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Fish assemblage and environmental patterns in the Río de la Plata estuary

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Abstract

The presence of persistent fish assemblage areas in estuaries can result from spatially structured environmental gradients, which determine a pattern of biological zonation. In the Río de la Plata estuary (36 °S, 56 °W), those assemblage areas were defined for summer, autumn, and spring of 1996. Cluster analysis identified groups of sampling stations with a similar species composition for each season. Our results identified three fish assemblage areas along the main axis of the estuary. These assemblages are persistent in specific composition and correspond to particular oceanographic environments throughout the year. The boundaries of the assemblage areas are associated with the highest horizontal gradients of salinity. Geographic variations of the boundaries, indicating contraction or expansion of fish assemblage areas, were associated with the spatial estuarine dynamics. The fish assemblage areas reflect the local pattern of habitat heterogeneity. This suggests that for large estuaries, the fish assemblage areas are indicators of this spatial scale of habitat heterogeneity, as defined by salinity and stratification of water column.

Keywords: estuaries; fish assemblages; temporal and spatial patterns; species composition; estuarine habitat; biological zonation; environmental pattern

1. Introduction

Geographic areas characterized by relatively homogeneous and persistent biological composition, referred to as 'species assemblage areas', are defined only on the basis of the geographic distribution of the species (Tyler, Gabriel, & Overholtz, 1982). Assemblages are groups of species that tend to co-occur together, because they have similar habitat preference or because they interact biologically (Mahon et al., 1998; Murawisky & Finn, 1998; Tyler et al., 1982). Species assemblages have been considered as appropriate indicators of habitat heterogeneity (Bulger, Hayden, Monaco, Nelson, & McCormick-Ray, 1993; Kremen, 1992; Monaco, Lowery, & Emmett, 1992; Noss, 1990), characterizing a particular section of the environmental gradient (Bulger et al., 1993; Kremen, 1992; Mahon & Smith, 1989; Monaco et al., 1992).

The environmental gradients in estuaries are very strong, with some species restricted to a particular section of it, thus demonstrating a zonation pattern (Raffaelli, Karakassis, & Galloway, 1991). Bulger et al. (1993) developed a scheme for identifying estuarine salinity zonations using distribution patterns of species assemblages.

Hierarchical classification methods to define fish assemblage areas have been used to map and identify fish communities (Colvocoresses & Musik, 1984; Gabriel, 1992; Gomes, Haedrich, & Rice, 1992; Gomes, Haedrich, & Villagarcia, 1995; Ishino, Iwassaki, Otsuka, & Kihara, 1983; Mahon et al., 1998; Mahon & Smith, 1989; Mariscal-Romero et al., 1998; de Mello, Castello, & Freire, 1992; Menni & Gostonyi, 1982;

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Menni & López, 1984; Menni & Stehmann, 2000; Prenski & Sánchez, 1988; Tyler et al., 1982).

The objective of this study was to develop a scheme of biological zonation for the Río de la Plata estuary through the identification of 'assemblage areas', based on the distribution (presence–absence) of fish species. Distribution by species abundance will be discussed in a future paper. Our results, based in the presence–absence of species and oceanographic data, identified three fish assemblage areas that persist in composition and correspondence to particular estuarine environments throughout time.

2. Material and methods

2.1. Study area

The Río de la Plata discharges into the Atlantic Ocean (36 °S, 56 °W) with a total average discharge of 20,000–25,000 $m^3\,s^{-1}$ (CARP, 1989) (Fig. 1). This freshwater input defines an estuarine system in which density fields are controlled by the salinity distribution. Based on its morphology and dynamics, the Río de la Plata estuary can be split into two regions (CARP, 1989), upper and lower, divided by Barra del Indio, a shallow bar across the river, centered in the line from Punta Piedras to Montevideo. The upper region has a pluvial regime and is entirely occupied by fresh water. The lower region is predominantly mixohaline, with its boundary with marine water defined by the isohaline surface of 27–30‰ (Practical Salinity Scale) which is highly variable and controlled by the wind field, and to a lesser extent by river discharge (Guerrero, Acha, Framiñan, & Lasta, 1997).

The mixohaline region has a surface area of 38,000 km^2 (Mianzan et al., 2001), with depths between 5 and 15 m. The main axis of the estuary is oriented NW-SE and its width changes from 95 km, between Punta Piedras and Montevideo, to 223 km at the mouth, between Punta Rasa and Punta del Este (Fig. 1).

