

Inter-estuarine and temporal patterns of the fish assemblage of subtropical subestuaries along the Río de la Plata coast (Uruguay)

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ABSTRACT

Fish assemblages in subestuaries have been poorly studied worldwide. In order to evaluate the inter-estuarine and temporal variability of the ichthyofauna of subestuaries along the Uruguayan coast of the Río de la Plata (RdIP), the Pando, Solís Chico and Solís Grande systems were sampled between 2011 and 2013. Fish biomass, abundance, species richness and diversity indices were analysed, defining fish assemblages characterised by a few species and great abundance. Estuarine resident and freshwater species represented 55.5% of the fish assemblage according to estuarine use guilds. Species occurrence was similar in the three subestuaries, but the relative abundances differed among them. The analysed community parameters showed a decreasing trend from west to east along the Uruguayan coast. Highest diversity and fish abundance were recorded in the Pando system located in the proximities of an important spawning area in the inner RdIP estuary. In the Solís Grande subestuary occurred the lowest species richness and fish abundance. The Solís Chico was characterised as a transitional subsystem. All three subestuaries showed an increase in species richness and abundance during high temperature periods, probably related to the life cycle of the species sharing habitats between the RdIP and the coastal subestuaries. This study constitutes the first step in assessing the fish assemblage patterns in coastal ecosystems of the RdIP and an approach about the ecological role of the subestuaries in the southwest Atlantic Ocean.

Descriptors: Species diversity, Ichthyofauna, Estuarine systems, Variability patterns, South American estuaries, Community parameters.

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RESUMO

As assembleias de peixes em subestuários têm sido pouco estudadas no mundo. A fim de avaliar a variabilidade inter-estuarina e temporal da ictiofauna dos subestuários ao longo da costa uruguaia do Rio da Prata, foram amostrados entre 2011 e 2013 os sistemas Pando, Solís Chico e Solís Grande. A biomassa e abundância de peixes, riqueza de espécies e índices de diversidade foram analisadas, definindo-se que as assembleias de peixes são caracterizadas por apenas algumas espécies e com grande abundância. Espécies residentes estuarinas e de água doce apresentaram 55,5% da assembleia de peixes conforme as guildas de uso do estuário. Embora, a ocorrência de espécies tenha sido semelhante nos três subestuários, a sua abundância relativa foi diferente. Os valores dos parâmetros da comunidade mostraram uma tendência decrescente de oeste para leste ao longo da costa uruguaia. Maior diversidade de peixes e abundância foram registradas no sistema do Pando, localizado nas proximidades de uma importante área de desova no estuário do Rio da Prata interior. No subestuário do Solís Grande foram encontrados menor riqueza e abundância de peixes. Solís Chico foi caracterizado como um subsistema de transição. Os três subestuários mostraram um aumento na riqueza e abundância durante os períodos de temperatura alta, provavelmente relacionada com o ciclo de vida das espécies que compartilham habitats entre o Rio da Prata e/ou os subestuários costeiros. Este estudo constitui o primeiro passo para avaliar os padrões de peixes no ecossistema costeiro do Rio da Prata e uma abordagem sobre o papel ecológico do subestuários no sudoeste do Oceano Atlântico.

Descritores: Diversidade de espécies, Ictiofauna, Sistemas estuarinos, Padrões de variabilidade, Estuários da América do Sul, Parâmetros comunitários.

INTRODUCTION

Estuaries represent areas of ecological significance for a great number of species. They are relevant as transitional environments for the breeding, feeding and sheltering of fish species, many of them of commercial importance (WHITFIELD, 1999; MCLUSKY; ELLIOTT, 2004; DAY et al., 2013). The ichthyofauna knowledge provides good indicators of ecosystem structure and health (WHITFIELD; ELLIOTT, 2002) and is often the object of management concerns. Estuarine fish are subjected to the environmental stress from estuaries, affecting the distribution, abundance and migration of fish species during their life cycle (ELLIOTT et al., 2007). Likewise, factors such as biogeography, shape and size of the estuary, as well as habitat availability, have also been suggested to impact on species occurrence (POTTER; HYNDES, 1999; WHITFIELD, 1999; VALESINI et al., 2004; GUTIÉRREZ-ESTRADA et al., 2008; FRANÇA et al., 2009; NICOLAS et al., 2010).

Considering the relevance of estuarine ecosystems, the fish fauna from the Río de la Plata estuary (RdIP), as well as, of the coastal estuaries along the Uruguayan-Argentinian coast has been previously studied (LAGOS, 2003; JAUREGUIZAR et al., 2004, 2016; ACUÑA PLAVAN et al., 2010; LORENZO et al., 2011; GURDEK et al., 2011, 2016; SOLARI et al., 2015; GURDEK; ACUÑA PLAVAN, 2016). The RdIP is one of the largest estuaries worldwide, connected permanently to the Atlantic Ocean. As a complex hydrodynamic environment, it is characterized by a salt-wedge regime (ACHA et al., 2008). The displacement of the estuarine front along the Uruguayan coast depends on the discharges from its main tributaries, the Uruguay and Paraná rivers, and predominant winds (FRAMIÑAN; BROWN, 1996; PIOLA et al., 2005, PIOLA et al., 2008; MÖLLER et al., 2008). The fish species of the RdIP have been mainly grouped into the Sciaenidae, Clupeidae, Mugilidae, Atherinopsidae, Engraulidae, Paralichthyidae and Pomatomidae families, some of them represented by species of commercial importance over the region (NORBIS et al., 2006; LORENZO et al., 2011). Among them species such as *Micropogonias furnieri*, *Brevoortia aurea* and *Macrondon ancylodon* present their reproductive areas in the RdIP during the austral spring (ACHA; MACCHI, 2000; MILITELLI et al., 2013).

