. tschudii* with the Argentinean coastal outer zone (Southern Outer Zone).

Our results show that bottom salinity has a stronger influence on the spatial structure of Río de la Plata estuary fish communities than bottom temperature, and confirm observations made in other estuaries

(Loneragan et al., 1987; Thiel et al., 1995; Able et al., 1997; Marshall and Elliott, 1998). This is likely related to specific differences in salinity tolerance (Able et al., 1997; Marshall and Elliott, 1998). Species from the same family are diagnostic species of different salinity regimes, as observed in skates (Menni and López, 1984; Menni and Stehmann, 2001) or in flatfish (Díaz de Astarloa, 1994). *P. orbignyanus*, a diagnostic species of the central area, is more euryhaline than *P. patagonicus* a diagnostic species of the outer area. *P. orbignyanus* uses estuarine nurseries such as Lagoa dos Patos in Brazil (Chao et al., 1982) and the Mar Chiquita lagoon in Argentina (Díaz de Astarloa, 1994).

The diagnostic species of the inner area included a freshwater visitor (*P. valenciennesi*) and an anadromous species (*N. barbus*) (Ringuelet et al., 1967). Fishes associated with the central area were mainly resident estuarine species (*M. furnieri*, *B. aurea*, *M. ancylodon*, *P. brasiliensis*, *P. orbignyanus*), and to a lesser degree, migrant estuarine (*Mugil* sp.) or marine (*M. americanus*) species (Rico, 2000). The resident estuarine species use Samborombón Bay (36°S 57°W) as a principal nursery area (Lasta, 1995). Finally, fishes associated with the outer area were marine species, either resident (*C. guatucupa*, *C. orbignyanus*, *D. tschudii*, *P. patagonicus*, *Percophys brasiliensis* and *A. castelnaui*) or migrant (*M. schmitti*, *S. bonapartii*, *S. brasiliensis*, *S. guggenheim*, *M. goodei* and *P. punctatus*) (Rico, 2000).

The seasonal distribution pattern of the areas (Fig. 2) reflects the seasonal discharge pattern of the Río de la Plata (Guerrero et al., 1997a,b). During autumn and winter, river discharge is maximum, and continental winds almost neutralize marine winds. Without wind stress the continental runoff is affected only by the Coriolis force, and the river turns north along the Uruguayan coast. During spring and summer, the marine winds overcome continental winds and Ekman drift forces waters southward generating a flow of freshwater along the Argentine coast, passing Punta Medanos (Guerrero et al., 1997a).

The comparison of the spatial (Fig. 2) and seasonal (Fig. 3) patterns showed that salinity and temperature influence different components of the assemblages. Temperature fluctuates over a wide range, but its effect on the distribution of water masses and organisms is less than that of salinity. The overall species

Table 5

Diagnostic species, determined using SIMPER analysis for three areas identified using multivariate analysis from four seasons (species for each area in matrix are diagnostic of season of top column)

