



Does the presence of the SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affect predator–prey interactions between shorebirds and polychaetes?

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Abstract

The burrowing crab *Chasmagnathus granulatus* is an important bioturbator that generates dense burrow assemblages (crab beds) characteristic of intertidal habitats of SW Atlantic estuaries. Crab bioturbation affects the topography and hydrodynamics of the sediment, increasing sediment water and organic matter content, decreasing sediment hardness and changing the grain size frequency distribution. In this study, we found that burrowing crabs can decrease the impact of predation by shorebirds on polychaetes. The polychaete *Laeonereis acuta* Treadwell has U-shaped burrows outside crab beds, which are associated with surface deposit-feeding while their burrows are mainly I-shaped inside which is associated with subsurface deposit feeding behavior. This pattern is likely the result of larger vertical sediment mixing inside crab beds due to crab burrowing. As a result of their feeding strategy, polychaetes appear on the surface more often outside crab beds, which increases their availability for shorebirds. In addition, shorebird species differentially use crab beds. The White-rumped Sandpiper, *Calidris fuscicollis* Vieillot, preferentially forage outside crab beds, meanwhile the Two-banded Plover *Charadrius falklandicus* Latham forage more frequently inside crab beds. However, experiments excluding shorebirds inside and outside crab beds showed negative effects of shorebirds only outside crab beds. Thus, our results show that the SW Atlantic burrowing crab *C. granulatus* affects the strength of the predator–prey interaction between shorebirds and polychaetes. © 2003 Elsevier Science B.V. All rights reserved.

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1. Introduction

Predation is one of the most important processes that influences the abundance and structure of prey populations (Paine, 1966). Survival and persistence of prey species varies with predation intensity (Micheli, 1996), but consumer feeding rates depend on prey abundance, behavior (Seitz et al., 2001) and habitat features like water depth and sediment type (Velasquez and Navarro, 1993; Micheli, 1996). On the other hand, variation in predator pressure may affect patterns of prey abundance (Power et al., 1985). However, differences in predation pressure may be caused by the absence of predators in some habitats or various physical or biological factors (Wootton, 1993). Therefore, factors affecting use of habitats of predators and their prey can in turn affect the intensity of the impact of predators on their prey.

Some of the most important predators of estuarine intertidal mudflats are shorebirds (Wilson, 1994). They usually spend their non-breeding season away from their breeding grounds and use estuaries as staging and stopover sites to obtain food (Kalejta, 1992a; Wilson, 1994). Due to their high-energy requirements, their feeding rates on benthic organisms are usually very high (Quammen, 1984; Botto et al., 1998). Some experimental studies have shown a strong effect of shorebirds on the abundance of invertebrate prey (Quammen, 1984; Botto et al., 1998), but others failed to find a significant impact (Raffaelli and Milne, 1987; Kalejta, 1993; Wilson, 1994; Sewell, 1996). In some cases, they do not affect densities of prey but affect their size structure (Godfray and Hassell, 1987). However, all evidence suggests that the importance of the effect of shorebirds on prey depends on many factors, but in soft intertidal, the characteristics of the substrate are important. Sediment grain size (Quammen, 1980), substrate penetrability and prey density affect capture rate directly (Myers et al., 1980). Moreover, sediment type may affect availability of invertebrates affecting their feeding behavior, abundance and growth rate (Newell and Hidu, 1982). Thus, any effect on sediment structure or quality is likely to affect the strength of predator–prey interactions between shorebirds and their infaunal prey.