A number of streams empty their waters into the Uruguayan coast of the RdIP, some of them forming small subestuaries (ACUÑA PLAVAN et al., 2015).

Among them, the Pando and Solís Grande subestuaries have been previously studied in terms of the benthic, planktonic and fish communities. In this sense, benthic and planktonic communities have been shown to describe different temporal patterns (GÓMEZ-ERACHE et al., 2000; CALLIARI et al., 2001; PASSADORE et al., 2007). Furthermore, these ecosystems have been suggested as nursery and juveniles areas for many commercial fish species (RETTA et al., 2006; DEFEO et al., 2009; ACUÑA PLAVAN et al., 2010; GURDEK et al., 2016). The fish assemblage has been studied providing daily (GURDEK et al., 2011), as well as monthly and spatial dynamics (ACUÑA PLAVAN et al., 2010, GURDEK et al., 2016). In spite of their proximity (~50 km), these estuaries have shown some differences in fish species composition and abundance. In this sense, the whitemouth croaker *Micropogonias furnieri* inhabit the Pando subestuary on high abundance and annual basis (ACUÑA et al., 2010; GURDEK; ACUÑA PLAVAN, 2014; GURDEK; ACUÑA PLAVAN, 2016), while the silverside *Odontesthes* sp. (Atherinopsidae) and the mullet *Mugil liza*, are the most abundant species according to spatial-temporal studies in the Solís Grande subestuary (GURDEK et al., 2011; 2016).

Further studies, including new systems, as well broader temporal scales, are needed in order to provide a more comprehensive description of the fish assemblage from the small subestuaries along the Uruguayan coast. The aim of this study was to provide a characterization of the spatial and temporal patterns of the fish assemblage of three subestuaries along the Uruguayan coast of the RdIP between 2011 and 2013: Pando, Solís Chico and Solís Grande. Results will contribute to a better understanding of subestuarine fish composition and dynamics.

MATERIAL AND METHODS

STUDY AREA

The Río de la Plata (RdIP) is one of the largest estuaries in the world, discharging an average of 23,000 m³ s⁻¹ into the Atlantic Ocean (BORÚS et al., 2013). The RdIP is subdivided in a fluvial (inner) and estuarine (outer) region; the outer region covering an area of 35,000 km² (FRAMIÑAN; BROWN, 1996). The Pando, Solís Chico and Solís Grande subestuaries are located in the outer region within a distance of 50 km along the Uruguayan coast of the RdIP estuary (Figure 1). These ecosystems

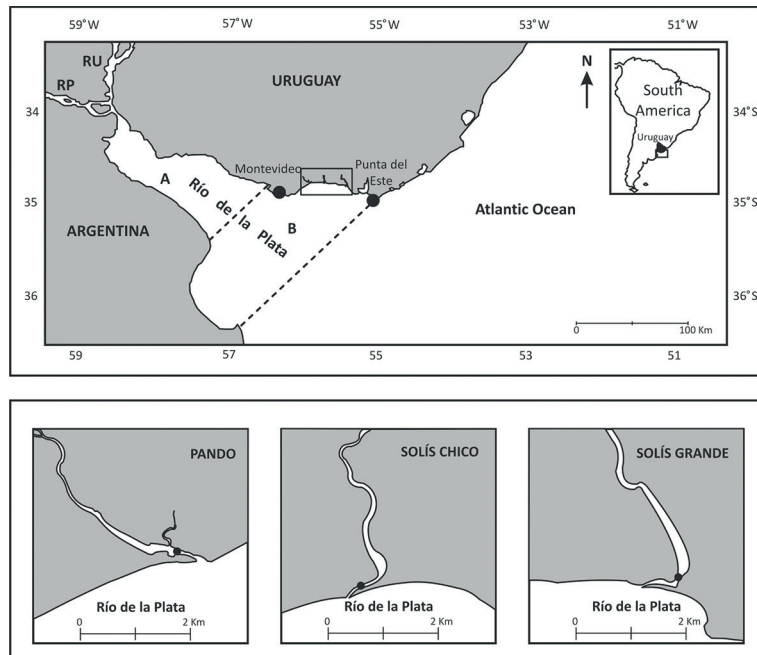


Figure 1. Location of the three sampling sites: Pando, Solís Chico and Solís Grande subestuaries of the Río de la Plata along the Uruguayan coast and fish sampling area in each estuary. A=upper and B=outer regions of the Río de la Plata. RU=Uruguay River; RP=Paraná River.

are subject to similar weather conditions but differ in morphology and human impacts associated with the basins (FREPLATA, 2003).

The Pando subestuary (P) (Figure 1) is the western estuary and the smallest one with a drainage basin of 973 km². The average flow is 6.4 m³ s⁻¹, the average depth is 1.5 m and the maximum mouth width is 220 m (FREPLATA, 2003). High nutrient concentrations are characteristic of the estuary with frequent episodes of oxygen undersaturated waters (GOYENOLA et al., 2009). The subestuary presents a salinity range between 0 and 14 and a temperature range between 13 and 25 °C during El Niño conditions (ACUÑA PLAVAN et al., 2010).

The Solís Chico subestuary (Sch) (Figure 1) lies between Pando and Solís Grande, has a drainage basin of 644 km², average flow of 5.4 m³ s⁻¹ and maximum width of 280 m (FREPLATA, 2003). The subestuary has a salinity range of 9-24 and a temperature range between 15 and 18 °C (GUTIÉRREZ et al., 2015). Population density around the basin is low and the main human activities are related to agriculture, forestry and summer tourism (GOYENOLA et al., 2009; ECHEVARRÍA et al., 2011).

