

Research Article

From fresh water to the slope: fish community ecology in the Río de la Plata and the sea beyond

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ABSTRACT. The spatial pattern of fish assemblages and its relationship with factors along an environment gradient, from fresh to marine water environment along the Río de la Plata estuary (36°S, 56°W) the shelf and part of the slope, was examined using data from 22 sampling stations. Fish were sampled from all station with an Engel type trawl (200 mm stretched mesh in the wings, 120 mm stretched mesh in the cod ends, 4 m vertical opening and 15 m horizontal aperture) towed at 4 knots for 20 to 30 min per set. Cluster analysis and ordination analysis MDS were used to define spatial distribution of fish assemblages based on fish composition (abundance and biomass). BIO-ENV process was used to estimate assemblage association with depth, temperature and salinity of surface and bottom waters. The results of these analyses showed that the fish community along the riverine-marine gradient was structured in four assemblages: riverine, estuarine, shelf and slope. These assemblages were found to differ significantly in their species composition. Each assemblage was characterized by several common and discriminator species and characterized by differing environmental conditions. Bottom salinity and bottom temperature were the environmental variables most strongly associated with differences in assemblage structure across the various areas. The changes in assemblage structure between areas were gradual, with no sharp boundaries.

Keywords: fish assemblages, riverine-marine gradient, environmental variables, estuary, Río de la Plata, Argentine.

Desde el agua dulce hasta el talud: ecología de comunidades de peces en el Río de la Plata y el mar adyacente

RESUMEN. Se analizó el patrón espacial de las asociaciones de peces y su relación con los factores ambientales a lo largo del gradiente desde el agua dulce en el Río de la Plata hasta la parte superior del talud. Los peces fueron muestreados en 22 estaciones con una red de arrastre de fondo tipo Engel (200 mm de abertura de malla en las alas, 120 en el copo, 4 m de abertura vertical y 15 m de abertura horizontal) con una velocidad de arrastre de 4 nudos durante 20 a 30 min. Para definir la distribución espacial de las asociaciones de peces basadas en la composición de la ictiofauna (abundancia y biomasa) se aplicó el análisis de agrupamiento jerárquico y el análisis de ordenación MDS y para estimar la relación entre estas asociaciones con la profundidad, la temperatura y la salinidad del agua en la superficie y el fondo, se utilizó el proceso BIO-ENV. Los resultados obtenidos demuestran que en la comunidad de peces a lo largo de este gradiente riverino-marino se pueden establecer cuatro asociaciones: riverina, estuarial, plataforma y talud. Estas asociaciones fueron significativamente diferentes en la composición de especies, cada una de ellas fue caracterizada por varias especies comunes y discriminantes y presentó diferentes condiciones ambientales. Concluimos que la salinidad y temperatura de fondo fueron las variables ambientales determinantes de la estructura de las asociaciones a través de las áreas. El cambio en la estructura entre las áreas fue gradual y con límites flexibles.

Palabras clave: asociaciones de peces, gradiente ribereño-marino, variables ambientales, estuario, Río de la Plata, Argentina.

INTRODUCTION

Large scale (kilometers) distribution pattern of fish result primarily from the species responses to their physical environment. Probably dominant abiotic variables act like a physiological sieve, playing a vital role in the structuring of a community (Remmert, 1983; Martino & Able, 2003). The main parameters known to affect the spatial pattern of freshwater communities are temperature and turbidity (Ringuelet, 1975); salinity and depth in estuarine communities (Loneragan *et al.*, 1987; Cyrus & Blaber, 1992; Thiel *et al.*, 1995; Wantiez *et al.*, 1996; Marshall & Elliot, 1998; Hyndes *et al.*, 1999; Martino & Able, 2003; Jaureguizar *et al.*, 2003, 2004), and temperature and depth (Menni & Gosztanyi, 1982; Menni & López, 1984; Prenski & Sánchez, 1988; Bianchi, 1992) in marine communities. Some components of the habitat, such as benthic community composition and substrate type further influence this organization within each environment.

The environmental gradient from shallow freshwater to deeper marine water is very strong, with some species restricted to a particular section of it, displaying a zonation pattern (Rafaelli *et al.*, 1991). Consequently, species assemblages have been considered appropriate indicators of habitat heterogeneity (Noss, 1990; Kremen, 1992; Monaco *et al.*, 1992; Bulger *et al.*, 1993), characterizing a particular section of the environmental gradient (Mahon & Smith, 1989; Kremen, 1992; Monaco *et al.*, 1992; Bulger *et al.*, 1993).

In the shelf and coastal systems of Argentina several studies on fish communities have been developed at diverse scales (Menni & Gosztanyi, 1982; Menni & López, 1984; Prensky & Sánchez, 1988; Jaureguizar *et al.*, 2003, 2004, 2006). However, fish communities from the fresh and brackish waters of the Río de la Plata have never been analyzed together with that from oceanic waters off the shelf break. Therefore, the aim of the present large scale study (over 400 km), is to analyze fish assemblages searching for correspondences between physical and biological patterns along the riverine–marine gradient. Our specific objectives are: 1) to define fish assemblages, 2) to characterize their community structure, identifying the common and discriminator species, 3) to estimate the influence of environmental factors (temperature, salinity and depth) on the spatial distribution of fish assemblage areas, and 4) to test if frontal boundaries between water masses separate fish assemblages.

MATERIALS AND METHODS

We analyzed the results obtained during the FREPLATA bottom-trawl survey on board the R/V “Eduardo L. Holmberg”, which was conducted in the spring (November 2001) between 34°37′–36°45′S and 53°57′–57°52′W. The biological and oceanographic information was collected at 22 sampling stations along the environment gradient from fresh shallow water (3.5 m) to marine deep water (323.5 m), along the Río de la Plata estuary (36°S, 56°W), the shelf and the upper the slope (Fig. 1). Fish were sampled from 22 bottom trawl sets with an Engel type trawl (200 mm stretched mesh in the wings, 120 mm stretched mesh in the cod ends, 4 m vertical opening and 15 m horizontal aperture) towed at 4 knots for 20 to 30 min per set. All sampling was conducted during daytime.

At each station, environmental conditions (depth, temperature and salinity of surface and bottom waters) were obtained using a conductivity-temperature-depth profiler (Sbe19) with a sampling rate of 3 scans 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 for salinity.

