



Interaction strength varies in relation to tidal gradient and spatial heterogeneity in an intertidal Southwest Atlantic estuarine food web



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ABSTRACT

Interaction strength is a key component in food-web dynamics being highly variable over time and space, depending on biotic and abiotic conditions. Intertidal soft bottom ecosystems are essential nursery and feeding sites for migratory shorebirds and marine fishes, which in turn affect infaunal assemblage and the food web dynamic. In these systems, organisms that modify the resource availability to other species (i.e. burrowing crabs) are expected to have significant consequences on infauna distribution and the interactions among organisms. Here we simultaneously evaluated the interaction strength of birds and fishes on infaunal prey in areas with and without crab bioturbation. Field experiments showed weak predator–prey interactions of both predators; however, birds exerted high impact on meiofauna inside bioturbated areas during the warm season. Moreover, the effect of fishes differed depending on bioturbation and another factor such as climatic events (e.g. El Niño Southern Oscillation (ENSO)). Thus, our results suggest that interaction strength of birds and fishes on prey are context dependent, varying between different areas, tidal time exposition, ENSO episode and seasons. Also, our results exemplify how the outcome of predator–prey interaction strength can depend on other factors such as the activity of other species that modify the environment.

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1. Introduction

The interaction strength of species is a key component in most food-web dynamics and is defined as the magnitude of the effect of one species on the abundance of other (e.g. Berlow et al., 1999; Laska and Wootton, 1998). The distribution of interaction strength of most species is highly skewed towards weak or no detectable effects on the abundance of other species, while a few have strong effects (e.g. Fagan and Hurd, 1994; O'Gorman et al., 2010). In addition, the strength of biological interactions is highly variable over time and space, depending on biotic and abiotic conditions (Peacor and Werner, 2004; Petraitis and Dudgeon, 1999). For example, interaction strength might depend on nutrient availability (Setälä et al., 1997), precipitation (Polis et al., 1997), latitude (Pennings and Silliman, 2005), predator identity and diversity (Bruno and O'Connor, 2005) or population size structure (see Harley, 2003 and references therein). Thus, given that interaction strength is context dependent, species that are weak interactors in a particular scenario can be strong interactors in others (Harley, 2003).

Weak interactors are able to magnify spatiotemporal variations in community structure (Berlow, 1999) or to promote the persistence and stability of communities at local (e.g. Christianou and Ebenman, 2005; Emmerson and Raffaelli, 2004) and landscape level (Maser et al., 2007). Since weak interactions are highly variable and widespread, they contribute to the maintenance of community biodiversity (Berlow, 1999; Otto et al., 2007). In two dimensional spatial habitats (e.g. rocky shores: Menge, 1995; Menge et al., 1994; Navarrete and Berlow, 2006) interaction strength is often strong and several times analogous to keystone species (e.g. O'Gorman and Emmerson, 2009; Power et al., 1996) producing dramatic trophic cascades. However, in three dimensional habitats (e.g. lakes: Shurin et al., 2002; reefs: Grabowski, 2004; kelp forest: Sala and Dayton, 2011; soft bottom: O'Gorman et al., 2010) weak interactions occur more often stabilizing communities (O'Gorman and Emmerson, 2009; O'Gorman et al., 2010) and, in these types of environment interactions are not strong probably because prey can use the third dimension to escape (see Jaksic, 1986).

In soft-bottom systems, despite the predominance of weak predator–prey interactions, strong top-down control can be exerted by predators such as birds and fishes (e.g. Hamilton et al., 2006; Heck and Valentine, 2007). Birds are important consumers in intertidal environments and usually strongly impact community structure due to their high energetic requirements (Wootton, 1997). Fishes are also important predators (Norton and Cook, 1999) and they use soft intertidal habitats as breeding

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(Green et al., 2009; Minello et al., 2003) and feeding sites (Kneib, 1997; Platell and Freewater, 2009). Birds and fishes have different energetic requirements and eat during limited periods in different moments of the tidal cycle (i.e. fishes during high tides and birds during low tides; Galbraith et al., 2002; Rozas, 1995). Thus predator–prey interaction of birds and fishes is expected to be variable along the tidal cycle.

Besides the variability along tidal cycle, predation rates in soft bottom intertidals can also be modified by the presence of structurally complex microhabitats (Beukers and Jones, 1997; Rozas and Zimmerman, 2000) such as those generated by bioturbation (e.g. Murray et al., 2002). Bioturbation can affect the distribution and interactions among infaunal organisms (Reise, 2002; Volkenborn et al., 2009). For example, burrows and pits can concentrate food (Reise, 2002) positively affecting infaunal prey abundance (Volkenborn et al., 2009), and consequently increasing the per capita prey capture by predators inside sites with burrows (e.g. the silverside fish *Odontesthes argentinensis*: Martinetto et al., 2005; the two-banded Plover *Charadrius falklandicus*: Botto et al., 2000). Bioturbation has also important macro-scale effects on the structure of sediments and on the soft-bottom assemblages (e.g. the south-western Atlantic intertidal burrowing crab *Neohelice* (= *Chasmagnathus*) *granulata*, Iribarne et al., 1997; the shrimp *Callinassa kraussi*, Pillay et al., 2007; the polychaete *Arenicola marina*, Volkenborn and Reise, 2006) in such a way that can affect extensive areas on estuarine and low energy intertidal mudflats.

The south-western Atlantic estuaries are important nursery and feeding areas for migratory and local birds (e.g. Botto et al., 1998; Mariano-Jelichich et al., 2003) and fishes (e.g. Cousseau et al., 2001; Valiñas et al., 2010). Particularly, the intertidal of these estuaries (from 32°S in southern Brazil to 42°S in the northern Argentinean Patagonia) is characterized by the presence of the crab *N. granulata* (e.g. Iribarne et al., 1997; Spivak et al., 1994). This important bioturbator removes large amounts of sediment (up to 5 kg m⁻² day⁻¹; Iribarne et al., 1997) and affects the sedimentary environment (Botto and Iribarne, 2000). Inside crab beds (i.e. large areas occupied by crabs) the sediment softness, organic matter, and water content are larger than outside crab beds (Escapa et al., 2004). Moreover, infauna is affected by bioturbation in a variety of ways; for example some groups are more abundant inside crab beds while other groups are less abundant there (Escapa et al., 2004). Birds (e.g. Botto et al., 1998) and fishes (e.g. Martinetto et al., 2005) feed on infauna in these areas. Nevertheless, several bird species avoid bioturbated areas probably because there is a decreased available area for predation inside crab beds (i.e. due to area occupied by burrow entrances, Escapa et al., 2004) and maximize the distance to burrows when foraging (Iribarne et al., 2005). Therefore, the distribution of benthic species and predators are strongly affected by crab bioturbation. Thus, the outcome of predator–prey interactions may be modified between sites with and without bioturbation (see Martinetto et al., 2005; Palomo et al., 2003).

In this context, the aim of our work was to evaluate the interaction strength of two different predators, birds and fishes, on intertidal soft bottom infaunal prey. Given the higher energetic requirements of birds, we hypothesized that these will have stronger effects than fishes. Moreover, considering that birds feed during low tide (thereafter “terrestrial predators”) and fishes during high tide (thereafter “aquatic predators”) we evaluated the interaction strength in two different tidal levels (lower and upper intertidal) and in two different sites; one with crab bioturbation (thereafter “inside crab bed”) and another without crab bioturbation (thereafter “outside crab bed”).

2. Materials and methods

2.1. Study site

The study was performed at the Mar Chiquita Coastal Lagoon (37° 40'S, 57° 23'W, Argentina; an UNESCO Man and the Biosphere Reserve),

in a tidal flat zone situated 2.5 km upstream from the lagoon inlet during a cold (2007) and a warm (2008) season. This coastal lagoon is a brackish water body (46 km²), permanently connected to the sea (Reta et al., 2001) with low tidal amplitude (≤ 1 m) and a wide salinity range (2 to 35; Spivak et al., 1994). Mudflats are surrounded by a large *Spartina densiflora* marsh area (Isacch et al., 2006). The burrowing crab *N. granulata* is distributed in the *S. densiflora* salt marsh and the intertidal mudflats, where there are large burrowing beds (Spivak et al., 1994). The present study was made in open intertidal mudflats, which are the only habitats flooded daily by tides. Due to logistic constraints to find more extensive areas with similar tidal heights and general environmental characteristics to perform a larger experiment, we selected two sites, one with active bioturbation by crabs (“inside crab bed”) and a paired site without crabs (“outside crab bed”). Inside each site we defined a lower intertidal level (regularly flooded) and an upper intertidal level (sediment exposed most of the time).