The Solís Grande subestuary (SG) (Figure 1) is the eastern and largest estuary with a drainage basin of 1,354 km², average flow 9.6 m³ s⁻¹, mean depth 2 m and

maximum width 330 m (FREPLATA, 2003). SG has the largest ranges of temperature (10-25 °C) and salinity (4-33) (CALLIARI et al., 2001). This estuary is also characterised by low population density with main human activities related to agriculture, livestock, forestry, and tourism (GOYENOLA et al., 2009; ECHEVARRÍA et al., 2011).

FISH SAMPLING

Sampling was carried out during two consecutive years: spring 2011 (October), autumn 2012 (May), late winter 2012 (September), spring 2012 (November) and late summer 2013 (March). The samplings were carried out simultaneously, except for spring 2012 (P y SG) and summer 2013 (P). Fish were collected using a beach seine net (12 m long with a central bag of 6.70 m long, mesh size 12 mm of cod-end and two lateral wings each of 5 m in length and of 2 m high). Additionally, to obtain a representative sampling of the species, two sets of gill nets (40 m long, 1.7 m high, each one with 4 different mesh sizes: 2, 3.5, 5.5 and 8 cm) were placed at 200 m downstream and 1000 m upstream of the trawl fishing area. Twelve hauls were made on each sampling period, six on each margin of the subestuaries at approximately

1 km from the mouth, starting at sunrise and finishing no later than noon. Two ropes of 25 m were joined to each end of the beach seine net. One of the ropes was retained on the beach while the other end, together with the net, was deployed by a small rowing boat. The haul was made manually and perpendicular to the shore, keeping the net as close to the bottom as possible to cover an area of ca. 300 m². All individuals were counted, measured to the nearest 0.1 cm and weighted to the nearest 0.1 g in field and laboratory. Juveniles and adults individuals were classified according to the maturity length available in literature.

Three replicates of Water temperature (°C) and salinity were measured directly in the field with multiparameter Ysi Pro-plus (USA) with a temperature resolution of 0.1 °C and 0.01 for salinity.

DATA ANALYSIS

Only data from the beach seine were used to evaluate fish assemblage parameters (biomass, numerical abundance, richness and diversity indexes). Fish biomass and abundance were expressed in grams and number of individuals per 1000 m², respectively. Additionally, considering the way fish use the estuary during their whole life cycle (based on the available literature), species were categorised by functional guilds according to FRANCO et al. (2008) and each species was assigned to an estuarine use functional guild (Table 2). The estuarine use functional guilds considered were marine stragglers, marine migrants, estuarine species, freshwater species, catadromous species and anadromous species. The percentage contribution of each functional guild to the total number of species was calculated. The Shannon and Simpson diversity indexes (SIMPSON, 1949; SHANNON; WEAVER, 1963) were used to analyse fish assemblage diversity. Assumptions of normality and homogeneity of variance were analysed by Shapiro Wilk's test (SHAPIRO; WILK, 1965) and Levene's test (based on the averages), respectively. When necessary, the data were previously transformed to Log (x) or Log (x+1). Parametric analysis of variance (ANOVA) or non-parametric Kruskal-Wallis was used depending on the fulfilment of the assumptions to contrast fish community parameters. A posteriori Tukey Test or Mann-Whitney was used to test multiple comparisons. Differences in fish assemblages among subestuaries were examined using non-metric multidimensional scaling (nMDS) by using the Bray-Curtis similarity index. Prior to calculation of the Bray Curtis index, the abundance (individuals x 1000 m²)

was transformed to fourth-root to reduce the contribution of the abundant species. Analysis of similarity (ANOSIM) was carried out on the above data to determine the significance of fish assemblage differences or similarities between subestuaries and periods. The level of significance used was $p=0.05$ (SOKAL; ROHLF, 1995). The PRIMER software package (Version 6.0, Inc.) and Past (Version 3.0) were utilized to conduct the analyses.

RESULTS

ENVIRONMENTAL VARIABLES

The average water temperature varied between seasons, showing an increase during spring 2012 (23.1 °C) and summer 2013 (23.8 °C) (Table 1). No differences were found between sites (Kruskal-Wallis, $p>0.05$). The salinity varied between 7.5 (autumn 2012) in Pando and 25.5 (autumn 2012) in the Solís Grande (Table 1).

FISH COMPOSITION AND SPECIES OCCURRENCE

Overall a total of 8,271 individuals belonging to 15 families and 18 species were recorded in the three subestuaries (Table 2). In terms of species richness the fish assemblage was represented by 33.3% estuarine species, 22.2% freshwater species, 16.7% marine stragglers, 11.1% marine migrants, 11.1% anadromous species and 5.6% catadromous species. While Sciaenidae and Clupeidae were the most abundant families in terms of species richness, other families such as Cyprinidae (represented by *Cyprinus carpio*), Pimelodidae (represented by *Pimelodus maculatus*) and Anablepidae (represented by *Jenynsia multidentata*) occurred with a single species and individual. Larvae individuals classified as Clupeidae were captured only in P, while *Gobiosoma parri*, *Hypleurochilus fissicornis* and *Syngnathus folletti* only in SCh (Table 2). All three subestuaries showed similar fish species composition (Table 2). However, they showed differences in terms of species relative abundance (Figure 2). In this sense, in the P subestuary, *Brevoortia aurea*, *Mugil liza*, *Micropogonias furnieri*, *Odontesthes argentinensis*, *Lycengraulis grossidens* and *Platanichthys platana* made up 99 % of all the fish sampled, with *B. aurea* and *M. liza* accounting for more than 50% of the total. While in Solís Chico, the fish assemblage was dominated by species such as *B. aurea*, *P. platana*, *M. liza*, *O. argentinensis* and *M. furnieri*, similar than in P (*B. aurea*, *M. liza*, *O. argentinensis*, *M. furnieri*). In Solís Grande, *O. argentinensis* dominated

Table 1. Average \pm standard deviation of temperature (T- °C) and salinity (S) of water in Pando (P), Solís Chico (SCh) and Solís Grande (SG) subestuaries during five seasons (Spr- spring 2011, Aut- autumn 2012, Win- winter 2012, Spr- spring 2012 and Sum- summer 2013).