Fish, identified to species, were ordered according Braga (1993), López & Miquelarena (1991), López *et al.* (2003), Menni *et al.* (1984) and Ringuelet *et al.* (1967). Biological data were recorded as catch

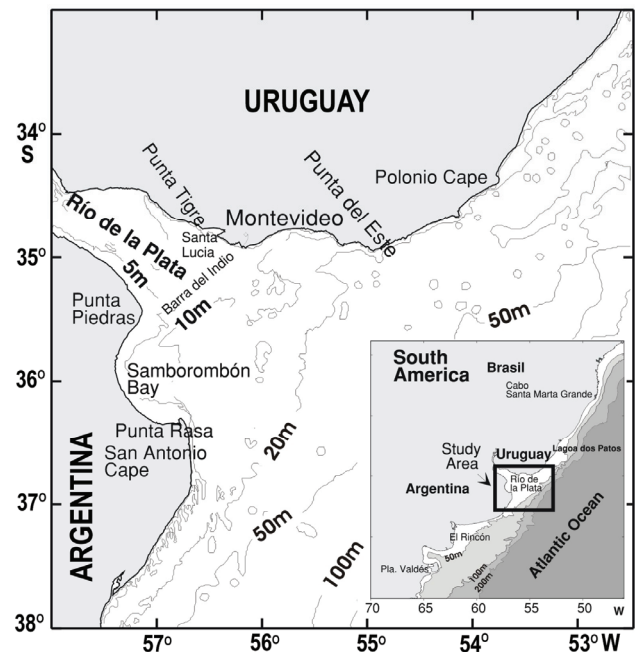


Figure 1. Location and bathymetry of the study area.

Figura 1. Localización y batimetría del área de estudio.

weights and number for each species. Fish biomass was measured as weight per unit area and abundance as thousands individual per unit area. Densities were calculated using the “swept area” method for each sampling station. Species biomass (ton nm^{-2}) and abundance (miles of individual nm^{-2}) by sampling station were used to obtain a grouping of stations (fish assemblage areas) based on species composition. The spatial trend or change in the fish assemblage areas was examined using two statistical techniques, cluster analysis and non-metric multidimensional scaling (MDS). These methods were carried out using the Bray-Curtis similarity index. Prior to calculation of the Bray Curtis index, the CPUE (ton and miles of individual) was $\log(x+1)$ scaled to reduce the contribution of the abundant species.

To determine whether or not major shifts in community structure have occurred between fish assemblage areas identified by Cluster and MDS analysis, we used an analysis of similarity ANOSIM (non-parametric analysis, permutation-based 1-way analysis of similarity). R-statistic values for pair-wise comparisons provided by ANOSIM were used to determine the dissimilarity between groups. Values close to 1 indicate very different composition, while values near zero show small difference. This methodology was used to test the null hypothesis that no changes in community structure were observed between fish assemblages (Clarke & Warwick, 2001).

ANOSIM only indicates whether the fish assemblage areas differ in species composition without reference to which species cause these differences. Since we were interested in how differences arose, we used SIMPER to determine which species typified and discriminated each fish assemblage area. The method is based on the analysis of Bray-Curtis (dis) similarity matrices derived from station compositions species. Within each assemblage area species were defined as common if they contributed to the top 90% of average similarity within the assemblage, or as discriminators if they contributed to the top 90% of dissimilarity between assemblage areas, and had a low ratio of average dissimilarity to its standard deviation. Through the similarity percentage procedure (SIMPER), 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 (Clarke & Warwick, 2001).

The BIO-ENV process was used to estimate the influence of depth, temperature and salinity of surface and bottom waters on the spatial distribution of fish assemblage areas. This process selects the abiotic variables that maximize the correlation rank (ρ) between the biotic and abiotic (dis) similarity matrices (Bray Curtis for biota, and Euclidean distance for environmental variables). Their rank was compared through a Spearman coefficient (ρ), which lies in the range (-1 to 1) with the extreme $\rho = -1$ and $+1$ corresponding to the cases where the two sets of ranks are in complete opposition or complete agreement (Clarke, 1993; Clarke & Warwick, 2001).

RESULTS

A total of 90 marine and freshwater species belonging to 81 genera and 54 families were caught across the transect (9 chondrichthyan and 45 osteichthyan taxa). Two marine species (*Trachurus lathami* and *Cynoscion guatucupa*) represented more than 50% of the total individual. *Trachurus lathami* represented 37.6% of the individual, followed by *Cynoscion guatucupa* who represented 22.51% of the total individual. In biomass, six species represented more than 50% of the total weight. The most abundant was *Trachurus lathami*, followed by *Macruronus magellanicus*, *Mustelus schmitti*, *Leporinus obtusidens*, *Nemadactylus bergi* and *Bassanago albescens* (Table 1).

Spatial pattern based on biomass and abundance

Four main groups of sampling stations were determined at a low similarity level (20%) in the cluster analysis for biomass (Fig. 2a) and abundance (Fig. 2b). The nMDS showed a low stress (0.04) in two dimensions and the plot of the two dimensions gave the same picture as the dendrograms (Figs. 2c and 2d). The agreement in the results of these two methods confirms the validity of species groups that define different zones (riverine, estuarine, shelf and slope assemblage areas), fish assemblage areas along the riverine-marine gradient (Figs. 2e and 2f).

The fish composition was significantly different between fish assemblage areas (ANOSIM, $p < 0.05$). They showed a similarity range between 33.3% and 76.2% for biomass, and between 32.0% and 57.2% for abundance (SIMPER, Table 1). The fish assemblage areas were characterized by several common and diagnostics species (SIMPER, Figs. 3 and 4), as well as by different environmental conditions (Table 2).

Riverine area (RA)

The riverine area was defined by sampling stations that covered the inner part of the Río de la Plata and

Table 1. Common species, identified by SIMPER analysis, of fish assemblages areas defined by multivariate analyses using biomass (ton nm⁻²) and abundance (thousands ind nm⁻²). It indicates the average similarity of each fish assemblage area and for each species indicates its average biomass (Bi. Av.) or average abundance (Ab. Av.) and its contribution in percentage to the area similitude (Contrib.). A: anadromous, E: estuarine, F: freshwater, M: marine.

Tabla 1. Especies comunes, identificadas por el análisis SIMPER, de las áreas de asociaciones de peces definidas por los análisis multivariados usando biomasa (t nm⁻²) o abundancia (miles ind nm⁻²). Se indica la similitud promedio de cada área de asociaciones de peces y para cada especie se indica su biomasa promedio (Bi. Av.) o abundancia promedio (Ab. Av.) y su contribución en porcentaje a la similitud del área (Contrib.) A: anádromo, E: estuarial, F: dulceacuícola, M: marina.