2.2. Effects of terrestrial vs. aquatic predators on infaunal community

To evaluate the effects of terrestrial and aquatic predators on infaunal community we made exclusion experiments that were deployed simultaneously at the two intertidal levels (upper and lower) and in the site with crab bioturbation and the site without crabs defined above. The experimental design consisted in five treatments (n = 10 for each treatment): 1) terrestrial predator exclusion (mainly excluded birds but also crabs and other occasionally predators from land during low tide), 2) aquatic predator exclusion (excluded mainly fishes but also crabs during high tide), 3) artifact control for terrestrial predator exclusion (hereafter “terrestrial control”), 4) artifact control for aquatic predator exclusion (hereafter “aquatic control”) and 5) natural control.

Terrestrial predator exclusions were cages (area: 1 m², height: 0.2 m, plastic mesh size: 2 cm opening; see Fig. 1) with roof and without floor. In the corners of the cages, hoops (constructed with security seals) were used to hold the plastic mesh to the PVC tubes (1.5 m high, 0.2 m buried in sediment) maintaining the cages in the same place when tides reached the cages. The lower borders of the cages (those borders in contact with the sediment) were equipped with buoys to keep cages floating during high tide but, allowing cages standing on the sediment during low tide. This cage design allowed fishes and crabs to have access to the sediment during high tide (i.e. cages floating) and avoided birds and crabs to enter during low tide (i.e. cages on the sediment). Aquatic predator exclusions were cages (area: 4 m², height: 1.2 m, net mesh opening size: 1 cm; see Fig. 1) without roof and without floor. Similar to terrestrial predator exclusions, in the corner of the cages hoops were attached and used to hold the cages to PVC tubes (following Martinetto et al., 2005). The lower borders of the mesh walls were buried 20 cm in the sediment. The upper borders of the mesh walls were equipped with buoys to keep the walls extended during high tide and over the sediment during low tide. This design excluded fishes and crabs during high tide (when mesh upper borders were floating) and allowed birds and crabs entrance during low tide (when mesh upper borders were on the sediment). Artifact controls (i.e. aquatic and terrestrial control) were made using the same materials but only with three sides to allow animals to enter during the complete tidal cycle. Natural controls were delimited areas (1 m²) without cages. Given that bird and fish assemblages could change depending the season, and the relative effect can vary with the abundances of individuals, this experiment was made during two periods: from August to October (i.e. cold season) and from January to March (i.e. warm season).

The experiments ran during 30 days and were monitored weekly to ensure the correct operation of all exclusions. Bird tracks were usually observed in aquatic exclusions and never found in terrestrial exclusions, showing that the experiment was functioning properly. At the end of the experiments we quantify from samples taken from the center of each experimental unit the abundance of macrofauna (# individuals·m⁻²), meiofauna (# individuals·cm⁻²), microalgae (microphytobenthos

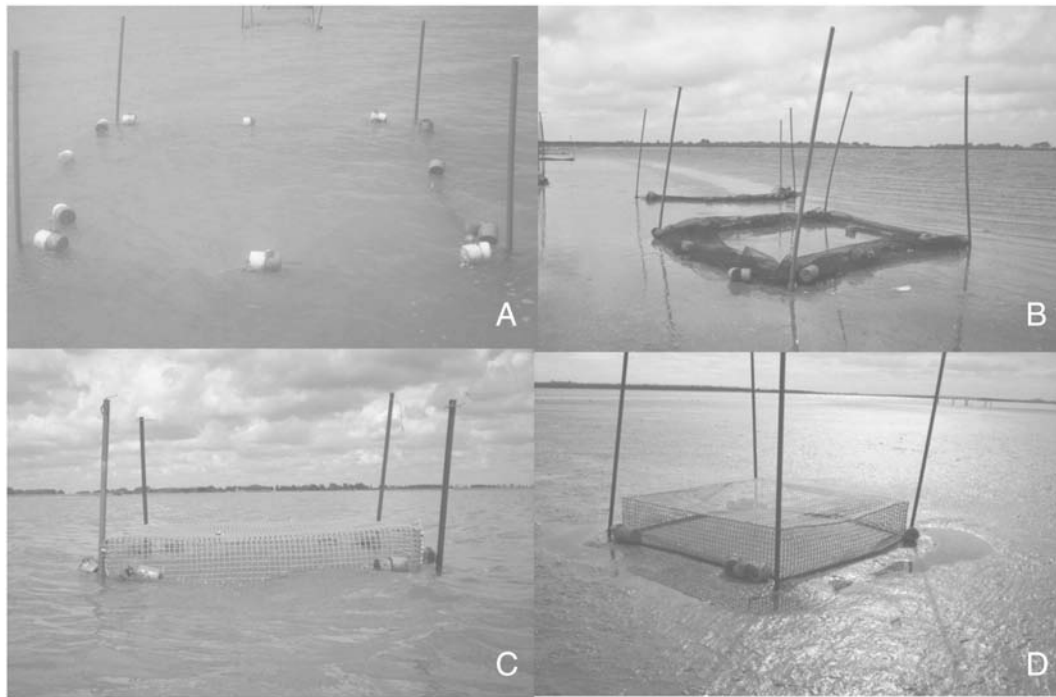


Fig. 1. Photograph to show aquatic predator exclusion during high tide (A) and low tide (B); and terrestrial predator exclusion during high tide (C) and low tide (D).

biomass as chlorophyll *a* concentration; $\mu\text{g}\cdot\text{cm}^{-2}$) and organic matter (percentage of ash free dry weight: AFDW).

Macrofauna samples (diameter and depth: 10 cm) were sieved through a 500 μm mesh and the retained organisms were preserved in formalin 5%, identified to species level and counted under binocular microscope ($10\times$). Organisms prey found were the polychaetes *Laeonereis acuta*, *Neanthes succinea*, *Heteromastus similis* and *Nephtys fluviatilis*. *L. acuta* was the most abundant species, contributing with more than 60% of the total number. Considering that other polychaetes were found in low abundances, statistical analysis was done adding all species (i.e. total polychaetes).

Meiofauna was obtained by sieving a sediment sample (diameter: 10 cm; depth: 2 cm) through a 250 μm mesh. Retained material was preserved in 4% formalin, stained with Bengal rose, identified and separated in broad taxonomic groups (e.g. nematodes), and individuals were counted under binocular microscope ($40\times$; following Higgins and Thiel, 1988; Valiñas et al., 2012).

Microalgal samples (two pooled samples of 2 cm diameter and depth per cage) were conserved in darkness and frozen (-18°C) for analysis. Pigments were extracted with 90% acetone and measured spectrophotometrically before and after acidification (following Lorenzen, 1967). Additionally, sediment samples (diameter and depth: 5 cm) to determine total organic matter content (hereafter OM) were taken, dried at 60°C until constant weight and then incinerated (sub-sample dry weight: 40 g; 550°C ; during 6 h). The difference in weight before and after incineration was used to estimate OM content as AFDW.

We also estimated the habitat use of birds and fishes as abundance of them inside and outside crab bed. The abundance of birds was estimated by focal observations ($n = 5$ per season) at low and ebbing tide using 10×50 binoculars (following Bruschetti et al., 2009), taking into account the species that were eating. The abundance of fishes was estimated by the identification and counting of the fishes retained in a beach seine (mesh size: 1 cm; $n = 5$ per season) towed for 270 m in a line parallel to the shore during high tide (Martinetto et al., 2005). To maintain a constant net opening the seine was towed by two people handling a 10 m rope. Differences between sites (inside and outside crab bed) in bird and fish abundances were analyzed with a *t*-test (Zar, 1999), independently for each season (cold and warm). Moreover,

to estimate habitat heterogeneity between sites, we evaluated density of crab burrows by counting the number of active burrows inside randomly distributed squares (1 m^2 , $n = 10$) in each season, site and tidal level.

The null hypothesis of no differences in the density of total polychaetes and meiofauna, and the null hypotheses of no differences in the concentration of chlorophyll *a* and OM among treatments (i.e. exclusions and controls) were analyzed with one-way ANOVA separately for each site, tidal level and season (Zar, 1999). Then corresponding post hoc Tukey tests (Zar, 1999) were performed when differences were found. Hereinafter, the normality and homoscedasticity of data were evaluated using the Shapiro–Wilk and Cochran test, respectively (Zar, 1999) and were used to discuss other sources of variations. When assumption could not be met, common transformations were used. If data transformation did not solve departure from assumptions, ANOVA test was carried out on untransformed data considering it robust to departures from the assumptions but taken into account in result interpretation (following Underwood, 1997).