	P	SCh	SG	P	SCh	SG	P	SCh	SG	P	SG	P
	Spr 2011			Aut 2012			Win 2012			Spr 2012		Sum 2013
T (°C)	14.7 \pm 0.7	15.2 \pm 0.8	14.1 \pm 1.1	16.3 \pm 0.4	17.8 \pm 0.6	17.6 \pm 0.6	14.2 \pm 0.1	15.2 \pm 0.2	16.3 \pm 1.6	23.1 \pm 1.3	20.2 \pm 0.6	23.8 \pm 3.5
S	20.9 \pm 6.2	21.4 \pm 5.8	21.8 \pm 8.7	7.5 \pm 7.3	13.4 \pm 9.2	25.5 \pm 8.0	8.4 \pm 0.2	9.9 \pm 2.2	9.9 \pm 5.3	13.6 \pm 7.0	20.1 \pm 4.5	21.1 \pm 0.5

the fish community (69%), followed by *Paralichthys orbignyanus* (12.7%) and *M. liza* (10.3%) (Figure 2). Estuarine resident species dominated the fish community in P (50%), SCh (33.3%) and SG (50%) subestuaries, followed by freshwater (16.7%) and anadromous species (16.7%) in P, marine stragglers (25%) in SCh and equal proportions of freshwater, marine migrants, anadromous and catadromous species (12.5%) in SG.

In relation to the temporal variability and environmental conditions some species patterns were observed. *Brevoortia aurea*, *M. liza*, *M. furnieri* and *L. grossidens* showed the highest density in P during summer, with an average water temperature and salinity of 23.8 °C and 21.1 respectively (Table 2; Table 1). *Micropogonias furnieri* was not caught during winter in any subestuary (Table 2). *Platanichthys platana* and *Odontesthes argentinensis* were mostly captured during autumn in all subestuaries with temperature values around 17 °C, however the salinity values were highly variable among the systems (Table 2; Table 1). *Paralichthys orbignyanus* on the other hand, was mostly caught in SG in autumn and spring 2012 (T values around 19 °C, S: 20.1-25.5) but also was only captured in SCh during autumn and in P during spring 2012 with similar temperature (mean 13.4) and salinity values (mean 13.6) (Table 2; Table 1).

Some differences were observed in the captures according to fishing gears (Table 2). However, *Micropogonias furnieri* and *Brevoortia aurea* presented high abundances regardless of the sampling gear. Some species were only captured by gill net depending on the site and sampling periods (e.g. *Pomatomus saltatrix* in P, *Pogonias cromis* in SCh and *M. furnieri* in SG). The length range of species was different between individuals caught by beach seine or gill net. Individuals captured by gill net were fundamentally represented by larger sizes. The most abundant species (i.e. *B. aurea*, *M. liza*, *O. argentinensis*, *M. furnieri*) presented the smallest sizes, denoting the occurrence of Clupeidae larvae during beach seine netting (Table. 2).

INTER-ESTUARINE AND TEMPORAL VARIATIONS IN FISH ASSEMBLAGES

According to spatial variability of the community parameters, the average biomass ranged from 979 \pm 1,220 g 1000 m² in SCh to 1,221 \pm 586 g 1000 m² in P (Figure 3 a). The highest biomass was found in SCh, as well as in SG during winter 2012 (Kruskal Wallis, $p < 0.05$) (Figure 3b). These values were recorded due to larger specimens of *Cyprinus carpio* (7,815 g) in SCh and *Paralichthys orbignyanus* (310.5 – 8,492 g) in SG. In other periods, the biomass was higher in P and SG than in SCh (e.g. spring 2011 and autumn 2012). In terms of density, the highest average abundance was registered in P (399 \pm 518 individuals 1000 m²) (Kruskal Wallis, $p < 0.05$), followed by SCh and SG (Figure 3 c). This pattern was found in all periods with the exception of winter 2012, when differences were only significant between P and SG (Mann Whitney, $p < 0.05$) (Figure 3 d). The highest abundance occurred during autumn 2012, in all three subestuaries (Kruskal Wallis, $p < 0.05$).

Once again, the average species richness and diversity was higher in P than in SG (Mann Whitney, $p < 0.05$) (Figure 3 e, g). There were differences between P and SG during spring 2011 and autumn 2012 (Kruskal Wallis, $p < 0.05$; Figure 3 f, h). SCh showed similarities and discrepancies with the P and SG according to the sampling period (in spring 2011 and autumn 2012). Autumn 2012 was the period with the highest occurrence of fish species in all subestuaries (Figure 3 f).

Regarding the comparison of fish diversity among the 3 subsystems when they were sampled together, results showed a minimum in diversity in all subestuaries during the winter, when mean temperature values ranged from 14.2 to 16.3 °C and salinities were lowest between 8.4 to 9.9 (Figure 3h; Table 1). Highest diversity occurred in autumn in all systems when temperature was higher (Figure 3h; Table 1).

The nMDS ordination based on individuals per species showed that P and SG are the most dissimilar systems, while SCh presents similarities with P and SG (Figure 4). Similarly, ANOSIM results, revealed that each estuary differed significantly with each other, although overlapping community characteristics ($R = 0.344$, $p < 0.05$). Paired

Table 2. Species, key to species abbreviations (Sa) and average of abundance (individuals 1000 m⁻²) sampled in the Pando (P), Solís Chico (SCh) and Solís Grande (SG) substuaries during spring 2011 (Spr-2011); autumn (Aut-2012), winter (Win-2012) and spring 2012 (Spr-2012) and summer 2013 (Sum-2013) by beach seine net. In brackets, gill net abundance (number of individuals per samples), EUG=estuarine use guild; ES=estuarine species; FW=freshwater species; MM=marine migrants; MS=marine stragglers; A=anadromous species, C=catadromous species. Not identified (n.i.). N=number of individuals; L=length range (cm). J/A correspond to the percentage of juveniles and adults.

