Fish diversity in the Río de la Plata and adjacent waters: an overview of environmental influences on its spatial and temporal structure

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The fish diversity and the main environmental factors affecting the spatial distribution of species, life history stages and community structure in the Río de la Plata (RdP) and adjacent waters are reviewed and analysed, with emphasis on the functional guild classification. The functional guild classification indicated that most species in the RdP were marine stragglers, zoobenthivores and oviparous species, although the biomass was dominated by estuarine species. Salinity had a stronger influence than temperature on the spatial pattern for all life stages, shallower and fresher waters are the preferred habitats of neonates and juveniles. During the breeding season (spring-summer), adults showed an intrusion into the inner part of RdP or to its adjacent nearshore waters from the offshore waters for spawning or mating, respectively. Variations in river discharge and wind patterns greatly affected the spatial extent of estuarine water, which ultimately influenced the domain of the main life-history stages (juveniles or adults) for both marine and estuarine fishes, as well as species and fish assemblage composition. The strong environmental gradient restricts some species and life-history stages to a particular section and defines three main fish assemblage areas. The composition of the fish assemblage is indicative of the recruitment of freshwater and marine species to the estuary in opposite ways, determined by the vertical stratification. Seasonal changes in the species composition were related to migration as a result of salinity and temperature variations and reproductive migrations to spawning and mating areas. This overview reveals that the RdP is under environmental variations that are likely to produce modifications to fish distribution and abundance that affect its fisheries. This context plus fish stock declines and changes in exploitation patterns could amplify the magnitude of the variations in the fisheries resources availability and affect the sustainability of fishing communities.

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Key words: community and population structure; estuary; fish conservation; fisheries management; physical characteristics and processes; reproductive pattern.

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INTRODUCTION

The Río de la Plata (RdP) drains about 20% of South America, discharging *c.* 22 000 m^3s^{-1} of fresh water to the continental shelf at 35°S, generating an estuarine system of *c.* 35 000 km^2 (Mianzan *et al.*, 2001). The interaction between freshwater discharge and the coastal seawater system generates an almost permanent salt wedge that defines the estuarine area bounded by two saline fronts: (1) the inner bottom front, where the halocline intersects the bottom and (2) the outer surface front, which shows the maximum horizontal gradient of salinity (Guerrero *et al.*, 1997*a*). The RdP discharge coupled with the wind pattern, plays a key role in the definition of the hydrographic conditions within the estuary and its adjacent marine coastal waters through the seasonal and interannual fluctuations in the tongue of low salinity waters (Guerrero *et al.*, 1997*a*; Simionato *et al.*, 2001).

Several reports and formal scientific papers covering different aspects of fish ecology and biology in the RdP and neighbouring waters have been produced, evidencing that the system is used by species in all the different life-history stages. Some species use the RdP as spawning or mating grounds, others as nursery or juvenile grounds, or just for feeding or even for occasional use. The spatial and temporal occurrence of most of the estuarine use functional groups (EUFGs) is related to hydrographic and oceanographic processes taking place in the RdP. Finally, the environmental changes impact at both synoptic (across the fish bottom fidelity and migration) and large scales (fish recruitment) on fish species availability and stock abundance to the coastal fisheries of Argentina and Uruguay. Fishing is one of the most important economic activities in both countries and many of the fish stocks lightly exploited during the 1970s have now reached or exceeded sustainable limits. Therefore, Argentina and Uruguay are taking urgent measures to manage their fish stocks, including the most important coastal commercial species [*Micropogonias furnieri* (Desmarest 1823) and *Cynoscion guatucupa* (Cuvier 1830)] (Defeo *et al.*, in press). Recent multispecies analysis shows long-term declines in ecosystem indicators, suggesting the short-term need to implement ecosystem-based fishery management initiatives (Defeo *et al.*, in press).

This overview is an attempt to draw together all available information on the response of fishes to environmental changes within the system, thereby contributing to a better understanding of the importance of freshwater supplies to estuaries on a local, regional and global scale. The aim of this paper is to show how and why the environment affects the fish community and life-history stages, and how these changes impact on the fisheries catches. This paper begins by describing the physical characteristics and processes that mainly affect the fish diversity, it then goes on to give a description of the biology of the main species inhabiting the estuary, followed by a characterization of the environmental influences on the spatial and seasonal patterns of both the fish community and the species' life history considering age and maturity. Finally, two issues are analysed for the first time: (1) the RdP fish diversity based on the estuarine use, the feeding and reproductive functional guild classification following Elliott *et al.* (2007), and (2) the influence of estuarine vertical stratification on the intrusion degree of freshwater and marine species to the inner part of the estuary. Throughout this review, by both new and published data analysis, the effect the environment has on fish distribution and abundance that determines fish availability to fishing is emphasized.
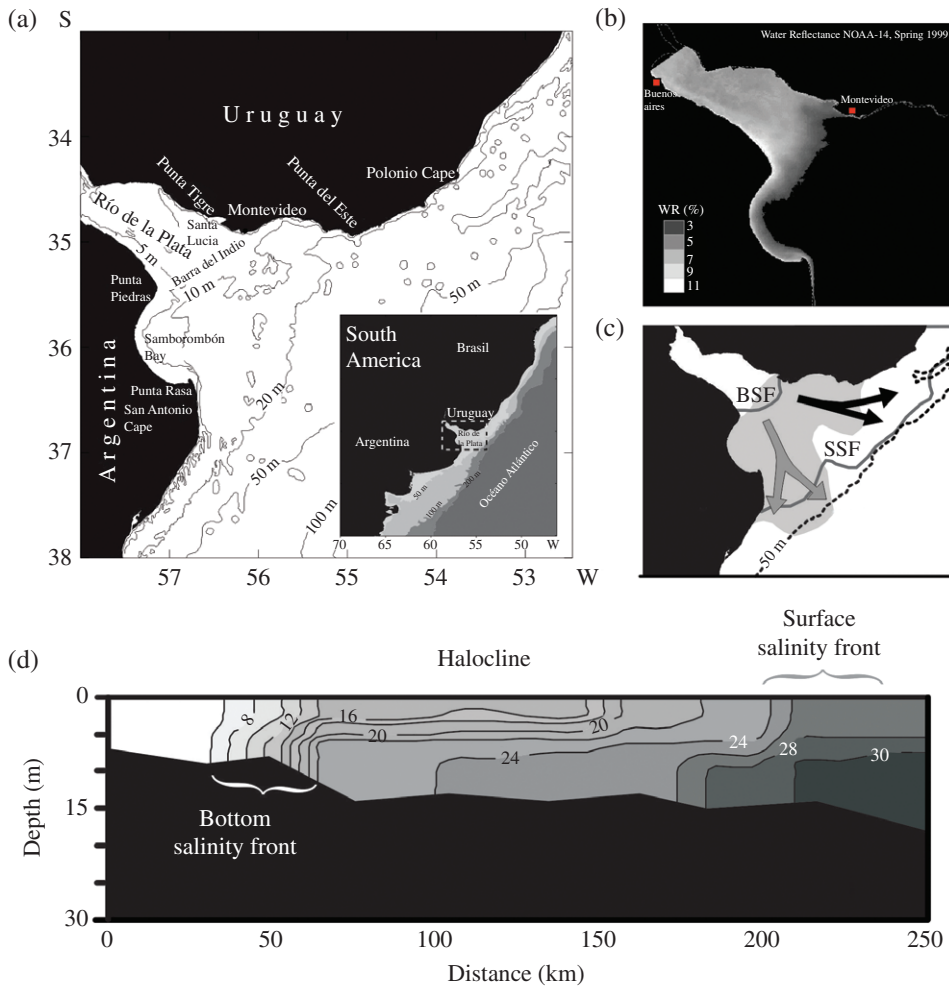
FIG. 1. (a) Location and bathymetry of the study area, (b) spring distribution of turbidity (Jaureguizar *et al.*, 2003*a*, 2003*b*), (c) seasonal distribution of estuarine water indicating the inner (bottom salinity front, BSF) and external boundary (surface salinity front, SSF) and (d) high resolution salinity distribution along a central transaction of the estuary (Guerrero *et al.*, 1997*a*, 1997*b*). ■, autumn–winter; ▨, spring–summer.

PHYSICAL CHARACTERISTICS AND PROCESSES

The RdP is an extensive microtidal shallow coastal plain estuary (Balay, 1961) located on the western South Atlantic coast [36° S; 56° W; Fig. 1(a)]. The interaction between the freshwater input, mainly coming from Paraná and Uruguay rivers with an average runoff of $22\,000\,\mathrm{m^3\,s^{-1}}$ (Jaime *et al.*, 2002), and the coastal shelf waters generates an estuarine system of *c*. $35\,000\,\mathrm{km^2}$ (Mianzan *et al.*, 2001) characterized by a salt wedge system (Guerrero *et al.*, 1997*a*).

The estuarine system is bounded by two persistent border fronts [Fig. 1(c), (d)]. The upper estuarine water boundary (riverine-mixohaline) occurs where the halocline intersects the bottom [bottom salinity front (BSF); Guerrero *et al.*, 1997*a*] and coincides

with the estuarine turbidity maximum zone [ETM, Fig. 1(b); Framiñan *et al.*, 1999; Jaureguizar *et al.*, 2003*a*]. On the other hand, the lower estuarine water boundary (mixohaline-coastal waters) is defined by the maximum horizontal gradient of surface salinity and identified by the extension of the 27–30 isohaline [surface salinity front (SSF); Guerrero *et al.*, 1997*a*, *b*]. This SSF displays higher spatial variability than the BSF [Fig. 1(c)], which remains mostly locked to a submersed shoal known as Barra del Indio (following the 10 m isobaths) in seasonal and interannual timescales (Framiñan & Brown, 1996; Guerrero *et al.*, 1997*a*; Framiñan *et al.*, 1999; Simionato *et al.*, 2001, 2007; Bava, 2004). The water column structure is highly influenced by atmospheric conditions, which determine the spatial and temporal distribution of temperature and salinity fields. Thermally, the estuarine waters show a warm period (December to March, 21–22° C) and a cold period (June to September, 10–12° C). For both periods, these waters are nearly vertically and horizontally homogeneous in temperature (Guerrero *et al.*, 1997*a*, *b*; Simionato *et al.*, 2010).