In north Argentinean estuaries, shorebirds are important Intertidal predators (Botto et al., 1998, 2000). The intertidal sediments of this region are highly disturbed by the burrowing crab *Chasmagnathus granulatus*. These crabs remove up to $5 \text{ kg m}^{-2} \text{ day}^{-1}$, generating large patches (“burrowing beds” of up to 40 crabs m^{-2}) of disturbed sediments (Iribarne et al., 1997; Botto and Iribarne, 2000). Their large burrow entrances (up to 15 cm diameter, up to 50 cm depth) work as fine-sediment traps contributing to the generation of soft sediment crab beds. As a result, sediment organic matter and water content increase, while permeability and hardness decrease (Botto and Iribarne, 2000). This bioturbation is an important and characteristic process in SW Atlantic estuarine environments (Botto and Iribarne, 2000) and could explain patterns of shorebird and infaunal distributions (Botto et al., 1998, 2000). In these areas, shorebirds showed differences in habitat use and foraging success between burrowing beds and areas where crabs are absent (Botto et al., 2000). For example, while the Two-banded Plover *Charadrius falklandicus* more frequently use the crab beds where they have higher capture rate of polychaetes and feeding efficiency, the White-rumped Sandpiper *Calidris fuscicollis* are more common and efficient outside burrowing areas (Botto et al., 2000). These differences are probably due to differences in sediment features and the feeding strategies between shorebird species.

In the areas previously described, the main prey of shorebirds is the polychaete *Laeonereis acuta*. This is an abundant species found in different types of sediment, and along the salinity gradient of estuarine areas, including burrowing beds of crabs (Gutierrez and Iribarne, 1999; Palomo et al., 1999; Palomo and Iribarne, 2000; Schwindt and Iribarne, 2000). They live in burrows with two (U-shaped) or one (I-shaped) connections to the surface (Palomo and Iribarne, 2000). Most of them live in the first 5 cm of sediment, but larger individuals live deeper (up to 10 cm). Their risk of being preyed on depends on shorebird feeding strategies (Pienkowski, 1981). This risk decreases with the depth of the burrows, since shorebirds move over the surface and have to dig or probe into the substrate to find prey only to a limited depth (Esselink and Zwarts, 1989). However, the risk of being captured by a visual forager also depends on how many times the worms move to the surface to feed or defecate (Pienkowski, 1983). Given that polychaete behavior can change in areas with different sediment characteristics, the presence of crab beds is likely to affect the feeding rates of shorebirds.

In this study, we address the question of whether the presence of the burrowing crab *C. granulatus* affects the interaction between shorebirds and their prey. First, we studied the possible effect of burrowing crabs on the distribution, burrowing and feeding behavior of the main prey of these shorebirds, the polychaete *L. acuta*. Then, given that shorebird species differently use areas with and without crabs (Botto et al., 2000), we evaluated with exclusion experiments, the overall effect of shorebirds on polychaete abundance and size-frequency distribution in both areas.

2. Methods

2.1. Study area

The study was conducted on the intertidal mudflats along Mar Chiquita coastal lagoon (38°00'S, 57°30'W, Argentina), from November 1998 to May 1999. The influence of the ocean creates an estuarine environment where the salinity is between 10 and 37 ppm and the tidal range up to 1.90 m (Fasano et al., 1982). Beaches of 500 m length and with the same tidal regime and similar benthic infauna were selected. Two types of areas were selected for the study: those with muddy sediment and active bioturbation by crabs (Iribarne et al., 1997; Botto and Iribarne, 1999, 2000) and those with sandy–muddy substrate, without the presence of crabs but located at the same tidal height. Hereafter the areas with crab burrows (densities higher than 15 burrows m⁻²) will be referred as “inside crab beds” and the areas without burrows and crab activity as “outside crab beds”.

2.2. Polychaetes inside and outside crab beds

2.2.1. Densities and size frequency distribution of polychaetes

Densities of polychaetes inside and outside crab beds were compared during the summer period. To evaluate temporal variation during the shorebird migratory season,

samples were taken from the mid-intertidal on December, January, February, and April. Ten Cores, 20 cm diameter and 10 cm long, were randomly taken from both areas and sieved through a 0.5-mm mesh screen. Organisms retained were identified and quantified under a binocular microscope (10×). Densities were compared between months and areas with a two-way ANOVA test. A log transformation was performed to adjust ANOVA assumptions. A posteriori LSD tests were used when necessary (Zar, 1999).