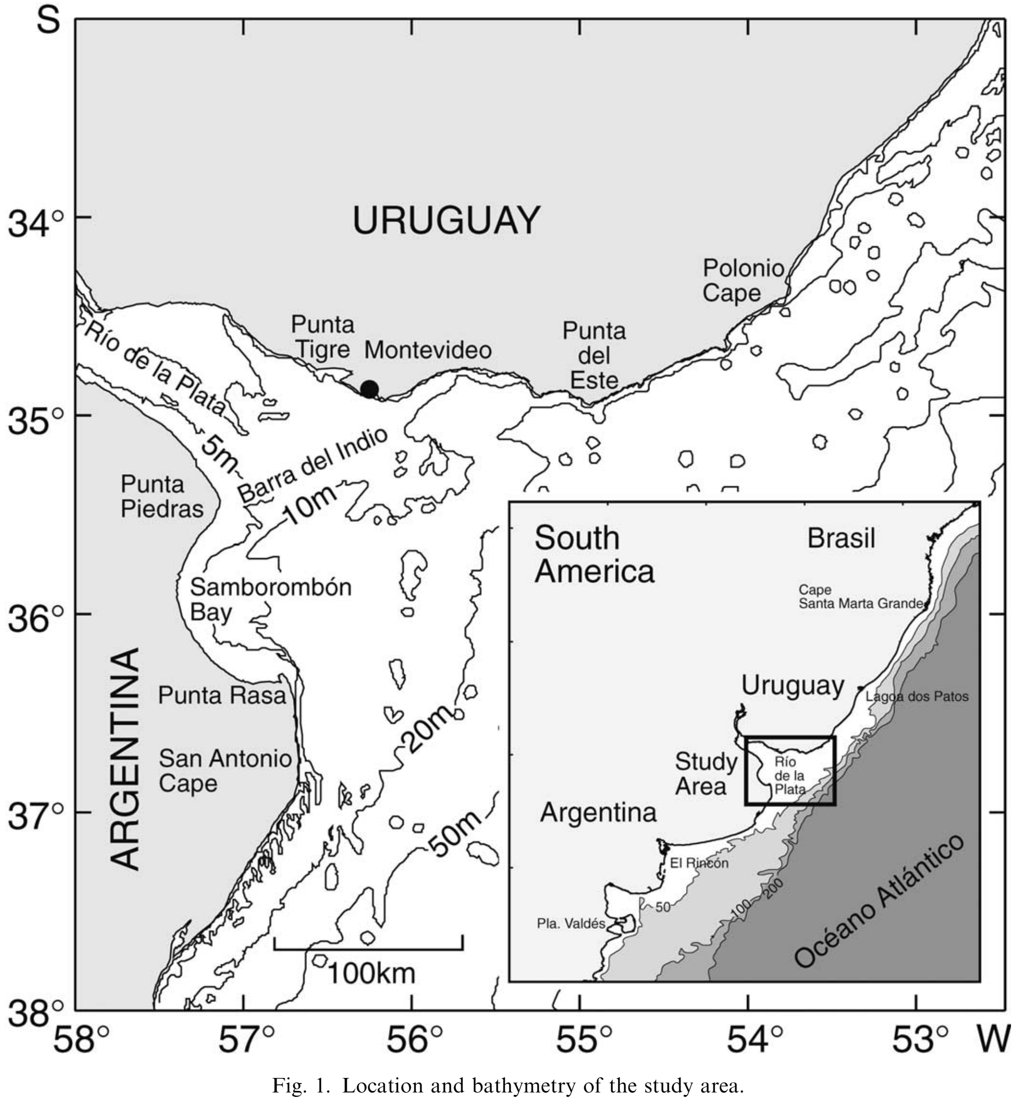


Fig. 1. Location and bathymetry of the study area.

Marine water penetrates as a lower layer into the riverine system as a salt wedge and defines an area of strong vertical stratification. However, moderate to strong onshore winds can destroy this stratification (Framiñan, Etala, Acha, Guerrero, Lasta, & Brown, 1999; Guerrero, Acha, et al., 1997).

Surface water temperatures show a warm period (December–March) with values from 21 to 22 °C and a cold period (June–September) with values from 10 to 12 °C. In each period, estuarine waters are almost fully thermally homogeneous in both vertical and horizontal scales (Guerrero, Acha, et al., 1997).

2.2. Sampling and data analysis

Biological and oceanographic data were obtained in summer (02/10–18), autumn (06/29–07/05), and spring (09/10–17 and 10/13–18) of 1996, during cruises of fisheries evaluation on board the R/V 'Eduardo L. Holmberg' from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). We conducted 167 fishing bottom trawls (55 in summer, 43 in autumn and 79 in spring) with an Engel type net (200 mm stretch of mesh in the wings and 120 mm stretch mesh in the cod end, 4 m of vertical opening and 15 m horizontal aperture) operating at 4 knots for 15 min in each station.

Temperature and salinity at each sampling station were obtained by Conductivity–Temperature-Depth ProfilerCTD (CTD) with a sampling rate of two scans per second and lowered at a speed of $0.5\,\mathrm{m\,s^{-1}}$. Data were reduced to a 1 m vertical resolution, with a precision of ±0.03 °C in temperature and ±0.05 units in salinity.

Fish species were identified according to Menni, Ringuelet, & Aramburu (1984). The fish assemblage areas were identified using cluster analysis using sampling stations (fish trawls) during each season. The un-weighted pair group method using the arithmetic averages cluster method was used. The Sorensen similarity index was applied to presence–absence data (Fagundes Netto & Gaelzer, 1991).

According to the occurrence of species in the study area, fish species were classified as *Permanent* (they occur at all seasons of the year) or *Temporary* (they occur only in some seasons).

Following Mahon et al. (1998), the affinity of species to each group of stations was determined calculating the standardized presence ($\mathrm{PE} = \mathrm{Fg}/\mathrm{Ft}$) for all species in each group, where: Fg = (number of trawls with presence of the species in the group/number of total trawls in the group); Ft = number of trawls with presence of the species in the study area/number of total trawls in the study area. This method limits each species to a single group in which it presents the highest standardized presence. The species affinity in each group was classified as *Exclusive* (present only in that group for all the sampling period) or *Common* (present in more than one group for some sampling periods).

Horizontal maps of bottom salinity were made to define the estuarine regions and their boundaries during each season. Also, vertical salinity sections along the northern coast of the estuary were graphed to establish the environmental boundaries identified by the fish assemblage areas.

A two-way analysis of variance (ANOVA), which considered, as factors of classification, the resulting groups from cluster and the seasons, and temperatures (surface and bottom), salinity (surface and bottom), difference in surface and bottom salinity and depth, as predictors variables, was used to determine spatial and temporal differences among groups. Diverse transformations were tested, but it was not possible to homogenize the variances (test of Bartlett), so, ANOVA was applied using a 0.01 level of maximum nominal significance in order to maintain greater control on the level of real significance associated with the ANOVA. In the case of existing significant differences, comparisons a posteriori were developed using the test of Scheffe. All mathematical analyses were carried out using STATISTICA software for Windows.

3. Results

3.1. Composition and distribution of fish assemblage areas

The ichthyofauna was composed of 59 species, representatives of 35 families and 18 orders (Table 1). Most species were marine euryhalines ($n = 52$), which inhabit the estuary *Permanently* ($n = 34$) or *Temporally* ($n = 18$); freshwater fauna was poor, represented by only seven species (Table 2).

Figs. 2A, 3A and 4A show, for all seasons, the sampling stations clustered together into three main areas as identified using cluster analysis. An area IV is defined in autumn. Each area was characterized by different species (Table 2), as well as different environmental conditions (Table 3).

Area I includes the stations from the inner zone, has the shallowest depth range, and has minimum bottom salinities ranging from 0.5 to 15 psu (Table 3). It has partial vertical salinity stratification for all seasons (Figs. 2B, 3B and 4B). The heterogeneity of their ichthyofauna is shown by the affinity of Exclusive and Permanent freshwater species (*Luciopimelodus pati* and *Parapimelodus valenciennesi*), together with euryhaline marine teleosts (*Micropogonias furnieri*, *Macrodon ancylodon* and *Brevoortia aurea*) (Table 2).

Area II corresponds to sampling stations with an intermediate depth range (means from 9.9 to 10.76 m), and defines the zone of the estuary with salinities between 14 and 29 psu (Table 3). It has high vertical saline

Table 1
Taxonomic list of species captured during summer, fall and spring of 1996

Chondrichthyes

- Triakidae
  - *Mustelus schmitti* Springer, 1939
- Callorhinchidae
  - *Callorhynchus callorhynchus* (Linné, 1758)
- Dasyatidae
  - *Dasyatis pastinaca* (Linné, 1758)
- Myliobatidae
  - *Myliobatis goodei* Garman, 1885
- Rajidae
  - *Psammobatis bergi* Marini, 1932
  - *Rioraja agassizi* (Müller & Henle, 1841)
  - *Atlantoraja castelnaui* (Miranda Ribeiro, 1907)
  - *Atlantoraja cyclophora* (Regan, 1903)
  - *Sympterygia acuta* Garman, 1877
  - *Sympterygia bonaparteii* Müller & Henle, 1841
- Rhinobatidae
  - *Rhinobatos horkelii* Müller & Henle, 1841
  - *Zapteryx brevirostris* (Müller & Henle, 1841)
- Squalidae
  - *Squalus acanthias* Linné, 1758
- Squatinidae
  - *Squatina guggenheim* Marini, 1936
- Torpedinidae
  - *Discopyge tschudii* Heckel, 1846