Summer	Autumn	Winter	Spring
Inner			
P. valenciennesi[a]	*P. valenciennesi*[a]		*P. valenciennesi*[a]
N. barbus[a]		*N. barbus*[a]	*N. barbus*[a]
Pimelodus albicans			*B. aurea*
M. furnieri		*Mugil* sp.	
Central			
B. aurea	*B. aurea*[a]	*B. aurea*[a]	
	M. furnieri[a]	*M. furnieri*[a]	*M. furnieri*[a]
M. ancylodon[a]	*M. ancylodon*[a]	*M. ancylodon*[a]	*M. ancylodon*[a]
P. brasiliensis	*P. brasiliensis*	*P. brasiliensis*	
P. orbignyanus	*P. orbignyanus*	*P. orbignyanus*	*P. orbignyanus*
M. americanus	*M. americanus*	*M. americanus*	
Mugil sp.[a]		*Mugil* sp.	*Mugil* sp.
Urophycis brasiliensis		*Urophycis brasiliensis*	
	Pomatomus saltatrix	*Pomatomus saltatrix*	
Lycengraulis grossidens		*M. goodei*	*P. patagonicus*
			P. signata
Outer			
C. guatucupa	*C. guatucupa*[a]	*C. guatucupa*[a]	*C. guatucupa*
S. bonapartii	*S. bonapartii*	*S. bonapartii*[a]	*S. bonapartii*
M. schmitti	*M. schmitti*	*M. schmitti*[a]	*M. schmitti*[a]
S. brasiliensis	*S. brasiliensis*	*S. brasiliensis*[a]	*S. brasiliensis*
C. orbignyanus	*C. orbignyanus*	*C. orbignyanus*	*C. orbignyanus*
A. castelnaui	*A. castelnaui*	*A. castelnaui*	*A. castelnaui*
P. punctatus	*P. punctatus*	*P. punctatus*	*P. punctatus*
S. guggenheim	*S. guggenheim*	*S. guggenheim*	*S. guggenheim*[a]
P. brasiliensis	*P. brasiliensis*	*P. brasiliensis*	*P. brasiliensis*
M. goodei[a]	*M. goodei*		*M. goodei*[a]
P. signata	*P. signata*	*P. signata*	
P. patagonicus	*P. patagonicus*	*P. patagonicus*	
Trachurus lathami		*Trachurus lathami*	*Trachurus lathami*
T. lepturus			*T. lepturus*
Peprilus paru			*Peprilus paru*
	D. tschudii	*D. tschudii*[a]	*D. tschudii*
	Umbrina canosai	*Umbrina canosai*	*Umbrina canosai*
	Prionotus nudigula	*Prionotus nudigula*	*Prionotus nudigula*
		Rioraja agassizi	*Rioraja agassizi*
M. furnieri[a]			*Pomatomus saltatrix*
		Engraulis anchoita	*Urophycis brasiliensis*

[a] Species groups that contribute to 50% of average dissimilarity.

composition of the three areas persisted seasonally, but there were significant differences in the relative biomass (t nm^{-2}) of diagnostic species. These differences are mainly due to the seasonal pattern of temperature in the estuary (Fig. 3, Table 9). The same has also been observed in other estuaries (e.g., Peel-Harvey (Australia): Loneragan et al., 1987; Elbe (Germany): Thiel et al., 1995; Humbert (England): Marshall and Elliott, 1998).

Seasonal changes observed in the fish assemblages studied here, suggest that these are caused mainly by seasonal migrations, as a result of salinity and temperature variations (e.g., *T. lepturus* and *D. tschudii*). Reproductive movements of *M. furnieri*, *M. schmitti* and

Table 6
Oceanographic (mean, S.D.) and biological data of the areas resultant of DCCA[a]

Area	Season	St	Z (m)		SS (ups)		BS (ups)		ST (°C)		BT (°C)	
			Mean	±S.D.	Mean	±S.D.	Mean	±S.D.	Mean	±S.D.	Mean	±S.D.
Inner	Summer	5	7.34	1.080	1.37	2.960	3.92	2.810	22.28	1.240	21.86	0.220
	Autumn	3	6.32	0.580	0.96	2.060	1.04	2.350	8.70	0.100	8.72	0.120
	Winter	1	9.00	–	0.80	–	1.30	–	9.70	–	9.50	–
	Spring	3	6.32	0.580	1.73	2.150	5.35	5.660	20.00	0.140	19.63	0.570
Central	Summer	17	10.17	3.470	11.95	5.610	19.06	4.070	22.23	0.620	21.96	0.390
	Autumn	18	7.61	1.440	11.08	7.430	22.27	6.490	9.12	0.500	10.03	0.820
	Winter	19	11.10	3.200	7.00	4.700	18.90	6.100	9.90	0.300	10.90	0.700
	Spring	13	9.17	2.440	13.68	9.050	23.22	3.410	19.23	0.440	18.11	0.750
Outer	Summer	34	13.06	3.880	16.41	6.920	27.86	3.910	22.26	0.970	21.34	1.320
	Autumn	25	14.29	3.080	24.96	6.530	32.45	1.470	9.42	0.700	10.20	0.790
	Winter	18	16.00	2.600	18.30	10.200	31.60	1.800	9.90	0.500	10.40	0.800
	Spring	25	13.98	3.470	24.15	7.230	30.54	2.320	17.97	1.160	15.71	1.600

[a] St, no. of sampling station; Z, total depth; SS, surface salinity; BS, bottom salinity; ST, surface temperature; BT, bottom temperature.

