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Biotic and environmental factors affect Southwest Atlantic saltmarsh use by juvenile fishes

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ABSTRACT

Fish habitat use is affected by biotic and environmental factors. These factors do not act in isolation; they commonly operate together, and can be modified by the presence of habitat structure, like vegetation. We studied at the Bahia Blanca estuary (38° 52′ S, 62 0°6′ W), the seasonal patterns of fish habitat use in a *Spartina alterniflora* saltmarsh and a contiguous tidal flat, and related them with biotic and environmental factors. The results showed that all fish species contributed to differences in the structure of fish assemblages between areas. The silverside *Odontesthes argentinensis* and the menhaden *Brevoortia aurea* were more abundant and smaller in size in the saltmarsh. In this area, the structure of fish assemblage was positively correlated with the structure of benthic community. The latter, was probably related to the high abundance of the polychaete *Laeonereis acuta*, the main benthic prey for fishes. Environmental factors that correlated with the structure of fish assemblages were particulate organic matter and sediment penetrability, both in the saltmarsh and in the tidal flat. This evidenced that in terms of physical and chemical factors studied, both areas present similar characteristics for fishes. This work highlights that saltmarshes in southern hemisphere provide both protection and food resources for fishes, and give support to the notion of saltmarshes as important fish habitat worldwide.

1. Introduction

Since fish are dominant macrofaunal components of estuarine habitat, several studies have focused on their patterns of habitat use (Akin et al., 2005; Whitfield, 1999). At large scales, the initial distribution of individuals is determined by larval dispersal patterns (Bell et al., 1988) while at small scales, patterns of habitat use may be affected by abiotic (e.g. temperature: Helland et al., 2007; salinity: Tolley et al., 2005; water turbidity: Cottenie and De Meester, 2003; sediment type: Díaz de Astarloa and Fabré, 2003) and biotic factors (e.g. food abundance: Connolly, 1994; predation: Akin et al., 2005; competition: Robertson and Gaines, 1986). The relative importance of abiotic and biotic conditions in structuring fish communities has received much attention in recent years. However, most of the studies have evaluated separately biotic (e.g. Cross and Stiven, 1997; Hollingsworth and Connolly, 2006) and abiotic factors (e.g. Malavasi et al., 2004; Rozas, 1995), and proportionally, less information is available on the effect of both factors working together (but see Layman et al., 2000; Selleslagh and Amara, 2008).

Within estuaries, saltmarshes are widely recognized as important nursery grounds that support valuable coastal fisheries (Cattrijsse et al., 1994; Paterson and Whitfield, 2003; Rountree and Able, 1992). Juveniles of many fish species use the flooded saltmarsh much more intensively than adjacent nonvegetated areas (Zimmerman and Minello, 1984) since they find shelter and protection from predation (Boesch and Turner, 1984; Kneib, 1997) as well as rich food areas (Hollingsworth and Connolly, 2006; Kneib, 1997). The presence of vegetation can modify biotic and abiotic conditions, having significant effects on habitat use by fish (e.g. Crinall and Hindell, 2004; Rozas and Minello, 1998). In saltmarshes, plants can affect fish habitat use directly through the provision of shelter (Minello et al., 2003), or indirectly by increasing food availability (Netto and Lana, 1997).

The role that saltmarshes plays for juvenile fishes has been reported from most regions of the world: North America (Rountree and Able, 1992; Rozas and Zimmerman, 2000), Europe (Cattrijsse et al., 1994; Green et al., 2009), Asia (Jin et al., 2007), Australia

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(Connolly et al., 1997; Platell and Freewater, 2009) and Africa (Le Quesne, 2000; Paterson and Whitfield, 2003). The Southwest (SW) Atlantic intertidal areas (from southern Brazil (32° S) to northern Argentinean Patagonia (42° S)) are globally important by virtue of their great extent (Isaach et al., 2006). They are characterized by extensive tidal flats surrounded by saltmarshes vegetated by *Spartina densiflora*, *Spartina alterniflora*, and *Sarcocornia perennis* (e.g. Isaach et al., 2006). Saltmarshes dominated by *S. alterniflora* occupy the mid-intertidal oceanic front of the saltmarsh as monospecific stands and are inundated daily by high tides (e.g. Isaach et al., 2006). In these saltmarshes, fish species can access directly to the vegetated area. The knowledge about nekton assemblages in SW *S. alterniflora* saltmarshes is scarce and even less is known about the role that these areas play for fishes and how biotic and environmental factors can influence their patterns of habitat use.

Information about southern hemisphere saltmarshes is very important because together with previous data from saltmarshes of different regions of the world, it will allow having a general notion of the role of these vegetated areas worldwide. In this context, the aim of the present study was to evaluate the spatial and temporal patterns of habitat use by fishes in a *S. alterniflora* saltmarsh in relation to a contiguous nonvegetated area, and the biotic and environmental factors that could explain fish distribution patterns in both areas.