Osteichthyes

- Congridae
  - *Conger orbignyanus* Valenciennes, 1847
- Atherinidae
  - *Atherinidae unid.* (Bonaparte, 1837)
- Batrachoididae
  - *Porichthys porosissimus* (Valenciennes, 1837)
- Clupeidae
  - *Brevoortia aurea* (Agassiz, 1829)
  - *Ramnogaster arcuata* (Jenyns, 1842)
- Engraulididae
  - *Anchoa marinii* Hildebrand, 1943
  - *Engraulis anchoita* Hubbs & Marini, 1935
  - *Lycengraulis grossidens* (Agassiz, 1829)
- Merlucciidae
  - *Merluccius hubbsi* Marini, 1933
- Phycidae
  - *Urophycis brasiliensis* (Kaup, 1858)
- Carangidae
  - *Parona signata* (Jenyns, 1842)
  - *Trachinotus marginatus* (Cuvier & Valenciennes, 1831)
  - *Trachurus lathami* Nichols, 1920
- Mugilidae
  - *Mugil* sp. (Linné,1758)
- Mullidae
  - *Mullus argentinus* Hubbs & Marini, 1933
- Percophidae
  - *Percophis brasiliensis* Quoy & Gaimard, 1824
- Pomatomidae
  - *Pomatomus saltatrix* (Linné, 1758)
- Scianidae
  - *Cynoscion guatucupa* (Cuvier, 1830)
  - *Macrodon ancylodon* Schneider, 1801
  - *Menticirrhus americanus* (Linné, 1758)
  - *Micropogonias furnieri* (Desmarrest, 1823)
  - *Paralonchurus brasiliensis* (Steindachner, 1875)
  - *Pogonias cromis* (Linné, 1766)
  - *Umbrina canosai* Berg, 1895
- Serranidae
  - *Acanthistius brasilianus* (Valenciennes, 1828)
- Sparidae
  - *Diplodus argenteus* (Valenciennes, 1830)
  - *Sparus pagrus* (Linné, 1758)
- Stromateidae
  - *Peprilus paru* (Linné, 1758)
  - *Stromateus brasiliensis* (Fowler, 1906)
- Trichiuridae
  - *Trichiurus lepturus* Linné, 1758
- Cynoglossidae
  - *Symphurus sp.* (Rafinesque, 1810)
- Paralichthyidae
  - *Paralichthys orbignyanus* (Valenciennes, 1939)
  - *Paralichthys patagonicus* Jordan, 1889
- Pleuronectidae
  - *Oncopterus darwini* Steindachner, 1875
- Triglidae
  - *Prionotus nudigula* Ginsburg, 1950
  - *Prionotus punctatus* (Cuvier 1829)
- Ariidae
  - *Netuma barbus* (Lacépède, 1803)
- Pimelodidae
  - *Luciopimelodus pati* (Valenciennes, 1840)
  - *Parapimelodus valenciennesi* (Kroyer, 1874)
  - *Pimelodus albicans* (Valenciennes, 1840)
- Loricariidae
  - *Loricariidae unid.* (Linné, 1758)
- Balistidae
  - *Balistes capriscus* (Gmelin, 1788)
- Curimatidae
  - *Leporinus fasciatus* (Gunter, 1864)
  - *Prochilodus platensis* (Holmberg, 1889)

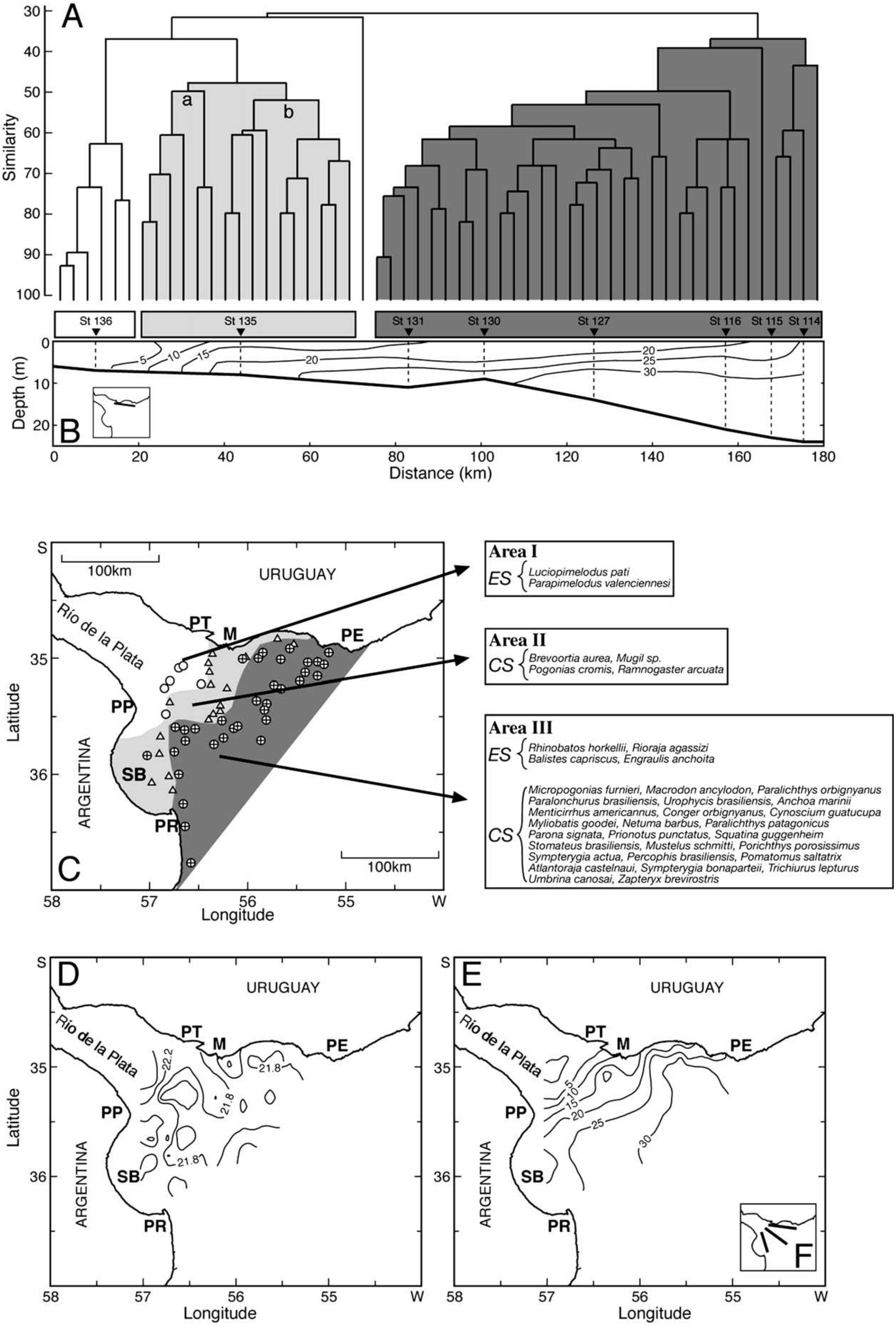
stratification (Figs. 2B, 3B and 4B). This area does not contain any Permanent species with Exclusive conditions. It shows great overlap of its fish composition, in particular, with marine species of the external Area III (Table 2). Area II showed two clear subgroups in summer (Fig. 2). The subgroup 'a' includes stations closer to the Argentine coast, with higher bottom salinities (mean 23.48 psu, SD 2.22). Its ichthyofauna was characterized by the presence of marine species (*Anchoa marinii*, *Paralichthys patagonicus*, *Parona signata*, *Pogonias cromis*, *Squatina guggenheim* and *Sympterygia bonapartei*). The subgroup 'b' includes stations close to the Uruguayan coast, with lower bottom salinities (mean 17.15 psu, SD 5.11), and was characterized by the presence of freshwater species (*Pimelodus albicans*) and marine species (*Conger orbignyanus*, *Menticirrhus americanus*, *Paralichthys orbignyanus*, *Peprilus paru*, *Prionotus punctatus*, *Ramnogaster arcuata* and *Symphurus* sp.).