	Sa	EUG	P			Aut-2012			Win-2012			Spr-2012			Sum-2013			Bench seine			Gill net			
			Sch	SG	P	SCh	SG	P	SCh	SG	P	SG	P	N	L	N	L	N	L	N	L	N	L	J/A
Clupeiformes																								
Engraulidae																								
<i>Lycengrulus grossidens</i> (Agassiz, 1829)	Lg	A	-	-	4.4	0.3 (1)	-	1.9	-	0.3	0.6 (2)	0.3	184.7 (2)	694	2.1-17.0	5	12.2-22.9	98.7/11.3						
Clupeidae																								
<i>Brevoortia anrea</i> (Agassiz, 1829)	Ba	ES	68.3	8.3 (15)	(7)	40.6 (14)	8.3 (3)	0.3 (2)	-	8.6 (29)	-	5.3 (69)	515.3 (35)	2,178	2.0-17.0	174	10.5-41.0	98.3/1.7						
<i>Platanichthys platana</i> (Regan, 1917)	Pp	FW	0.8	-	-	127.5	11.4	3.3	-	10.3	-	0.3	1.9	725	2.2-9.3		46.1	95.9/4.1						
Larvas n. i.	Cl	-	-	-	-	-	-	-	5.6	-	-	-	9.7	55	1.6-2.6			100/0						
Cypriniformes																								
Cyprinidae																								
<i>Cyprinus carpio</i> (Linnaeus, 1758)	Cc	FW	-	-	-	-	-	-	-	0.3	-	-	-	1	75.0			0/100						
Siluriformes																								
Ariidae																								
<i>Gentidens barbatus</i> (Lacepède, 1803)	Gb	A	8.3	0.6	-	-	-	-	-	-	-	-	-	11	8.5-10			100/0						
Pinelodidae																								
<i>Pinelodus maculatus</i> (Lacepède, 1803)	Pm	FW	-	-	-	-	-	-	-	-	-	-	(1)			1	28.8	100/0						
Mugiliformes																								
<i>Mugil liza</i> Günther, 1880	Ml	C	0.8	0.6 (1)	2.1	53.3	15.8 (1)	1.7	21.7	0.6	66.1	4.4	313.9 (1)	1,992	2.1-32.0	4	18.3-40.3	99.1/0.1						
Atheriniformes																								
Atherinopsidae																								
<i>Odontesthes argentinensis</i> (Valenciennes, 1836)	Oa	ES	48.3	7.2 (3)	5.4	107.2	19.4 (3)	36.4 (1)	16.1	1.67 (1)	14.7 (8)	13.6	12.2 (11)	954	1.6-38.0	27	21.9-44.8	80.3/19.7						
Perciformes																								
Sciaenidae																								
<i>Menticirrhus americanus</i> (Linnaeus, 1758)	Ma	ES	-	(1)	0.8 (3)	-	-	-	-	-	(4)	-	2.2 (1)	10	3.9-14.3	9	16.8-40	73.7/26.3						
<i>Microgogonias furnieri</i> (Desmarest, 1823)	Mf	ES	-	-	(2)	40.8 (36)	25.0 (14)	(2)	-	-	59.7 (18)	(2)	213.6 (39)	1,226	1.9-19.3	113	11.8-41.0	99.6/0.4						
<i>Pogonias cromis</i> (Linnaeus, 1766)	Pe	ES	-	(2)	-	0.3	(1)	-	-	-	(5)	-	(1)	1	13.6	9	21.3-53.8	30/70						
Pomatomidae																								
<i>Pomatomus saltatrix</i> (Linnaeus, 1766)	Ps	MM	-	-	-	-	-	(1)	-	-	(1)	-	0.3 (10)	1	16.8	12	14.3-33.8	100/0						
Gobiidae																								
<i>Gobiosoma parri</i> (Ginsburg, 1933)	Gp	MS	-	-	-	0.6	-	-	-	-	-	-	-	2	2.9-4.2			0/100						
Blenniidae																								
<i>Hyppleurochilus fassiacornis</i> (Quoy & Gaimard, 1824)	Hf	MS	-	-	-	0.6	-	-	-	-	-	-	-	2	2.9-4.2			0/100						
Carangidae																								
<i>Trachinotus marginatus</i> (Cuvier, 1832)	Tm	MM	-	-	-	-	-	0.3	-	-	(1)	-	-	1	21	1	22	100/0						
Syngnathiformes																								
Syngnathidae																								
<i>Syngnathus foliatus</i> (Herald, 1942)	Sf	MS	-	-	-	0.6	-	-	-	-	-	-	-	2	14.7-14.9			0/100						
Pleuronectiformes																								
Paralichthyidae																								
<i>Paralichthys orbignyanus</i> (Valenciennes, 1839)	Po	ES	-	-	-	2.2	5.0	-	0.6	1.4 (1)	5.3	-	-	61	3.1-90.0	1	30.7	98.2/1.8						
Cyprinodontiformes																								
Anableptidae																								
<i>Jenynsia multidentata</i> (Jenyns, 1842)	Jm	FW	-	-	-	0.3	-	-	-	-	-	-	-	1	4.9			100/0						