The surface waters show a dominant bi-modal discharge characterized by the spring-summer and autumn-winter modes [Fig. 1(c)], as a result of most frequent (synoptic and intra-seasonal) winds acting along those seasons, and is constrained by the coastline orientation (Guerrero *et al.*, 1997*a*; Simionato *et al.*, 2001, 2004, 2007). During cold months, a weak dominance of offshore winds and a weak maximum in the RdP discharge, allow the extension of a freshwater plume along the Uruguayan coast, resulting in a coastal water intrusion into the estuary across the Argentinean coast (Guerrero *et al.*, 1997*a*; Simionato *et al.*, 2004). During spring and summer, dominant north-east winds force the estuarine waters southward along the Argentine coast as far as 37° S, while the subtropical shelf waters penetrate from the north down to Punta del Este (Uruguay), constraining the north north-east drift. The southward overshooting of the estuarine waters interacts and then mixes with coastal shelf waters up to the shelf break limit (Guerrero *et al.*, 1997*a*; Lucas *et al.*, 2005).

The wind has differential effects on the vertical structure of water masses. Winds stronger than $10 \, \text{m s}^{-1}$ (south-easterlies in particular) cause a breakage of the salt wedge, whereas the remaining winds directions favour its maintenance (Guerrero *et al.*, 1997*a*; Meccia *et al.*, 2013). Also, the wind produces a recirculation between surface and bottom layers (Simionato *et al.*, 2007). When wind blows from directions between north-west and east it produces an inflow (outflow) of bottom (surface) waters, while the outflow (inflow) of bottom (surface) waters occurs when the wind directions are between south-east and west (Simionato *et al.*, 2007).

The RdP runoff variability is highly correlated with the El Niño-Southern Oscillation (ENSO) cycles (Robertson & Mechoso, 1998) and triggers large variations in the spatial distribution of particular environmental conditions and the frontal position (Framiñan & Brown, 1996; Bava, 2004). The freshwater discharge time series showed large variations [Fig. 2(a)], having reached extreme maximum values in 1983 (87 800 $\text{m}^3 \, \text{s}^{-1}$), 1998 (71 700 $\text{m}^3 \, \text{s}^{-1}$) and 2009 (34 500 $\text{m}^3 \, \text{s}^{-1}$) associated with El Niño and extreme minimum values associated with La Niña (*e.g.* 1970–1971, 1973–1975, 1988, 1995–1996, 2005 and 2010–2011). Variations in the discharge have a strong effect on the inner part of the estuarine region, as was observed in the location of the ETM zone. During months with higher discharges than the average ones, a downstream displacement of the ETM was observed, while the upstream displacement occurred related to a decrease in the freshwater discharge [Fig. 2(b)].
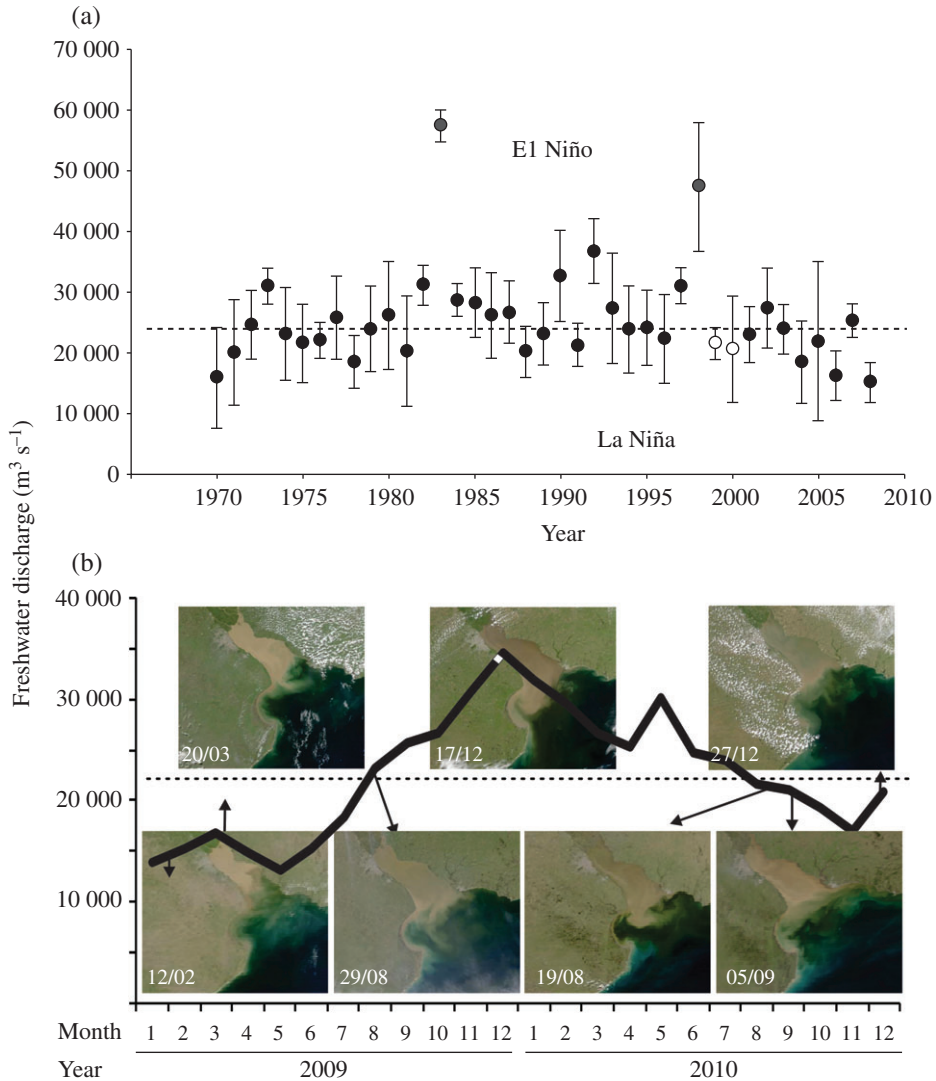
FIG. 2. (a) Time series of annual freshwater discharge of Río de la Plata (mean ± S.D.), indicating the averages (----, 22 000 m³ s⁻¹, Jaime *et al.*, 2002), and the main El Niño (●) and La Niña (○) years and (b) monthly freshwater discharge from January 2009 to December 2010 and the estuarine turbidity spatial distribution (imagine MODIS-Aqua Quasi True Colour).

FISH DIVERSITY AND FUNCTIONAL GROUPS

FISH DIVERSITY

A total of 119 fish species (24 Chondrichthyes and 95 Osteichthyes, 25 orders and 64 families) inhabit the RdP estuary (Table I; Cousseau, 1985; Boschi, 1988; Jaureguizar *et al.*, 2003*a*; FREPLATA, 2004; Jaureguizar, 2004; Solari *et al.*, 2009; García *et al.*, 2010). The number of species decreases with the diminishing of the saltwater intrusion

along its main axes (Cousseau, 1985; Boschi, 1988) and the inner and outer salinity boundaries of estuarine waters coincide with species richness minimum (among riverine and estuarine fish assemblages) and maximum (among the estuarine and coastal shelf fish assemblages), respectively (Barletta *et al.*, 2010).

ESTUARINE USE FUNCTIONAL GROUP

The EUFG, which defines the overall ecological use of an estuary by a given species (Elliott *et al.*, 2007), based on the presence of species (Table I) showed that most species were marine (stragglers 44·5% and migrant 10·9%), followed by freshwater stragglers (23·5%) and estuarine (15·1%). Based on the annual mean biomass of species (Jaureguizar *et al.*, 2004), RdP was dominated by estuarine species (46·5%) and marine migrants (41·8%). This could be related to the scale of the estuarine area (35 000 km^2) and the river mouth length (*c.* 257 km) that allow the intrusion of marine species along with saltwater penetration. Forced by the wind and low freshwater discharge conditions, even the intrusion of marine species associated with subtropical water masses may occur, such as *Balistes capriscus* Gmelin 1788 (García & Menni, 1982), *Eucinostomus melanopterus* (Bleeker 1863) (Solari *et al.*, 2010), *Selene vomer* (L. 1758), *Dactylopterus volitans* (L. 1758) and *Trachinotus carolinus* (L. 1766) (A. Solari, pers. obs.), among others. The high presence of freshwater species (straggler 23·5% and migrants 4·2%) occurs in shallow waters or tributaries (Acuña Plavan *et al.*, 2010; Solari *et al.*, 2015). In deeper waters freshwater species are occasionally observed and their presence is related to low salinity spread by the high freshwater discharge or to natural processes of species biology [*Parapimelodus valenciennesis* (Kroyer 1874), *Leporinus obstusidens* (Valenciennes 1837) and *Luciopimelodus pati* (Valenciennes 1840); Jaureguizar *et al.*, 2004)]. In this group, the presence of *Cyprinus carpio carpio* (L. 1758) and *Oreochromis niloticus* (L. 1758) should be mentioned, two exotic species with great adaptive powers and damaging effect over certain native species and the general ecosystem. The occurrence of anadromous species is related to the use of the RdP estuary as a nursery area during spring and summer [*Genidens barbus* (Lacépède, 1803)] or spawning area during autumn [*Lycengraulis grossidens* (Spix & Agassiz, 1829)] (Fuster de Plaza & Boschi, 1961; Ringuelet *et al.*, 1967).

FEEDING MODE FUNCTIONAL GROUP

The feeding mode functional group (FMFG), which defines the primary feeding method used by a given species (Elliott *et al.*, 2007) showed that most of species were zoobenthivores species (37%), followed by zooplanktivores (25·2%) and piscivores (21·8%) (Table I). Based on the annual mean biomass of species (Jaureguizar *et al.*, 2004), RdP was dominated by zoobenthivores species (52·2%), followed by piscivores (30·4%) and zooplanktivores (14·2%). This indicates that organisms related to bottom mainly sustain the RdP fish community. A transect from fresh to marine waters reflects the transition from a fish community influenced by muddy deposits originating from the river to marine fish species, where energy flow from the bottom deposits is probably less relevant and the zooplankton production becomes more important (García *et al.*, 2010). The freshwater species were mainly bottom or detritus feeders (omnivores 24·2 and detritivores 18·2%, respectively), while the marine fish species, migrant or stragglers, were zoobenthivores (46·2 and 47·2%, respectively) and piscivores (30·8 and 32·1%, respectively).