Biomass						
Riverine (76.2%)			Estuarine (39.6%)			
Species	Av. Bi.	Contrib.	Species	Av. Bi.	Contrib.	
F <i>Paraloricaria vetula</i>	452.83	12.03	E <i>Micropogonias furnieri</i>	503.13	34.84	
F <i>Pimelodus albicans</i>	420.8	11.4	E <i>Macrodon ancylodon</i>	211.78	14.07	
F <i>Leporinus obtusidens</i>	675.85	10.92	E <i>Brevoortia aurea</i>	32.42	13.73	
F <i>Pterodoras granulosus</i>	408.78	10.65	F <i>Pimelodus albicans</i>	54.41	5.53	
F <i>Cyprinus carpio</i>	390.09	10.54	M <i>Prionotus punctatus</i>	156.03	5.27	
F <i>Luciopimelodus pati</i>	101.14	7.51	F <i>Parapimelodus valenciennis</i>	41.46	4.79	
F <i>Prochilodus lineatus</i>	74.96	5.55	F <i>Luciopimelodus pati</i>	20.14	3.51	
A <i>Netuma barba</i>	443.7	5.40	M <i>Sympterygia bonapartii</i>	32.95	3.45	
F <i>Parapimelodus valenciennis</i>	43.97	5.36	E <i>Paralonchurus brasiliensis</i>	16.85	2.40	
F <i>Pimelodus maculatus</i>	54.71	5.08	E <i>Anchoa marinii</i>	39.04	2.36	
F <i>Ageneiosus valenciennesi</i>	13.23	3.65	M <i>Conger orbignyanus</i>	8.27	2.15	
F <i>Rhinodoras dorbignyi</i>	11.17	2.91				
Shelf (45.7%)			Slope (33.3%)			
Species	Av. Bi.	Contrib.	Species	Av. Bi.	Contrib.	
M <i>Trachurus lathami</i>	2461.31	23.45	M <i>Squalus acanthias</i>	24.3	22.58	
M <i>Mustelus schmitti</i>	1135.9	16.91	M <i>Merluccius hubbsi</i>	593.41	20.03	
M <i>Squatina guggenheim</i>	136.75	13.93	M <i>Bassanago albescens</i>	1400.77	18.29	
M <i>Percophis brasiliensis</i>	591.08	13.87	M <i>Squalus mitsukurii</i>	7.95	17.56	
M <i>Prionotus nudigula</i>	26.03	5.89	M <i>Macruronus magellanicus</i>	2318.77	9.78	
M <i>Stromateus brasiliensis</i>	66.13	4.39	M <i>Helicolenus dactylopterus lahillei</i>	154.48	7.31	
M <i>Mullus argentinae</i>	37.76	3.01				
M <i>Pagrus pagrus</i>	138.99	2.58				
E <i>Micropogonias furnieri</i>	51.31	2.41				
M <i>Discopyge tschudii</i>	109.62	2.25				
M <i>Atlantoraja castelnaui</i>	30.03	1.94				
Abundance						
Riverine (57.2%)			Estuarine (45.7%)			
Species	Av. Bi.	Contrib.	Species	Av. Bi.	Contrib.	
F <i>Parapimelodus valenciennis</i>	1454.85	15.21	E <i>Micropogonias furnieri</i>	531.69	17.24	
F <i>Pimelodus albicans</i>	473.33	12.63	M <i>Prionotus punctatus</i>	810.32	15.16	
E <i>Micropogonias furnieri</i>	3128.6	11.09	E <i>Brevoortia aurea</i>	58.05	9.42	
F <i>Luciopimelodus pati</i>	242.86	10.1	M <i>Sympterygia bonapartii</i>	41.79	8.98	
A <i>Lycengraulis grossidens</i>	125.23	6.72	E <i>Anchoa marinii</i>	1511.19	8.95	
F <i>Paraloricaria vetula</i>	497.11	6.48	E <i>Paralonchurus brasiliensis</i>	235.34	7.15	

F	<i>Leporinus obtusidens</i>	339.77	5.39	M	<i>Conger orbignyanus</i>	22.24	6.14
F	<i>Pterodoras granulosus</i>	215.09	5.03	E	<i>Macrodon ancylodon</i>	8601.98	5.4
F	<i>Rhinodoras dorbignyi</i>	134.05	4.07	M	<i>Cynoscion guatucupa</i>	32776.24	5.27
F	<i>Cyprinus carpio</i>	79.25	4.04	M	<i>Paralichthys patagonicus</i>	37.72	5.11
F	<i>Pimelodus maculatus</i>	95.85	3.15	M	<i>Parona signata</i>	107.11	4.67
F	<i>Prochilodus lineatus</i>	38.33	2.7				
F	<i>Ageneiosus valenciennis</i>	27.83	2.55				
A	<i>Netuma barba</i>	144.79	2.33				
	Shelf (48.2%)				Slope (32.0 %)		
	Species	Av. Bi.	Contrib.		Species	Av. Bi.	Contrib.
M	<i>Trachurus lathami</i>	53599.16	23.73	M	<i>Squalus mitsukurii</i>	59.78	22.3
M	<i>Percophis brasiliensis</i>	677.05	14.12	M	<i>Bassanago albescens</i>	13646.54	18.91
M	<i>Mustelus schmitti</i>	993.16	12.62	M	<i>Merluccius hubbsi</i>	1099.21	17.29
M	<i>Prionotus nudigula</i>	283.66	10.41	M	<i>Squalus acanthias</i>	14.96	17.29
M	<i>Squatina guggenheim</i>	120.31	9.58	M	<i>Helicolenus dactylopterus lahillei</i>	672.6	8.74
M	<i>Mullus argentinae</i>	660.79	5.37	M	<i>Macruronus magellanicus</i>	3861.9	8.69
M	<i>Stromateus brasiliensis</i>	290.14	5.3				
M	<i>Pagrus pagrus</i>	403.73	2.59				
M	<i>Discopyge tschudii</i>	141.66	1.93				
E	<i>Micropogonias furnieri</i>	33.99	1.90				
M	<i>Prionotus punctatus</i>	36.20	1.82				
M	<i>Thyrsopterus lepidopodea</i>	39.69	1.69				

characterized by fresh water, shallow depth and the highest water temperature of the study area (Figs. 2e and 2f, Table 2). Its fish composition showed the highest similarity (73.2% for biomass and 57.2% for abundance), and was mainly dominated by freshwater species. *Paraloricaria vetula*, *Pimelodus albicans*, *Leporinus obtusidens*, *Pterodoras granulosus*, *Cyprinus carpio*, *Luciopimelodus pati*, *Prochilodus lineatus*, *Netuma barba*, *Parapimelodus valenciennis*, *Pimelodus maculatus*, *Ageneiosus valenciennesi* and *Rhinodoras dorbignyi* were common species in both analyses (Table 1). The ichthyofauna was mainly discriminated by *Ageneiosus valenciennesi*, *Brochiloricaria chauliodon*, *Cyprinus carpio*, *Hypostomus laplatae*, *Leporinus obtusidens*, *Pachyurus bonariensis*, *Paraloricaria vetula*, *Pimelodus maculatus*, *Prochilodus lineatus*, *Pterodoras granulosus*, *Rhinodoras dorbignyi*, *Pimelodus albicans*, *Luciopimelodus pati*, *Parapimelodus valenciennis* and *Lycengraulis grossidens* (Figs. 3 and 4). *Catathyridium jenynsi* and *Eigenmannia virescens* were also diagnostic species for the abundance analysis (Fig. 4).