Area III is the deepest zone in the estuary (means from 12.63 to 16 m), with salinities between 25 and 34 psu (Table 3), and partial salinity stratification (Figs. 2B, 3B and 4B). It is characterized by the largest

Table 2
Standardized presence of species according to area

			Area I			Area II			Area III			Area IV
			Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Fall
Permanent species												
D	ES	*Luciopimelodus pati*	**9.17**	**10.75**	**6.58**							
D	ES	*Parapimelodus valenciennesi*	**9.17**	**10.75**	**6.58**							
M	CS	*Micropogonias furnieri*	1.02	**1.16**	1.02	1.02	1.04	**1.11**	**5.43**	0.83	0.97	0.77
M	CS	*Pogonias cromis*			**3.29**	3.44	**1.48**	2.82				
M	CS	*Brevoortia aurea*	1.93		**2.58**	**1.99**	**1.48**	2.21	1.93		0.32	
M	CS	*Mugil* sp.			0.51	**2.67**	**1.48**	**4.34**	**2.04**		0.23	
M	CS	*Ramnogaster arcuata*				**3.44**	**1.33**	**5.64**		0.61		
M	CS	*Macrodon ancylodon*	1.45		1.20	1.27	**1.48**	**3.59**	**4.34**		0.27	
M	CS	*Paralichthys orbignyanus*	0.65		0.94	1.96	**1.48**	**3.22**	**3.27**		0.43	
M	CS	*Paralonchurus brasiliensis*	0.37		0.33	1.10	**1.43**	**2.54**	**5.87**	0.23	0.75	
M	CS	*Urophycis brasiliensis*			0.29	2.15	**1.21**	**1.47**	**3.44**	1.12	1.04	
M	CS	*Anchoa marinii*				0.69	**1.48**	**3.76**	**7.33**		0.50	
M	CS	*Menticirrhus americanus*				0.86	**1.33**	**4.70**	**6.88**	0.61	0.25	
M	CS	*Conger orbignyanus*				0.63	**1.13**	2.63	**7.50**	0.74	0.79	**1.72**
M	CS	*Myliobatis goodei*	0.61			0.46	**1.11**	**1.46**	**7.33**	0.77	1.11	**1.79**
M	CS	*Netuma barbus*	2.18		2.47	1.31	0.74	**2.82**	**3.49**	**3.07**	0.19	
M	CS	*Paralichthys patagonicus*				0.16	1.08	**2.82**	**8.75**	**1.40**	0.75	0.65
M	CS	*Parona signata*				0.33	1.11	**0.59**	**8.28**	**1.32**	1.33	0.51
M	CS	*Prionotus punctatus*				0.43	0.99	**2.02**	**8.02**	**1.23**	0.96	**1.91**
M	CS	*Sympterygia bonapartei*				0.49	1.10	**3.13**	**7.86**	**1.39**	0.66	0.46
M	CS	*Sympterygia acuta*					0.89	**1.88**	**9.17**	**2.46**	0.99	
M	CS	*Cynoscion guatucupa*			0.27	0.33	1.03	0.71	**8.29**	**1.30**	**1.24**	**1.30**
M	CS	*Squatina guggenheim*				0.18	0.74	0.64	**8.68**	**2.46**	**1.32**	1.43
M	CS	*Stromateus brasiliensis*				1.59	1.06	0.75	**4.94**	**1.54**	**1.29**	0.51
M	CS	*Umbrina canosai*					0.21	1.13	**9.17**	**4.39**	**1.19**	2.05
M	CS	*Mustelus schmitti*					0.91	0.26	**9.17**	**2.39**	**1.42**	
M	CS	*Porichthys porosissimus*					1.11	0.38	**9.17**	**1.54**	**1.39**	
M	CS	*Percophis brasiliensis*					0.42		**9.17**	**4.39**	**1.49**	
M	CS	*Pomatomus saltatrix*					**0.89**		**9.17**	0.61	1.49	**4.30**
M	CS	*Atlantoraja castelnaui*					**1.30**		**9.17**	0.77	**1.49**	
M	CS	*Trichiurus lepturus*				0.80		2.42	**7.03**		0.85	**14.33**
M	CS	*Zapteryx brevirostris*						**1.41**	**9.17**	**6.14**	1.12	
M	ES	*Rhinobatos horkelii*							**9.17**	**6.14**	**1.49**	
M	ES	*Rioraja agassizi*							**9.17**	**6.14**	**1.49**	
M	ES	*Balistes capriscus*							**9.17**	**6.14**	**1.49**	
M	ES	*Engraulis anchoita*							**9.17**	**6.14**	**1.49**	
Temporary Species												
M	ES	Pimelodidae	**9.17**									
D	CS	*Pimelodus albicans*	**7.33**		**5.93**	0.69						
D	CS	Atherinidae		**2.69**	**6.58**		1.11					
D	ES	*Leporinus fasciatus*			**6.58**							
D	ES	Loricaridae			**6.58**							
D	ES	*Prochilodus platensis*			**6.58**							
M	ES	*Rioraja cyclophora*					**1.48**					
M	ES	*Lycengraulis grossidens*				2.19		**5.64**	**3.33**			
M	ES	*Sympterygia* sp.						**3.76**			0.50	
M	CS	*Mullus argentinus*							**9.17**			
M	ES	*Oncopterus darwini*							**9.17**			
M	ES	*Psammobatis bergi*								**6.14**		
M	CS	*Prionotus nudigula*					0.49			**4.10**		
M	ES	*Sparus pagrus*								**6.14**		
M	CS	*Squalus acanthias*					0.99			**2.05**		
M	CS	*Symphurus* sp.				0.86	0.74		**6.88**	**3.07**		
M	ES	*Trachinotus marginatus*							**9.17**			
M	CS	*Peprilus paru*				0.60			**7.57**		**1.49**	
M	ES	*Trachurus lat hami*							**9.17**		**1.49**	
M	ES	*Merluccius hubbsi*									**1.49**	
M	ES	*Paralichthys* sp.									**1.49**	
M	ES	*Prionotus* sp.									**1.49**	
M	ES	Rajidae									**1.49**	
M	ES	*Callorhynchus callorhynchus*									**1.49**	
M	ES	*Dasyatis pastinaca*									**1.49**	
M	CS	*Discopyge tschudii*					0.74			**3.07**	**1.49**	
M	CS	*Acanthistius brasilianus*					0.85			**2.63**	**1.49**	
M	CS	*Diplodus argenteus*					0.89			1.23	**1.49**	**2.87**