C. guatucupa could results of other factors disguised by temperature.

T. lepturus is a cosmopolitan species being among the more abundant benthopelagic teleost of the continental shelf of southern Brazil (Haimovici, 1997). Its high densities in the estuary are associated with the penetration of subtropical continental water masses during warm periods forced by the southward flow of southern Brazil waters (Pereira, 1989; Lima et al., 1996). The intrusion of this water masses near the mouth of the estuary could imply a southward shift of the subtropical shelf front reported by Piola et al. (2000). An event of this type was reported in summer

Table 7
R-statistic values and their significance levels for pair-wise comparisons of species composition of each areas for different seasons using ANOSIM

Season combinations	Areas		
	Inner	Central	Outer
Summer vs. spring	0.508*	0.069	0.547***
Summer vs. autumn	0.518*	0.238***	0.558***
Summer vs. winter	0.520	0.151***	0.649***
Spring vs. autumn	0.185	0.141*	0.462***
Spring vs. winter	0.111	0.026	0.154**
Winter vs. autumn	0.111	0.068	0.26***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

2000 associated with a diminishing in the Río de la Plata mean continental discharge (Guerrero, personal communication). Consistently, during spring and summer, waters within the Uruguayan sector of the estuary are warmer and more saline (Guerrero et al., 1997a,b).

Decreasing temperature in the outer estuarine zone together with the intrusion of shelf water from the south during winter (Piola and Rivas, 1997), may be associated with relatively large densities of *D. tschudii*. This cold water species is considered a Magellanic form belonging the "Inner shelf mixed fauna" (Menni and Gosztonyi, 1982; Menni and López, 1984).

The euryhaline species *M. furnieri* performs most of its life cycle in estuarine water (Acha et al., 1999). Juveniles (<32 cm TL) are abundant in the inner part of the Río de la Plata, while adults are abundant toward the offshore regions (Cotrina, 1986; Cousseau et al., 1986; Jaureguizar et al., 2003). Spawning, which takes place between November and April, occurs in the inner zone and coincides with the bottom salinity front (Acha et al., 1999). Higher biomasses of *M. furnieri* during summer appear to be associated with the reproductive movements from the outer estuary to the spawning areas. This spawning migration coincides with an increase in the size of individuals caught by the artisanal fishery of Pajas Blancas (near Montevideo, Uruguay) during the fishing seasons (November–January) (Norbis et al., 1992).

Table 8
Diagnostic species, determined using SIMPER, for the external area from four seasons (species for each pair-wise comparison in matrix are diagnostic of season of top column)

	Summer	Autumn	Winter	Spring
Summer		C. guatucupa[a] S. bonapartii S. brasiliensis	M. schmitti[a] S. brasiliensis[a] D. tschudii[a] C. guatucupa[a] P. punctatus[a] A. castelnaui S. guggenheim S. bonapartii	M. schmitti[a] S. guggenheim[a] P. punctatus[a] M. goodei[a] C. guatucupa P. patagonicus S. bonapartii S. brasiliensis A. castelnaui P. brasiliensis
Autumn	M. furnieri[a] T. lepturus[a] M. ancylodon[a] P. signata M. goodei M. schmitti S. guggenheim Prionotus punctatu P. patagonicus Peprilus paru P. signata		M. schmitti[a] S. brasiliensis[a] M. furnieri[a] D. tschudii[a] P. punctatus[a] S. guggenheim A. castelnaui S. bonapartii P. signata M. goodei C. orbignyanus M. ancylodon	M. schmitti[a] S. guggenheim[a] P. punctatus[a] M. furnieri[a] M. goodei[a] S. bonapartii P. patagonicus S. brasiliensis A. castelnaui D. tschudii P. brasiliensis P. signata
Winter	M. furnieri[a] M. ancylodon[a] T. lepturus P. signata	C. guatucupa[a]		M. schmitti[a] P. punctatus[a] S. guggenheim[a] M. goodei[a] A. castelnaui S. bonapartii P. patagonicus Trachurus lathami P. signata P. brasiliensis
Spring	M. furnieri[a] M. ancylodon[a] T. lepturus M. goodei	C. guatucupa[a]	S. brasiliensis[a] C. guatucupa[a] M. furnieri[a] D. tschudii	

[a] Species groups that contribute to 50% of average dissimilarity.