2. Materials and methods

2.1. Study area

The study was performed at the Bahía Blanca estuary; a large macrotidal embayment (2300 km^2) affected by semidiurnal tides that reach up to 4 m in height (Perillo and Piccolo, 1999). This estuary has extensive tidal flats surrounded by saltmarshes mostly dominated by species of *Spartina* (*S. densiflora* and *S. alterniflora*) and by *S. perennis* (e.g. Isaach et al., 2006). At the studied site (Villa del Mar, 38° 52′ S, 62 0°6′ W), *S. alterniflora* occupies the lower intertidal zone; the middle zone is dominated by *S. perennis* while *S. densiflora* is restricted to a narrow strip on the higher part of the saltmarsh (~ 3 m width). During low tide, both the saltmarsh and a wide area of the tidal flat are exposed. Sample collection was carried out in the low saltmarsh.

The sampling design was planned as a two-habitat comparison, sampling a paired vegetated and nonvegetated area (hereafter, “saltmarsh” and “tidal flat” respectively) over a year.

2.2. Spatial and temporal variability in fish assemblage structure and fish size distribution

To assess differences in fish abundance between the saltmarsh and the tidal flat and among seasons, fish were collected seasonally in both areas during one year, using a beach seine towed 50 m parallel to the coast. Samples (n = 7) were taken 1 h after high tide, when the saltmarsh and the tidal flat were simultaneously inundated and water levels were similar. The captured individuals were identified, counted and measured (total length, accuracy 0.01 mm). Given logistic and economic constrains, fish samplings were performed in a *S. alterniflora* saltmarsh at Villa del Mar over several days. Every day 3 to 5 tows were performed in both areas and then averaged. Each day was considered as a replicate.

From the overall number of species collected, only the silverside *Odontesthes argentinensis* was abundant enough to make seasonal comparisons between the saltmarsh and the tidal flat. The remaining species were not well represented in the samples during the fall, winter and spring, so comparisons between areas were made only for the summer. Differences in fish assemblage structure between the saltmarsh and the tidal flat were explored using multivariate analysis (PRIMER 6 software package, Clarke and Warwick, 2001) based on Bray–Curtis dissimilarities on fourth-root transformed data (Clarke and Warwick, 2001). Then the significance of differences was analyzed with one-way analyses of similarities (ANOSIM). Non-metric multidimensional scaling (nMDS) ordinations were obtained to illustrate sample similarities between areas. Fish species most responsible for the multivariate pattern were identified using a similarity percentages analysis (SIMPER) on abundance data. Species that contributed at least 10% dissimilarity were considered important differentiators between areas (e.g. Bulleri et al., 2005). Differences in the abundance of these species between the saltmarsh and the tidal flat were evaluated with t_c tests (Zar, 1999). The t_c value is equal to the t value when sample sizes are the same, but degrees of freedom decrease as the difference between variances of the 2 groups increases (Zar, 1999). When assumptions of parametric statistics could not be met and there were no possible transformations, Mann–Whitney tests was used (Conover, 1980). For *O. argentinensis*, differences in abundance between areas and seasons were evaluated using two-way ANOVA with subsequent Tukey's HSD tests (Zar, 1999).

To evaluate differences in fish size distribution between areas, fish samples within each season were pooled and a Kolmogorov–Smirnov test (Zar, 1999) was performed independently for each species. Comparisons were made with individuals collected in summer for the whitemouth croaker *Micropogonias furnieri* and the menhaden *Brevoortia aurea*, and for *O. argentinensis* collected in autumn, winter and spring separately. The test was not performed for the Jenyns's sprat *Ramnogaster arcuata* and *O. argentinensis* collected in summer due to low abundance of these species.

2.3. Spatial variation in food abundance for fishes

One of the main functions attributed to saltmarshes is their role as feeding areas for fishes (e.g. Hollingsworth and Connolly, 2006; Kneib, 1997). To assess differences in food abundance for fish between the saltmarsh and the tidal flat, samples of benthos (macro and meiofauna) and zooplankton were obtained during summer. Since the general objective of this work was to evaluate the relationship between biotic and environmental factors with fish assemblage structure, and due to the fact that only one species was collected during autumn, winter and spring seasons, variables were only measured during summer when several fish species were present in the study area. The same approach was used for environmental variables (see Section 2.4).

For macrofauna, 7 sediment samples (10 cm in diameter and 10 cm deep) were randomly collected at each area. Samples were sieved through a 500 μm mesh, and the retained organisms were identified and quantified under a binocular microscope (10×). Also for meiofauna, 7 samples of sediment were extracted in each area (10 cm in diameter and 3 cm deep), sieved with a 62 μm mesh and fixed in 4% formalin. A subsample was stained with Bengal Rose to facilitate individual's visualization. Organisms retained were identified, classified and counted under a binocular microscope (40×).