Value in bold indicate area with highest presence value. M, Marine; D, Fresh water. ES, Exclusive; CS, Common.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St 135
St 131
St 130
St 127
St 116
St 115
St 114
B
Depth (m)
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20
25
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Distance (km)
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100
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URUGUAY
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PT
M
PE
PP
SB
PR
ARGENTINA
Latitude
35
36
Longitude
58
57
56
55
W
Area I
ES
Luciopimelodus pati
Parapimelodus valenciennesi
Area II
CS
Brevoortia aurea, Mugil sp.
Pogonias cromis, Ramnogaster arcuata
Area III
ES
Rhinobatos horkellii, Rioraja agassizi
Balistes capriscus, Engraulis anchoita
CS
Micropogonias furnieri, Macrodon ancylodon, Paralichthys orbignyanus
Paralonchurus brasiliensis, Urophycis brasiliensis, Anchoa marinii
Menticirrhus americannus, Conger orbignyanus, Cynoscium guatucupa
Myliobatis goodei, Netuma barbus, Paralichthys patagonicus
Parona signata, Prionotus punctatus, Squatina guggenheim
Stomateus brasiliensis, Mustelus schmitti, Porichthys porosissimus
Sympterygia actua, Percophis brasiliensis, Pomatomus saltatrix
Atlantoraja castelnaui, Sympterygia bonaparteii, Trichiurus lepturus
Umbrina canosai, Zapteryx brevirostris
D
22.2
21.8
21.8
21.8
E
5
10
15
20
25
30
F

presence of marine Permanent species ($n = 16$). Four of these are Exclusive (*Balistes capriscus*, *Engraulis anchoita*, *Rioraja agassizi* and *Rhinobatos horkelii*) and 12 are Common (Table 2). In spring (Fig. 4), this area showed two subgroups. Subgroup 'a' comprise stations with higher bottom salinities (mean 28.20 psu, SD 2.99), located both in the central part of the Area and near the Uruguayan coast. It was characterized by the presence of marine species (*Anchoa marinii*, *Balistes capriscus*, *Dasyatis pastinaca*, *Menticirrhus americanus*, *Paralichthys orbignyanus*, *Rioraja agassizi*, *Sympterygia acuta*, *Sympterygia bonapartei* and *Trachurus lathami*). The subgroup 'b' clustered central stations and coastal stations from both banks, and had a 25.81 psu mean bottom salinity (SD 2.62). The fish fauna was characterized by *Acanthistius brasilianus*, *Callorhynchus callorhynchus*, *Discopyge tschudii*, *Engraulis anchoita*, *Macrodon ancylodon* and *Merluccius hubbsi*.

In fall (Fig. 3), the Area IV included three sampling stations near Punta del Este, with depth, temperature and bottom salinity similar to Area III, but with lower surface salinities (mean 19.06 psu, SD 4.8) and higher difference in surface and bottom salinity than Area III (Table 3). Its ichthyofauna was characterized by the close affinity of *Conger orbignyanus*, *Myliobatis goodei*, *Prionotus punctatus*, *Cynoscion guatucupa*, *Pomatomus saltatrix*, *Atlantoraja castelnaui* and *Diplodus argenteus*.

The variation in the composition of Temporary species in each area, indicates that the largest intrusion of temporary freshwater species into Area I happens in spring ($n = 5$). The amount of Temporary marine species in Area III is similar for all seasons. Most Temporary species that enter Area III also make it to Area II (Table 2).

3.2. Depth, temperatures and salinities of fish assemblage areas

3.2.1. Depth

Overall depth ranges between 6 m (Punta Tigre–Punta Piedras zone, Fig. 1) and 23 m (mouth of the estuary). Significant differences in depth were found between areas I and III for three seasons ($p < 0.003$ for summer and autumn, and $p < 0.018$ for spring). Area II showed no significant differences with Areas I and III. There were no differences in depth within each area ($p = 0.61$) (Table 3).

3.2.2. Temperature

Horizontal distribution of temperature was nearly homogeneous for all seasons, with a weak increase of temperature gradients during spring. Mean minimum and maximum temperatures were found during autumn and summer, respectively (Table 3) and were significantly different ($p < 0.00001$).

Surface temperatures (SST) showed no significant differences between areas throughout the year ($p = 0.028$), even though Scheffe test indicated significant differences ($p < 0.0002$) in bottom temperatures between Area I and Areas II and III during spring.

3.2.3. Salinities

For all seasons, a strong salinity gradient was evident along the estuary, with low salinities upriver and high salinities closer to the mouth of the estuary. The region with bottom salinities of 5–10 psu (between Punta Tigre and Punta Piedras, Fig. 1) had strongest horizontal gradients, bounded by regions with weaker gradients (Figs. 2E, 3E and 4E). Figs. 2B, 3B and 4B show a high vertically stratified zone, limited by partially stratified ones, mainly during summer and spring. The inner limit of the surface salinity (SS) front is observed between the isohaline 25–30.