2.3. Interaction strength

The interaction strength of both predators (fishes and birds) on their prey (total polychaetes and meiofauna abundance), were calculated on the basis of dynamics indexes (DI; Wootton, 1997) from data obtained from the habitat use of birds and fishes, and the abundance of total polychaetes and total meiofauna (i.e. all groups as nematodes + ostracods + foraminiferans).

$$DI = (\ln(N/D))/Yt$$

where *N* is the abundance of prey in natural control (i.e. where predators are present); *D* is the abundance of prey in terrestrial or aquatic exclusion (i.e. where predators are absent); *Y* is the abundance of the predator (estimated as habitat use); and *t* is the time interval in days that each experiment runs (i.e. cold or warm season).

To calculate the index, each value of *N* and *D* was randomly taken from the total of 10 replicates of each treatment ($n = 99$ times for polychaetes and meiofauna index), selecting all valid indexes for statistical

Table 1Results of one way ANOVAs and t_c -test during cold season for each variable, in different sites and intertidal levels.

	Inside crab bed		Outside crab bed	
	Lower intertidal	Upper intertidal	Lower intertidal	Upper intertidal
Total polychaetes	$F_{4, 45} = 0.19^a$	$F_{4, 45} = 0.9$	$F_{4, 45} = 1.08^c$	$F_{4, 45} = 3.76^{*,a}$
Total meiofauna	$F_{4, 45} = 1.57$	$F_{4, 45} = 0.97^b$	$F_{4, 45} = 1.11$	$F_{4, 45} = 0.57$
Nematods	$F_{4, 45} = 0.19$	$F_{4, 45} = 1.13^b$	$F_{4, 45} = 0.52^b$	$F_{4, 45} = 0.31$
Ostracods	$F_{4, 45} = 2.56$	$F_{4, 45} = 0.25$	$F_{4, 45} = 1.8$	$F_{4, 45} = 1.28$
Foraminiferans	$F_{4, 45} = 1.15$	$F_{4, 45} = 0.56^a$	$F_{4, 45} = 0.7$	$F_{4, 45} = 0.42$
% Organic matter	$F_{4, 45} = 0.7$	$F_{4, 43} = 3.87^{*,c}$	$F_{4, 41} = 0.94$	$F_{4, 43} = 0.74^c$
Chlorophyll a	$F_{4, 45} = 2.12$	$F_{4, 44} = 0.42$	$F_{4, 44} = 1.91$	$F_{4, 45} = 3.38^*$
DI on total meiofauna	$t_c = 3.35^{**}$	$t_c = 0.81$	$t_c = 9.48^{**}$	$t_c = -3.02^{**}$
	df = 113.7	df = 115.1	df = 103.2	df = 100

^a Data transformed to square root ($x + 1$).^b Data transformed to square root.^c Data transformation was not possible.* $p < 0.05$.** $p < 0.01$.

analysis. The Y value was the mean abundance for each species (birds and fishes) in each season. We included those bird species that were observed eating during focal observations and those fishes that in the bibliography are recognize to consume infaunal prey (following Martinetto et al., 2005; Valiñas et al., 2010 for fishes). The time interval t was estimated as the duration of experiments minus the duration time during ebb (for fishes) or flood (for birds) tides. We considered the period of time in which each predator had access to the food from the intertidal

levels (fishes = 12 h in the low intertidal and 8 h in the high intertidal; birds: 8 h in both); t indicator was calculated considering that half of the day in which the tide is low, and the other half in which the tide is high following tidal table of Servicio de Hidrografía Naval (<http://www.hidro.gov.ar>) tidal cycles were corroborated in the field. Given that both sites (inside and outside crab bed) were chosen with similar conditions, tidal exposure did not change between sites. Particular cases observed in the field, such as many days in which the mudflat

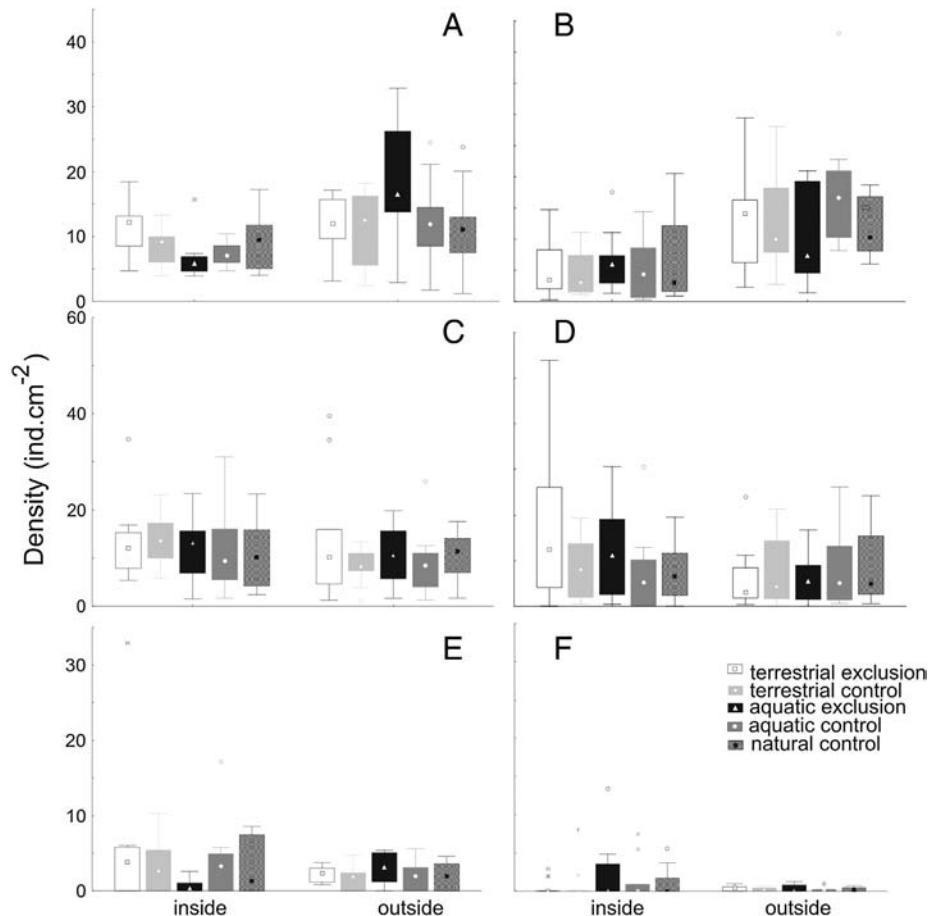


Fig. 2. Density among treatments and sites during cold season of ostracods in lower (A) and upper tidal levels (B); nematodes in lower (C) and upper tidal levels (D) and foraminiferans in lower (E) and upper tidal levels (F). In this and the following figures, symbols within the boxes denote the median, boxes denote 25 and 75 percentile (50% of data). Circles outside the boxes are outliers and asterisks are extremes. All data are presented prior to transformations. Different letters denoted differences among treatments.

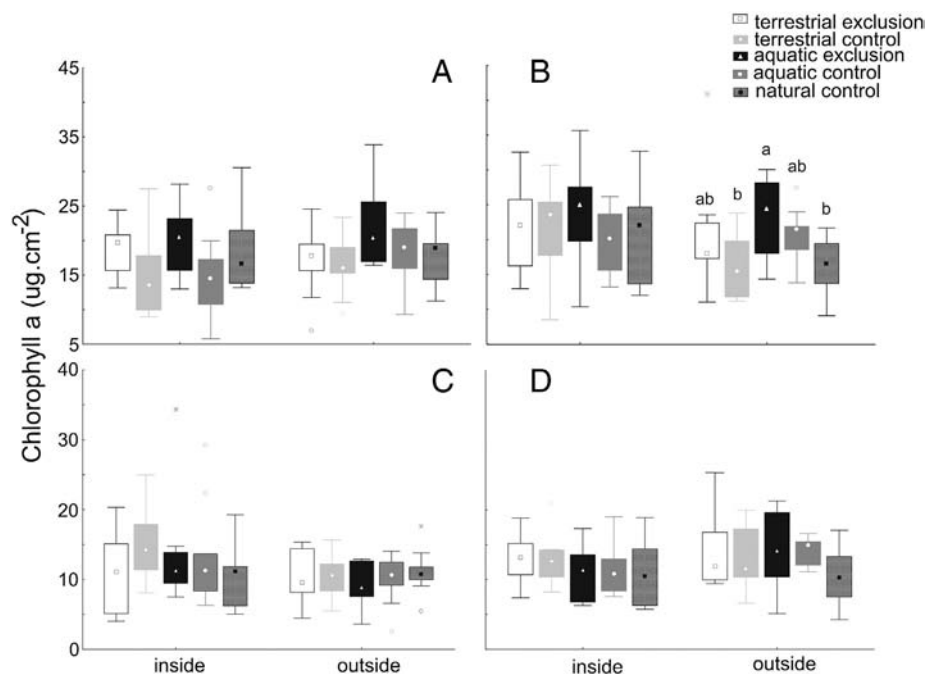


Fig. 3. Concentration of chlorophyll *a* among treatments and sites during cold season in lower (A) and upper tidal levels (B); and during warm season in lower (C) and upper tidal levels (D).

was flooded, were included in the fish index calculation and were subtracted to the bird index. All these data were obtained in the field, given that experiments were weekly controlled.