To assess differences in zooplankton abundance between the saltmarsh and the tidal flat, zooplankton samples (n = 7) were collected in both areas with a 65 μm mesh net, which was towed 30 m parallel to the coast. Samples were fixed in 4% formalin and were examined under a microscope (4×) in a 5 ml Bogorov chamber (10 × 10 cm). In those samples, where organisms density was very high, aliquots of samples (n = 3, volume = 5 ml) were extracted and organisms were identified and counted on the camera. The average abundance was calculated from the 3 sub-samples and extrapolated to the total volume collected.

Differences in macrofauna, meiofauna and zooplankton composition between the saltmarsh and the tidal flat were explored separately using multivariate analysis (PRIMER software package, Clarke and Warwick, 2001), following the same procedure used for the analysis of fish assemblage structure. Differences in the abundance of species that contributed to dissimilarities between the saltmarsh and the tidal flat were evaluated with t_c tests (Zar, 1999).

2.4. Environmental variables

Environmental characteristics can also affect the distribution patterns of fishes in saltmarshes (e.g. Malavasi et al., 2004; Rozas, 1995). For this reason, physical and chemical variables of the water and the sediment (sediment penetrability, water turbidity, in vivo chlorophyll *a* and particulate organic matter (POM)) were measured in summer to assess whether they differ between the saltmarsh and the tidal flat. Sediment penetrability (n = 7) was measured with a hand penetrometer, and was calculated as the pressure (kg cm^{-2}) needed to introduce a piston into the sediment to a standard depth. To determine water turbidity and in vivo chlorophyll *a*, water samples were collected (n = 7) in each area and measured with a handheld fluorometer (detection range: turbidity, 0.5–150 NTU; chlorophyll, 0.05–300 mg chl^{-1}). For POM, water samples (n = 7, volume: 500 ml) were collected at 20 cm above the sediment. In the laboratory, samples were filtered through a Whatman GF/C filter previously burned for 2 h at 500 °C. The filters with samples were dried at 60 °C for 72 h, weighed, incinerated at 500 °C for 6 h and weighed again. POM content was measured as ash-free dry weight. All samples were collected approximately 1 h after high tide, on the same days that fish sampling was made. Three to five replicates per day were obtained and averaged, and days were considered replicates. Differences between areas in the environmental variables measured were evaluated using t_c tests (Zar, 1999).

2.5. Relationship between fish assemblage structure, food abundance and environmental variables

The relationships between fish assemblages and benthic and zooplanktonic composition were analyzed separately for each area using RELATE (PRIMER software, Clarke and Warwick, 1994). This routine correlates similarity measures from two matrices using a Spearman Rank correlation. A ρ value is then calculated by comparing this correlation with a large number of random (Monte Carlo) simulations. The multivariate BIOENV procedure (PRIMER software, Clarke and Warwick, 1994) was used to explore the potential relationships between the environmental variables and fish assemblage structure in the saltmarsh and in the tidal flat separately. This analysis compares the fish similarity matrix with the distance environmental matrix and selects the best explanatory variables maximizing the rank correlation between them.

3. Results

3.1. Spatial and temporal variability in fish assemblage structure and fish size distribution

Four fish species were collected both in the saltmarsh and in the tidal flat: *O. argentinensis*, *B. aurea*, *M. furnieri* and *R. arcuata* (Table 1). The structure of the fish assemblages was different between areas (ANOSIM: R = 0.26, $p<0.05$, Fig. 1a). SIMPER analysis showed that all species (*O. argentinensis*: 24.18%, *M. furnieri*: 36.47%, *B. aurea*: 20.83% and *R. arcuata*: 18.51%) contributed to the dissimilarities between saltmarsh and the tidal flat. The abundance of *O. argentinensis* was different between seasons ($F_{3,50} = 7.55$, $p<0.001$) and areas ($F_{1,50} = 13.27$, $p<0.001$). This species was more abundant in the saltmarsh than in the tidal flat (Tukey test, $p<0.05$, Fig. 2) and in spring than in summer (Tukey test, $p<0.05$, Fig. 2). The abundance of *B. aurea* was also higher in the saltmarsh than in the tidal flat (t_c value = 2.27, df = 12, $p<0.05$, Fig. 3a). No differences in the abundance of *R. arcuata* (t_c value = 0.09, df = 12, $p>0.9$, Fig. 3b) and *M. furnieri* were found between areas (Z = 0.83, df = 12, $p>0.4$, Fig. 3c).