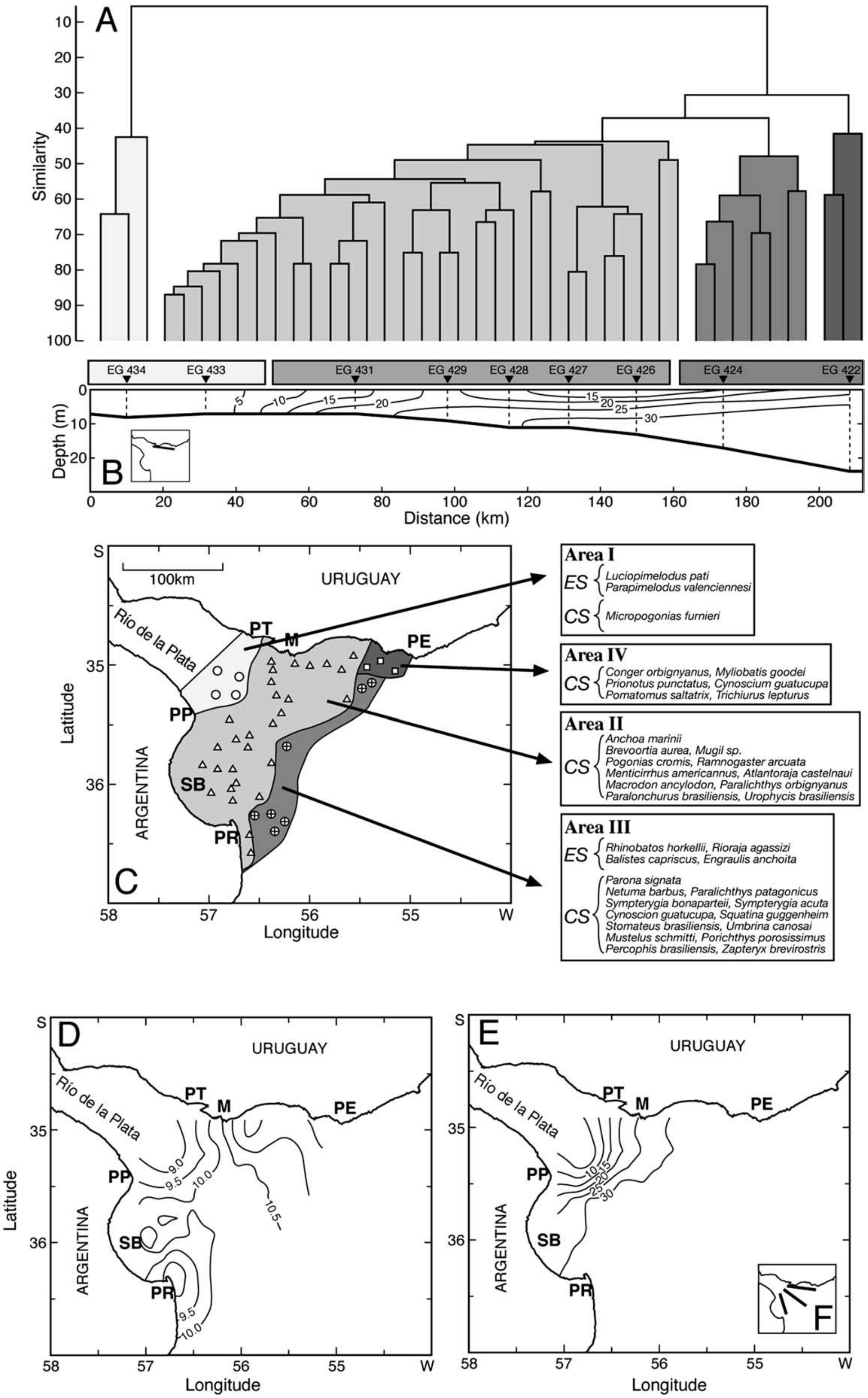
Significant differences ($p < 2.25 \times 10^{-5}$) were observed between the autumn salinity maximum and the spring–summer salinity minimum (Table 3). Significant differences in SS between Areas I and II correspond to autumn ($p < 1.21 \times 10^{-6}$) and spring ($p < 0.0007$), while differences between Areas I and III were found during the whole study period ($p < 2.9 \times 10^{-5}$).

Bottom salinities differed significantly ($p < 0.0015$) between all areas during summer and between Areas II and III in autumn and spring ($p < 0.05$). Relevant seasonal significant differences were found in bottom salinity in Area II between autumn and summer–spring. The difference between surface and bottom salinity (DS) showed no significant difference between areas throughout the year ($P = 0.447$). Maximum differences in salinity values were found in the Area II and the minimum ones in the Area I (Table 3).

4. Discussion

This study shows that the Río de la Plata estuarine ichthyofauna had a permanent spatial structure from its mouth through the innermost zone of the estuary (Figs. 2C, 3C and 4C). This pattern, with differences in species composition between zones, was also observed by Boschi (1988) in relation to bottom salinity concentrations (<0.5, 0.5–30, >30‰). Abella, Arena, and Nion (1979) as well as Cousseau (1985) describe the same pattern, based on geographical areas defined by

Fig. 2. (A) Dendrogram of the cluster analysis results corresponding to summer, (B) location of the groups on the distribution of the salinity along of Sampling Station (St) on the north transect of high resolution. (C) Area of distribution of the groups and species affinity [(ES) Exclusive species, (CS) Common species] corresponding to each group. Distribution of (D) temperature and (E) salinity of bottom. (F) Location of the oceanographic transects of high resolution (North, Central and South).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S
100km
URUGUAY
Río de la Plata
PT
M
PE
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SB
PR
ARGENTINA
C
Latitude
Longitude
58
57
56
55
W
35
36
Area I
ES
Luciopimelodus pati
Parapimelodus valenciennesi
CS
Micropogonias furnieri
Area IV
CS
Conger orbignyanus, Myliobatis goodei
Prionotus punctatus, Cynoscium guatucupa
Pomatomus saltatrix, Trichiurus lepturus
Area II
CS
Anchoa marinii
Brevoortia aurea, Mugil sp.
Pogonias cromis, Ramnogaster arcuata
Menticirrhus americannus, Atlantoraja castelnaui
Macrodon ancylodon, Paralichthys orbignyanus
Paralonchurus brasiliensis, Urophycis brasiliensis
Area III
ES
Rhinobatos horkellii, Rioraja agassizi
Balistes capriscus, Engraulis anchoita
CS
Parona signata
Netuma barbus, Paralichthys patagonicus
Sympterygia bonaparteii, Sympterygia acuta
Cynoscion guatucupa, Squatina guggenheim
Stomateus brasiliensis, Umbrina canosai
Mustelus schmitti, Porichthys porosissimus
Percophis brasiliensis, Zapteryx brevirostris
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the relief of the bottom, configuration of the coast and current and tidal regimes (SIHN, 1972). On the other hand, consistent differences between fish assemblage areas defined by fish density (t/nm^2) were reported in autumn by Anganuzzi (1983) and Prenski and Sánchez (1988), during winter by Díaz de Astarloa, Aubone and Cousseau (1999), and for spring by Lasta, Bremec, and Mianzan (1998). The present study defines the zonation of the estuary by the permanent spatial pattern of three main fish assemblages, on the bases of species co-occurrence throughout the year.

Our sampling station groups defined in Figs. 2A, 3A and 4A, are associated with a particular oceanographic vertical environmental structure (Figs. 2B, 3B and 4B). Their differences in the species composition (Table 2) reflect the transition from a marine species assemblage, characteristic of the external zone (Area III), to a fish assemblage dominated mostly by freshwater species in the inner zone (Area I). The external zone (Area III) and the central zone (Area II) are similar in species composition and geographic distribution to that observed by other authors (Anganuzzi, 1983; Díaz de Astarloa et al., 1999; Lasta et al., 1998; Prenski and Sánchez, 1988). Díaz de Astarloa et al. (1999) define an internal area with traits agreeing with the results obtained in the present work.