To evaluate differences between sites on the size of available prey, and to find possible recruitment events, size frequency distributions of polychaetes were obtained for each area and time. The worms found in the samples were measured using a caliper (accuracy 0.01 mm) when they were completely quiet and elongated. As many individuals were broken, their lengths were estimated from the jaw size. The jaws were measured (accuracy 0.001 mm) using a binocular microscope (40×) and a regression model was constructed using the length of intact worms as the independent factor and the length of jaws as the dependent one (Esselink and Zwarts, 1989). A log transformation was performed to adjust the linear regression model and regression least squares analysis was performed to test the model (Neter et al., 1990). The size frequency distributions of polychaetes were compared between areas with a Kolmogorov–Smirnov test (Conover, 1980) for each month independently. Comparisons between months were also made within areas.

2.2.2. Burrow shapes

Burrow shapes of polychaetes were identified inside and outside crab beds as an indicator of trophic mode (Tsutsumi and Taniguchi, 1998) to evaluate changes in prey behavior between sites. This identification was performed only once because it was not expected to change temporally. Sediment cores (10 cm diameter, 15 cm depth) were taken in each area. These cores were broken in the field to expose the burrows that were easily distinguished due to their brownish colored walls. Burrows were characterized as either I-shaped if they were straight and with one connection to the surface or U-shape when having two connections to the surface (Palomo and Iribarne, 2000). To compare burrow shape between areas (outside and crab beds), only large polychaetes (between 24.5 and 40 mm) were selected because small animals have always U-shaped burrows (Palomo and Iribarne, 2000). A Kolmogorov–Smirnov analysis was performed to test if polychaete size differed between samples. A χ^2 test (Zar, 1999) was used to compare the percentage of occurrence of U- and I-shaped burrows outside and inside crab beds.

2.2.3. Body condition of polychaetes

Given that areas with crabs have increased organic matter content (Botto and Iribarne, 2000), the indirect effect of crabs on polychaetes could be an increase on their food acquisition. To evaluate this hypothesis we compared the body condition of polychaetes inside and outside of crab beds. Body condition, as a measure of prey profitability, can affect shorebird prey selection (Esselink and Zwarts, 1989). To obtain a measure of body condition, we fitted the relationship between wet weight polychaete length as independent variable. Wet weight was determined after polychaetes were dried with a tissue paper during 2 min. Polychaete body condition was defined as the relationship between wet

weight and polychaete length. Then the two regression slopes from outside and crab bed were compared between areas with a Parallelism test (Zar, 1999).

2.2.4. Behavior of polychaetes

An experiment was performed to study surface activity of polychaetes outside and inside crab bed, given that this can be a measure of the risk of being preyed on by visual foragers. During low tide, wet sediment areas (the areas used by shorebirds to forage; personal observation) were chosen to observe the surface behavior of polychaetes. Plots of 100 cm² were randomly selected and observations were performed during 20 min and were replicated five times inside and outside crab beds. Observations were made after waiting in the place for 10 min, to prevent disturbance of the polychaetes. Each time a polychaete appeared on surface was recorded to estimate the number of appearances on surface per minute per area. The densities of polychaetes in the plots were determined afterwards with the core sampler. A *t*-test with separate variances (thereafter *t_c*; Zar, 1999) was performed to compare the number of appearances per polychaete between areas. Also, given that with the observation of surface activity could not be differentiated the head from the tail, the position of the head of 100 polychaetes on each area was observed directly from their burrows. Differences on the occurrence of each position (up or down) were compared between areas with a χ^2 test (Zar, 1999).

Another behavior that was also considered to affect predation risk is the fragmentation capacity of polychaetes. Some worms can fragmentize their tails to reduce predation risk. Nereid polychaetes are usually capable of regenerating the posterior end but cannot regenerate lost heads (Brusca and Brusca, 1990). To test if *L. acuta* have the capacity to fragment, an experiment was performed. Sediment cores were extracted and opened to expose burrows. When polychaetes were observed inside, they were captured randomly from the end or from the head (100 times each) with a fine-ended clamp. The percentage of fragmented worms was calculated.