The size distribution of *O. argentinensis* showed differences between the saltmarsh and the tidal flat in autumn (Dmax = 0.05, $p<0.01$) and spring (Dmax = 0.03, $p<0.001$). In autumn, individuals under 70 mm were more abundant in the saltmarsh while individuals between 70 and 100 mm were more abundant in the tidal flat (Fig. 4a). In spring, the same pattern described for the fall was observed, with a higher proportion of smaller sizes, in this case under 80 mm in the saltmarsh and the opposite pattern, with higher proportion of individuals over 80 mm in the tidal flat (Fig. 4c). No differences in size distribution between areas were found for *O. argentinensis* in winter (Dmax = 0.25, $p>0.1$, Fig. 4b). For *B. aurea*, size distribution was also different between areas (Dmax = 0.01, $p<0.001$), showing a higher proportion of smaller individuals in the saltmarsh and the opposite pattern in the tidal flat, with a higher proportion of larger individuals (Fig. 5a). No differences in size distribution between the saltmarsh and the tidal flat were found for *M. furnieri* (Dmax = 0.25, $p>0.05$; Fig. 5b).

3.2. Spatial variation in food abundance for fishes

The macrofauna was composed by two polychaete species (*Capitella capitata* and *Laeonereis acuta*), one species of small gastropod (*Heleobia australis*) and one unidentified priapulid species with differences between the saltmarsh and the tidal flat (ANOSIM: R = 0.52, $p<0.001$; Fig. 1b). SIMPER analysis showed that *L. acuta* (15.70%) and *H. australis* (83.03%) were the species that most contributed to differences between areas (55.78%). The abundance of *L. acuta* was higher in the saltmarsh (t_c value = 3.35, df = 12, $p<0.01$; Fig. 6a), while *H. australis* was more abundant in the tidal flat (t_c value = 3.56, df = 12, $p<0.01$; Fig. 6b).

The meiofauna was composed by nematodes, ostracods, foraminiferans and copepods, with differences between the saltmarsh and the tidal flat (ANOSIM: R = 0.73, $p<0.05$; Fig. 1c). SIMPER analysis showed that all meiofaunal groups contributed significantly to differences between areas (foraminiferans, 36.75%; nematodes, 25.79%; copepods 19.03%; ostracods, 19.02%). The abundances of all groups were higher in the tidal flat than in the saltmarsh (nematodes, t_c value = 4.58, df = 12, $p<0.001$; ostracods, t_c value = 3.75, df = 6.21, $p<0.01$; foraminiferans t_c value = 4.72, df = 12, $p<0.001$; copepods, t_c value = 3.54, df = 6.07, $p<0.05$; Fig. 7a–d).

The zooplankton community was composed of: nauplii larvae, polychaete larvae, gastropod larvae, cladocerans, copepods, ostracods and foraminiferans. No differences were found in the composition of the zooplankton assemblage between the saltmarsh and the tidal flat (ANOSIM: R = 0.04, $p>0.2$, Fig. 1d).

3.3. Environmental variables

Sediment penetrability was higher in the tidal flat than in the saltmarsh (t_c value = 2.76, df = 6.32, $p<0.05$, Table 2). No differences were detected in water turbidity (t_c value = 1.19, df = 7.70, $p>0.2$, Table 2), in POM content (t_c value = 0.03, df = 12, $p>0.9$, Table 2) nor in in vivo chlorophyll *a* between areas (t_c value = 1.53, df = 12, $p>0.1$, Table 2).

Table 1
Absolute and relative abundance of fishes collected from saltmarsh and tidal flat at Villa del Mar saltmarsh.

Scientific name	Common name	Saltmarsh		Tidal flat	
		n	%	n	%
Odontesthes argentinensis	Silverside	696	30.26	169	26.45
Micropogonias furnieri	White-mouth croaker	661	28.74	262	41
Brevoortia aurea	Brazilian menhaden	929	40.39	172	26.92
Ramnogaster arcuata	Jenyn's sprat	14	0.61	36	5.63
Total		2300		639	