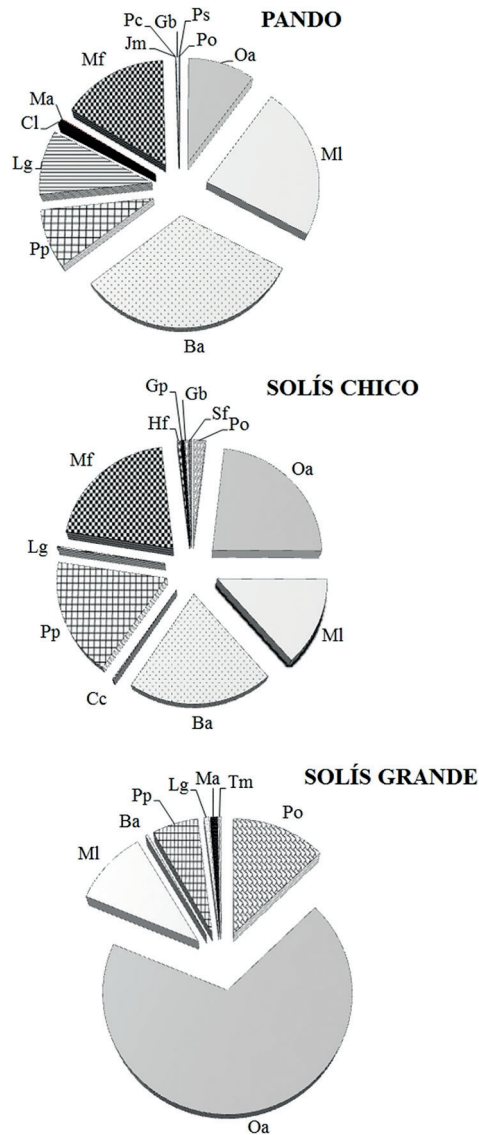


Figure 2. Relative abundance of fish species (individuals 1000 m⁻²) based on beach seine in the Pando (P), Solís Chico (SCh) and Solís Grande (SG) subestuaries. Key of species abbreviations in Table 2.

comparisons indicated a significant difference between P and SG ($R=0.431, p<0.05$). However, there were not significant differences between P and SCh ($R=0.138, p>0.05$), or between SCh and SG ($R= 0.481, p>0.05$), showing a more similar community between P and SCh.

DISCUSSION

FAMILIES AND SPECIES COMPOSITION

The families and species found in the three subestuaries sampled in the present study are similar to those found

in subestuaries and other estuarine ecosystems along the Uruguayan coast (RETTA et al., 2006; ACUÑA PLAVAN et al., 2010; TEIXEIRA DE MELLO et al., 2011), southern coast of Brazil (CHAO et al., 1985; VIEIRA; MUSICK, 1994; RAMOS; VIEIRA, 2001), north eastern coast of Argentina (GONZÁLEZ-CASTRO et al., 2009; SOLARI et al., 2009; COUSSEAU et al., 2011; BRUNO et al., 2013; SOLARI, 2013).

Fish assemblages from Pando, Solís Chico and Solís Grande subestuaries were characterised by a few dominant species (*Micropogonias furnieri*, *Brevoortia aurea*, *Mugil*

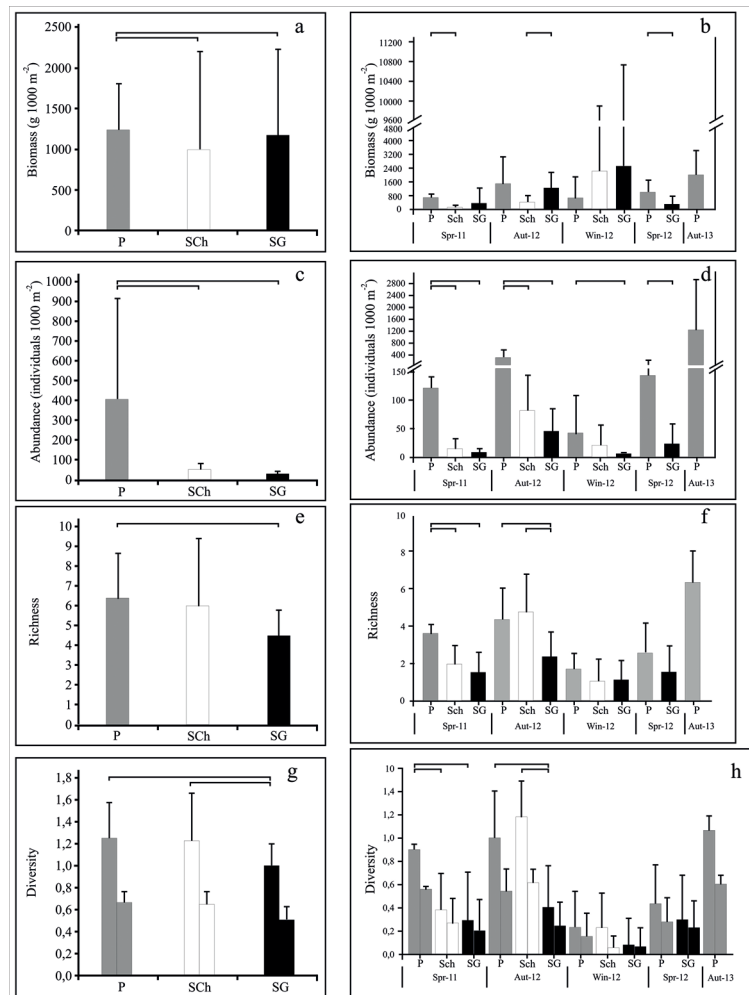


Figure 3. Biomass (g 1000 m⁻²) (a,b), abundance (c,d) (individuals 1000 m⁻²), richness (e,f) and diversity indices (g,h) (Shannon index: left bar; Simpson index: right bar) from the fish community from the Pando (P=grey column), Solis Chico (Sch=white column) and Solis Grande (SG=black column) subestuaries during spring 2011 (Spr-11), autumn (Aut-12), winter (Win-12) and spring (Spr-12) 2012 and summer 2013 (Sum-13). The columns represent mean values and the vertical bars on top of the columns are standard deviations. Horizontal lines represent significant differences between subestuaries ($p < 0.05$).