Two clear subgroups were determined in the abundance analysis (Fig. 2a). The “subgroup a” included the inner stations of the riverine area, with

lowest salinity and highest temperature (Table 2, Fig. 2e). The “subgroup a” was discriminated by the highest abundance of *Paraloricaria vetula*, *Leporinus obtusidens*, *Pterodoras granulosus*, *Cyprinus carpio*, *Pimelodus maculatus*, *Netuma barba*, *Pachyurus bonariensis*, *Prochilodus lineatus*, *Ageneiosus valenciennesi*, *Eigenmannia virescens*, *E. trilineata*, *Hypostomus laplatae*, *Brochiloricaria chauliodon*, *Catathyridium jenynsi*, *Rhinodoras dorbignyi*, *Luciopimelodus pati*, *Pimelodus albicans* and *Odontesthes bonariensis*. The “subgroup b”, corresponds to outer stations of the Riverine area, bordering the estuarine area, with lower temperature and highest salinity (Table 2, Fig. 2e). The ichthyofauna of this subgroup was discriminate by the highest abundance of *Lycengraulis grossidens*, *Parapimelodus valenciennis*, *Micropogonias furnieri*, *Macrodon ancylodon*, *Brevoortia aurea* and *Anchoa maringii*.

Estuarine area (EA)

The estuarine area comprised the sampling stations with intermediate salinity and temperatures (Figs. 2e and 2f, Table 2). Its fish community showed an intermediate similarity (39.6% for biomass and 45.5% for abundance). The species that most contributed to

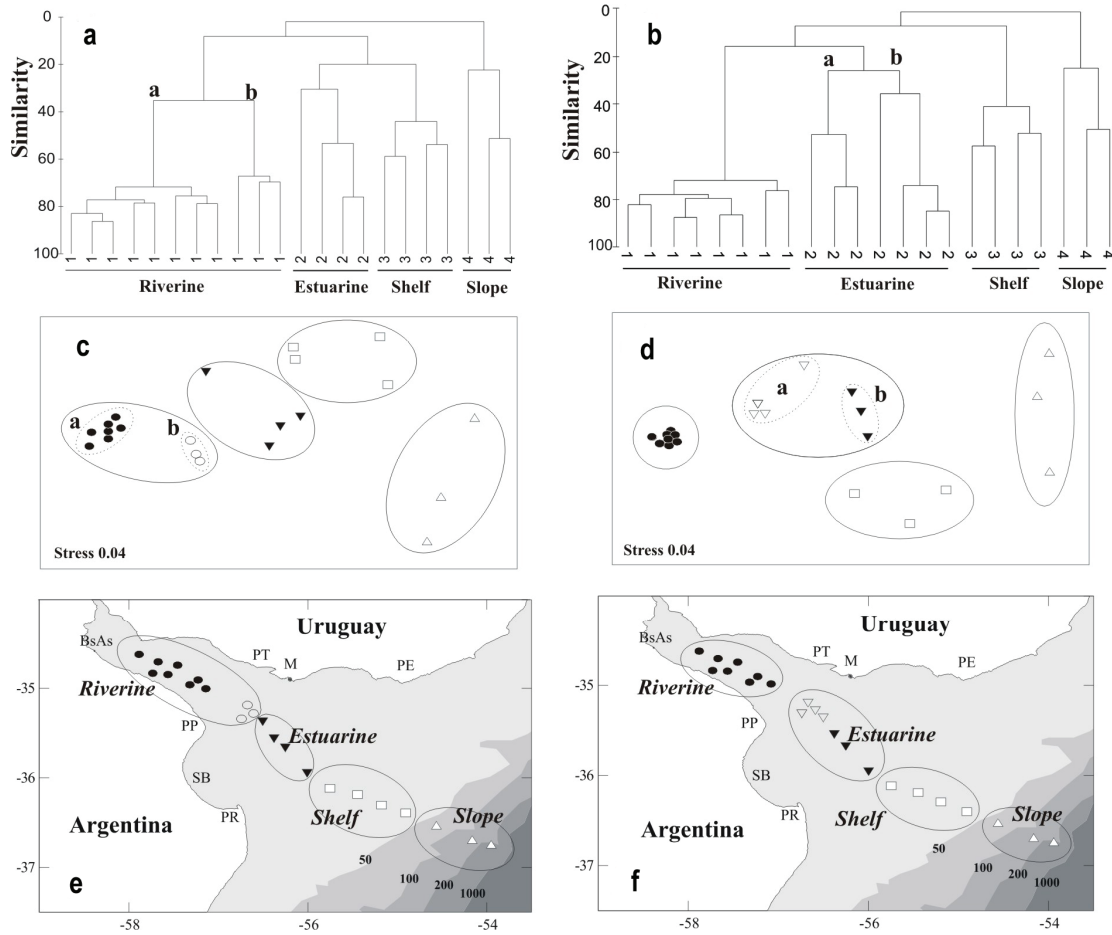


Figure 2. Dendrograms of the cluster analysis (a, b), nMDS diagrams (c, d) and location of the fish assemblage areas (e, f) defined for abundance and biomass analysis.

Figura 2. Dendrogramas de los análisis de agrupamiento jerárquico (a, b), diagramas del nMDS (c, d) y localización de las áreas de asociaciones de peces (e, f) definidas para los análisis de abundancia y biomasa.

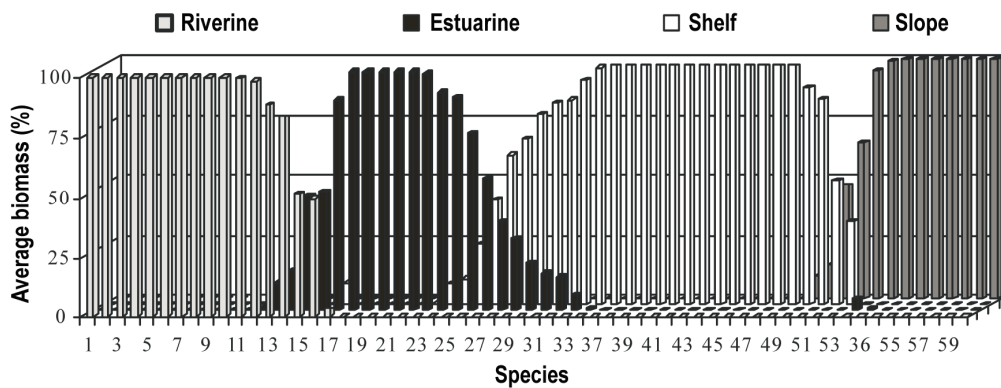


Figure 3. Biomass contrast of the discriminator species, identified by SIMPER analysis, for the fish assemblage areas defined by multivariate analyses using biomass ($t\ nm^{-2}$). Species that contribute to top 90% of dissimilarity between the fish assemblage areas.

Figura 3. Contraste de biomasa de las especies discriminantes, identificadas por análisis SIMPER, para las áreas de asociaciones de peces definidas por los análisis multivariados usando biomasa ($t\ nm^{-2}$). Especies que contribuyen al 90% superior de la disimilitud entre las áreas de asociaciones de peces.