The null hypothesis of no differences between DI of predators (i.e. birds or fishes) on their prey (i.e. total meiofauna or total polychaetes) for each tidal level, site and season was analyzed with *t*-tests (corrected *t*-test for unequal variances which is equal to *t*-test if variances are the same; Welch approximation; Zar, 1999).

3. Results

Results are reported for each season separately.

3.1. Cold season

In the lower intertidal level, the abundance of total polychaetes, total meiofauna, nematodes, ostracods and foraminiferans were not different among treatments inside or outside crab bed (see Table 1; Fig. 2A, C and E). There were no differences in chlorophyll *a* (hereafter chl *a*; Fig. 3A), and OM content (Fig. 4A) between treatments inside or outside crab bed (see Table 1).

In the upper intertidal level, differences among treatments were found for total polychaetes outside crab bed, where density was higher inside aquatic predator exclusion than terrestrial predator exclusion; however there were no differences inside crab bed (see Table 1).

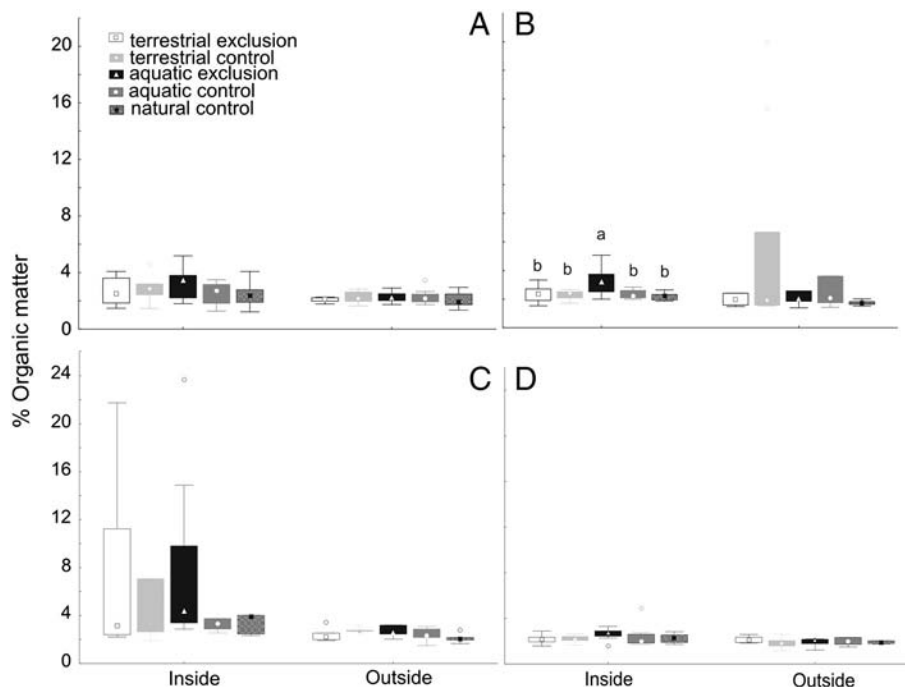


Fig. 4. Organic matter percentage among treatments and both sites during cold season in lower (A) and upper tidal levels (B); and during warm season for lower (C) and upper tidal levels (D).

Table 2

Summary of abundances of the different bird species found during the experiment period in different sites and seasons.

Species	Season			
	Cold		Warm	
	Inside crab bed	Outside crab bed	Inside crab bed	Outside crab bed
<i>Himantopus melanurus</i>	2	201	10	41
<i>Larus atlanticus</i>	7	–	–	–
<i>Larus maculipennis</i>	9	43	5	–
<i>Tringa flavipes</i>	–	45	–	112
<i>Tringa melanoleuca</i>	1	10	15	73
<i>Haematopus palliatus</i>	–	–	10	–
<i>Pluvialis squatarola</i>	–	–	–	2
<i>Charadrius falklandicus</i>	–	19	–	19
<i>Limosa haemastica</i>	–	–	–	2
<i>Calidris fuscicollis</i>	–	–	–	112

Density of total meiofauna, ostracods, nematodes and foraminiferans were not different between treatments inside or outside crab bed (Table 1, Fig. 2B, D and F).

ANOVA showed no differences for concentrations of chl *a* inside crab bed (see Table 1), but analysis outside crab bed showed that concentration was higher in aquatic predator exclusion than in the natural control (Table 1; Fig. 3B). OM showed no differences outside crab bed, but inside crab bed percentage of OM was higher in aquatic predator exclusion than on the other treatments (see Table 1; Fig. 4B).

Abundance of birds was low (see Table 2) and birds were mainly found outside the crab bed (square root transformed data, $t = -3.4$, $df = 7$, $p < 0.05$). The most frequently observed migratory birds eating during the experimental periods were the greater yellowlegs (*Tringa melanoleuca*), the lesser yellowlegs (*Tringa flavipes*), the two-banded plover (*Charadrius falklandicus*), and local species like the Olrog's gull (*Larus atlanticus*), the brown-hooded gull (*Larus maculipennis*), and the South American stilt (*Himantopus melanurus*).

The most abundant fish species found was the silverside (*Odontesthes argentinensis*, see Table 3) and there was no difference between inside and outside crab bed ($t = 0.65$, $df = 8$, $p = 0.5$). Only occasionally it was also found the flatfish (*Paralichthys orbignyanus*), the gray mullet (*Mugil platanus*), the Brazilian menhaden (*Brevoortia aurea*), the Jenyns's sprat (*Rammogaster arcuata*) and the River Plate sprat (*Platanichthys platana*). Density of crab burrows was very low in this season and the densities of active burrows (burrow $\cdot m^{-2}$) in the lower intertidal level (mean (SD) inside crab bed: 0.96 (1.06); outside crab bed: 1.12 (1.05)) were higher than in the upper intertidal level (inside crab bed: 0.76 (0.83); outside crab bed: 0.24 (0.52)).

3.2. Warm season

Compared to the cold season, the total densities of polychaetes increased 100%, although it continued to be low with respect to other years (e.g. Palomo et al., 2003). In the lower intertidal level abundances of total polychaetes were not different among treatments inside or

outside crab bed (see Table 4). ANOVAs showed no differences among treatments for abundances of total meiofauna, ostracods, foraminiferans (Table 4; Fig. 5A and E), chl *a* (Table 4; Fig. 3C) and OM content (Table 4; Fig. 4C), inside or outside crab bed. Differences among treatments were found for nematodes inside crab bed (Table 4; Fig. 5C) increasing the density in aquatic control and aquatic predator exclusion in relation to terrestrial predator exclusion and natural control; however no differences were found for the same group outside crab bed (Table 4; Fig. 5C).

In the upper tidal level, no differences were found among treatments inside or outside crab bed for abundances of total polychaetes, foraminiferans, chl *a* and OM percentage, inside or outside crab bed (Table 4; Figs. 3D, 4D and 5F). Differences among treatments were found for abundances of total meiofauna inside the crab bed, increasing the abundance in aquatic predator exclusion than terrestrial control (see Table 4). There was also difference in the abundance of nematodes inside crab bed, with higher value in aquatic predator exclusion with respect to terrestrial control (Table 4; Fig. 5D). However, outside crab bed, differences were found for abundance of ostracods (Table 4; Fig. 5B), showing higher abundance in aquatic predator exclusion than all other exclusion treatments.

Abundance of birds was similar to the cold season (see Table 2), but there was small abundance inside crab bed compared to outside crab bed (square root transformed data, $t = -3.2$, $df = 7$, $p < 0.05$). The same species observed during cold season were found eating during this season, although other species such as the white-rumped sandpiper (*Calidris fuscicollis*), the Hudsonian godwit (*Limosa haemastica*), the black-bellied plover (*Pluvialis squatarola*), and the American oystercatcher (*Haematopus palliatus*) were found. The white-rumped sandpiper and lesser yellowlegs were the more abundant species, reaching up to 60% of observed birds. In this season, the abundance of fishes was more than twice larger than in the cold season being the silverside the most abundant (Table 3), followed by the Brazilian menhaden. The fish assemblage was similar to that found in the cold season, and only two new fish species were caught: the white-mouth croaker (*Micropogonias furnieri*) and the Atlantic sabretooth anchovy (*Lycengraulis grossidens*);

Table 3

Summary of abundances of the different fish species found during the experiment period in different sites and season.