liza, *Odontesthes argentinensis*, *Paralichthys orbignyanus*) with high abundance and mainly belonging to the category resident estuarine species. It is a typical characteristic from temperate estuaries worldwide (BLABER, 2002; VEIGA et al., 2006; GONZÁLEZ-CASTRO et al., 2009; ACUÑA PLAVAN et al., 2010; VASCONCELOS et al., 2011; GURDEK et al., 2016). The composition of fish assemblages in the subestuaries of the Uruguayan coast also included marine stragglers and freshwater species of occasional temporal and estuarine occurrence. For instance, *Syngnathus folletti*, *Hyleurochilus fissicornis* and *Gobiosoma parri*, occurred only in Sch, while

the freshwater species *Pimelodus maculatus*, *Jenynsia multidentata* and *Cyprinus carpio* were captured only in P and Sch. The sampling site, i.e. the mouth of the subestuary, was probably the determinant factor for the low capture of freshwater species. Marine species were under-represented in all three subestuaries in contrast to many estuarine systems (FRANCO et al., 2008; NICOLAS et al., 2010; CARDOSO et al., 2011).

Regarding the fishing gear, some differences were observed in the captures. Differences in catches according to the fishing gear indicate gear selectivity (schools, patchy distribution, species characteristics) (ELLIOTT;

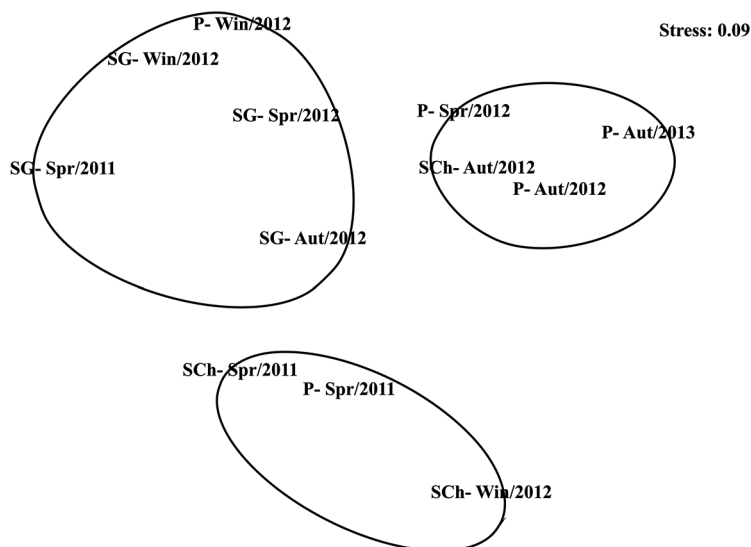


Figure 4. Multi-Dimensional Scaling (MDS) based on abundance of fish samples collected in the Pando (P), Solís Chico (SCh) and Solís Grande (SG) subestuaries during different sampling periods. Spr/2011 (spring 2011), Aut/2012 (autumn 2012), Win/2012 (winter 2012), Spr/2012 (spring 2012), Sum/2013 (summer 2013).

HEMINGWAY, 2002). It is important to include different sampling gears to enhance the representation of the fish community (FRANCO et al., 2012).

INTER-ESTUARINE PATTERNS IN FISH ASSEMBLAGES

In general terms, the abundance, species richness and diversity followed an eastward decreasing trend among subestuaries; probably related to the estuarine-ocean gradient regarding of the RdIP (JAUREGUIZAR et al., 2004; LORENZO et al., 2011; LAGOS, 2003). This feature supports the study of RETTA et al. (2006) who found that abundance and species richness decreases from the inner to the outer part of the Uruguayan coast of RdIP. In order to understand the spatial distribution of fish assemblages from the P, SCh and SG subestuaries, it is necessary to consider their links with the larger RdIP estuary. These subestuaries are influenced by the highly dynamic RdIP system, where freshwater discharge and regional winds, and tides to a lesser extent, displace and mix its waters (NAGY et al., 2008; JAUREGUIZAR et al., 2016). Variation in spatial distribution of fish assemblage in estuaries can be attributed to contrasting marine conditions (HARRISON; WHITFIELD, 2006; GONZÁLEZ-CASTRO et al., 2009; NICOLAS et al., 2010). The SG subestuary presented the lowest abundance, richness and diversity of the community probably related to the estuarine-ocean gradient of the RdIP (FRAMIÑAN; BROWN, 1996; JAUREGUIZAR

et al., 2016). In this subestuary dominated *Odontesthes argentinensis*, a shallow-water pelagic fish known by its marine affinities and inhabits both estuarine and inshore waters (MORESCO; BEMVENUTI, 2006). The large phenotypic plasticity of this species allows it to adapt to a wide range of salinities (LLOMPART et al., 2013). We need to highlight the high abundance and diversity of species in the P subestuary probably related to the proximity to reproduction and breeding areas located in the inner RdIP estuary (ACHA; MACCHI, 2000; ACHA et al., 2008) such *Micropogonias furnieri* and *Brevoortia aurea* species. Regarding the fish assemblage composition of SCh, it showed more similarities with P than with SG. This could be associated to the location of SCh in between both systems. It is worthwhile highlight that SG is located next to the RdIP external limit. Outer conditions of the RdIP probably affect the SCh composition in a more similar way than it does to P. The SCh subestuary can be considered a transitional ecosystem.