TABLE I. List of species indicating the functional groups classification suggested by Elliott *et al.* (2007): estuarine use functional groups (es, estuarine; ms, marine stragglers; mm, marine migrants; fs, freshwater stragglers; fm, freshwater migrants; an, anadromous), feeding mode functional groups (dv, detritivores; op, miscellaneous/opportunist; ov, omnivores; pv, piscivores; zv, zoobenthivores; zp, zooplanktivore) and reproductive mode functional groups (v, viviparous, species in which the female produces live progeny; W, ovoviviparous, species producing egg case in which the young developed; o, oviparous, producing eggs that are liberated into the surrounding waters). The species in this last group (o) can be sub-divided into the following five categories considering the type of egg produced: op, produced pelagic eggs; ob, produced eggs which settle on the substratum; ov, produced adhesive eggs that become attached to substrata and vegetation; og, one or the other parent guards their eggs externally; os, one or the other parent protects their eggs for a period in a part of their body. The species records (x) from different authors are indicated (1, Cousseau, 1985; 2, Jaureguizar *et al.*, 2003*a*, 2003*b*; 3, Jaureguizar, 2004; 4, Solari *et al.*, 2009; 5, FREPLATA, 2004)

Class	Order	Family	Specie	EUFG	FMFG	RMFG	1	2	3	4	5
Chondrichthyes	Carcharhiniformes	Sphyrnidae	*Sphyrna zygaena*	ms	pv	v	x				
		Triakidae	*Galeorhinus galeus*	ms	pv	v	x		x		
			Mustelus fasciatus	ms	zb	v	x				
			Mustelus schmitti	mm	zb	v	x	x	x		x
	Chimaeriformes	Callorhinchidae	*Callorhynchus callorhynchus*	ms	zb	w	x	x	x		
	Hexanchiformes	Hexanchidae	*Notorynchus cepedianus*	ms	op	v					x
	Lamniformes	Lamnidae	*Alopias vulpinus*	ms	pv	v	x				
	Rajiformes	Dasyatidae	*Dasyatis pastinaca*	ms	zb	w	x	x	x		
		Myliobatidae	*Myliobatis freminvillii*	ms	zb	v	x				
			Myliobatis goodei	mm	zb	v	x	x	x		x
		Rajidae	*Atlantoraja platana*	ms	zb	w	x				
			Atlantoraja castelnaui	ms	pv	w	x	x	x		
			Atlantoraja cyclophora	ms	zb	w	x	x	x		
			Psammobatis bergi	ms	zb	w	x	x	x		
			Psammobatis extenta	ms	zb	w	x				
			Rioraja agassizi	ms	zb	w	x	x	x		
			Sympterygia acuta	ms	zb	w	x	x	x		
			Sympterygia bonapartii	mm	zb	w	x	x	x		
		Rhinobatidae	*Rhinobatos horkelii*	ms	zb	v	x	x	x		

TABLE I. Continued

Class	Order	Family	Specie	EUFG	FMFG	RMFG	1	2	3	4	5
	Squaliformes	Squalidae	*Zapterix brevirostris*	ms	zb	v	x	x	x		
	Squatiniformes	Squatinidae	*Squalus acanthias*	ms	pv	v	x	x	x		
			Squatina argentina	ms	pv	v	x				
			Squatina guggenheim	mm	pv	v					x
	Torpeniformes	Narcinidae	*Discopyge tschudii*	ms	zb	v	x	x	x		
Osteichthyes	Acipenseriformes	Acipenseridae	*Acipenser baerii baerii*	fs	pv	ov					
	Anguiliformes	Congridae	*Conger orbignyanus*	ms	pv	ob	x	x	x	x	x
			Pseudoxenomystax albescens	ms	pv	ob	x			x	x
	Atheriniformes	Atherinopsidae	*Odontesthes argentinensis*	es	zp	ov	x	x		x	x
			Odontesthes bonariensis	fm	zp	ov	x	x		x	
	Batrachoidiformes	Batrachoididae	*Porichthys porosissimus*	ms	pv	op	x	x	x	x	x
	Characiformes	Anostomidae	*Leporinus obtusidens*	fs	ov	ob		x		x	
		Characidae	*Astyanax eigenmanniorum*	fs	zp	ob				x	
			Astyanax pampa	fs	zp	ob				x	
			Bryconamericus iheringii	fs	zp	ob				x	
			Cheirodon interruptus	fs	ov	ob				x	
			Hyphessobrycon anisitsi	fs	zp	ob				x	
			Hyphessobrycon togoi	fs	zp	ob				x	
			Oligosarcus jenynsii	fs	zp	ob				x	
			Salminus brasiliensis	fs	pv	ob				x	
		Curimatidae	*Cyphocharax spilotus*	fs	dv	ob				x	
			Cyphocharax voga	fs	dv	ob				x	
	Cynodontidae		*Raphiodon vulpinus*	fs	pv	ob	x			x	
	Erythrinidae		*Hoplias malabaricus*	fs	pv	og				x	
	Prochilodontidae		*Prochilodus lineatus*	fs	dv	ob		x			
	Clupeiformes	Clupeidae	*Brevoortia aurea*	fs	zp	op	x	x	x	x	x
			Platanichthys platana	es	zp	op	x			x	x

Table I. Continued

Class	Order	Family	Specie	EUFG	FMFG	RMFG	1	2	3	4	5
		Engaraulidae	*Ramnogaster arcuata*	es	zp	op	x	x		x	x
			Anchoa marinii	es	zp	op	x	x		x	x
			Engraulis anchoita	ms	zp	op	x	x			
			Lycengraulis grossidens	an	zp	op	*x*	x		x	x
	Cypriniformes	Cyprinidae	*Cyprinus carpio carpio*	fm	op	ov	x				
	Cyprinodontiformes	Anablepidae	*Jenynsia multidentata*	fm	zp	w	x				
		Poeciliidae	*Cnesterodon decemmaculatus*	fs	dv	w	x				
	Gadiformes	Merlucciidae	*Merluccius hubbsi*	ms	pv	op	x	x	x	x	x
		Phycidae	*Urophycis brasiliensis*	ms	pv	op	x	x	x	x	x
	Gasterosteiformes	Syngnathidae	*Hippocampus punctulatus*	ms	zp	os	x			x	x
			Syngnathus folletti	es	zp	os				x	x
	Gymnotiformes	Ramphichthyidae	*Eigenmannia virescens*	fs	zp	ov	x				
	Mugiliformes	Mugilidae	*Mugil liza*	es	dv	op	*x*	*x*	*x*	*x*	*x*
	Perciformes	Blenniidae	*Hypleurochilus fissicornis*	ms	zb	ov	x				
		Carangidae	*Parona signata*	mm	pv	op	x	x	x	x	x
			Selene vomer	mm	zp	op				*x*	
			Trachinotus carolinus	mm	zp	op				*x*	
			Trachinotus marginatus	ms	zp	op		x			*x*
			Trachurus lathami	ms	zp	op		x	x	x	
			Trachurus picturatus australis	ms	zp	op	x	x		x	
			Vomer setapinnis	ms	zp	op	*x*	x			
		Cheilodactylidae	*Nemadactylus bergi*	ms	zb	op		x	x		
		Cichlidae	*Australoheros facetus*	fs	op	og				x	
			Oreochromis niloticus	fs	ov	os				*x*	
		Gerreidae	*Eucinostomus gula*	es	zb	op	x				
			Eucinostomus melanopterus	es	zb	op					*x*
		Gobiidae	*Gobiosoma parri*	ms	zb	ob	v				*x*

Table I. Continued

Class	Order	Family	Specie	EUFG	FMFG	RMFG	1	2	3	4	5
		Haemulidae	*Boridia grossidens*	ms	zb	op	×				
		Mullidae	*Mullus argentinae*	ms	zp	op	×	×			
		Nototheniidae	*Paranotothenia magellanica*	*ms*	*ov*	op				×	
		Percophidae	*Percophis brasiliensis*	ms	pv	ob	×	×	×	×	
		Pomatomidae	*Pomatomus saltatrix*	*ms*	pv	op	×	×	×	×	×
		Sciaenidae	*Cynoscion guatucupa*	mm	pv	op				×	
			Cynoscion striatus	ms	pv	op	×				
			Macrodon ancylodon	es	pv	op	×	×	×	×	×
			Menticirrhus americanus	es	zb	op	×	×	×	×	×
			Micropogonias furnieri	es	zb	op	×	×	×	×	×
			Paralonchurus brasiliensis	es	zb	op	×	×	×	×	×
			Pogonias cromis	es	zb	op	×	×	×	*x*	*x*
			Umbrina canosai	ms	zb	op	×	×	*x*		
		Scombridae	*Scomber japonicus*	*ms*	pv	op	×	×	×		×
		Serranidae	*Acanthistius patachonicus*	ms	zb	ov	×	×	×		
			Dules auriga	ms	zb	ov	×		*x*		
		Sparidae	*Diplodus argenteus*	ms	zb	ob	×	×	×	×	×
			Pagrus pagrus	*mm*	*zb*	*ob*	*x*	*x*	*x*		
		Stromateidae	*Prepilus paru*	*ms*	zp	op	×	×			×
			Stromateus brasiliensis	*mm*	zp	op	×	×	×	×	×
		Trichiuridae	*Trichiurus lepturus*	*ms*	pv	op	×	×	×	×	×
		Uranoscopidae	*Astroscopus sexspinosus*	*ms*	zp	op	×	×	×	×	×
	Pleuronectiformes	Cynoglossidae	*Symphurus jenynsi*	es	zb	op		×			×
			Symphurus plagusia	es	zb	op		×		*x*	
		Paralichthyidae	*Etropus longimanus*	ms	zb	op	×				
			Paralichthys orbignyanus	es	zb	op	*x*	×	×	×	*x*
			Paralichthys patagonicus	*mm*	pv	op	×	×	×	×	

TABLE I. Continued

Class	Order	Family	Specie	EUFG	FMFG	RMFG	1	2	3	4	5
		Pleuronectidae	*Xystreurys rasile*	ms	zb	op			x		
			Oncopterus darwini	es	zb	op	x	x		x	
	Scorpaeniformes	Dactylopteriae	*Dactylopterus volitans*	mm	zb	ob				x	
		Triglidae	*Prionotus nudigula*	ms	zb	op	x	x	x		
			Prionotus punctatus	mm	zb	op	x	x	x	x	x
	Siluriformes	Ariidae	*Genidens barbus*	an	zb	os	x	x	x		x
		Auchenipteridae	*Trachycystes* sp.	fs	ov	os					
		Callichthyidae	*Corydoras paleatus*	fs	ov	ov				x	
		Doradidae	*Rhinodoras dorbignyi*	fs	zb	ov					x
		Heptapteridae	*Pimelodella laticeps*	fm	zp	ov				x	
			Rhamdia quelen	fs	zp	ov				x	
		Loricariidae	*Hypostomus commersoni*	fs	dv	ov		x			
			Loricariichthys anus	fs	dv	ov		x		x	
		Pimelodidae	*Luciopimelodus pati*	fs	pv	ob	x	x			x
			Parapimelodus valenciennesi	fs	ov	ob	x	x		x	x
			Pimelodus albicans	fm	ov	ob	x	x		x	x
			Pimelodus maculatus	fs	ov	ob	x				
	Tetraodontiformes	Balistidae	*Balistes capriscus*	ms	zb	og	x	x			
		Tetraodontidae	*Lagocephalus laevigatus*	ms	pv	op	x				