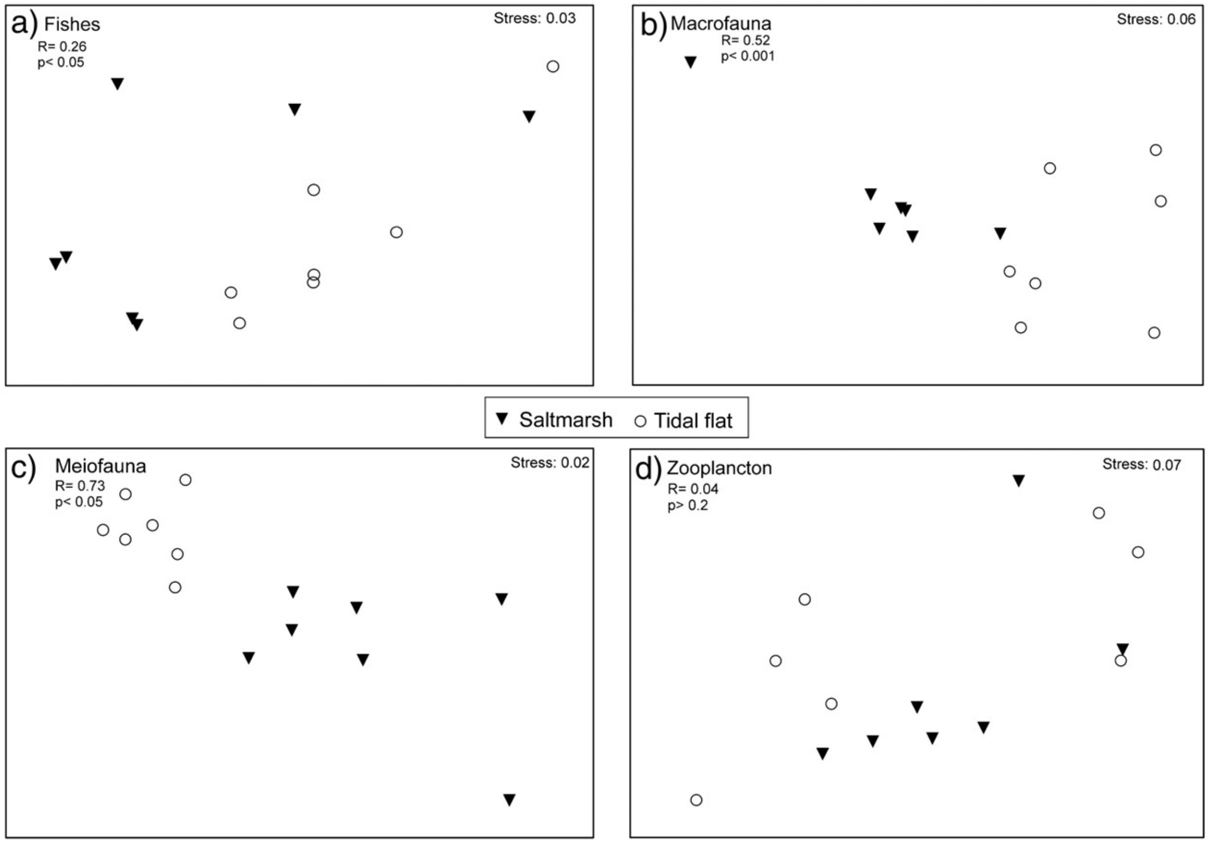

Fig. 1. Non-metric multidimensional scaling (nMDS) plots on four-root transformed data comparing a) the structure of fish assemblages b) macrofaunal, c) meiofaunal and, d) zooplankton composition between the saltmarsh and the tidal flat during summer season.

3.4. Relationship between fish assemblage structure, food abundance and environmental variables

Fish assemblages were positively correlated with the structure of the benthic community in the saltmarsh ($\rho = 0.48$, $p < 0.05$), but no correlation was found in the tidal flat ($\rho = 0.34$, $p > 0.05$). No correlation between fish assemblage structure and zooplankton was found for any of the two studied areas (saltmarsh, $\rho = -0.25$, $p > 0.05$; tidal flat, $\rho = 0.21$, $p > 0.05$).

Regarding the environmental factors, POM and sediment penetrability were the variables that better explained the structure of the fish assemblage, both in the saltmarsh (BIOENV, $\rho = 0.75$) and in the tidal flat (BIOENV, $\rho = 0.62$).

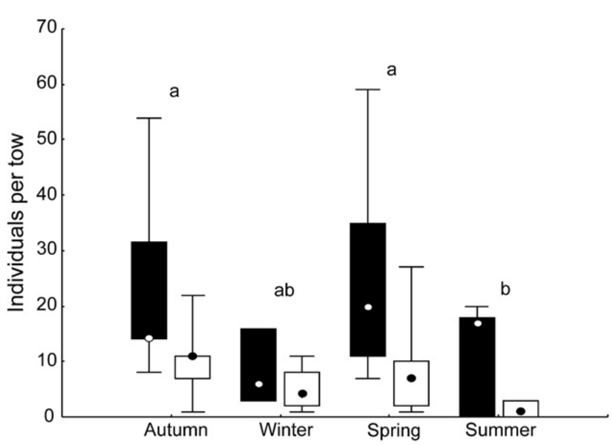

Fig. 2. Abundance of *Odontesthes argentinensis* in the saltmarsh (black boxes) and in the tidal flat (empty boxes). Hereafter, box plots are constructed with limits of boxes being the 75th and 25th percentiles, lines represent 10th and 90th percentiles. Marks inside boxes are medians.

4. Discussion

Our work showed that fish assemblage's structure differed between the saltmarsh and the tidal flat, and that all fish species were contributing to such differences. The abundance of *O. argentinensis* and *B. aurea* was higher in the saltmarsh where smaller sizes of both species were found in higher proportion. In this area, fish assemblage structure was positively correlated with biotic and environmental variables (benthic fauna composition, POM and sediment penetrability) while in the tidal flat it was only correlated with environmental variables (POM and sediment penetrability).