2.3. Shorebirds predation

2.3.1. Shorebird abundance

To evaluate differential use of areas by shorebirds, six areas 150 m long, 60 m width were selected at low tide, three inside crab beds and three outside crab beds. In each area, observations were carried out at low tide using 10 × 70 binoculars once a week from November 1998 to May 1999. Birds were counted and described as resting or feeding. Bird species were identified following the field guide of Narosky and Yzurieta (1987). A repeated measures three-way ANOVA test was used to detect differences in the abundance of species outside and inside crab beds (Zar, 1999). A posteriori multiple comparison tests were performed due to the significant interaction between factors (Underwood, 1997).

2.3.2. Effects of shorebirds

To evaluate if the effect of shorebirds on polychaetes is different inside and outside crab beds, we performed a shorebirds exclusion experiment and examined the effect of

shorebird predation on polychaete abundance and size-frequency distribution. The experiment had two treatments: (1) shorebirds exclusion, using 1×1 m wire roofs (2 cm mesh) to exclude birds, (2) control, areas located nearby without roofs. Roofs were deployed 10 cm above the sediment, with a PVC stake (2 cm diameter) on each corner. Previous experiments (Botto et al., 1998) showed that these roofs prevent shorebirds from using the areas underneath and have no further effect on the infauna. The design without walls allows crabs and fishes to enter. Birds exclusions were examined every other day to see if there were bird tracks underneath. The experiment was repeated four times in four separate locations (December, January, February and April) to test for temporal changes during the summer. At the end of each experiment (December 10, January 15, February 19 and April 1), a core (20 cm diameter, 10 cm depth) was extracted from the center of each replicated unit. Samples were sieved through a 0.5-mm mesh screen. Organisms retained were identified and quantified under a binocular microscope ($10\times$). t_c -tests were used to compare densities between control and roofs plots on each area for each month. Polychaetes were also measured in the laboratory and lengths of broken worms were estimated with the regression jaw size-total length model previously described. Kolmogorov–Smirnov two sample tests were used to compare polychaetes size frequency distributions between treatments for each area (Conover, 1980).

To analyze possible confounding effects of roofs on the sediment characteristics (Hall et al., 1990), sediment samples (3 cm diameter, 5 cm depth) were obtained from each replicate (roofs and controls) at the end of the experiment in April. The organic matter content, water content and grain size distribution were analyzed. Water content was determined on the basis of the difference between wet and dry weight (after drying at 70°C up to constant weight). Organic matter content was determined from the same sample combusted at 550°C during 6 h obtaining the ash-free dry weights (AFDW). A two-way ANOVA was used to evaluate differences in water content or AFDW between treatments for each area (Zar, 1999). Grain size distribution was determined by sieve and sedimentation analysis following Carver (1971). The samples were sieved through a series of six different mesh size openings from 2000 to $62\ \mu\text{m}$ and mesh size was expressed according to the phi scale (Gray, 1981). Pipeting technique was performed to separate grains from 62 to $3.9\ \mu\text{m}$. Grain size distributions of the different treatments and places were compared using Kolmogorov–Smirnov tests (Conover, 1980).

3. Results

3.1. Densities and size frequency distribution of polychaetes

In both areas, sediment samples contained only the polychaete *L. acuta*. Other polychaete species (*Neanthes succinea* and *Heteromastus similis*) were rarely found (one or two individuals per species per monthly sampling). Thus, we only included *L. acuta* in our data analysis. Densities of polychaetes were higher during December and April than January and February (ANOVA, $F=8.75$, $df=3, 72$, $P<0.001$) and

high inside than outside crab beds ($F=10.30$, $df=1$, 72 , $P<0.002$), but the interaction between month and areas was not significant ($F=0.81$, $df=3$, 72 , $P>0.05$, Fig. 1).

The regression model to estimate the length of broken worms was: \log_{10} worm length = $0.846 + 0.129 \cdot \text{jaw length}$, ($r^2=0.78$, $n=315$, $P<0.001$). Size frequency distribution of polychaetes changed between areas in December and January (Kolmogorov–Smirnov, $P<0.05$; Fig. 2). The relative frequency of the small polychaetes increased in crab beds in comparison to outside crab beds in both months. Independent comparisons between months in both areas showed that the size frequency distribution changed in almost all months (see Table 1).