(1) *Ageneiosus valenciennesi*, (2) *Brochiloricaria chauliodon*, (3) *Cyprinus carpio*, (4) *Hypostomus laplatae*, (5) *Leporinus obtusidens*, (6) *Pachyurus bonariensis*, (7) *Paraloricaria vetula*, (8) *Pimelodus maculatus*, (9) *Prochilodus lineatus*, (10) *Pterodoras granulosus*, (11) *Netuma barba*, (12) *Rhinodoras dorbignyi*, (13) *Pimelodus albicans*, (14) *Luciopimelodus pati*, (15) *Parapimelodus valenciennis*, (16) *Lycengraulis grossidens*, (17) *Micropogonias furnieri*, (18) *Anchoa marinii*, (19) *Brevoortia aurea*, (20) *Conger orbignyanus*, (21) *Cynoscion guatucupa*, (22) *Percophis brasiliensis*, (23) *Macrodon ancylodon*, (24) *Prionotus punctatus*, (25) *Parona signata*, (26) *Sympterygia bonapartii*, (27) *Paralichthys patagonicus*, (28) *Myliobatis goodei*, (29) *Trichiurus lepturus*, (30) *Mustelus schmitti*, (31) *Rioraja agassizi*, (32) *Squatina guggenheim*, (33) *Stromateus brasiliensis*, (34) *Trachurus lathami*, (35) *Acanthistius brasiliensis*, (36) *Atlantoraja castelnaui*, (37) *Dules auriga*, (38) *Galeorhinus galeus*, (39) *Mullus argentinae*, (40) *Myliobatis goodei*, (41) *Pagrus pagrus*, (42) *Percophis brasiliensis*, (43) *Prionotus nudigula*, (44) *Pseudopercis semifasciata*, (45) *Squalus megalops*, (46) *Thyrsitops lepidopodea*, (47) *Zapterys brevirostris*, (48) *Discopyge tschudii*, (49) *Xystreuryx rasile*, (50) *Nemadactylus bergi*, (51) *Merluccius hubbsi*, (52) *Urophycis brasiliensis*, (54) *Coelorhynchus marinii*, (55) *Genypterus blacodes*, (56) *Helicolenus dactylopterus lahillei*, (57) *Macruronus magellanicus*, (58) *Patagonotothem ramsayi*, (59) *Squalus acanthias*, (60) *Squalus mitsukurii*.

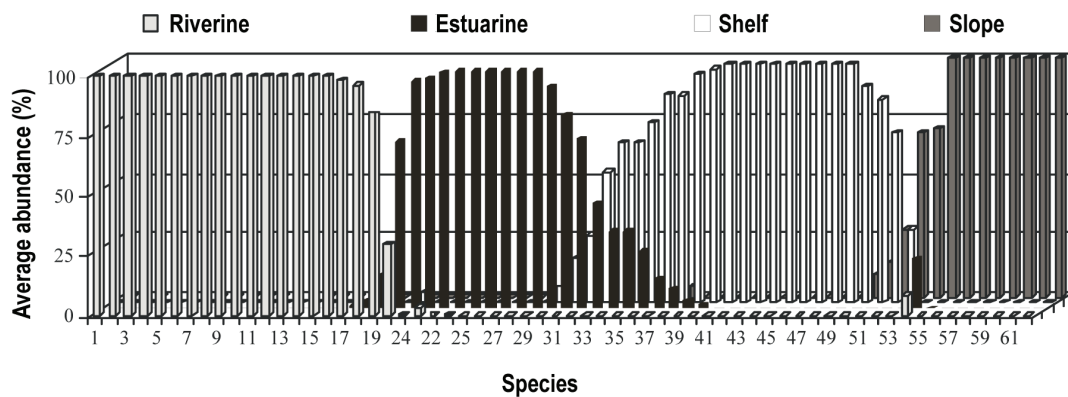


Figure 4. Abundance contrast of the discriminator species, identified by SIMPER analysis, for the fish assemblage areas defined by multivariate analyses using abundance (Thousands ind nm⁻²). Species that contribute to top 90% of dissimilitude between the fish assemblages areas.

Figura 4. Contraste de abundancias de las especies discriminantes, identificadas por análisis SIMPER, para las áreas de asociaciones de peces definidas por los análisis multivaridos usando abundancia (miles ind nm⁻²). Especies que contribuyen al 90% superior de la disimilitud entre las áreas de asociaciones de peces.

(1) *Ageneiosus valenciennesi*, (2) *Brochiloricaria chauliodon*, (3) *Catathyridium jenynsi*, (4) *Cyprinus carpio*, (5) *Eigenmannia virescens*, (6) *Hypostomus laplatae*, (7) *Leporinus obtusidens*, (8) *Luciopimelodus pati*, (9) *Pachyurus bonariensis*, (10) *Paraloricaria vetula*, (11) *Parapimelodus valenciennesi*, (12) *Pimelodus albicans*, (13) *Pimelodus maculatus*, (14) *Prochilodus lineatus*, (15) *Pterodoras granulosus*, (16) *Rhinodoras dorbignyi*, (17) *Netuma barba*, (18) *Lycengraulis grossidens*, (19) *Micropogonias furnieri*, (20) *Brevoortia aurea*, (21) *Prionotus punctatus*, (22) *Macrodon ancylodon*, (23) *Anchoa marinii*, (24) *Percophis brasiliensis*, (25) *Conger orbignyanus*, (26) *Cynoscion guatucupa*, (27) *Engraulis anchoita*, (28) *Symphurus jenynsi*, (29) *Sympterygia acuta*, (30) *Parona signata*, (31) *Sympterygia bonapartii*, (32) *Paralichthys patagonicus*, (33) *Mustelus schmitti*, (34) *Rioraja agassizi*, (35) *Trichiurus lepturus*, (36) *Porichthys porosissimus*, (37) *Myliobatis goodei*, (38) *Squatina guggenheim*, (39) *Stromateus brasiliensis*, (40) *Trachurus lathami*, (41) *Atlantoraja castelnaui*, (42) *Dules auriga*, (43) *Mullus argentinae*, (44) *Pagrus pagrus*, (45) *Percophis brasiliensis*, (46) *Prionotus nudigula*, (47) *Squalus megalops*, (48) *Thyrsitops lepidopodea*, (49) *Zapterys brevirostris*, (50) *Discopyge tschudii*, (51) *Nemadactylus bergi*, (52) *Xystreuryx rasile*, (53) *Merluccius hubbsi*, (54) *Urophycis brasiliensis*, (55) *Bassanago albescens*, (56) *Coelorhynchus marinii*, (57) *Genypterus blacodes*, (58) *Helicolenus dactylopterus lahillei*, (59) *Macruronus magellanicus*, (60) *Patagonotothem ramsayi*, (61) *Squalus acanthias*, (62) *Squalus mitsukurii*.

the similarity were *Micropogonias furnieri*, *Macrodon ancylodon*, *Brevoortia aurea*, *Prionotus punctatus*, *Sympterygia bonapartii*, *Paralichthys brasiliensis*, *Anchoa marinii*, and *Conger orbignyanus* (Tables 1

and 2). *Pimelodus albicans*, *Parapimelodus valenciennis* and *Luciopimelodus pati* in the biomass analysis, as *Cynoscion guatucupa*, *Paralichthys patagonicus*, and *Parona signata* in the abundance

Table 2. Oceanographic (mean, standard deviation) data of the fish assemblages areas defined by multivariate analyses using biomass ($t\text{ nm}^{-2}$) or abundance (thousands ind nm^{-2}). Z: total depth (m), ST: surface temperature, BT: bottom temperature, SS: surface salinity, BS: bottom salinity.