Species	Season			
	Cold		Warm	
	Inside crab bed	Outside crab bed	Inside crab bed	Outside crab bed
<i>Odontesthes argentinensis</i>	7	26	338	247
<i>Paralichthys orbignyanus</i>	1	–	–	–
<i>Mugil platanus</i>	1	–	–	–
<i>Brevoortia aurea</i>	1	–	68	54
<i>Micropogonias furnieri</i>	–	–	11	1
<i>Rammogaster arcuata</i>	1	–	–	–
<i>Platanichthys platana</i>	1	–	–	–
<i>Lycengraulis grossidens</i>	–	–	4	8

Table 4Results of one way ANOVAs and t_c -test during warm season for each variable, in different sites and intertidal levels.

	Inside crab bed		Outside crab bed	
	Lower intertidal	Upper intertidal	Lower intertidal	Upper intertidal
Total polychaetes	$F_{4, 45} = 0.71^a$	$F_{4, 45} = 0.84$	$F_{4, 45} = 0.58$	$F_{4, 45} = 0.66^c$
Total meiofauna	$F_{4, 44} = 2.14$	$F_{4, 45} = 3.91^*$	$F_{4, 45} = 1.15$	$F_{4, 44} = 1.45$
Nematods	$F_{4, 44} = 3.1^{*,b}$	$F_{4, 45} = 3.23^*$	$F_{4, 45} = 0.78$	$F_{4, 44} = 0.39$
Ostracods	$F_{4, 44} = 0.83$	$F_{4, 45} = 1.7$	$F_{4, 45} = 1.67$	$F_{4, 44} = 8.38^{**}$
Foraminiferans	$F_{4, 44} = 1.64$	$F_{4, 45} = 0.82$	$F_{4, 45} = 0.34$	$F_{4, 44} = 0.53$
% Organic matter	$F_{4, 38} = 0.12$	$F_{4, 40} = 0.66^b$	$F_{4, 28} = 1.82^b$	$F_{4, 38} = 1.09^c$
Chlorophyll a	$F_{4, 45} = 0.76$	$F_{4, 45} = 0.71$	$F_{4, 45} = 0.31$	$F_{4, 45} = 1.45$
DI on total meiofauna	$t_c = 1.34$	$T_c = -7.77^{**}$	$t_c = 12.8^{**}$	$t_c = 0.48$
	df = 98	df = 98	df = 142.7	df = 121.1

^a Data transformed to square root ($x + 1$).^b Data transformed to square root.^c Data transformation was not possible.* $p < 0.05$.** $p < 0.01$.

and there were no difference between sites ($t = 0.31$, $df = 8$, $p = 0.75$). Density of crab burrows ($\text{burrow} \cdot \text{m}^{-2}$) was higher in warm than in cold season, with higher values inside crab bed and in the lower intertidal level (mean (SD)); inside crab bed, lower level: 6.55 (2.32); upper level: 2.2 (1.85). Outside crab bed, lower level: 2 (2.05); upper level: 0.

3.3. Interaction strength

Dynamic index (DI) showed that interaction strength is mainly weak (near zero; i.e., DI between ± 0.08 with some cases near to 0.1). For total

polychaetes, several replicates registered zero as prey abundances, thus data of DI are shown graphically (Fig. 6). For DI of predators on total polychaetes, the index of aquatic predators (i.e. fishes) was more variable than the index of terrestrial predators (i.e. birds) during cold season in both sites and levels, with more negative values and high variances inside crab bed (Cochran test in all cases $p < 0.001$; see Fig. 6A and B); DI of birds on polychaetes was near zero with exception inside the crab bed.

During the warm season the results were the opposite, showing that DI of fishes on polychaetes was almost zero in both sites and levels; however DI of birds on polychaetes was more variable and with high

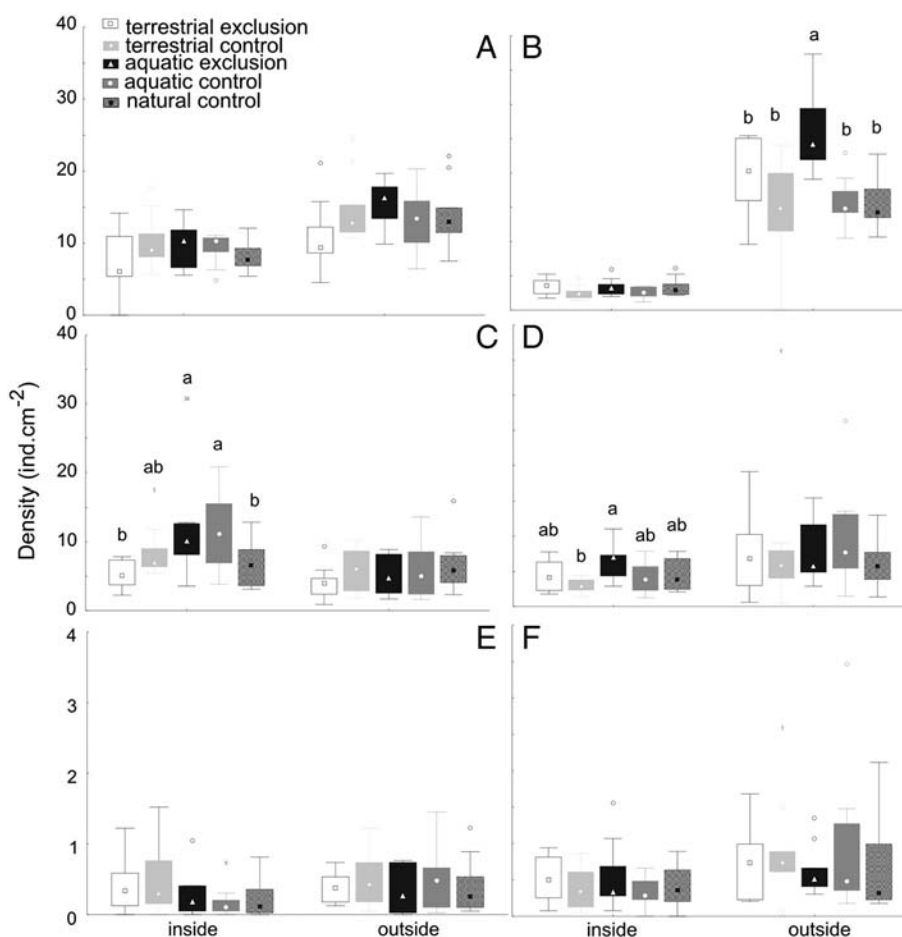


Fig. 5. Density among treatments and sites during warm season of ostracods in lower (A) and upper tidal levels (B); nematodes in lower (C) and upper tidal level (D) and foraminiferans in lower (E) and upper tidal level (F).

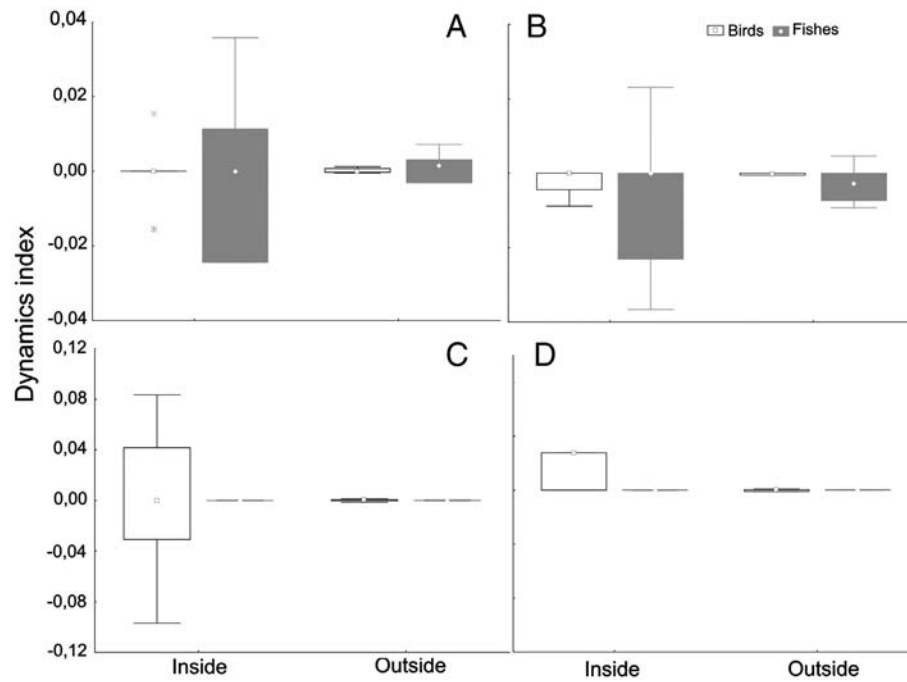


Fig. 6. Dynamics index (DI) between different sites and predators on total polychaetes during cold season to lower (A) and upper tidal levels (B); and during warm season for lower (C) and upper tidal levels (D).

variances especially inside crab bed in both levels (Cochran test in all cases $p < 0.001$; see Fig. 6C and D).