REPRODUCTIVE MODE FUNCTIONAL GROUP

The reproductive mode functional group (RMFG), which indicates how and, in some cases, where an estuarine species reproduces (Elliott *et al.*, 2007), reflects that the majority of the species in the RdP are oviparous (78·2%; producing pelagic eggs 39·5%, eggs that settle on the substratum 20·2% and adhesive eggs 11·8%), followed by viviparous (11·8%) and ovoviviparous (10·1%) (Table I). Based on the annual mean biomass of species (Jaureguizar *et al.*, 2004), RdP was dominated by oviparous (76·8%; producing pelagic eggs, 74·7% eggs that settle on the substratum 1·4%), followed by viviparous (18·3%) and ovoviviparous (4·3%). Among the freshwater species, while most of the straggler species (57·1%) produced eggs that settle on the substratum, most of the migrant species (60%) produce adhesive eggs [*e.g. C. carpio carpio*, *Odontesthes bonariensis* (Valenciennes 1835), *Pimelodella laticeps* (Eigenmann 1917)]. There are only two freshwater viviparous species, the migrant *Jenynsia multidentata* (Jenyns 1842) and the straggler *Cnesterodon decemmaculatus* (Jenyns 1842). Moreover, only freshwater stragglers (14·2%) showed eggs with parental protection, one parent or the other guards their eggs externally [*Australoheros facetus* (Jenyns 1842), *Hoplias malabaricus* (Bloch 1796), *Hypostomus commersoni* (Valenciennes 1836) and *Loricariichthys anus* (Valenciennes 1836)] or protects them inside the mouth for a period of time (*O. niloticus* and *Trachycorystes* sp.). The estuarine species mainly produced pelagic eggs (88·9%), whose spawning area within the estuary is related either to the salinity front [*e.g. M. furnieri*, *Macrodon ancylodon* Schneider 1801, *Pogonias cromis* (L. 1766), *Brevoortia aurea* (Agassiz 1829), *Ramnogaster arcuata* (Jenyns 1842)] or not [*e.g. Paralonchurus brasiliensis* (Steindachner 1875) and *Menticirrhus americanus* (L. 1758)]. There was only one species whose male protects the eggs in an incubation bag [*Syngnathus folletti* (Herald 1942)]; another one produced adhesive eggs that are able to attach to substrata and the vegetation [*Odontesthes argentinensis* (Valenciennes 1835)], and both of them inhabit the inshore waters of Bahía Samborombón (Lasta, 1995) that offer extensive flooding plains and vegetation providing both protection from currents and abundant food. The marine species were mainly oviparous (63·6%) producing pelagic eggs or viviparous (21·2%). There are two species that showed some kind of parental protection, *B. capriscus* (guards eggs externally) and *Hippocampus punctulatus* Guichenot 1850 (protects their eggs in a part of their body). Other marine species have their spawning or mating area within the adjacent waters of the RdP, either within open coastal waters [*C. guatucupa*, *Paralichthys patagonicus* Jordan 1889, *Prionotus punctatus* (Cuvier 1829) and *Parona signata* (Jenyns 1842)] or within nearshore waters along Uruguayan and Argentinean coasts (*Mustelus schmitti* Springer 1939, *Myliobatis goodei* Garman 1885 and *Squatina guggenheim* Marini 1936). Juvenile individuals of these species are generally found in the RdP waters.

ENVIRONMENTAL INFLUENCE ON DISTRIBUTION OF FISH SPECIES, LIFE-HISTORY STAGES, AND FISH ASSEMBLAGE STRUCTURE AND ESTUARINE TROPHIC FOOD WEB

The seasonal and interannual variations in the species spatial distribution, stages of life history and community structure, reflected the combined influence of coastal shelf water masses along the south-western Atlantic coastal system (SWACS) and the

RdP discharge pattern that acts mainly across the species physiological constraint to salinity.

FISH SPECIES DISTRIBUTION

The species spatial distribution pattern changes seasonally in an onshore and offshore direction, as well as in a north and south direction primarily associated with salinity distribution. During winter, the cool and high salinity waters cover a greater area of SWACS and this allows a wider northern distribution of marine species associated with shelf waters (*e.g. Discopyge tschudii* Garman 1885 and *Prionotus nudigula* Ginsburg 1950), forcing their intrusion into the southbound coast of the RdP (Jaureguizar *et al.*, 2004, 2007; Cortés *et al.*, 2011*a*). Due to physiological constraints, the spatial distribution of *D. tschudii* is restricted to high salinity (>32·2; Cortés *et al.*, 2011*a*) and the boundary between searobins (*Prionotus* spp.) species distribution is linked to 29–30 (Jaureguizar *et al.*, 2007). During spring, low salinity conditions in adjacent waters of RdP along the Argentinean coast produce a reduction in the northern flow of cool and high salinity waters, thus restricting the northern distribution of *D. tschudii* and its intrusion into the RdP estuary (Cortés *et al.*, 2011*a*). These conditions also produce an offshore extended distribution of species related to estuarine waters (*P. punctatus*; Jaureguizar *et al.*, 2007).

The interannual variation in the spatial distribution of fish species (*P. nudigula* and *D. tschudii*) is higher in spring than in winter (Jaureguizar *et al.*, 2007; Cortés *et al.*, 2011*a*), evidenced through variations at a regional scale in the spatial coverage (*D. tschudii*, *c.* 35%) or in the species boundary location (*P. punctatus v. P. nudigula*, 200 km) within the coastal system. For *D. tschudii*, a northward winter extension that forces its intrusion into the RdP along the bottom layer (springs 1994, 1999 and 2005) is forced by the advection of cold waters over the coastal area. This fact may be modulated by the strength and location of the Malvinas (Falkland) Current and predominant synoptic wind conditions. In spring, when the dominant wind direction is from north-northeast-east (1994, 1999 and 2005), warm and low saline (<28) surface waters (up to 10 m deep) are pushed downstream from the upper part of estuary, and the mass transport is compensated by a net inflow of cold and saline (>30) bottom waters upstream. The *D. tschudii* bottom intrusion into the RdP is stopped by the progression of adverse wind conditions as observed during 1998 and 2003. During these spring periods, the dominance of south and south-west winds pushed surface waters (up to 10 m deep) upstream towards the upper part of the RdP; the net outflow of warm and fresh bottom waters downstream in the estuary restricts the progression of the *D. tschudii* intrusion, even forcing them back into the coastal system (Cortés *et al.*, 2011*a*).

The border zone between presence and absence of *D. tschudii* and for *Prionotus* spp. is near the location where the 29–30 isohaline intersects the bottom, which corresponds to the bottom signal of the SSFs (Guerrero *et al.*, 1997*a*). These salinities has similar values to those (25–27 isohaline) observed in Chesapeake Bay and Delaware Bay (Bulger *et al.*, 1993; Able *et al.*, 2001), which indicate the transition between the estuary and the coastal waters. The Atlantic *Prionotus* spp. spatial distribution (*P. punctatus* associated with estuarine waters *v. P. nudigula* inhabiting the coastal shelf system) denotes that the southward extension of this transition has an interannual variation of around 200 km during spring, mainly related to the wind driven discharge of estuarine waters from the RdP (Jaureguizar *et al.*, 2007). The minimum *P. punctatus* southward

extension into the coastal system (1995) occurs when weak onshore wind stress is dominant (4·8 m s^{-1}), and the freshwater discharge is low. When the alongshore wind stress dominates the area and the freshwater discharge is the highest, the *P. punctatus* intrusion into the coastal system is maximum (1994). Under similar freshwater discharge (1999 with 18 780 m^3 s^{-1} and 1995 with 19 725 m^3 s^{-1}), the alongshore wind stress (5·8 m s^{-1}, year 1999) following an opposed wind condition drives an intermediate intrusion of *P. punctatus* into the coastal system (Jaureguizar *et al.*, 2007).

LIFE HISTORY STAGES DISTRIBUTION (ESTUARINE AND MARINE SPECIES)

Although the entire life cycle of some estuarine (*i.e. M. furnieri,* Fig. 3) and marine species (*e.g. M. schmitti*, *S. guggenheim*, *C. guatucupa*, *Percophis brasiliensis* Quoy & Gaimard 1824 and *P. patagonicus*) seems to occur within the SWACS, life-history stages show differences in habitat preference that are associated with ontogenetic movements from the nursery area to deeper waters throughout individual development. Environmental variables have a significant influence on the life stage spatial pattern [Fig. 3(c)], where salinity has a stronger influence than temperature (Jaureguizar *et al.*, 2003b, 2006a; Vögler *et al.*, 2008; Cortés *et al.*, 2011b). As observed in other coastal systems including estuaries and bays, the selection of inshore waters by neonates and juveniles (RdP: *M. furnieri,* Jaureguizar *et al.*, 2003b, 2008; Solari *et al.*, 2015; coastal shelf ecosystem: *M. schmitti*, Cortés *et al.*, 2011b; *S. guggenheim*, Colonello *et al.*, 2007; Vögler *et al.*, 2008; *C. guatucupa,* Jaureguizar *et al.*, 2006a; *P. brasiliensis,* C.A. Barreto, unpubl. data, http://hdl.handle.net/1834/3017/; *P. patagonicus,* C. Riestra, unpubl. data, http://hdl.handle.net/1834/4065/) is related to predator protection, food availability or environmental conditions which promote faster growth. Neonates and juveniles show a persistent preference for inshore habitats throughout the seasons. In contrast, adults shows a penetration towards the estuarine ecosystem inner area for spawning [*M. furnieri,* Fig. 3(a)] or the coastal ecosystem inshore area for mating (*C. guatucupa*, *P. brasiliensis*, *P. patagonicus*, *M. schmitti* and *S. guggenheim*) during the reproductive seasons (austral spring-summer).