Tabla 2. Datos oceanográficos (media, desvió estándar) de las áreas de asociaciones de peces definidas por los análisis multivariados usando biomasa ($t\text{ nm}^{-2}$) o abundancia (miles ind nm^{-2}). Z: profundidad total (m), ST: temperatura superficial, BT: temperatura del fondo, SS: salinidad superficial, BS: salinidad del fondo.

	Biomass					
	Riverine	Estuarine			Shelf	Slope
		Ia	Ib	Total		
Z	7.88 ± 1.53	4.5 ± 1.91	8.66 ± 1.15	6.29 ± 2.69	28 ± 12.75	151.66 ± 107.51
ST	20.55 ± 0.35	20.29 ± 0.89	19.62 ± 1.16	20 ± 0.99	18.41 ± 1.59	15.33 ± 0.99
BT	20.46 ± 0.45	19.63 ± 0.65	18.9 ± 0.91	19.32 ± 0.803	14.88 ± 2.11	6.99 ± 2.28
SS	0.08 ± 0.02	3.58 ± 2.79	18.46 ± 4.84	9.96 ± 8.66	26.85 ± 4.48	33.45 ± 0.3
BS	0.08 ± 0.02	6.69 ± 5.71	20.7 ± 4.71	12.7 ± 8.93	31.61 ± 1.45	33.82 ± 0.25

	Abundance					
	Riverine	Estuarine			Shelf	Slope
	Ia	Ib	Total			
Z	7.87 ± 1.53	4.33 ± 2.31	6.91 ± 2.33	7.75 ± 2.06	28 ± 12.75	151.66 ± 107.51
ST	20.54 ± 0.34	20 ± 0.85	20.4 ± 0.54	19.99 ± 1.21	18.41 ± 1.59	15.33 ± 0.99
BT	20.46 ± 0.44	19.82 ± 0.68	20.28 ± 0.56	18.96 ± 0.75	14.88 ± 2.11	6.99 ± 2.28
SS	0.08 ± 0.02	3.99 ± 3.27	1.15 ± 2.34	14.43 ± 8.98	26.85 ± 4.48	33.45 ± 0.3
BS	0.08 ± 0.02	4.19 ± 3.38	1.2 ± 2.44	19.07 ± 5.04	31.61 ± 1.45	33.82 ± 0.25

analysis were also identified as common species (Table 1). Discriminator species were *Micropogonias furnieri*, *Anchoa marinii*, *Brevoortia aurea*, *Conger orbignyanus*, *Cynoscion guatucupa*, *Paralichthys brasiliensis*, *Macrodon ancylodon*, *Prionotus punctatus*, *Parona signata*, *Sympterygia bonapartii* and *Paralichthys patagonicus* (Figs. 3 and 4). In the abundance analyses, *Engraulis anchoita*, *Symphurus jenynsi* and *Sympterygia acuta* (Fig. 4) were also identified as discriminators.

In the biomass analysis two subgroups were defined (Fig. 2b). The “subgroup a” included the inner stations of the estuarine area, with lower salinity and depth (Fig. 2f, Table 2). The ichthyofauna was mainly discriminated by the presence of the freshwater species (*Pimelodus albicans*, *Parapimelodus valenciennis*, and *Luciopimelodus pati*), anadromous species (*Lycengraulis grossidens*) and estuarine species (*Brevoortia aurea* and *Micropogonias furnieri*). The “subgroup b” covered the outer station of estuarine area (Fig. 2f). The ichthyofauna was discriminated by estuarine and marine species.

Shelf area (SHA)

This assemblage area included the sampling stations outside the Río de la Plata (Figs. 2e and 2f). It was

salty, intermediate depth and cool (Table 2). The ichthyofauna within this area showed an intermediate similarity (45.7% for biomass and 48.2% for abundance), and was mainly dominated by marine species. *Trachurus lathami*, *Mustelus schmitti*, *Squatina guggenheim*, *Percophis brasiliensis*, *Prionotus nudigula*, *Stromateus brasiliensis*, *Mullus argentinae*, *Pagrus pagrus*, *Micropogonias furnieri*, *Discopyge tschudii* were common species in both analyses (Tables 1 and 2). The ichthyofauna in this area was mainly discriminated by *Myliobatis goodei*, *Trichiurus lepturus*, *Mustelus schmitti*, *Rioraja agassizi*, *Squatina guggenheim*, *Stromateus brasiliensis*, *Trachurus lathami*, *Atlantoraja castelnaui*, *Dules auriga*, *Mullus argentinae*, *Myliobatis goodei*, *Pagrus pagrus*, *Percophis brasiliensis*, *Prionotus nudigula*, *Squalus megalops*, *Thyrstlops lepidopodea*, *Zapteryx brevirostris*, *Discopyge tschudii*, *Xystreureys rasile* and *Nemadactylus bergi* (Figs. 3 and 4). Also, *Acanthistius brasilianus*, *Galeorhinus galeus* and *Pseudopercis semifasciata* in the biomass analysis (Fig. 3), and *Porichthys porosissimus* in the abundance analysis (Fig. 4), were identified as discriminator species.

Slope area (SLA)

This assemblage area covered the zone with the greatest depths, highest salinities, and lowest

temperatures (Figs. 2e and 2f, Table 2). The fish community of this area showed the lowest similarity (33.3% for biomass and 32.0% for abundance). *Squalus mitsukurii*, *S. acanthias*, *Bassanago albescens*, *Merluccius hubbsi*, *Helicolenus dactylopterus lahillei* and *Macruronus magellanicus* were identified as common species in both analysis (Tables 1 and 2). The ichthyofauna was mainly discriminated by *Coelorhynchus marinii*, *Genypterus blacodes*, *Helicolenus dactylopterus lahillei*, *Macruronus magellanicus*, *Patagonotothen ramsayi*, *Squalus acanthias* and *S. mitsukurii* (Figs. 3 and 4). Also, *Merluccius hubbsi*, *Urophycis brasiliensis*, and *Bassanago albescens* were identified as discriminator species in the abundance analysis (Fig. 4).

Relationship with environmental factors

The BIO-ENV process analysis identified the surface and bottom salinity ($\rho = 0.848$ and $\rho = 0.819$ respectively) as the factors having the greatest influence on the fish assemblages distribution based on biomass. Bottom temperature ($\rho = 0.828$) was the next most influential factor on the fish assemblages distribution based on abundance (Fig. 5). As the faunistic ordination is not unidimensional, it is not desirable to have only one factor providing the best fit to the fish assemblage distribution areas. For both analyses the combination of temperature and bottom salinity present the best correlation coefficient ($\rho = 0.906$ and 0.917 respectively) (Fig. 5).