3.2. Burrows shape

Polychaete sizes did not differ between areas (K-S test, $n=30$, $P>0.1$). Polychaete burrows outside crab beds showed a smaller proportion (56%) of U-shaped burrows than inside crab beds (87%, $\chi^2=4.71$, $n=40$, $P<0.05$).

3.3. Body condition of polychaetes

The relationship between polychaete length and weight was different inside and outside of crab beds (Parallelism test, $F=11.27$, $df=1$, $P<0.001$). Inside crab beds the slope ($b=0.963$, S.D.=0.042) was higher than outside crab beds ($b=0.817$, S.D.=0.051). The lines crossed in the point polychaete length = 10.7 mm; wet weight = 0.003 g, which indicates that polychaetes larger than 10.7 mm inside crab bed are heavier than the ones outside. The great proportion of the organisms found in the sediment were larger than 10.7 mm, consequently most of the polychaetes inside crab beds were in better body condition.

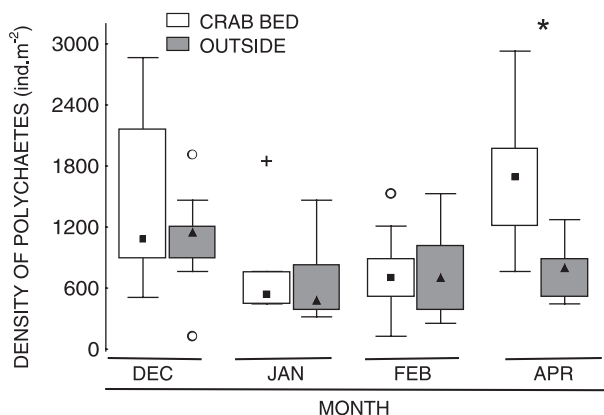


Fig. 1. Polychaetes densities outside and inside crab bed from December to April. A two-way ANOVA test was used to compare densities between areas and months. A posteriori LSD test was performed to detect differences. Box plots are constructed with percentiles. Limits of boxes are the 75th and 25th percentile, lines represent 10th and 90th percentiles, squares or triangles inside boxes are medians, circles outside boxes are outliers.

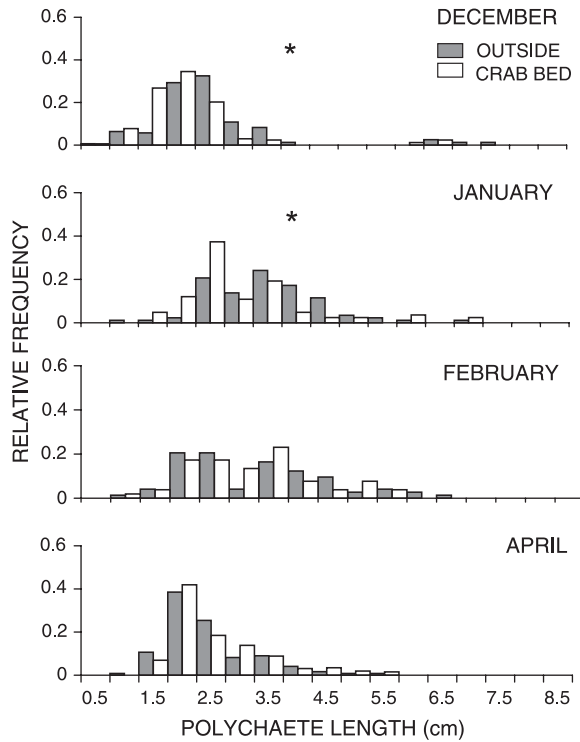


Fig. 2. Size frequency distribution of the polychaetes outside and inside crab beds on December, January, February and April. Kolmogorov–Smirnov tests were used to compare areas within each month.

3.4. Behavior of polychaetes

Polychaetes were more frequently seen on the surface outside than inside crab beds ($x_{\text{outside}} = 0.025$ (S.D. = 0.013) surfacing min^{-1} ; $x_{\text{inside}} = 0.003$ (S.D. = 0.007) surfacing min^{-1} ; $t_c = 4.01$, $df = 4.005$, $P < 0.05$).