Estuarine species

The spatial distribution of *M. furnieri* stages shows that juveniles occupy the inner and shallow waters of the RdP estuarine area and adults are common towards the offshore regions [Fig. 3(a)] mainly influenced by bottom salinity spatial distribution (Jaureguizar *et al.*, 2003b, 2008). Juveniles persistently inhabit waters with low bottom salinity and depth matching the ETM zone [Jaureguizar *et al.*, 2003b, Fig. 3(b),(c)]. The ETM [Fig. 3(c),(d)] is a region of high *M. furnieri* larval abundance (Braverman *et al.*, 2009), high plankton concentration (Mianzan *et al.*, 2001; Kogan, 2005; Berasategui *et al.*, 2006) and high prey abundance (Schiariti *et al.*, 2006; Giberto, 2008), offering protection to juveniles from avian predation (Favero *et al.*, 2000, 2001; Mauco *et al.*, 2001).The ETM may also link the two main nursery areas of the estuary, Samborombón Bay and Santa Lucia River (beside Punta Tigre; Fig. 3) (Jaureguizar *et al.*, 2003b). During spring, there is an adult stage penetration towards the inner area of the RdP associated with reproductive movements from the outer zone to the spawning area (Macchi *et al.*, 1996; Jaureguizar *et al.*, 2003b), producing the rise in the size of individuals captured by the artisanal fishery of Pajas Blancas (near Montevideo,
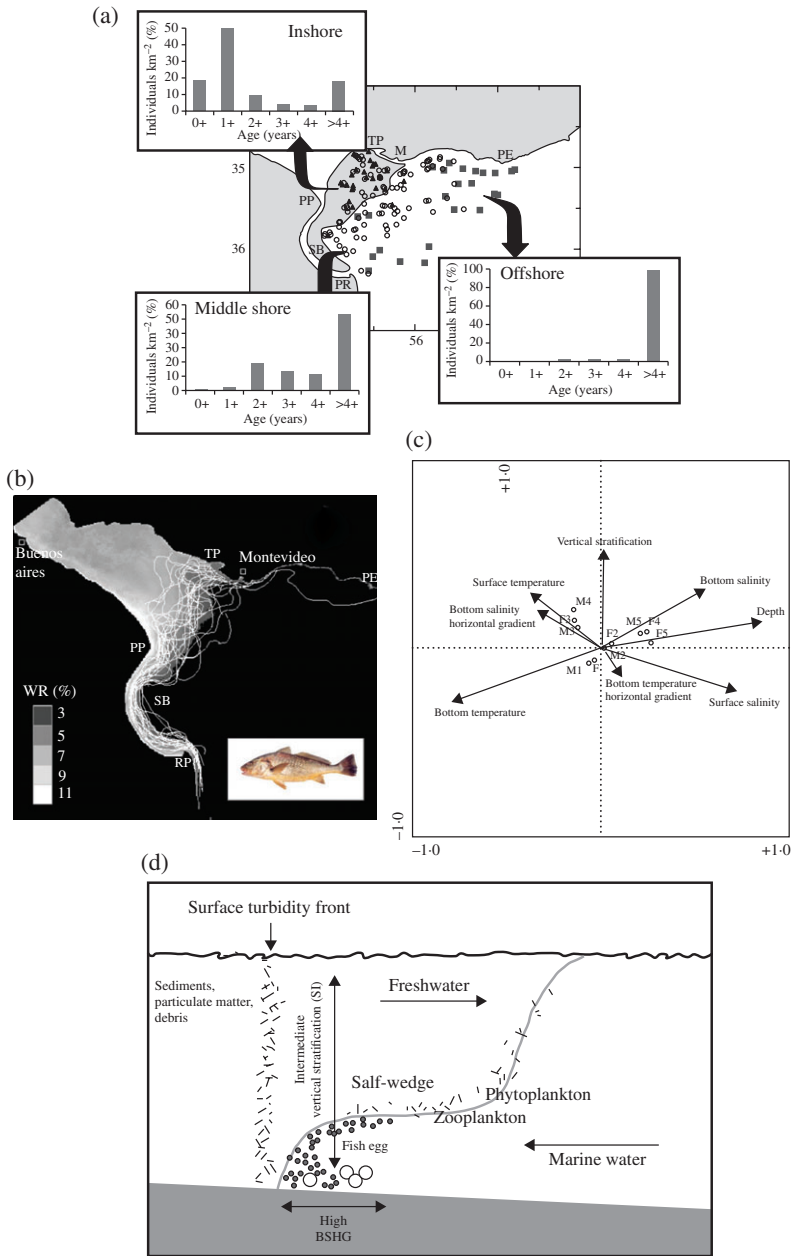
FIG. 3. Spatial distribution of life stages of *Micropogonias furnieri* and their relationship with the environmental variables in the Río de la Plata during spring: (a) distribution areas for defined sampling stations groups (▲, Inshore; ○, middle shore; ■, offshore) showing their age classes structure and (b) turbidity spatial distribution (%WR, percentage of water reflectance; redrawn from Jaureguizar *et al.*, 2003*b*), (c) environmental preference per sex (M, male; F, female) and maturity stages [1, inmature; 2, developing and partially pent; 3, gravid (with hydrated oocytes) or running; 4, spent; 5, resting] (redrawn from Jaureguizar *et al.*, 2008) and (d) diagram of hypothetical spawning ground on the vertical section (redraw from Bava *et al.*, 1996). PE, Punta del Este; PP, Punta Piedras; PR, Punta Rasa; SB, Samborombón Bay; PT, Punta Tigre; M, Montevideo.

Uruguay) (Norbis *et al.*, 1992). Spawning takes place between November and April (Macchi & Christiansen, 1996) and overlaps geographically with the BSF (Macchi & Christiansen, 1996; Macchi, 1997; Acha *et al.*, 1999; Militelli, 2007; Jaureguizar *et al.*, 2008). Although juveniles and spawning individuals inhabit similar depths and bottom salinities [Fig. 3(a),(b)], the spawning ground is more linked to water with high bottom salinity horizontal gradient (BSHG) and moderate water column vertical stratification (SI) [Macchi, 1997; Jaureguizar *et al.*, 2008; Fig. 3(c),(d)].

Micropogonias furnieri spawning strategy in the RdP does not coincide with the general pattern that characterizes temperate marine fishes with estuarine dependence, which spawn in marine areas and use estuaries as nursery habitats (Day *et al.*, 1989; Nordlie, 2003). The spatial scale (35 000 km^2) and stable environmental gradients of the RdP allow for a favourable combination of properties that guarantees a reproductive success (enrichment, concentration, transport and retention processes; Bakun, 1996). Within the RdP estuary, enrichment of nutrients (silicate, nitrite, nitrate and phosphate; Carreto *et al*., 1986; Calliari *et al*., 2009) associated with the freshwater discharge (22 000 m^3 s^{-1}; Jaime *et al.*, 2002), leads to high production for both food items for larvae and prey abundance for fishes. Therefore, the retention within the zone with high BSHG [Fig. 3(b)], whatever the wind direction (Simionato *et al.*, 2008), provides both hydrological (preventing drift or advection to the adjacent marine coastal water) and nutritional stability during and immediately after spawning events, which favours *M. furnieri* planktonic eggs and larvae development. Militelli (2007) classifies this species together with other sciaenids (*M. ancylodon* and *P. cromis*) and other species like *B. aurea* (Acha & Macchi, 2000); and *R. arcuata* (Rodrigues *et al.*, 2008) as estuarine spawning species associated with the BSF.

Marine species

Even though *C. guatucupa* is a marine migrant species along the RdP, it is a resident species in adjacent waters. The specific association between its life stages and the environmental conditions (Jaureguizar *et al.*, 2006*a*) means that synoptic environmental conditions (on a short time scale) along the coast determine the population age-class structure available in the region [Fig. 4(a); Jaureguizar & Guerrero, 2009]. Neonates and juveniles inhabit brackish, warmer and shallow water (outer RdP estuarine area) while adults are more abundant in waters with high bottom salinities and depths, and low temperatures (Jaureguizar & Guerrero, 2009). Under spring and summer conditions, where cool and high salinity waters cover a greater area of the Uruguayan coast (similar to 1998-El Niño and 1999-La Niña years), a wider distribution of *C. guatucupa* adults is observed and even an intrusion into the northern portion of the RdP estuary (Jaureguizar & Guerrero, 2009). When spring wind blows mainly from the west (1994 and 2003 years), as in autumn and winter conditions, however, the wind forces an outflow of estuarine brackish waters along the Uruguayan coast (north-northeast drift) allowing a wider distribution of juveniles along the coast and an adult dispersion from the inshore Uruguayan coast (Jaureguizar & Guerrero, 2009). Therefore, variations in the predominant synoptic environmental conditions can have strong effects on *C. guatucupa* population dynamics, affecting the age of fishing mortality or reproductive success through the use of the nearshore as a spawning area.

Considering the coastal circulation (Palma *et al.*, 2004; Simionato *et al.*, 2004), and the spatial distribution and age-class frequency in the estuarine and marine coastal areas observed by Jaureguizar *et al.* (2006*b*), these authors suggest that *C. guatucupa* spawns
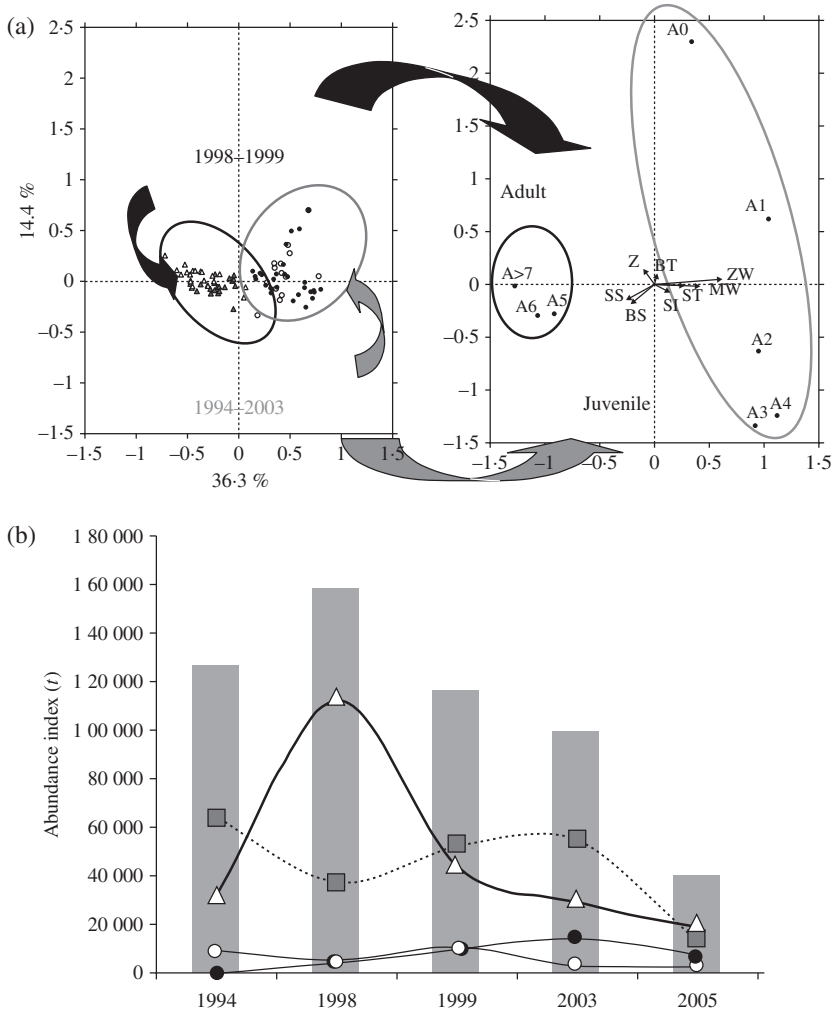
Fig. 4. Environmental influence on the distribution and abundance of the life stages of *Cynoscion guatucupa* during the spring bottom trawl survey of Río de la Plata. (a) CCA ordination diagrams showing the spatial pattern of sampling station based on the age-class composition during fourth spring (○, 1994; ▲, 1998; △, 1999; ●, 2003) and the spatial distribution per age (years)-class (A#) with respect to six environmental variables (BT, bottom temperature; BS, bottom salinity; Z, depth; SI, Simpson index; MW, meridional wind; ZW, zonal wind). The percentage of variance of age-class data explained by each axis (redrawn from Jaureguizar & Guerrero, 2009) is indicated. (b) Spring abundance index by total (▣) and total length size (L_T; ●, < 20 cm; ▣, $20 < L_T > 30$ cm; △, $30 < L_T > 43$ cm; ○ >43 cm) estimated in five bottom trawl survey (redrawn from Aubone & Ruarte, 2008).