During spring, adult *M. schmitti* arrive at the coast to reproduce, and juveniles move greater depths (Massa, 1998). The adults occur in the Río de la Plata during autumn and winter, but are absent in spring (Massa, personal communication). This agrees with its increased biomass in the Atlantic Uruguayan coast when water temperature ranges from 13 to 16 °C (Meneses and Paesch, 1999).

The higher biomass of *C. guatucupa* in autumn appears related to the arrival of adults at the coastal area from the North or from intermediate shelf waters (Cousseau et al., 1986) after the reproductive period. Reproductive activity takes place along the coastal zone at high salinities, and from October to early April with a peak in spring (Macchi, 1998).

The salinity, besides influencing the fish assemblage, may affect the relative use of the estuary by age-classes of the same species (e.g., *M. furnieri*: Jaureguizar et al., 2003). Some of the estuarine

Table 9
Canonical coefficients ($100 \times c$) and intra-set correlations ($100 \times r$) of environmental variables with the first two axes of DCCA for all seasons[a]

Variable	Coefficient			Correlation	
	Axis 1	Axis 2		Axis 1	Axis 2
Z	15.70	−7.47		62.70	−23.31
ST	104.95	−35.27		−39.95	−88.58
BT	129.49	3.51		−53.41	−82.45
SS	8.47	−10.18		63.98	−34.98
BS	42.88	−1.40		84.32	−17.64
Spe-data	11.4	3.4		14.8	
Spe-env	60.8	19.1		79.9	
Eigenvalue	0.442	0.132			
Var-total	71.06	21.22			

[a] Z, depth; SS, surface salinity; BS, bottom salinity; ST, surface temperature; BT, bottom temperature; Spe-env, percentage variance of species–environment relation; Spe-data, percentage variance of species data; Eigenvalue, measure of the importance of each of the axes; Var-total, percentage total variance.
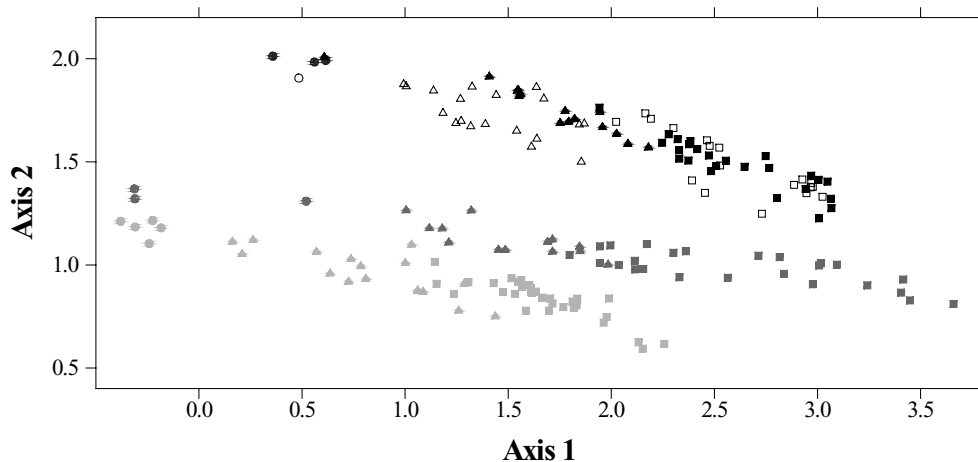

Fig. 3. DCCA ordination diagram of all sampling stations classified by the measured environmental factors: (◐) summer (inner), (●) autumn (inner), (○) winter (inner), (●) spring (inner); (▲) summer (middle), (▲) autumn (middle), (△) winter (middle), (▲) spring (middle); (■) summer (outer), (■) autumn (outer), (□) winter (outer), (■) spring (outer).