Table 1
Kolmogorov–Smirnov tests comparing size frequency distributions of polychaetes between months

Month	Outside		Crab bed	
	d_{max}	P -level	d_{max}	P -level
December–January	0.50	0.001	0.54	0.001
December–February	0.34	0.001	0.57	0.001
December–April	0.11	0.1	0.33	0.001
January–February	0.23	0.05	0.18	0.1
January–April	0.52	0.001	0.34	0.001
February–April	0.32	0.001	0.34	0.001

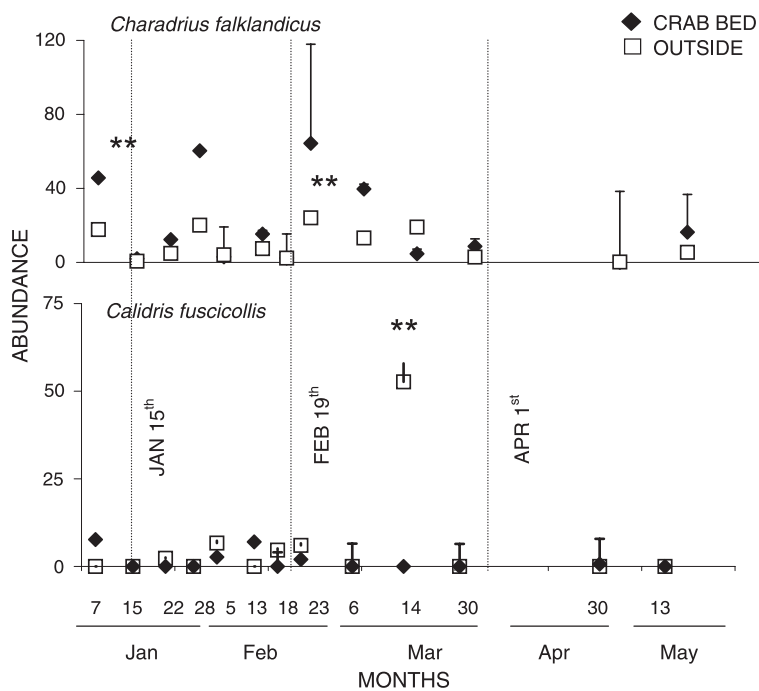


Fig. 3. Mean abundance (+1 S.D.) of the shorebirds *C. falklandicus* and *C. fuscicollis* inside and outside crab beds, vertical lines with dates indicate the monthly experiments periods.

The occurrence of the head-up position worms outside crab beds was significantly greater than inside crab beds ($\chi^2 = 10.08$, $n = 100$, $P < 0.001$). 100% of the polychaetes fragmented their tails when pressure hard enough to take them outside their burrows was

Table 2

Three-way repeated measures ANOVA results for two areas, inside and outside crab beds and two shorebirds species (*C. fuscicollis* and *C. falklandicus*)

Source	df	MS	F	P
<i>Between</i>				
Area	1	1152.41	1.538	0.250
Species	1	4000.61	5.339	0.049
Area × Species	1	3491.30	4.660	0.062
Error	8	749.20		
<i>Within</i>				
Time	12	505.64	3.434	0.0003
Area × Time	12	1055.49	7.166	<0.0001
Species × Time	12	447.86	3.040	0.001
Area × Species × Time	12	531.16	3.606	0.0001
Error	96	147.28		

Time was considered as the repeated factor.

applied. However, no polychaete fragmented their heads when a similar force was applied to the head region.