Differences of biomass, abundance and species diversity among three subestuaries may also respond to inherent estuarine factors such as shape, size, depth, habitat-type availability and freshwater flow of the estuary (BLABER, 2000; HARRISON; WHITFIELD, 2006; FRANÇA et al., 2012) and factors influencing the connection to the RdIP system (e.g. mouth width and opening). In this regard, the morphology of the lower section of P and SCh determines

a more direct connection with the brackish waters of the RdIP (FREPLATA, 2003; ECHEVARRÍA et al., 2011). The SCh has a large area occupied by salt marshes located near the sampled area (FREPLATA, 2003), which could explain the high diversity specified in taxonomic terms (some species captured only there) and evenness (the lack of dominance). These habitats provide shelter and food resources to the fish community, hence influencing the community parameters found along the estuaries (FRANÇA et al., 2009; NICOLAS et al., 2010).

TEMPORAL VARIABILITY OF FISH ASSEMBLAGES

Species richness and abundance varied temporally in the three subestuaries, with peaks in warm periods and lows in cold periods. Temperature is the primary abiotic factor controlling life history patterns of fish (THIEL et al., 1995; HARRISON; WHITFIELD, 2006). In Mar Chiquita coastal lagoon, Argentina, species such as *Brevoortia aurea*, *Micropogonias furnieri*, *Mugil liza* and *Odontesthes argentinensis* were more abundant during the warm season (October-March) (COUSSEAU et al., 2011). On the other hand, low species richness is a common pattern found during the cold seasons (autumn-winter) (JAMES et al., 2007; FRANÇA et al., 2008; SELLESLAGH; AMARA, 2008; CARDOSO et al., 2011; FOWLER; BOOTH, 2013). From October 2002 to March 2003, ACUÑA PLAVAN et al. (2010) found a seasonal variability in the abundance of the fish community of P subestuary with a high predominance of *B. aurea* and *M. furnieri* during March 2003 (late summer).

For instance, estuarine resident species showed higher abundances during winter in Portuguese small estuaries while seasonal species using these areas as nurseries or feeding grounds were higher during summer and autumn (CARDOSO et al., 2011). Estuaries represent a fundamental link for numerous fish species, which use them during specific life stages (in an obligatory or opportunistic way) (VASCONCELOS et al., 2011). The use of the estuary of large RdIP estuary according to the life cycle of species could explain the temporal patterns in the subestuaries. The spatial and temporal distribution of fish assemblages in the RdIP has been extensively studied (DÍAZ DE ASTARLOA et al., 1999; JAUREGUIZAR et al., 2003a, 2006; GARCÍA et al., 2010; LORENZO et al., 2011) finding an occurrence of similar species between RdIP and the three subestuaries. This is the case of estuarine species, such as *M. furnieri*, *Menticirrhus americanus*, *Pogonias cromis*, *B. aurea* and *Paralichthys orbignyanus*, marine migrant species represented by *Trachinotus marginatus*, catadromous species such as *Mugil liza* and anadromous species like *Genidens barbatus*. The life cycles (maturity, spawning, larval and juvenile growth) of these species occur within a specific period and location in the RdIP (JAUREGUIZAR et al., 2003b; ACHA et al., 2008; LORENZO et al., 2011; MILITELLI et al., 2013). The large RdIP estuary allows reproductive opportunities for fish species as well as constitutes the habitat of fish larvae, developing similar ecological functions than the oceanic coastal systems. In this sense, the life cycle of the whitemouth croaker *M. furnieri* is related to the RdIP system but also to smaller subestuarine systems, as shown in figure 5. According

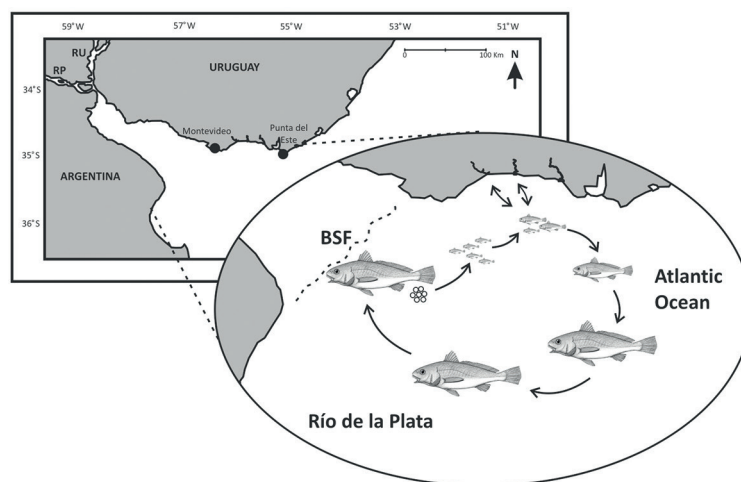


Figure 5. Schematic design of life cycle of *Micropogonias furnieri* in the Río de la Plata estuary and Uruguayan coast. The fish size and arrows direction show the adults spawning distribution in the bottom salinity front (BSF), subadults in the mouth of the RdIP and juveniles distributed between the subestuaries of the Uruguayan coast and RdIP. Pando=P; Solís Chico=SCh; Solís Grande=SG. Modified from GOYENOLA et al. (2009).

to JAUREGUIZAR et al. (2003b) the younger age classes (<2 years) are located in the same region of the RdIP during early winter and spring. A higher abundance of the same age classes of the species were registered in P from November 2002 to March 2003 (from spring to summer) by ACUÑA PLAVAN et al. (2010), as well as of juveniles during March 1999 and January 2000 (summer) by MARTÍNEZ and RETTA (2002). ACHA et al. (2008) suggested a displacement of the young-of-the-year *M. furnieri* individuals to shallow and protected areas of the Uruguayan coast after spawning season.

The role of subestuaries in the life cycle of fish species, and hence the connectivity between their populations and the ones from larger estuaries should receive further attention.

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