M. furnieri, *B. aurea* and *R. arcuata* were found only during summer, showing a seasonal use of the saltmarsh and the tidal flat. This is in accordance with previous research that demonstrated that many fish species use saltmarsh and contiguous nonvegetated areas during early juvenile stages (Jin et al., 2007; Rountree and Able, 1992; Salgado et al., 2004), but then move out onto the continental shelf (Able and Fahay, 1998; Salgado et al., 2004). The silverside *O. argentinensis* was collected throughout the year, indicating that this species is a permanent inhabitant of the studied area.

O. argentinensis and *B. aurea* were more abundant in the saltmarsh, where smaller sizes of both species were found in higher proportion. Increased food resources appear to be associated with high growth rates in vegetated habitats (Levin et al., 1997; Sogard, 1992). It has been observed that many young fishes use shallow estuarine habitats like saltmarshes, where they exploit abundant food supplies to maintain rapid growth (Boesch and Turner, 1984; Kneib, 1993). These high growth rates reduce the time that young fish spend during its life in size classes that are more vulnerable to predators (Beck et al., 2001).

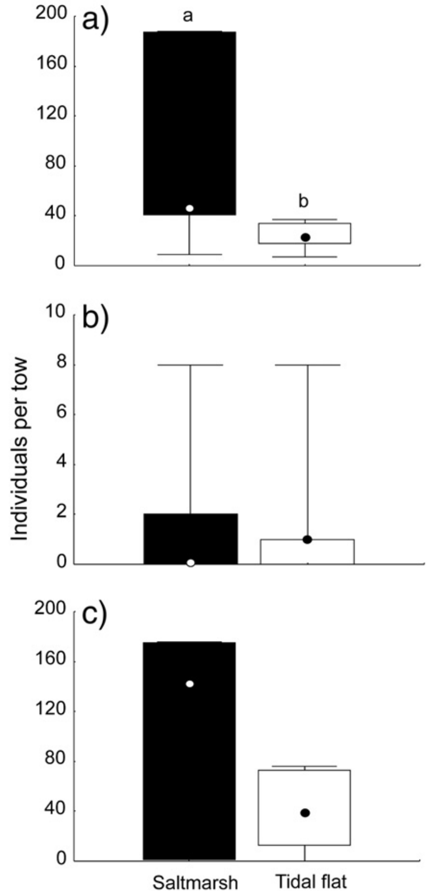

Fig. 3. Abundance of (a) *Brevoortia aurea*, (b) *Ramnogaster arcuata* and (c) *Micropogonias furnieri* in the saltmarsh (empty boxes) and in the tidal flat (white boxes). Different letters denote significant differences between areas.

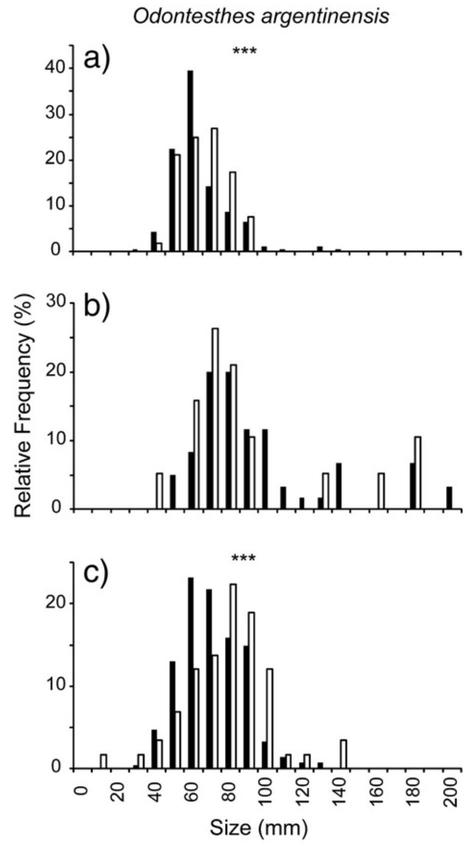

Fig. 4. Size–frequency distribution of *Odontesthes argentinensis* collected in the saltmarsh (black bars) and in the tidal flat (empty bars) in (a) autumn (b) winter and (c) spring. Asterisks denote differences in size distribution between areas.

In this way they increase the survivorship of early juvenile fishes (Sogard, 1997). In the other hand, the importance of structure is that structurally complex habitats such as saltmarshes provide animals protection (Platell and Freewater, 2009; Rozas and Zimmerman, 2000), by decreasing the ability of predators to detect, capture or manipulate their preys (Seitz et al., 2001; Sih et al., 1992). When using *S. alterniflora* saltmarsh, small size fishes could be taking advantage by accelerating growth and also by reducing the predation risk of birds such as *Podiceps major*, *Phalacrocorax brasilianus* and *Larus dominicanus* all of which have been reported as fish consuming at the Bahia Blanca estuary (Delhey and Petracci, 2004).