4. Shorebirds predation

4.1. Shorebirds abundance

Seven species of shorebirds were observed foraging at the study sites. Lesser Yellowlegs (*Tringa flavipes*), Greater Yellowlegs (*Tringa melanoleuca*), Black-bellied Plover (*Pluvialis squatarola*), Red Knot (*Calidris canutus*) and Hudsonian Godwit (*Limosa haemastica*) were observed only sporadically and are not included in the analysis. The Two-banded Plover (*C. falklandicus*), and White-rumped Sandpiper (*C. fuscicollis*) were the only species considered in the analysis since they were the most abundant (>90%). The Two-banded Plover arrived to the lagoon in January and reached a

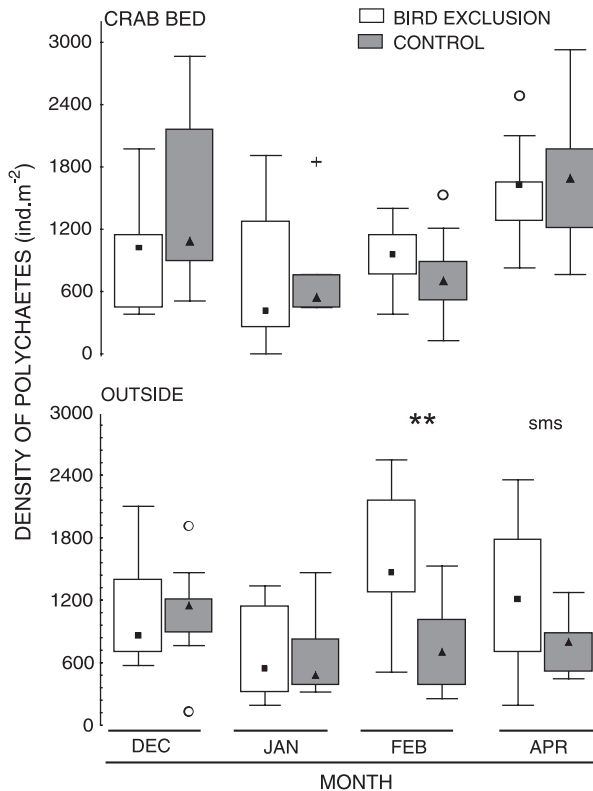


Fig. 4. Density of polychaetes vs. months for both areas, inside and outside crab beds, sms means statistical marginal significance.

maximum density of 60 ind ha⁻¹ inside crab beds and 27 ind ha⁻¹ outside crab beds (Fig. 3). The White-rumped Sandpiper arrived at the lagoon on January and the maximum density inside crab beds was 7 ind ha⁻¹, meanwhile outside crab beds was 53 ind ha⁻¹ in March (Fig. 3). Repeated measures ANOVA showed no differences in shorebird abundance between areas, but there were temporal differences between shorebirds species (Table 2). Interactions between areas × time, shorebirds × time and areas × shorebirds × time were also significant. Because a significant third-order interaction was found, testing lower order interactions or main effects was not possible (Underwood, 1997). Results from multiple comparisons showed that shorebirds species occupied different areas in different times. White-rumped Sandpiper was more abundant outside crab beds on March 14. Two-banded Plover was more abundant inside crab beds on January 7 and February 23 (Fig. 3).