During the cold season, in the lower level, DI of predators on total meiofauna showed the same pattern for both sites (inside and outside crab bed), this being higher predation impact of fishes than birds (see Table 1; Fig. 7A). However in the upper level DI of birds on total meiofauna showed the lower values outside crab bed (Table 1;

Fig. 7B). Moreover, DI of fishes on total meiofauna inside crab bed in both tidal levels showed higher variances than other indexes.

In the lower level during the warm season, outside crab bed DI showed that fishes had more negative impact on total meiofauna than birds (Table 4; Fig. 7C), however higher variance of DI of birds was found inside crab bed than in all other treatments (Fig. 7C). For the upper level, inside crab bed, the DI of birds on meiofauna was lower

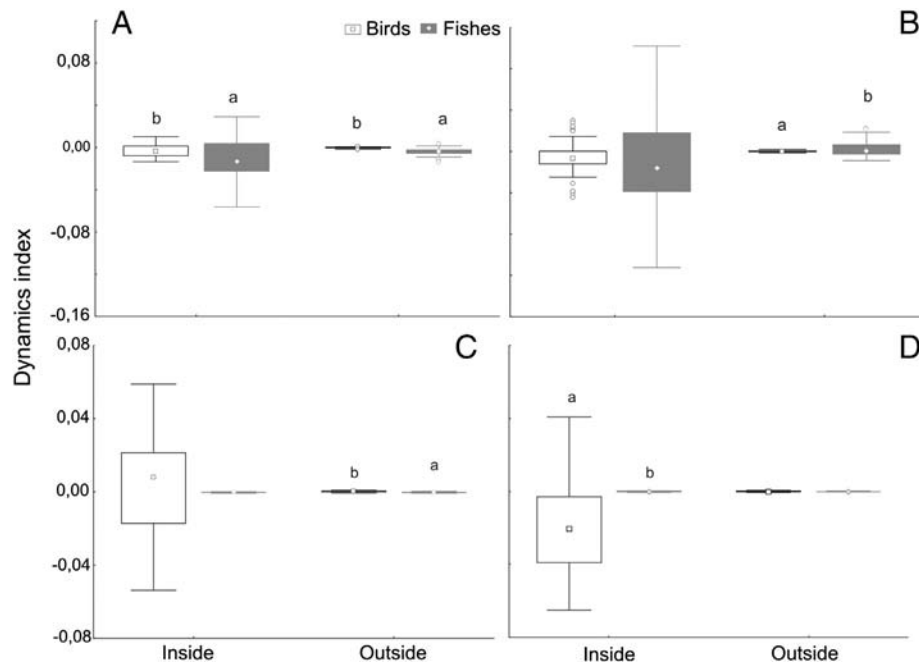


Fig. 7. Dynamics indexes (DI) between different sites and predators on meiofauna during cold season in lower (A) and upper tidal levels (B); and during warm season for lower (C) and upper tidal levels (D).

than the other index (Fig. 7D). Outside crab bed no differences were found between DI of different predators (Table 4, Fig. 7D).

4. Discussion

Our results show that weak interactions prevail. During the warm season, interaction strength of birds was highly variable for both prey items, with large negative effects on meiofauna in the upper tidal level. During the cold season, however, fishes exhibit broad variation in their impact on prey, especially inside crab bed and for meiofaunal organisms.

Predation is an important source of variability in many communities, producing changes in prey abundance (Hidalgo et al., 2011; Navarrete, 1996), and in the species composition and diversity (Hillebrand, 2003; Pillay et al., 2009). However, in a given spatial and temporal interval, predation rates can change depending on factors such as seasons, time of day (Abugov, 1982) or environmental temperature, especially when predators are birds (e.g. Duriez et al., 2005). Several intertidal areas in the south-western Atlantic region are stop-over sites for migratory shorebirds that arrive to feed and rest during the warm season (e.g. Morrison and Ross, 1989; Myers and Myers, 1979). In these intertidals, birds use in different ways areas with and without crabs (Botto et al., 1998, 2000; our results), where the abundances of prey and feeding behavior are also different (Botto and Iribarne, 1999; Palomo et al., 2003). For example, the white-rumped sandpiper, and the greater and the lesser yellowlegs are most frequently found outside crab beds (Botto et al., 2000), where there is higher availability of prey items (Palomo et al., 2004). In our work, we found similar patterns of habitat use for predators and prey. Density of prey was high outside bioturbated areas where the migratory birds spend more time feeding. However, the interaction strength of birds on polychaetes and on meiofauna was highly variable inside crab bed in both tidal levels, showing negative effects of birds in the upper intertidal level. This may be either due to the low density of prey or to the foraging rates of several birds that change depending on the intensity of crab bioturbation (e.g. *C. falklandicus*; Botto et al., 2000). Therefore, our results show that birds, though being in relatively low abundances, can have an impact on their prey especially at the high intertidal. This may be facilitated by crabs, because their activity ameliorates the sediment physical harshness making the intertidal area physically more homogeneous, allowing some organisms to extend their distribution to upper levels (Escapa et al., 2004).

The interaction strength of fishes on polychaetes and on meiofauna suggests that predation by fishes is high during the cold season. Previous works showed that fishes decrease polychaete abundances (Martinetto et al., 2005, 2007) and consume meiofaunal groups such as ostracods, nematodes and foraminiferans, which in some cases represent the 20% of the fish diet (Valiñas et al., 2010). Additionally, the year in which our experiment was carried out (i.e. 2007) corresponded to El Niño Southern Oscillations year (ENSO; see also Canepuccia et al., 2010 for a study in this region), which causes an increase in precipitation from southern Brazil to central Argentina (Viles and Goudie, 2003), promoting flooding in the pampas and coastal marshes (e.g. Alberti et al., 2007; Canepuccia et al., 2007). During these periods mudflats remained mostly covered by freshwater, changing lagoon water level and salinity (Martinetto et al., 2007). These conditions could generate system-wide ecological changes (e.g. Lubchenco et al., 1991; Tylanakis et al., 2008). For example, the access of fishes to intertidal mudflats (which is controlled by tides; Rozas, 1995), and prey availability would be higher during ENSO, when the intertidal stayed flooded for much longer time due to intense raining in the area. In those conditions the interaction strength of fishes on polychaetes, may result in the negative impact of predation on meiofauna inside and outside crab bed.

Inside crab bed interaction strength (both kind of predators, seasons and tidal levels) was more variably and had higher variances than areas without bioturbation (see Results, Figs. 6 and 7). In soft bottom systems, predator–prey interactions and predation rates can change because of the activity of bioturbator organisms (e.g. Martinetto et al., 2005;

Palomo et al., 2003). In our work the presence of strong bioturbators could indirectly modify predator–prey interactions, probably because bioturbation enhances sediment structural complexity, modifying the abundance, the behavior and the availability of prey (e.g. Botto and Iribarne, 1999; Palomo et al., 2003). Thus, although interactions in our work were weak but highly variable, they may also be important (e.g. Berlow, 1999; Navarrete and Menge, 1996). Similarly, the effect of bioturbation organisms may be more complex than expected, affecting predator–prey interactions with different magnitudes and directions (e.g. Alvarez et al., 2013; Martinetto et al., 2005). In consequence, our results suggest that in intertidal systems, impact of predation can change not only due to abundance and distribution of the involved species, but also depending of changes in tidal cycles and presence of bioturbator organisms.