in coastal waters at a very shallow depths. The main spawning area is not well defined within the RdP region, but during the beginning (November; Macchi & Acha, 1998) and the end (March; Militelli & Macchi, 2006) of the reproductive season, spawning take place primarily in a reduced area in front of Punta del Este shore (Uruguay). Nevertheless, in December 2003, the highest concentrations of spawning females were located in the external sector coinciding with a temperature bottom front (Militelli &

Macchi, 2006). *Cynoscion guatucupa* like *Umbrina canosai* Berg 1895 are classified by Militelli (2007) as marine spawners, whose spawning always occurs in marine waters (>30). Other species such as *P. brasiliensis*, *P. patagonicus* and *P. signata* may be included in this group. These species also show a higher reproductive activity in the outer estuarine area (Macchi & Acha, 1998; Rodrigues *et al.*, 2007; Militelli, 2011).

The environment also has an influence on the spatial distribution of shark, skate and ray size-classes (*M. schmitti*: Menni, 1985; Cortés *et al.*, 2011*a*, *b*; *S. guggenheim*: Vögler *et al.*, 2008; *Sympterygia bonapartii* Müller & Henle 1841; Mabragaña *et al.*, 2002) and reproductive stages (*S. guggenheim*: Colonello *et al.*, 2007; *Zapterix brevirostris* (Müller & Henle 1841): Colonello, 2009) within the SWACS. Salinity has a stronger influence than temperature during spring (Vögler *et al.*, 2008; Cortés *et al.*, 2011*a*, *b*) due to SAWCS physical dynamics that forces a freshwater tongue along the Argentine coast. The neonates and juveniles (<50 cm L_T) of *M. schmitti* shows seasonal persistence to shallower and fresher habitats. These habitats are warm and have high abundance of their main prey during spring (crustaceans and polychaetes; Belleggia *et al.*, 2012), allowing *M. schmitti* neonates and juveniles to maximize their growth rate. The adults (both sexes) prefer deeper and warmer waters in winter, while in spring they show segregation by sex, with females inhabiting shallower waters than males (Cortés *et al.*, 2011*b*). The spring environmental preference by sex is also observed in *S. guggenheim*, where the preferred salinity range by adult males (27·8–35·5) and females (24·8–35·4; gravid and non-gravid) shows significant differences (Vögler *et al.*, 2008). In both shark species, adults are associated with the deepest coastal waters during winter, which coincides with the period (autumn and winter) of highest abundance in the outer shelf waters (between 50 and 130 m depth, *M. schmitti,* Pereyra *et al.*, 2008; *S. guggenheim,* Vögler *et al.*, 2008). The observed predominance of neonates and juveniles in coastal waters and larger individuals in the outer shelf water indicates that the winter size class distribution pattern seems to be associated with ontogenetic movements from the nursery area to deeper waters. During the reproductive season, parturition of both species takes place in spring and early summer (Colonello *et al.*, 2007) and adult males and females display a differential migration towards the nursery area (shallow coastal waters, <30 m). *Squatina guggenheim* females have a 3 year reproductive cycle and differ from *M. schmitti* females which have an annual reproductive cycle that determines that migration movements related to mating and parturition do not affect all the reproductive population, and therefore the migration is less intense than in other species (Vooren & Klippel, 2005). Considering the similar female behaviour of these two shark species and according to the Vögler *et al.* (2008) hypothesis for *S. guggenheim,* birth and nursery areas must be located adjacent to the RdP discharge along the coastal zones of both Uruguay (*c.* 34–35° S) and northern Argentina (*c.* 35–38° S). For *M. schmitti,* the relative use of these areas as nursery and mating grounds shows interannual variation affected by the environmental conditions (Fig. 5, Cortés, 2012). The juveniles (37 to 56 cm L_T) and medium-sized adults (57 to 75 cm L_T) are the most influential stages in *M schmitti* population growth rate (F. Cortés, unpubl. data; http://www.oceandocs.org/bitstream/1834/2597/1/Cortes_2007.pdf/). Therefore, the environmental conditions could have a considerable impact on *M. schmitti* population growth rate through the restriction of the use of suitable habitats for growth and reproduction.

The coastal area is also used by juveniles of *Z. brevirostris* and by pregnant females that inhabit this shallow area from spring and summer until parturition, which mainly
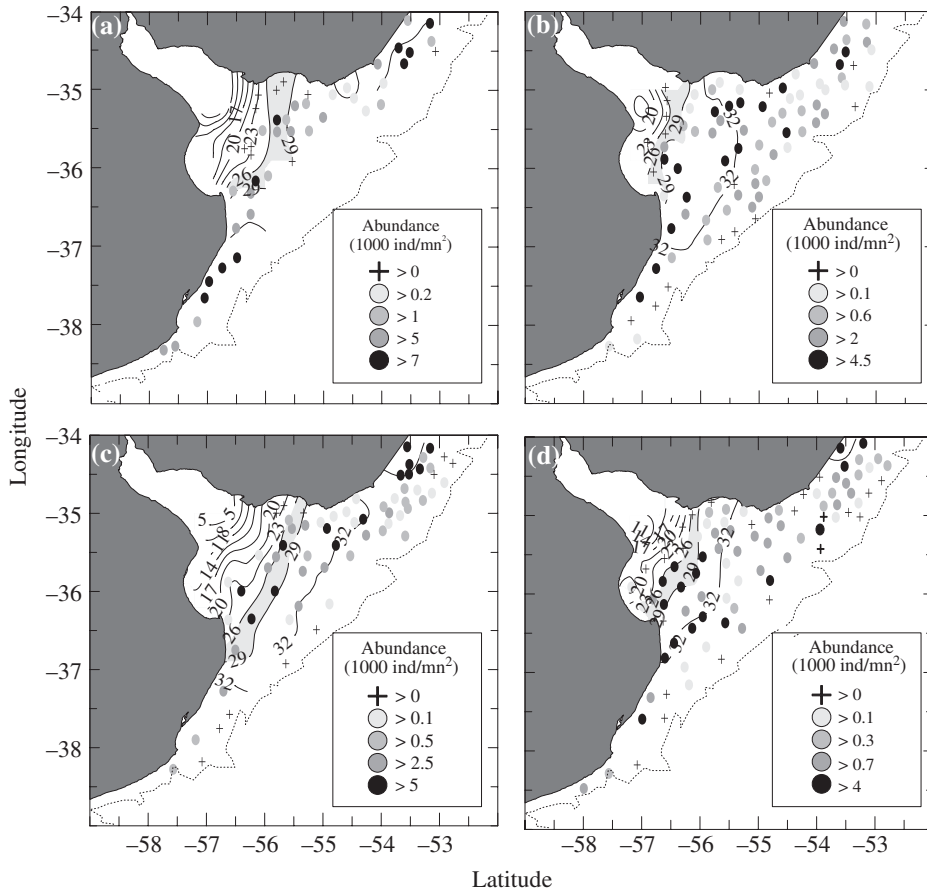
FIG. 5. Variation in the spatial distribution of *Mustelus schmitti* abundance under different salinity pattern conditions during spring in (a) 1998, (b) 1999, (c) 2003 and (d) 2005. Shadow area indicates the salinity range preferred by *M. schmitti*. Points indicate the sampling stations and abundance of *M. schmitti* during research surveys (redrawn from Cortés *et al.*, 2009). The legend shows for each year the set of ordered abundance data divided into five equal parts.

occurs during autumn and winter. After the reproductive season, the rest of the adult females and males migrate to deep waters, although the female 3-year reproductive cycle (Colonello, 2009; Colonello *et al.*, 2011) would determine that migration movements related to mating and parturition do not affect all the reproductive population. *Zapteryx brevirostris* selects sandy bottoms to feed on polychaetes and lancelets, where the highest fishing activity occurs (Barbini *et al.*, 2011).

The ecological relationship of Chondrichthyes still remains poorly known, but available information reveals that many shark species use the SWACS as feeding grounds [*M. schmitti* (Belleggia *et al.*, 2012), *S. guggenheim* (Vögler *et al.*, 2003, 2009), *Galeorhinus galeus* De Buen 1950 (Lucifora *et al.*, 2006), *Notorynchus cepedianus* (Poey 1861) (Lucifora *et al.*, 2002, 2005a) and Z. *brevirostris* (Barbini *et al.*, 2011)], mating grounds [*M. schmitti* (Menni, 1985; Cousseau *et al.*, 1998), *S. guggenheim* (Colonello *et al.*, 2007), *G. galeus* (Lucifora *et al.*, 2004), *Carcharias taurus* Rafinesque 1810

(Lucifora *et al.*, 2002; Lucifora, 2003) and *S. bonapartii* (Mabragaña *et al.*, 2002)] and nursery grounds [*M. schmitti* (Cousseau, 1986; Menni, 1986; Menni *et al.*, 1986), *S. guggenheim* (Colonello *et al.*, 2007; Vögler *et al.*, 2008), *G. galeus* (Lucifora *et al.*, 2004), *Carcharhinus brachyurus* (Günther 1870) (Lucifora *et al.*, 2005*b*) and *N. cepedianus* (Menni & García, 1985; Lucifora, 2003)], suggesting that the environment could influence spatial and temporal habitat use.