According to the species classification proposed by Rico (2000), following Whitfield (1999), different kind of species were associated with the areas defined in the present work. Diagnostic species for the inner area of the estuary include one freshwater straggler species (*Parapimelodus valenciennesi*) and one anadromous species (*Netuma barbus*) that enter estuaries and rivers for reproduction (Sverliej, Lopez, Delfino Schenke, & Espinach Ros, 1998). Fish associated with middle area were predominantly estuarine resident species (*Micropogonias furnieri*, *Brevoortia aurea*, *Macrodon ancylodon*, *Paralonchurus brasiliensis* and *Paralichthys orbignyanus*) and, to a lower degree, migrant species, estuarine (*Mugil* sp.) and marine (*Menticirrhus americanus*). The estuarine resident species use Samborombón Bay as main nursery area (Lasta, 1995). In contrast with the middle area, fish associated with the outer area were predominantly marine species, either straggler (*Cynoscion guatucupa*, *Conger orbignyanus*, *Discopyge tschudii*, *Paralichthys patagonicus*, *Percophis brasiliensis* and *Atlantoraja castelnaui*) or migrant species (*Mustelus schmitti*, *Sympterigia bonapartei*, *Stromateus brasiliensis*, *Squatina guggenheim*, *Myliobatis goodei* and *Prionotus punctatus*). The last group has species (*Cynoscion guatucupa* and *Paralichthys patagonicus*) that occurred more frequently in shelf wasters, and carried on reproductive activity in coastal zones with salinities over 28 psu (Macchi and Acha, 1998). The role of the estuary as reproductive area is probably less important for these species.

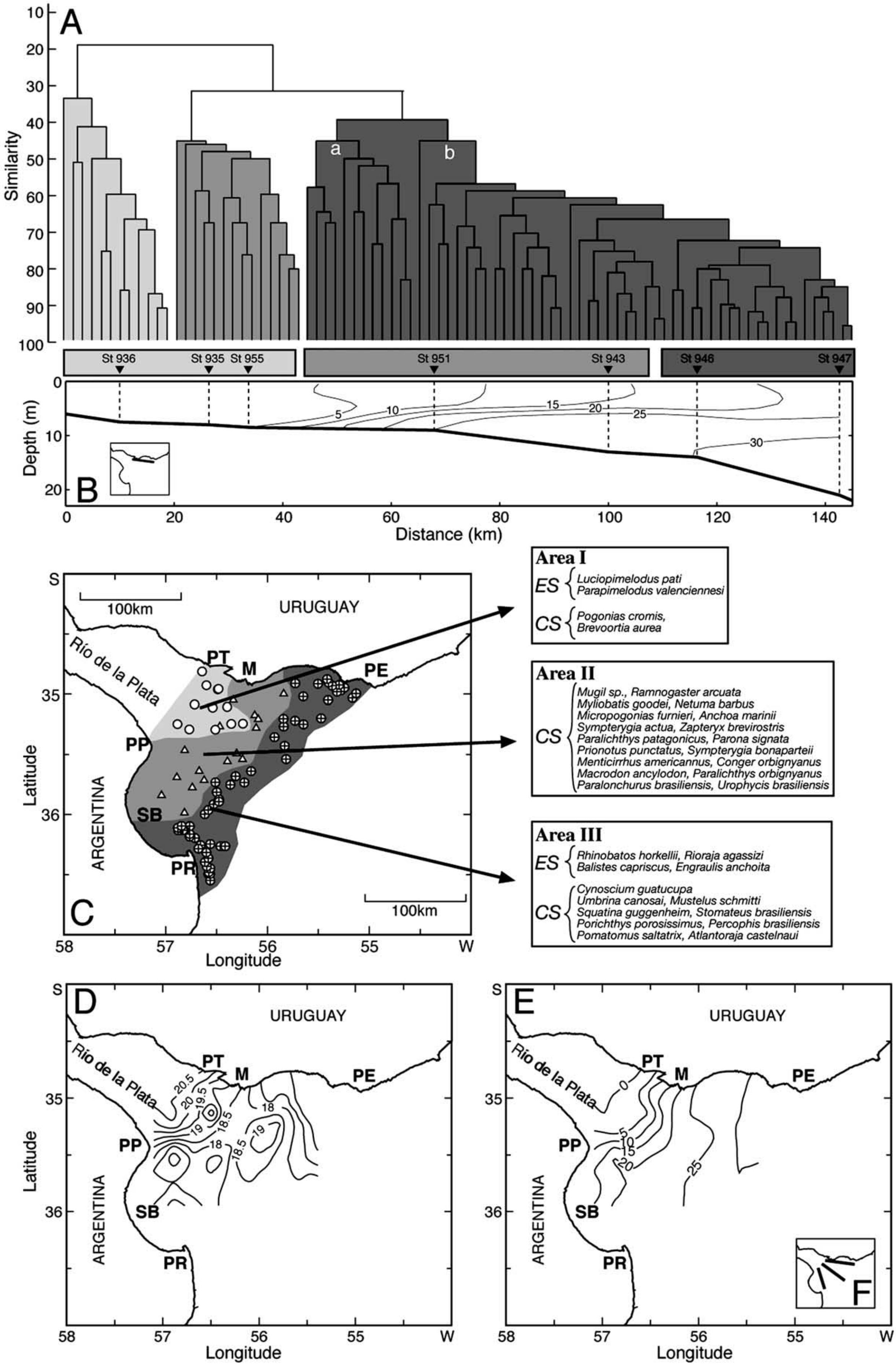
The salinity vertical structure (Figs. 2B, 3B and 4B), showed the presence of shelf water intrusion along the bottom. This allowed the incursion of marine species toward the head of the estuary. This near permanent physical characteristic (Guerrero, Acha, et al., 1997) would explain how some members of the family Sciaenidae (*Micropogonias furnieri*, *Macrodon ancylodon*) and *Brevoortia aurea* (Clupeidae) can reach the tip of the salt wedge (Area I) using the bottom salinity front. This area was defined as the ecotone between the estuary and riverine fresh water (Acha, Mianzan, Lasta, & Guerrero, 1999). A similar situation was observed in the Peel-Harvey estuary, Australia (Loneragan, Potter, Lenanton, & Caputi, 1987). The decrease in the number of species along the different sections of the environment as observed in Table 2, is correlated with the diminishing salt water intrusion, This feature has been observed with less spatial resolution by Boschi (1988) and Cousseau (1985).

The vertical salinity structure also defined three distinctive stratification conditions (Mianzan et al., 2001), spatially correlated to the geographical areas delimited by the fish assemblages (Figs. 2B, 3B and 4B). The central Area II represents the estuarine mixohaline area where conditions of high vertical stratification (Guerrero, Acha, et al., 1997), are limited by zones of maximum horizontal salinity gradients (Mianzan et al., 2001).