Table 10
R-statistic values and their significance levels for pair-wise comparisons of estuarine species composition for different seasons using ANOSIM ($P < 0.01$)

Season combinations	R-value
Summer vs. spring	0.250***
Summer vs. autumn	0.332***
Summer vs. winter	0.268***
Spring vs. autumn	0.215***
Spring vs. winter	0.047*
Winter vs. autumn	0.105***

* $P < 0.05$.
*** $P < 0.001$.

species, such as *M. furnieri*, could have different age-classes distribution along the salinity gradient, and the influence of each age-class on the fish community structure would be distinct. Then, the species contribution to the average dissimilarity between fish assemblages of the estuary would be different for the same species due to difference in age class distribution. As a result, it seems clear that future studies relative to spatial and seasonal variations of assemblage structures in this and other estuaries should consider using different age classes of the same species as distinct species.

Table 11
Diagnostic species determined using SIMPER analysis, for estuary from four seasons (species for each pair-wise comparison in matrix are diagnostic of season of top column)

	Summer	Autumn	Winter	Spring
Summer		*C. guatucupa*[a]	*M. schmitti*[a]	*M. schmitti*[a]
		S. bonapartii[a]	*S. brasiliensis*[a]	*B. aurea*[a]
		B. aurea[a]	*B. aurea*[a]	*S. guggenheim*[a]
		M. schmitti	*M. goodei*[a]	*M. goodei*[a]
			C. guatucupa[a]	*Prionotus punctatu*[a]
			S. guggenheim	*C. guatucupa*
			S. bonapartii	*S. bonapartii*
			P. punctatus	*P. patagonicus*
			A. castelnaui	*P. brasiliensis*
			D. tschudii	*S. brasiliensis*
			C. orbignyanus	
Autumn	*M. furnieri*[a]		*M. schmitti*[a]	*M. schmitti*[a]
	M. ancylodon[a]		*S. brasiliensis*[a]	*S. guggenheim*[a]
	T. lepturus[a]		*M. furnieri*[a]	*M. goodei*
	M. goodei		*M. ancylodon*[a]	*P. punctatus*
	P. signata		*M. goodei*	*S. bonapartii*
	Mugil sp.		*D. tschudii*	*S. brasiliensis*
	P. brasiliensis		*A. castelnaui*	*P. patagonicus*
	S. guggenheim		*S. guggenheim*	*P. brasiliensis*
	N. barbus		*C. orbignyanus*	*P. signata*
			P. punctatus	
			P. signata	
Winter	*M. furnieri*[a]	*C. guatucupa*[a]		*M. schmitti*[a]
	M. ancylodon[a]	*B. aurea*[a]		*S. guggenheim*[a]
	T. lepturus[a]	*S. bonapartii*		*M. goodei*[a]
	P. signata			*P. punctatus*
	Mugil sp.			*S. bonapartii*
				A. castelnaui
				P. patagonicus
				P. signata
Spring	*M. furnieri*[a]	*C. guatucupa*[a]	*M. furnieri*[a]	
	M. ancylodon[a]	*M. furnieri*[a]	*B. aurea*[a]	
	P. signata	*B. aurea*[a]	*S. brasiliensis*[a]	
	T. lepturus	*M. ancylodon*[a]	*M. ancylodon*[a]	
	Mugil sp.		*C. guatucupa*	
			D. tschudii	

[a] Species group that contribute to 50% average dissimilarity.

In any given area, environmental characteristics play an initial role in structuring fish associations. Within this underlying structure biological interaction results in further pattern. We propose an explanation of how the environment influences fish associations both spatially and temporally in the Río de la Plata estuary. The variations explained by the considered factors suggest that the salinity gradient is the main factor resulting in the spatial distribution of assemblages. Changes in water temperature exert a seasonal influence on the relative abundance of fish species within these assemblages.

Fisheries science and management are shifting their focus from single species to ecosystems. This has been precipitated in part by analyses indicating that intensive fishing has caused significant changes in the overall abundance, productivity, and community structure of fish communities in marine ecosystem (ICES, 2000). The present study allowed us to define the characteristics and spatial boundaries for the fish

communities in the Río de la Plata estuarine system, in which fishing take place. Such knowledge is pre-requisite for managing fishing in an ecosystem context, where the identification of fish assemblage patterns and their environmental determinants are becoming important tools for the management and protection of essential habitats and for maintaining sustainable fisheries.

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