FISH ASSEMBLAGE STRUCTURE (SPATIAL AND TEMPORAL DISTRIBUTION)

The strong environmental salinity gradient from shallow fresh waters to deep marine waters restricts the fish species distribution to a particular section of this gradient (Fig. 6), displaying a specific distribution pattern with regard to the ichthyofaunal composition (Boschi, 1988; Jaureguizar *et al.*, 2003*a*, 2004, 2006*b*; Pereiro, 2007; Barletta *et al.*, 2010; García *et al.*, 2010). Within the RdP estuary, persistent fish assemblage areas [inner (I), central (II) and outer (III), Jaureguizar *et al.*, 2003*a*, 2004, Fig. 6(a)] reflect the intrusion of marine species towards the head of the estuary allowed by the shelf water intrusion along the bottom [Fig. 6(b)], where the fish assemblage is usually dominated by freshwater species [Fig. 6(c)].

The composition of the inner estuarine area shows the highest ichthyofaunal heterogeneity with the occurrence of freshwater stragglers (*L. pati* and *P. valenciennesi*), anadromous species (*G. barbus*) and estuarine species (*M. furnieri*, *M. ancylodon* and *B. aurea*). Fishes associated with the central estuarine area are mainly estuarine species [*B. aurea*, *M. furnieri*, *M. ancylodon*, *P. brasiliensis*, *Paralichthys orbignyanus* (Valenciennes 1939)*, Mugil liza* Günther 1880 and *M. americanus*] and showed great overlap with marine species associated with the outer estuarine area. The fishes linked to the outer estuarine area were marine species, either migrants [*C. guatucupa*, *P. patagonicus*, *M. schmitti*, *S. bonapartii*, *Stromateus brasiliensis* (Fowler 1906), *S. guggenheim*, *M. goodei* and *P. punctatus*] or stragglers [*Conger orbignyanus* Valenciennes 1847, *D. tschudii*, *P. brasiliensis* and *Atlantoraja castelnaui* (Miranda Ribeiro 1907)] (Jaureguizar *et al.*, 2003*a*, 2004, 2006*b*).

Fish assemblages show consistent seasonal and temporal boundaries associated with frontal zones. The border between inner and central estuarine areas is near the location where halocline intersects the bottom [Figs 1(d) and 6(b)] and corresponds to the BSF defined by Guerrero *et al.* (1997*a*). This represents the maximum downstream intrusions of freshwater species into the estuary (*Pimelodus maculatus* Lacépède 1803, *L. pati*, *P. valenciennis*, *L. obtusidens*, *P. lineatus* and species of Loricariidae) and the upstream incursion of marine species through the shelf water intrusion along the bottom (Jaureguizar *et al.*, 2003*a*, 2004, 2006*b*; Jaureguizar, 2004). The degree of intrusion of freshwater and marine species to the estuary is determined by the vertical stratification of the water column during spring 1995 [DCCA, Fig. 7(a)]. When the RdP showed a strong stratification [transect I, Fig. 7(d)], it allowed the maximum intrusion of freshwater (*e.g. P. maculates* and Loricariidae spp.) and marine species (*C. guatucupa*) in the opposite sense towards the estuary [Fig. 7(b), (c)]. As the vertical stratification was broken and the water column became homogenous [the isohalines were more vertical, from transect I to transect III, Fig. 7(d)], the RdP showed lesser incursion of freshwater and marine species and the inner zone was more dominated by estuarine species
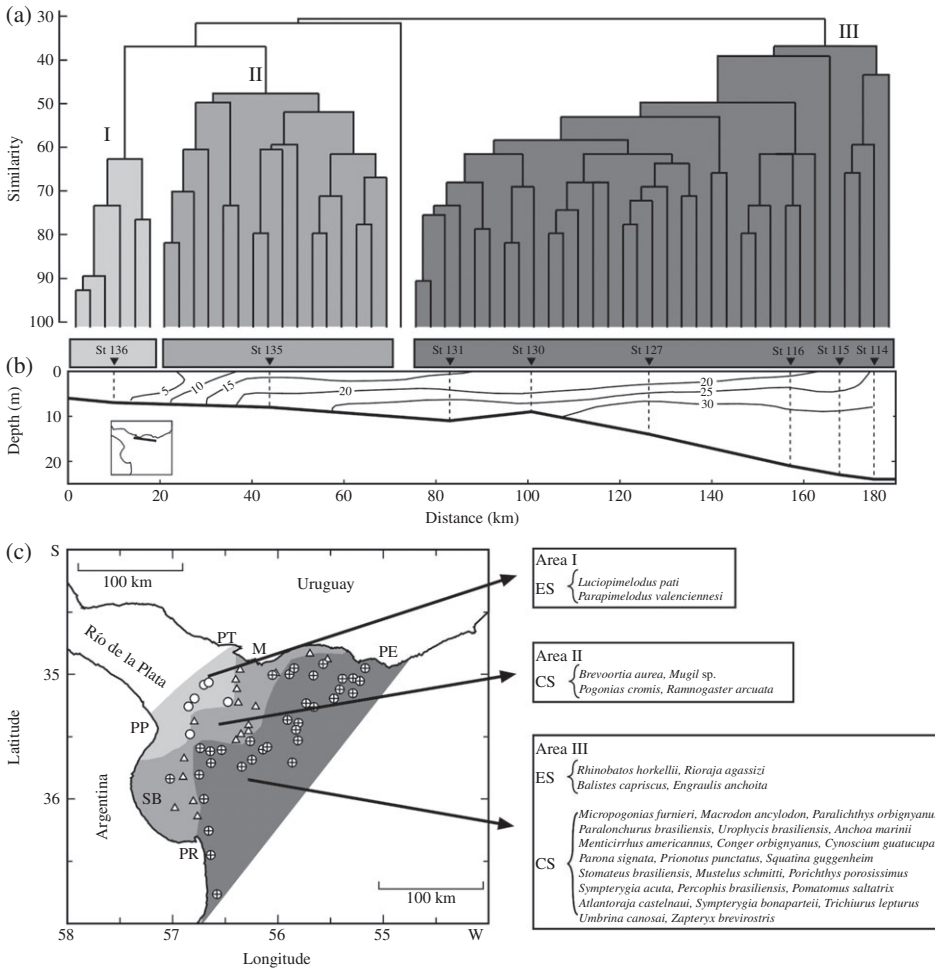
FIG. 6. Spatial pattern of fish assemblages areas in the Río de la Plata estuarine area corresponding to summer: (a) dendogram of the cluster analysis of sampling stations based on the species composition, (b) location of identified clusters on the distribution of the salinity along of sampling stations on the north transect of high resolution and (c) area of distribution of the clusters of sampling stations (I, inner area; II, central area; III, outer area) and their species affinity (ES, exclusive species; CS, common species) corresponding to each cluster (redrawn from Jaureguizar *et al.*, 2004). St, sampling station; PE, Punta del Este; PP, Punta Piedras; PR, Punta Rasa; SB, Samborombón Bay; PT, Punta Tigre; M, Montevideo. The symbols in the maps indicate the sampling stations location and their corresponding fish assemblage area.

[*M. furnieri*, *B. aurea*, *M. ancylodon*, *P. brasiliensis* and *M. liza*, Fig. 7(b), (c)]. The border zone between the central and outer areas [Fig. 6(b)] coincides with the maximum horizontal gradient of surface salinity, related to the boundary among the estuary and the coastal shelf waters (Jaureguizar *et al.*, 2007). This boundary limits the presence of marine species [*e.g. B. capriscus*, *Rioraja agassizi* (Müller & Henle 1841)*, Rhinobatos horkelii* Müller & Henle 1841*, Psammobatis bergi* Marini 1932*, Merluccius hubbsi* Marini 1933*, Trachurus lathami* Nichols 1920 and *Callorhinchus callorynchus* (L. 1758)] within the estuary (Jaureguizar *et al.*, 2003*a*).

FIG. 7. Fish species composition in the inner frontal zone of Río de la Plata under different stratification conditions, at the same time during spring. (a) Detrended canonical correspondence analysis ordination diagram of the sampling stations based on the species composition with respect to five environmental variables (BT, bottom temperature; BS, bottom salinity; ST, surface temperature; SS, surface salinity; SI, Simpson index). The fourth sampling station groups defined for DCCA axis 1 (G1, black; G2, grey; G3, white; G4, little grey) and its correspondent transect (I, II, III) are indicated. (b) The average species composition for the fourth sampling station groups. (c) Their spatial distribution. (d) Location on the salinity section of each transect. The numbers at the top axis indicate the sampling station name and the corresponding group.

At seasonal and temporal scales, fish assemblages are persistent in specific composition and the geographic variations of their boundaries indicate a contraction or expansion of fish assemblage areas associated with water masses dynamics (Fig. 8), as a consequence of both river flow and winds (Jaureguizar *et al.*, 2003*a*, 2004, 2006*b*). Seasonal changes in the fish assemblage composition suggest that these changes are generally caused by seasonal migrations, as a result of salinity and temperature variations (*e.g. Trichiurus lepturus* L. 1758 and *D. tschudii*) and by reproductive movements for spawning (*M. furnieri* and *C. guatucupa*) and mating (*M. schmitti*) areas (Jaureguizar *et al.*, 2004). *Trichiurus lepturus* is an abundant benthopelagic teleost on the southern Brazil continental shelf (Haimovici *et al.*, 1989) and its higher densities in the RdP estuarine waters are coupled with the subtropical continental water mass penetration during warm periods forced by the southward flow of southern Brazil waters (Jaureguizar *et al.*, 2004). On the other hand, decreasing temperature in the outer estuarine

zone caused by the cold (<16° C) shelf water intrusion from the south is associated with relatively large densities of *D. tschudii* (Jaureguizar *et al.*, 2004; Cortés *et al.*, 2011*a*). The seasonal variation in the spatial coverage of fish assemblage areas (Jaureguizar *et al.*, 2003*a*, 2004) reflects the seasonal discharge pattern of the RdP (Fig. 8; Guerrero *et al.*, 1997*b*). During autumn and winter, when the RdP low salinity tongue turns northward, the central area extends mainly along the Uruguayan coast, reaching Punta del Este during winter and an outer area intrusion on the Argentine coast is observed. During spring and summer, the southward flow of fresh water along the Argentine coast beyond Punta Médanos (Guerrero *et al.*, 1997*a*), influences the retraction of the central area along the Uruguayan coast and consequently the outer area locates near Montevideo (Fig. 8).