DISCUSSION

A clear spatial pattern of fish assemblages have been identified along the environment gradient from the fresh and shallow water (3.5 m) to marine and deeper water (323.5 m) along the Río de la Plata estuary (36°S, 56°W), the shelf and the upper slope (Fig. 5). The fish assemblage areas (riverine, estuarine, shelf and slope) were consistently distinguishable by their environmental conditions and by their constituent species. Each area showed consistent boundaries, with slight variations in their geographical location between both analyses, which occur near the location of frontal zone. The factors that have most influence on their spatial distributions are bottom salinity and temperature. The changes in the fish assemblage structure were gradual, demonstrating a gradient in change from riverine to marine communities rather than a distinct single transition (Fig. 5).

The riverine area is mainly dominated by freshwater (*Paraloricaria vetula*, *Pimelodus albicans*, *Leporinus obtusidens*, *Pterodoras granulosus*, *Cyprinus carpio*, and *Luciopimelodus pati*), and anadro-

mous species (*Netuma barba*, *Lycengraulis grossidens*). The anadromous species, *N. barba* during spring and early summer, and *L. grossidens* during the autumn and early winter, penetrates into the Río de la Plata and rivers from the Plata basin to spawn (Fuster de Plaza & Boschi, 1961; Ringuelet *et al.*, 1967; Ringuelet, 1975; Jaureguizar *et al.*, 2003; Menni, 2004). Fish associated with the estuarine area were predominantly estuarine resident species (*Micropogonias furnieri*, *Anchoa marinii*, *Brevoortia aurea*, *Paralonchurus brasiliensis*, and *Macrondon ancyllodon*), and to a lower degree occasional freshwater species (*Pimelodus albicans*, *Parapimelodus valenciennis*, and *Luciopimelodus pati*) and marine species, either straggler (*Cynoscion guatucupa*, *Conger orbignyanus* and *Paralichthys patagonicus*) or migrant (*Prionotus punctatus* and *Sympterygia bonapartii*). The estuarine resident species use Samborombón Bay as the main nursery area (Lasta, 1995). The straggler species (*C. guatucupa* and *P. patagonicus*) occurred more frequently in shelf waters, and carried on reproductive activity in coastal zones with salinity over 28 (Macchi & Acha, 1998). The shelf and slope fish assemblages were dominated by marine species. *Trachurus lathami*, *Mustelus schmitti*, *Squatina guggenheim*, *Prionotus nudigula* and *Percophis brasiliensis* characterized the shelf area. In contrast with the shelf area, the slope assemblage was dominated by marine species associated with deep water (*Squalus acanthias*, *Merluccius hubbsi*, *Macruronus magellanicus*, *Helicolenus dactylopterus lahillei* and *Basanago albescens*).

The boundary between fish assemblage areas occurs near the location of frontal zone. The riverine–estuarine border is near the location where the halocline intersects the bottom (Fig. 5), and corresponds to the bottom salinity front defined by Guerrero *et al.* (1997a, 1997b). This represents the boundary for intrusions of freshwater species into the estuary (*Luciopimelodus pati*, *Parapimelodus valenciennis*, *Leporinus obtusidens*, *Prochilodus lineatus* and species of Loricariidae) (Boschi, 1988; Jaureguizar *et al.*, 2003). The border zone between the estuarine and shelf areas coincides with the location of the maximum horizontal gradient of surface salinity (Guerrero *et al.*, 1997a, 1997b), indicating the boundary between the estuary and the continental coastal waters (Mianzan *et al.*, 2001). The persistent salinity vertical structure (Guerrero *et al.*, 1997a, 1997b) in the estuarine area (Fig. 5), shows the presence of a shelf water intrusion along the bottom, which allows the incursion of marine species toward the head of the estuary (Jaureguizar *et al.*, 2003). This zone is the limit for the presence in the estuary of

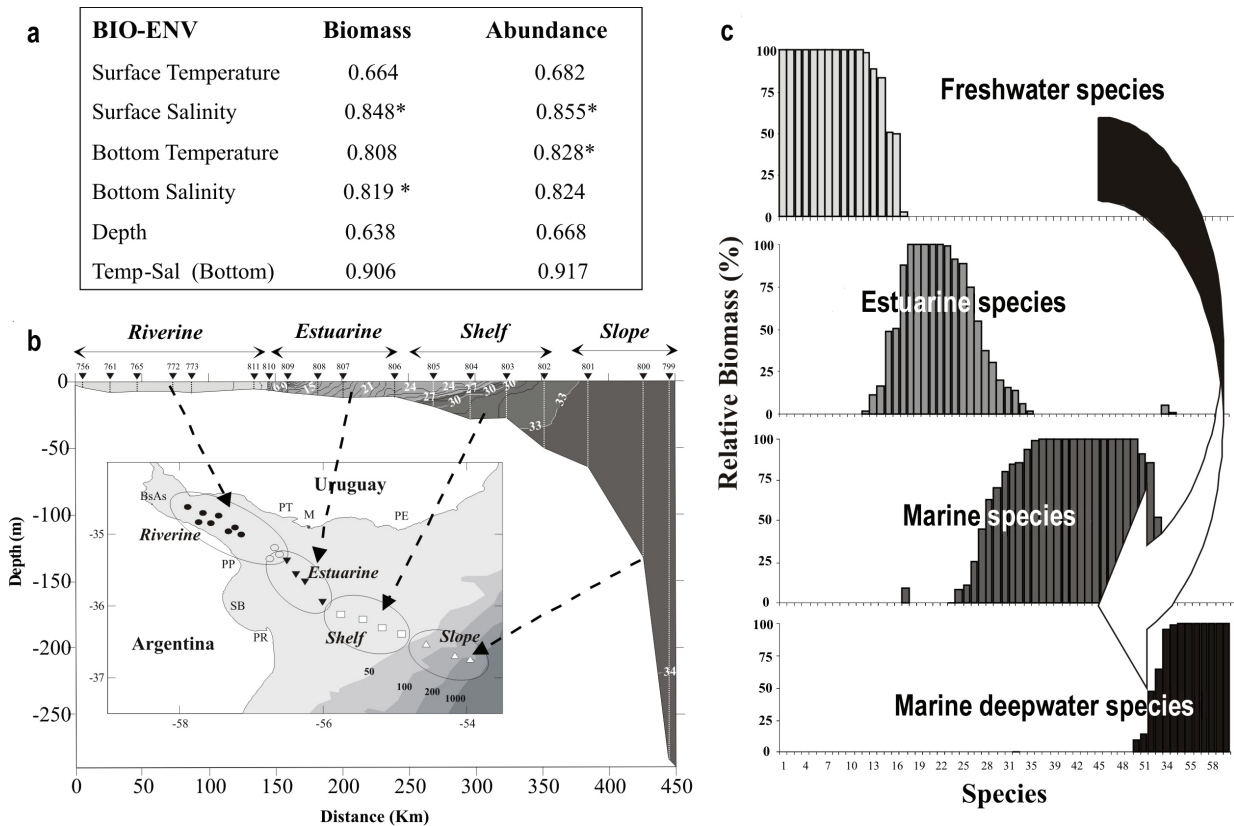


Figure 5. a) Combination of the environmental variables yielding the best matches of biotic (species biomass or abundance, Bray Curtis similarity), and abiotic (Euclidean distance) similarity matrices, as measured by weighted Spearman correlation by means of BIO-ENV process. Z: depth (m), ST: surface temperature ($^{\circ}$ C), BT: bottom temperature ($^{\circ}$ C), SS: surface salinity, BS: bottom salinity, b) Location of the fish assemblage areas defined by biomass on the distribution of salinity along the sampling station, and their area of distribution, and c) Relative biomass (%) of the species by fish assemblage area defined by multivariate analyses using biomass (ton nm^{-2}).