In soft-bottom sediments, fishes can strongly reduce the abundances of infaunal (Fleeger et al., 2008) and epifaunal prey (Posey et al., 2006), affect microalgal biomass (Deegan et al., 2007), and change composition of community by direct (e.g. Fleeger et al., 2008) or indirect interactions (e.g. Heck and Valentine, 2007). Likewise, other predators such as snails (Silliman and Bertness, 2002; Silliman and Zieman, 2001) or birds (Hamilton et al., 2006; Johnson et al., 2009) can have similar effects. However, top-down effects are often difficult to detect because infaunal responses can be vary along environmental gradients as inundation (Fleeger et al., 2008) and salinity (Deegan et al., 2007). Our results show that top-down effects by top consumers (fishes and birds) were weak (see also Johnson and Fleeger, 2009) and highly variable depending mainly on seasonality and tidal gradients. Birds affect meiofaunal organisms and exhibit higher effects than fishes in warm season, while fishes in the cold season have stronger effects (especially on meiofauna). Birds can use all intertidal and their abundances increase in summer (e.g. Botto et al., 2000; Mariano-Jelicich et al., 2003), while fishes have the access for food limited by tidal cycle and their abundances do not change along the year. Moreover both predators use in different ways areas with and without crab bioturbation (see Botto et al., 2000; Martinetto et al., 2005). Thus, our results suggest that top-down effects of fishes and birds could be compensated, fishes exhibiting strong effects in cold season and birds are the main predators in warm seasons (see also Johnson et al., 2009).

Our results show that interaction strength of both predators, fishes and birds, are mainly weak. However, although weak, the importance of the different predators is determined by environmental context as the grade of bioturbation generated by crabs, the tidal time exposition (due to tidal cycle or ENSO episode) and seasonality, changing the sign and magnitude of interactions. Therefore, our work, including others (e.g., Harley, 2003; Wootton and Emmerson, 2005), exemplify how the outcome of interaction strength between predators and prey may result from a complex link between organisms and their habitats, and how this outcome depends dynamically on background community composition and temporal–spatial scale.

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References

- Abugov, R., 1982. Species diversity and phasing of disturbance. *Ecology* 63, 289–293.

- Alberti, J., Montemayor, D., Alvarez, F., Méndez Casariego, A., Luppi, T., Canepuccia, A., et al., 2007. Changes in rainfall pattern affect crab herbivory rates in a SW Atlantic salt marsh. *J. Exp. Mar. Biol. Ecol.* 353, 126–133.
- Alvarez, M.F., Esquiús, K.S., Addino, M., Alberti, J., Iribarne, O., Botto, F., 2013. Cascading top-down effects on estuarine intertidal meiofaunal and algal assemblages. *J. Exp. Mar. Biol. Ecol.* 440, 216–224.
- Berlow, E., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Berlow, E., Navarrete, S., Briggs, C., Power, M., Menge, B.A., 1999. Quantifying variation in the strengths of species interactions. *Ecology* 80, 2206–2224.
- Beukers, J.S., Jones, G.P., 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114, 50–59.
- Botto, F., Iribarne, F., 1999. Effect of the burrowing crab *Chasmagnathus granulata* (Dana) on the benthic community of a SW Atlantic coastal lagoon. *J. Exp. Mar. Biol. Ecol.* 241, 263–284.
- Botto, F., Iribarne, O.O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuar. Coast. Shelf Sci.* 51, 141–151.
- Botto, F., Iribarne, O.O., Martínez, M.M., Delhey, K., Carrete, M., 1998. The effect of migratory shorebirds on the benthic species of three Southwestern Atlantic Argentinean Estuaries. *Estuaries* 21, 700–709.
- Botto, F., Palomo, G., Iribarne, O., Martínez, M.M., 2000. The effect of Southwestern Atlantic burrowing crabs on habitat use and foraging activity of migratory shorebirds. *Estuaries* 23, 208–215.
- Bruno, J.F., O'Connor, M.I., 2005. Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.* 8, 1048–1056.
- Bruschetti, M., Bazterrica, C., Luppi, T., Iribarne, O., 2009. An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon. *J. Exp. Mar. Biol. Ecol.* 375, 76–83.
- Canepuccia, A., Isacch, J., Gagliardini, D., Escalante, A.H., Iribarne, O.O., 2007. Waterbird response to changes in habitat area and diversity generated by rainfall in a SW Atlantic coastal lagoon. *Waterbirds* 30, 541–553.
- Canepuccia, A.D., Alberti, J., Pascual, J., Alvarez, G., Cebrían, J., Iribarne, O.O., 2010. ENSO episodes modify plant/terrestrial-herbivore interactions in a southwestern Atlantic salt marsh. *J. Exp. Mar. Biol. Ecol.* 396, 42–47.
- Christianou, M., Ebenman, B., 2005. Keystone species and vulnerable species in ecological communities: strong or weak interactors? *J. Theor. Biol.* 235, 95–103.
- Cousseau, M., Díaz de Astarloa, J., Figueroa, D., 2001. La ictiofauna de la laguna Mar Chiquita. In: Iribarne, O. (Ed.), *Reserva de biosfera Mar Chiquita: características físicas, biológicas y ecológicas*. Editorial Martín, Mar del Plata, Argentina, pp. 187–203.
- Deegan, L.A., Bowen, J.L., Drake, D., Fleeger, J.W., Friedrichs, C.T., Galván, K.A., Hobbie, J.E., Hopkinson, C., 2007. Susceptibility of salt marshes to nutrient enrichment and predation removal. *Ecol. Appl.* 17, 42–63.
- Duriez, O., Fritz, H., Binet, F., Tremblay, Y., Ferrand, Y., 2005. Individual activity rates in wintering Eurasian woodcocks: starvation versus predation risk trade-off? *Anim. Behav.* 69, 39–49.
- Emmerson, M.C., Raffaelli, D., 2004. Predator-prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 73, 399–409.
- Escapa, M., Iribarne, O., Navarro, D., 2004. Effects of the intertidal burrowing crab *Chasmagnathus granulatus* on infaunal zonation patterns, tidal behavior, and risk of mortality. *Estuaries* 27, 120–131.
- Fagan, W., Hurd, L., 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. *Ecology* 75, 2022–2032.
- Fleeger, J.W., Johnson, D.S., Galván, K.A., Deegan, L.A., 2008. Top-down and bottom-up control of infauna varies across the saltmarsh landscape. *J. Exp. Mar. Biol. Ecol.* 357, 20–34.
- Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* 25, 173–183.
- Grabowski, J.H., 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85, 995–1004.
- Green, B.C., Smith, D.J., Earley, S.E., Hepburn, L.J., Underwood, G.J.C., 2009. Seasonal changes in community composition and trophic structure of fish populations of five salt marshes along the Essex coastline, United Kingdom. *Estuar. Coast. Shelf Sci.* 85, 247–256.
- Hamilton, D.J., Diamond, A.W., Wells, P.G., 2006. Shorebirds, snails, and the amphipod (*Corophium volutator*) in the upper Bay of Fundy: top-down vs. bottom-up factors, and the influence of compensatory interactions on mudflat ecology. *Hydrobiologia* 567, 285–306.
- Harley, C.D.G., 2003. Species importance and context: spatial and temporal variation in species interactions. In: Kareiva, P., Levin, S.A. (Eds.), *The Importance of Species: Perspectives on Expendability and Triage*. Princeton University Press, New Jersey, USA, pp. 44–68.
- Heck Jr., K., Valentine, J., 2007. The primacy of top-down effects in shallow benthic ecosystems. *Estuar. Coast.* 30, 371–381.
- Hidalgo, F., Firstater, F., Lomovasky, B., Iribarne, O., 2011. Effects of a predatory starfish on substrate colonization by a dominant mussel. *Mar. Ecol. Prog. Ser.* 432, 103–114.
- Higgins, R.P., Thiel, H., 1988. *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, USA.
- Hillebrand, H., 2003. Opposing effects of grazing and nutrients on diversity. *Oikos* 100, 592–600.
- Iribarne, O., Bortolus, A., Botto, F., 1997. Between-habitat differences in burrow characteristics and trophic modes in the southwestern Atlantic burrowing crab *Chasmagnathus granulata*. *Mar. Ecol. Prog. Ser.* 155, 137–145.
- Iribarne, O., Bruschetti, M., Escapa, M., Bava, J., Botto, F., Gutiérrez, J., Palomo, G., Delhey, K., Petracchi, P., Gagliardini, A., 2005. Small and large-scale effect of the SW Atlantic burrowing crab *Chasmagnathus granulatus* on habitat use by migratory shorebirds. *J. Exp. Mar. Biol. Ecol.* 315, 87–101.
- Isacch, J., Costa, C., Rodríguez, L., Conde, D., Escapa, M., Gagliardini, D., Iribarne, O., 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *J. Biogeogr.* 33, 888–900.
- Jaksic, F.M., 1986. Predator-prey interactions in a terrestrial and intertidal ecosystems: are the differences real? *Rev. Chil. Hist. Nat.* 59, 9–17.
- Johnson, D.S., Fleeger, J.W., 2009. Weak response of saltmarsh infauna to ecosystem-wide nutrient enrichment and fish predator reduction: a four-year study. *J. Exp. Mar. Biol. Ecol.* 373, 35–44.
- Johnson, D., Fleeger, J., Deegan, L., 2009. Large-scale manipulations reveal that top-down and bottom-up controls interact to alter habitat utilization by saltmarsh fauna. *Mar. Ecol. Prog. Ser.* 377, 33–41.
- Kneib, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr. Mar. Biol.* 35, 163–220.
- Laska, M.S., Wootton, J.T., 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79, 461–476.
- Lorenzen, C.J., 1967. Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. *Limnol. Oceanogr.* 12, 343–346.
- Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., et al., 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* 72, 371–412.
- Mariano-Jelicich, R., Favero, M., Silva, M.P., 2003. Fish prey of the black skimmer *Rynchops niger* at Mar Chiquita, Buenos Aires province, Argentina. *Mar. Ornithol.* 31, 199–202.
- Martinetto, P., Iribarne, O., Palomo, G., 2005. Effect of fish predation on intertidal benthic fauna is modified by crab bioturbation. *J. Exp. Mar. Biol. Ecol.* 318, 71–84.
- Martinetto, P., Ribeiro, P., Iribarne, O., 2007. Changes in distribution and abundance of juvenile fishes in intertidal soft sediment areas dominated by the burrowing crab *Chasmagnathus granulatus*. *Mar. Freshw. Res.* 58, 194–203.
- Maser, G.L., Guichard, F., McCann, K.S., 2007. Weak trophic interactions and the balance of enriched metacommunities. *J. Theor. Biol.* 247, 337–345.
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.* 65, 21–74.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C.G., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Mar. Ecol. Prog. Ser.* 246, 39–59.
- Morrison, R.I.G., Ross, R.K., 1989. Atlas of Nearctic shorebirds on the coast of South America. *Can. Wildl. Serv. Spec. Publ.* 2, 131–323.
- Murray, J., Meadows, A., Meadows, P., 2002. Biogeomorphological implications of micro-scale interactions between sediment geotechnics and marine benthos: a review. *Geomorphology* 47, 15–30.
- Myers, J.P., Myers, L.P., 1979. Shorebirds of coastal Buenos Aires Province, Argentina. *Ibis* 121, 186–200.
- Navarrete, S.A., 1996. Variable predation: effects of whelks on a mid-intertidal successional community. *Ecol. Monogr.* 66, 301–321.
- Navarrete, S.A., Berlow, E., 2006. Variable interaction strengths stabilize marine community pattern. *Ecol. Lett.* 9, 526–536.
- Navarrete, S.A., Menge, B.A., 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecol. Monogr.* 66, 409–429.
- Norton, S.F., Cook, A.E., 1999. Predation by fishes in intertidal. In: Horn, M.H., Martin, K.L.M., Chotkowski, M.A. (Eds.), *Intertidal Fishes: Life in Two Worlds*. Academic Press, San Diego, CA, pp. 223–263.
- O'Gorman, E.J., Emmerson, M.C., 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proc. Natl. Acad. Sci. U. S. A.* 106, 13393–13398.
- O'Gorman, E.J., Jonsson, U., Emmerson, M.C., 2010. Interaction strength, food web topology and the relative importance of species in food webs. *J. Anim. Ecol.* 79, 682–692.
- Otto, S.B., Rall, B.C., Brose, U., 2007. Allometric degree distributions facilitate food web stability. *Nature* 450, 1226–1229.
- Palomo, G., Botto, F., Navarro, D., Escapa, M., Iribarne, O., 2003. Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator-prey interactions between shorebirds and polychaetes? *J. Exp. Mar. Biol. Ecol.* 290, 211–228.
- Palomo, G., Martinetto, P., Iribarne, O., 2004. Changes in the feeding behavior of the deposit-feeding polychaete *Laeonereis acuta* on soft sediments inhabited by burrowing crabs. *Mar. Biol.* 145, 657–667.
- Peacor, S.D., Werner, E.E., 2004. How independent are species-pair interaction strengths on other species in the food web? *Ecology* 85, 2754–2763.
- Pennings, S.C., Silliman, B.R., 2005. Linking biogeography and community ecology: latitudinal variation in plant-herbivore interaction strength. *Ecology* 86, 2310–2319.
- Petraitis, P.S., Dudgeon, D., 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Ecology* 80, 429–442.
- Pillay, D., Branch, G., Forbes, A., 2007. Effects of *Callinassa kraussi* on microbial biofilms and recruitment of macrofauna: a novel hypothesis for adult-juvenile interactions. *Mar. Ecol. Prog. Ser.* 347, 1–14.
- Pillay, D., Branch, G.M., Steyn, A., 2009. Complex effects of the gastropod *Assiminea globulus* on benthic community structure in a marine-dominated lagoon. *J. Exp. Mar. Biol. Ecol.* 380, 47–52.
- Platell, M.E., Freewater, P., 2009. Importance of saltmarsh to fish species of a large south-eastern Australian estuary during a spring tide cycle. *Mar. Freshw. Res.* 60, 936–941.
- Polis, G.A., Anderson, W.B., Holt, R.D., Anderson, B., Polis, A., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Ann. Rev. Ecol. Syst.* 28, 289–316.
- Posey, M.H., Alphin, T.D., Cahoon, L., 2006. Benthic community responses to nutrient enrichment and predator exclusion: influence of background nutrient concentrations and interactive effects. *J. Exp. Mar. Biol. Ecol.* 330, 105–118.