Changes in environmental conditions in the coastal system, in particular the influence of high freshwater discharge of the RdP during El Niño years associated with high precipitation (Robertson & Mechoso, 1998; Camilloni & Barros, 2000) produces a movement of the estuarine assemblage areas towards the continental shelf (years 1983 and 1998, Fig. 9). Depending on the spring dominant wind pattern, their expansion occurs along the estuary main axis (1998) or along the Argentine coast (1983). Moreover, decreases in the freshwater discharge of the RdP estuary during La Niña years produced upstream movements of the estuarine assemblage areas (years 1981 and 1999, Fig. 9), consequently the marine fish assemblage areas cover a greater portion of the estuary. Under normal freshwater discharge, the boundaries of the fish assemblages are relatively more stable (Jaureguizar *et al.*, 2006*b*).

ENVIRONMENTAL INFLUENCE ON CATCHES OF SMALL-SCALE FISHERIES AND CRUISE-BASED FISHERY EVALUATION

It is clear that climatic variability (*e.g.* changes in salinity and temperature distribution, wind fields and hydrological cycles at annual to decadal time scales) affects the fish abundance and distribution in RdP and its adjacent coastal waters, which could have major effects on their population dynamics. The scarcity of long-term biological observations (*e.g.* physiology, growth and reproductive capacity, mortality, and prey abundance) in the RdP has limited knowledge of the variability in different time scales of these important variables as well as the consequences of environmental forcing.

The high spatial variation (200 km, *c.* 35% of area) in the coastal water distribution alters the fish distribution at different layers, from community level (fish assemblage) to single species level (*P. nudigula, P. punctatus, D. tschudii* and *M. schmitti)* and their life-history stage (*M. furnieri* and *C. guatucupa)*. Environmental variation determines the fish availability for a specific area, and due to short travel distances of the small-scale fishery, it affects the production of these fisheries in the inner (*M. furnieri*, Norbis *et al.*, 1992) and outer (Jaureguizar *et al.*, 2015) areas of the RdP estuary. Therefore, the available fish population in the fishing area is one of the most important factors that determines small-scale fisheries production. *Mustelus schmitti* which is available to the artisanal fishery in the southern boundary of RdP estuary (Partido de La Costa, Argentina) during austral spring and summer seasons, is associated with reproductive migration from deep to shallow waters (Cortés *et al.*, 2011*b*). The *M. schmitti* yield (individuals $100 \, m^{-1} \, 24 \, h^{-1}$) during the 2008 and 2009 fishing season was higher than
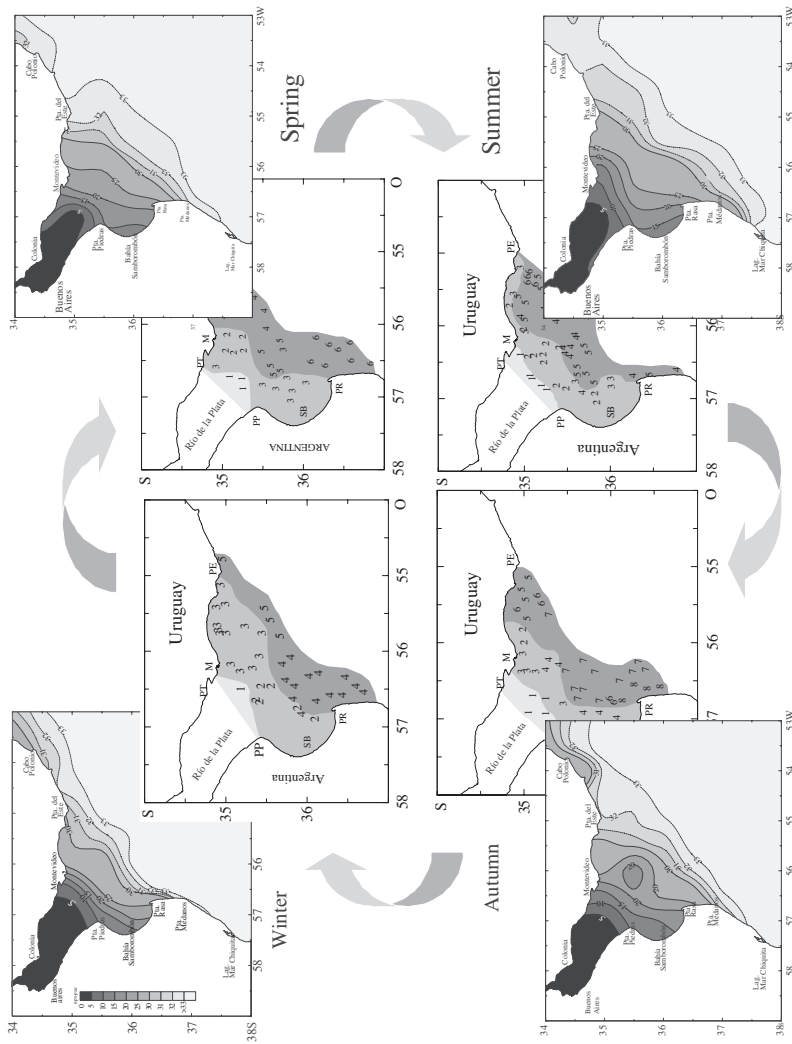
Fig. 8. Relationship between the seasonal variation in the spatial distribution pattern of bottom salinity (redrawn from Guerrero *et al.*, 1997*b*) and its corresponding fish assemblage areas (redrawn from Jaureguizar *et al.*, 2004) in the Río de la Plata estuarine zone. The shallow areas indicate the three main fish assemblage area (inner, central and outer estuarine areas) where the number show the position of sampling station and indicate the subareas within the main areas (Jaureguizar *et al.*, 2004). PE, Punta del Este; PP, Punta Piedras; PR, Punta Rasa; SB, Samborombón Bay; PT, Punta Tigre; M, Montevideo.

FIG. 9. Relationship between the spring inter-annual variation in the spatial coverage of the three main estuarine fish assemblage areas [0, inner (IEA); 1, central (CEA); 2, outer (OEA) estuarine areas; 3 and 4, marine areas (MA) redrawn from Jaureguizar *et al.* (2006*a*, 2006*b*)] in (a) 1981, (b) 1983, (c) 1998 and (d) 1999, and (e) freshwater discharge anomaly of Río de la Plata. The shallow areas indicate the three main fish assemblage area and the number show the position of sampling station.

during the 2009–2010 season (Fig. 10) and this difference was related to the environment. The temporal series of satellite-derived surface chlorophyll-*a* (CSAT, mg m^{-3}) related to salinity (Piola *et al.*, 2008) and the habitat association of *M. schmitti* (Cortés, 2012), shows that when the salinity was higher than 28, the fishery was more productive, while the decline in yield was associated with lower salinities along the coast (Fig. 10).

In the same way, the environment with its differential influence on the habitat used by size composition, age and maturity stages affects the basic information (catch numbers) obtained during the fish stock assessment cruises. This is the case with the marine migrant species *C. guatucupa* (Fig. 4), whose population age-class structure available in the RdP and adjacent Uruguayan coast is determined by the synoptic environmental conditions along the coast (Jaureguizar & Guerrero, 2009). The environmental dynamics affects the availability of different length size classes for the commercial fishery and evaluation cruises. This fact alters the catch per unit effort (CPUE) and the total biomass values estimated from assessment cruises for *C. guatucupa* (Fig. 4). Considering this, the commercial fishery CPUE does not follow a fixed pattern, thus it is unproportional to biomass and the *C. guatucupa* abundance is unexplained (Perrotta & Ruarte, 2009).

Taking into account the high environmental dynamics of the RdP and the strong habitat association of fish species stage, size and age, monitoring programmes need to be designed considering all of these objectives as part of a dynamic and reflective process that integrates science and management. Understanding how habitat associations change over time with species and stage will provide new knowledge that is necessary to delineate essential fish habitats in order to refine spatial fisheries management approaches.
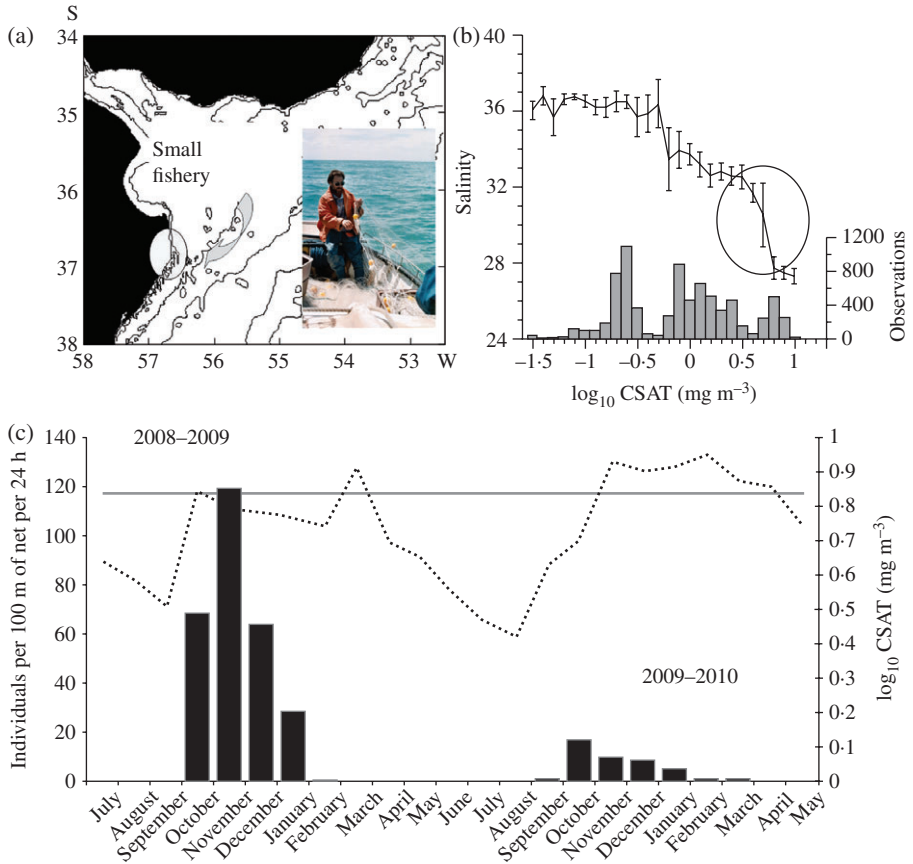
FIG. 10. Association between salinity pattern and the *Mustelus schmitti* yield during two austral spring and summer season (2008–2009 and 2009–2010) in a small-scale fishery settled in the southern boundary of Río de la Plata: (a) location of the small-scale fishery of Partido de la Costa, (b) relationship among chlorophyll satellite (CSAT) and salinity in the Río de la Plata (redrawn of Piola *et al.*, 2008) and (c) monthly yield of *M. schmitti*. The grey line indicates the CSAT values related to external front of Río de la Plata estuarine water (salinity *c*. 28).

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