The concept that saltmarshes are extensively used by juvenile fishes because it provides enhanced foraging opportunities due to their high productivity (Hollingsworth and Connolly, 2006; Kneib, 1997) has been based on studies on benthic prey abundance (e.g. Jackson, 1985; Lana and Guiss, 1992). Nevertheless, until now, there are no studies in the literature that compare zooplankton prey abundance between saltmarshes and adjacent tidal flats. The results of the present work showed that, for planktivorous fishes (*O. argentinensis* < 80 mm; Martinetto et al., 2005; *B. aurea*; Giangiobbe and Sanchez, 1993), both the saltmarsh and the tidal flat offer the same advantages in terms of feeding habitat, because the abundance of zooplankton did not differ between areas. Nevertheless, the higher abundance of planktivorous fishes in the saltmarsh could be evidence that the preference for the vegetated area by this trophic group could not be related, at least directly, with food abundance. The latter strengthens our previous conclusions about the role of the saltmarsh as refuge areas for fish.

The structure of fish assemblage in the saltmarsh was correlated with the structure of benthic community, which could be an evidence of the role of this habitat as feeding ground for benthivorous fishes (*O. argentinensis* > 80 mm, Martinetto et al., 2005; *M. furnieri*, Hozbor and García de la Rosa, 2000). Polychaetes have been reported as important prey for several fish species in saltmarshes (e.g. *Solea solea*, Cabral, 2000; *Platichthys flesus*, Hampel et al., 2005). The polychaete *L. acuta* was the unique benthic prey found in the gut contents of juveniles of *O. argentinensis* and *M. furnieri* in SW *S. alterniflora* saltmarshes (M. Valiñas., unpub. data). It was also found that benthivorous fish affected the highest

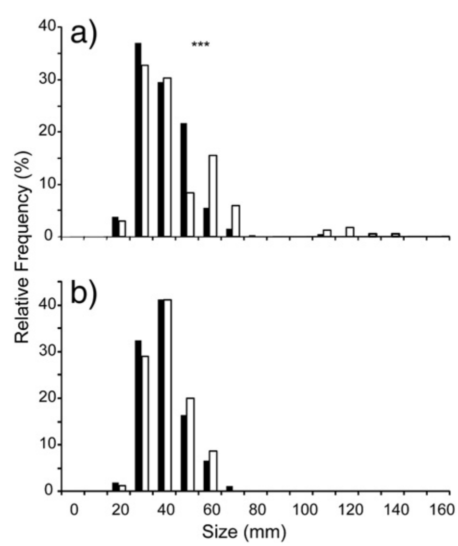

Fig. 5. Size–frequency distribution of (a) *Brevoortia aurea* and (b) *Micropogonias furnieri* collected during summer in the saltmarsh (black bars) and in the tidal flat (empty bars). Asterisks denote differences in size distribution between areas.

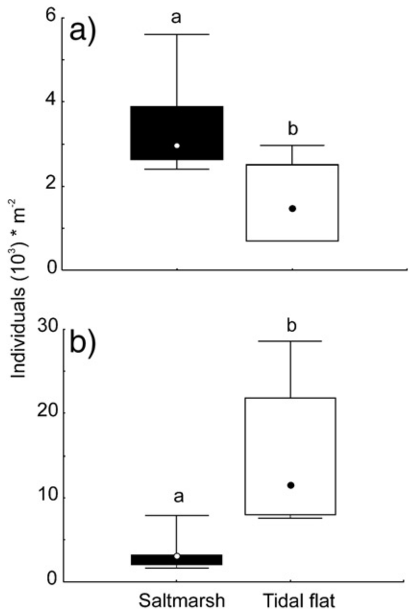

Fig. 6. Abundance of macrofaunal prey (a) *Laeonereis acuta*, (b) *Heleobia australis* in the saltmarsh (empty boxes) and in the tidal flat (white boxes). Different letters denote significant differences between areas.

sizes of polychaetes in the saltmarsh (M. Valiñas., unpub. data). Though, as mentioned previously, vegetation can interfere in the detection, capture, and manipulation of prey (e.g. Halpin, 2000; Platell and Freewater, 2009; Rozas and Zimmerman, 2000), it has also been observed that, for small fishes plants do not represent a physical obstacle (e.g. *Nannoperca australis*, Warfe and Barmuta, 2004). Thus, for benthivorous fishes, saltmarshes could be a better feeding area than tidal flats due to the higher abundance of polychaetes, which in turn could be explaining the correlation found between fishes and benthos.