- Power, M.E., Tilman, D., Estes, J., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *Bioscience* 46, 609–620.
- Reise, K., 2002. Sediment mediated species interactions in coastal waters. *J. Sea Res.* 48, 127–141.
- Reta, R., Martos, P., Perillo, G.M.E., Piccolo, M.C., Ferrante, A., 2001. Características hidrográficas del estuario de la laguna de Mar Chiquita. In: Iribarne, O. (Ed.), *Reserva de biosfera Mar Chiquita: características físicas, biológicas y ecológicas*. Editorial Martín, Mar del Plata, Argentina, pp. 31–52.
- Rozas, L.P., 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18, 579–590.
- Rozas, L.P., Zimmerman, R.J., 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). *Mar. Ecol. Prog. Ser.* 193, 217–239.
- Sala, E., Dayton, P.K., 2011. Predicting strong community impacts using experimental estimates of per capita interaction strength: benthic herbivores and giant kelp recruitment. *Mar. Ecol.* 32, 300–312.
- Setälä, H., Rissanen, J., Markkola, A.M., 1997. Conditional outcomes in the relationship between pine and ectomycorrhizal fungi in relation to biotic and abiotic environment. *Oikos* 80, 112–122.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5, 785–791.
- Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. *Proc. Natl. Acad. Sci. U. S. A.* 99, 10500–10505.
- Silliman, B.R., Zieman, J.C., 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology* 82, 2830–2845.
- Spivak, E., Anger, K., Luppi, T., Bas, C., Ismael, D., 1994. Distribution and habitat preferences of two grapsid crab species in Mar Chiquita coastal lagoon (Province of Buenos Aires, Argentina). *Helgoländer Meeresun.* 48, 59–78.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance*. Cambridge University Press, Cambridge.
- Valiñas, M., Acha, E.M., Iribarne, O., 2010. Habitat use and feeding habits of juvenile fishes in an infrequently flooded Atlantic saltmarsh. *Mar. Freshw. Res.* 61, 1154–1163.
- Valiñas, M.S., Molina, L.M., Addino, M., Montemayor, D.I., Acha, E.M., Iribarne, O.O., 2012. Biotic and environmental factors affect Southwest Atlantic saltmarsh use by juvenile fishes. *J. Sea Res.* 68, 49–56.
- Viles, H.A., Goudie, A.S., 2003. Interannual, decadal and multi-decadal scale climatic variability and geomorphology. *Earth-Sci. Rev.* 61, 105–131.
- Volkenborn, N., Reise, K., 2006. Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformations. *J. Exp. Mar. Biol. Ecol.* 330, 169–179.
- Volkenborn, N., Robertson, D., Reise, K., 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. *Helgol. Mar. Res.* 63, 27–35.
- Wootton, J.T., 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecol. Monogr.* 67, 45–64.
- Wootton, J.T., Emmerson, M.C., 2005. Measurement of interaction strength in nature. *Ann. Rev. Ecol. Syst.* 36, 419–444.
- Zar, J.H., 1999. *Biostatistical Analysis*, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.