The border zone between the external and internal areas coincides with the location of the maximum horizontal gradient of SS (Guerrero, Acha, et al., 1997), indicating the boundary between the estuary and the continental coastal waters (Mianzan et al., 2001). This zone is the limit for the presence in the estuary of marine species (*Balistes capriscus*, *Engraulis anchoita*, *Rioraja agassizi*, *Rhinobatus horkelii*, *Oncopterus darwini*, *Mullus argentinus*, *Psammobatis bergi*, *Sparus pagrus*, *Trachinotus marginatus*, *Merluccius hubbsi*, *Trachurus lathami*, *Callorhynchus callorhynchus* and *Dasyaatis pastinaca*) (Table 2). Similar results were observed for Chesapeake Bay and Delaware Bay (Able, Light, Nemerson & Busch, 1997; Bulger et al., 1993), who identified the 25–27 psu isohaline as the edge of the brackish water for strictly marine species.

The border zone between the internal and central areas is near the location where the halocline intersects the bottom, and corresponds to the bottom salinity fronts defined by Guerrero, Acha, et al. (1997). This represents the boundary for intrusions of freshwater species into the estuary (*Luciopimelodus pati*, *Parapimelodus*

Fig. 3. (A) Dendrogram of the cluster analysis results corresponding to fall, (B) location of the groups on the distribution of the salinity along of Sampling Station (St) on the north transect of high resolution. (C) Area of distribution of the groups and species affinity [(ES) Exclusive species, (CS) Common species] corresponding to each group. Distribution of (D) temperature and (E) salinity of bottom. (F) Location of the oceanographic transects of high resolution (North, Central and South).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Río de la Plata
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ARGENTINA
SB
PR
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Latitude
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Longitude
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W
Area I
ES { Luciopimelodus pati, Parapimelodus valenciennesi
CS { Pogonias cromis, Brevoortia aurea
Area II
CS { Mugil sp., Ramnogaster arcuata, Myliobatis goodei, Netuma barbus, Micropogonias furnieri, Anchoa marinii, Sympterygia actua, Zapteryx brevirostris, Paralichthys patagonicus, Parona signata, Prionotus punctatus, Sympterygia bonapartei, Menticirrhus americannus, Conger orbignyanus, Macrodon ancylodon, Paralichthys orbignyanus, Paralonchurus brasiliensis, Urophycis brasiliensis
Area III
ES { Rhinobatos horkellii, Rioraja agassizi, Balistes capriscus, Engraulis anchoita
CS { Cynoscium guatucupa, Umbrina canosai, Mustelus schmitti, Squatina guggenheim, Stomateus brasiliensis, Porichthys porosissimus, Percophis brasiliensis, Pomatomus saltatrix, Atlantoraja castelnaui
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Table 3
Physical oceanographic measurements and biological data of the areas defined by cluster analysis

	Number		Depth (m)		SS		SB		TS (°C)		TB (°C)		DS	
Area	St	Sp	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD	Mean	±SD
I														
Summer	6	11	7.08	0.970	4.15	5.053	8.47	7.681	22.51	1.260	21.75	0.266	4.36	8.220
Fall	4	4	6.50	0.577	1.42	2.001	2.10	2.350	8.67	0.096	8.72	0.101	3.26	5.852
Spring	12	12	7.29	0.656	1.80	2.300	7.75	6.926	20.87	0.694	19.42	0.906	5.03	5.536
II														
Summer	16	26	9.99	2.045	14.34	5.189	20.27	5.226	22.31	0.730	21.83	0.349	5.70	4.645
Fall	29	36	10.52	3.055	21.61	7.045	28.30	5.355	9.16	0.472	10.09	0.723	7.34	5.466
Spring	14	29	10.76	2.790	13.65	5.648	19.79	5.015	19.90	1.349	17.79	0.781	6.14	5.883
III														
Summer	33	12	14.11	3.870	19.47	6.065	28.58	3.220	22.27	0.710	21.69	0.419	8.92	5.453
Fall	7	29	16.00	3.651	30.55	4.514	33.42	1.126	9.73	0.436	10.15	0.680	2.88	3.582
Spring	53	43	12.63	2.963	21.93	3.579	27.84	2.982	20.18	0.900	17.78	1.395	5.92	4.636
IV														
Fall	4	14	18.60	3.055	19.06	4.800	33.60	0.228	10.27	1.330	11.40	0.320	14.61	4.610

St, number of sampling station; Sp, number of species; Z, total depth; SS, surface salinity; SB, bottom salinity; TS, surface temperature; TB, bottom temperature; DS, difference in surface and bottom salinity.

valenciennesi, *Leporinus fasciatus*, *Prochilodus platensis* and species of Loricariidae) (Table 2). The patterns of occurrence of species in the border areas of this zone limit, suggest that this boundary does not represent one barrier for marine species dispersion up-water (Area I) as sharp as it does for freshwater species dispersion down-water (Area II) (Table 2). This has been also observed in Chesapeake Bay (Wagner, 1999). The surface and bottom salinity fronts are boundaries recognized by the species of the mixohaline area of the estuary, instead of 0.5 and 30.0‰ as defined by Boschi (1988). According to species composition (Table 2), this area is a transition zone between fresh waters and marine waters, characterized by the absence of elements of its own, and by the great overlapping of common species with bordering areas.

The variation in the occurrence of temporary species (Table 2) and the geographic position of the boundaries that produce the contraction and expansion of the areas are associated with the oceanographic dynamics of the estuary. In autumn, when the river flow is minimum, it discharge along the Uruguayan coast (Guerrero, Lasta, Acha, Mianzan, & Framiñan, 1997) and the central area is wider (Fig. 3C). During this season, the horizontal distribution of bottom salinities above 25 reveals the intrusion of fresher northwest waters on the Uruguayan coast (Fig. 3E). This facilitates species coming from the north into the external zone of the estuary (Area III) also observed by Cousseau (1985).

In spring–summer (Figs. 2C and 4C), when the marine water shows more upriver penetration (Guerrero, Lasta, et al., 1997), central and external areas are displaced toward the inside of the estuary and reduce its extension. At the same time the internal area expands by the increased discharge of continental water over salt water. These results denote the persistence of the identified boundaries. The influence of environmental changes that occurred during the course of the investigation can be detected as displacement in the geographical boundaries of the species assemblages.

In conclusion, the distinctive physical characteristics of the Río de la Plata estuary, which has a microtidal amplitude (Balay, 1961) and small seasonality in the discharge of continental water, generate a stable environmental gradient (Mianzan et al., 2001). This gradient determines the persistent extension and penetration of marine species inside the estuary, and reciprocally of freshwater species (Lalli & Parsons, 1997). During the studied year, the constant spatial restriction of species produces persistent fish assemblages in each particular oceanographic estuarine zone. These assemblages characterize these areas better than individual species.

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Fig. 4. (A) Dendrogram of the cluster analysis results corresponding to spring, (B) location of the groups on the distribution of the salinity along of Sampling Station (St) on the north transect of high resolution. (C) Area of distribution of the groups and species affinity [(ES) Exclusive species, (CS) Common species] corresponding to each group. Distribution of (D) temperature and (E) salinity of bottom. (F) Location of the oceanographic transects of high resolution (North, Central and South).

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