Environmental factors can also influence saltmarsh habitat use by fishes (e.g. Malavasi et al., 2004; Rozas, 1995). In this work, the sediment penetrability was correlated with fish assemblage structure both in the saltmarsh and in the tidal flat, even when this variable differed between areas. Sediment penetrability plays an important role in the foraging efficiency of organisms that feed on benthic community (Mouritsen and Jensen, 1992). Tactile predators, like *M. furnieri*, select habitats with high sediment penetrability (Chao and Musick, 1977; Valiñas et al., 2010) to penetrate deeper into the substrate and thereby increase prey capture efficiency (Kuwae et al., 2010; Mouritsen and Jensen, 1992). The vegetated and nonvegetated areas that we studied are characterized by a soft substrate composed mostly by fine sand, silt and clay (M. Addino, pers. comm.) This could benefit prey capture and could explain the correlation found between sediment penetrability and fish assemblage structure in both areas.

Another environmental variable that correlated with fish assemblage's structure both in the saltmarsh and in the tidal flat was POM. POM concentration is used as an indicator of food availability in the water column (e.g. Martinetto et al., 2007). However, given that no correlation was observed between the fish assemblage structure and the composition of zooplankton and *in vivo* chlorophyll *a* (as an indirect measure of phytoplankton abundance), this variable would not be associated, at least directly, with food availability. It is possible that sediment penetrability and POM concentration were correlated because substrates highly penetrable are more easily resuspended, enhancing POM levels in the water column (Valeur et al., 1995). Thus, the correlation between POM and fish assemblages would be a spurious correlation. Nevertheless, more information is needed to confirm this hypothesis.

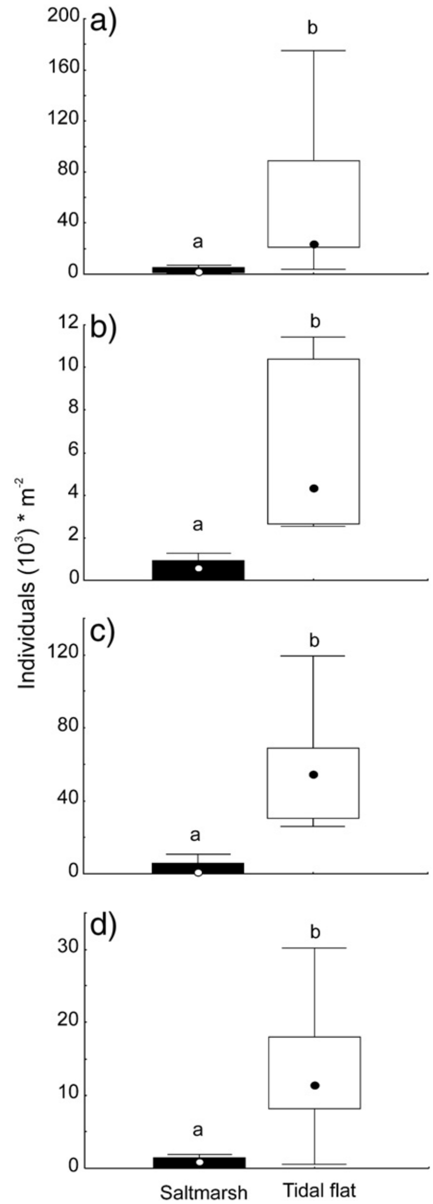

Fig. 7. Abundance of meiofaunal prey (a) nematodes, (b) ostracods (c) foraminiferans, and (d) copepods in the saltmarsh (empty boxes) and in the tidal flat (white boxes). Different letters denote significant differences between areas.

In summary, *S. alterniflora* saltmarsh in SW Atlantic coasts supported significantly greater densities of fishes than nonvegetated sites and constitute an important ecosystem for these organisms. The presence of juvenile of different species emphasizes the importance of the vegetated areas as a nursery ground, where organisms encounter suitable conditions for their development. Although both biotic and environmental factors influenced the habitat use by juvenile fish, the latter would not be responsible for the differences in the structure of the fish assemblage between areas. In terms of the physical and chemical factors studied,

Table 2
Means (SD) of environmental variables measured in the saltmarsh and in the tidal flat. Asterisks denote significant differences between areas.

Environmental variable	Saltmarsh	Tidal flat	*P*
Sediment penetrability (kg cm^{-2})	0.64 (0.57)	0.03 (0.09)	<0.05*
POM (g m^{-3})	35.8 (13.65)	35.58 (9.18)	0.97
Water turbidity (NTU)	20.66 (3.24)	24.78 (8.52)	0.25
In vivo chlorophyll *a* (μg l^{-1})	19.64 (1.84)	18.47 (0.86)	0.15

both areas present identical characteristics for fishes. This work provides information about southern hemisphere saltmarshes, gives support to the notion of saltmarshes as important fish habitats worldwide, and underscores the need for recognition of these vegetated areas in management plans for fishes.

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