Figura 5. a) Combinación de variables ambientales que producen la mejor coincidencia entre las matrices de similitud biótica (biomasa o abundancia de especies, similitud de Bray Curtis) y abiótica (distancia de Euclidean), medida por la correlación de Spearman pesada mediante el proceso BIO-ENV. Z: profundidad (m), ST: temperatura superficial ($^{\circ}$ C), BT: temperatura del fondo ($^{\circ}$ C), SS: salinidad superficial, BS: salinidad del fondo, b) Localización de las áreas de asociaciones de peces definidas usando biomasa sobre la distribución de la salinidad a lo largo de las estaciones de muestreo, y sus áreas de distribución, y c) Biomasa relativa (%) de las especies por área de asociación definida por los análisis multivariados usando biomasa (ton nm^{-2}).

marine species as *Mullus argentinus*, *Sparus pagrus*, *Merluccius hubbsi* and *Trachurus lathami* (Boschi 1988; Jaureguizar *et al.*, 2003). Similar results were observed for Chesapeake and Delaware bays (Bulger *et al.*, 1993; Able *et al.*, 1997), who identified the 25-27 isohaline as the edge of the brackish water for strictly marine species. The shelf-break front is near the border between shelf and slope fish assemblages. This front is a permanent feature that characterized the border of the shelf, and its inner boundary lies between 90 and 100 m isobaths (Acha *et al.*, 2004). Here the sub Antarctic waters meet the cooler and more saline water of the Malvinas current, thus

producing a thermohaline front (Martos & Piccolo, 1988; Lutz & Carreto, 1991).

Each assemblage was associated to different water masses, with differences in species composition, reflecting a transition from a fish community influenced by muddy deposits originated in the river, dominated by bottom or detritus feeders, to a fish community where the presence of marine pelagic or semi pelagic species becomes more important, and probably energy flow originating from bottom deposits is less important. In the first case the main energy flow come from detritus. In the second case, species feeding on small pelagic fish or crustaceans

indicate that the energy derived from the phytoplankton and zooplankton production becomes more important.

Most of the freshwater species are bottom or bottom related species, omnivorous and euriphagic (Ringuelet, 1975; Menni, 2004). *Pterodoras granulosus* feed on fruit, seed, vegetables, crustaceans and fish (Panattieri & Del Barco, 1982; Darrigran & Colautti, 1994; Ferriz *et al.*, 2000). *Leporinus obtusidens* has a similar diet, but includes small fish and mollusk (Mastrarrigo, 1950; Ringuelet *et al.*, 1967). Due to their euriphagy, all these species have changed their diet because of the invasion by *Corbicula fluminea* and *Limnoperna fortunei*, mollusk from southeast Asian, in the Río de la Plata basin (Ferriz *et al.*, 2000; García & Protogino, 2005). *Netuma barba* is a benthophagous species. Juveniles of *Lycengraulis grossidens* are planktophagous and adults are ichthyophagous (Ringuelet *et al.*, 1967).

Most of species in the estuarine area have benthic habits and feed on mollusks and crustaceans. *Micropogonias furnieri* adults mainly prey upon *Mactra isabelleana* and secondarily upon shrimps, cephalopods and polychaetes (Sánchez *et al.*, 1991). Only *Brevoortia aurea* is planktophagous, preying on diatoms, dinoflagellates, and copepods (Sánchez, 1999), but detritus has also been observed in its diet (Giangiobbe & Sánchez, 1993). In the shelf and slope, the feeding habits show a transition from benthic diet, basically mollusks, crustaceans and small fish, to a more benthopelagic diet composed by small pelagic fish and deep water crustaceans and occasionally zooplankton. Among fishes of these communities, *Squalus acanthias* prefers to prey on pelagic communities. The main food items are ctenophores, teleost fishes (*Merluccius hubbsi*, *Stromateus brasiliensis*, *Engraulis anchoita*, *Nemadactylus bergi*, notothenids and mictophids and cephalopods, occasionally epibenthic macrocrustaceans (Menni, 1985; García de la Rosa & Sánchez, 1997). *Mustelus schmitti* feed on crustaceans, polychaetes and fishes (Olivier *et al.*, 1968; Menni, 1985). The principal dietary component of *Squatina guggenheim* is bony fish, followed by crustaceans, shrimps, molluscs and polychaetes. The bony fish are mainly pelagic fishes such as *Engraulis anchoita*, followed by demersal fishes such as *Cynoscion guatucupa* and *Patagonotothen ramsayi*, *Notothenia longipes* and *Merluccius hubbsi* (Cousseau, 1973; Vögler *et al.*, 2003). *Helicolenus dactylopterus lahillei* feeds on benthic and pelagic species, such as ctenophores, salps, crustaceans, squids and fishes (Cousseau & Perrotta, 2000). Adult *Merluccius hubbsi* mainly feed on pelagic and demersal-pelagic species, with the more

common prey being zooplanktonic crustaceans amphipods and euphausiids, cephalopods, fishes, and epibenthic microcrustaceans (Angelescu *et al.*, 1958; Angelescu & Cousseau 1969; Cordo, 1981; Angelescu & Prenski, 1987; Ruiz & Fondacaro, 1997; Sánchez & García de la Rosa, 1999). Juveniles mainly prey on zooplankton and secondarily on cephalopods and epibenthic macrocrustaceans. *Trachurus lathami* feed on copepods and chaetognaths (Cousseau, 1967). *Percophis brasiliensis* feed on fishes and squids (San Román, 1972). *Macruronus magellanicus* is an eurybatic species, able to adapt to different depths and hydrological conditions. It feeds upon pelagic crustaceans, amphipods, cephalopods and small fishes like sardines and notothenids (Angelescu & Gneri, 1961; Bezzi, 1984; Sánchez & Prenski, 1996; Sánchez, 1999).

In conclusion, the significant changes in the species composition of fish assemblages along the riverine-marine gradient indicate it as appropriate indicators of a heterogeneous habitat. Although the environmental variables, salinity and temperature, play an important role in the habitat differentiation, the change in the food energy source from benthic or detritus production to phytoplankton and zooplankton production evidence its importance in the demersal fish structuring.

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