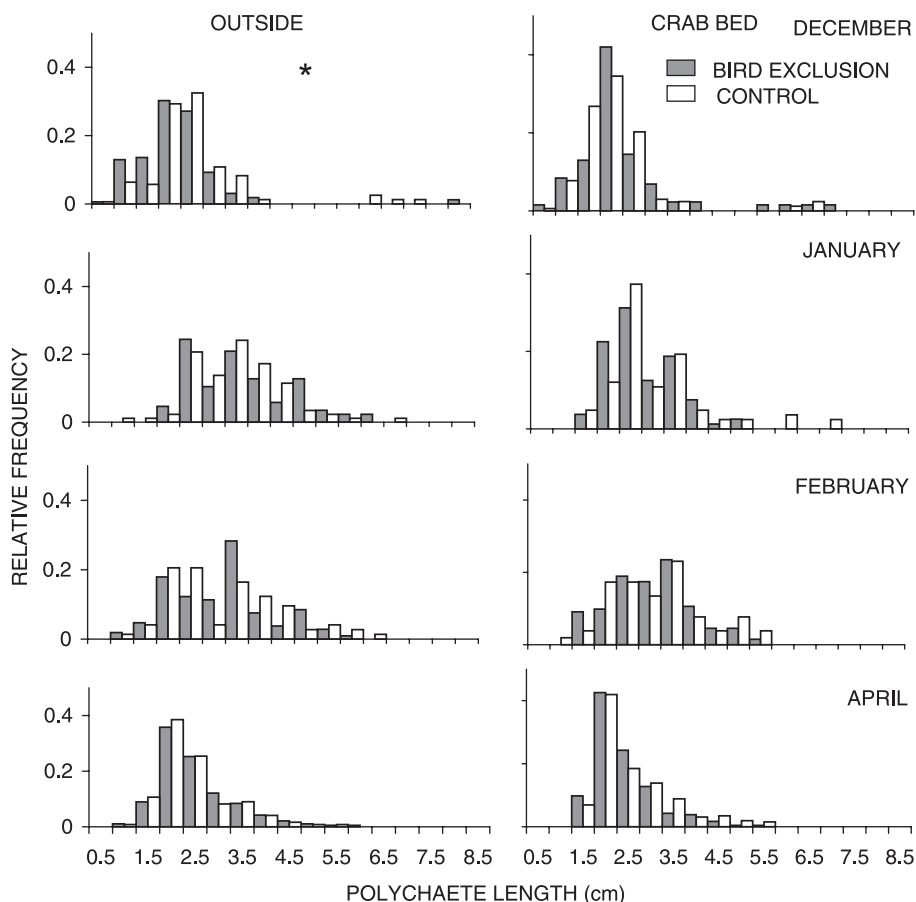


Fig. 5. Size frequency distribution on bird exclusions and controls for the monthly experiment and the two sites.

Table 3

Two-way ANOVA of the water and organic matter content outside and inside crab bed (area) for ceiling and control plots (treatment)

Factor	df	MS	F ratio
<i>Water content</i>			
Area	1	0.245	1.319 ns
Treatment	1	0.129	0.698 ns
Interaction	1	0.245	1.319 ns
Error	15	0.185	
<i>Organic matter</i>			
Area	1	6.314	12.276**
Treatment	1	0.349	0.678 ns
Interaction	1	0.014	0.029 ns
Error	15	0.514	

df, degrees of freedom; MS, mean square. Here and thereafter *= $P < 0.05$, **= $P < 0.01$, ***= $P < 0.005$ and ns = not significant.

4.2. Effect of shorebirds

Exclusion of shorebirds showed that the density of polychaetes did not change between treatments, except in February and April. In these months outside crab beds, the density of polychaetes decreased significantly in the control (February, $t_c = 3.08$, $df = 15.95$, $P < 0.01$; April, $t_c = 1.895$, $df = 11.68$, $P < 0.082$ (marginally significant, Fig. 4).

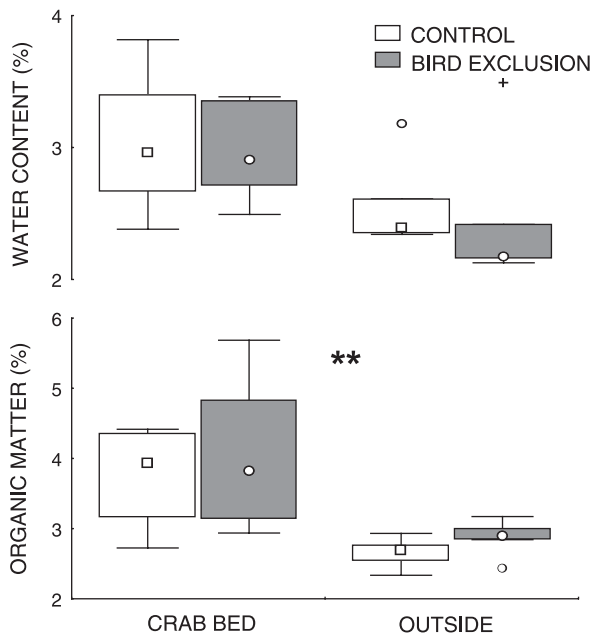


Fig. 6. Water content (%) and organic matter content of the surface sediment of bird exclusion and control of the experiments. A two-way ANOVA was performed to test differences between treatments and areas.

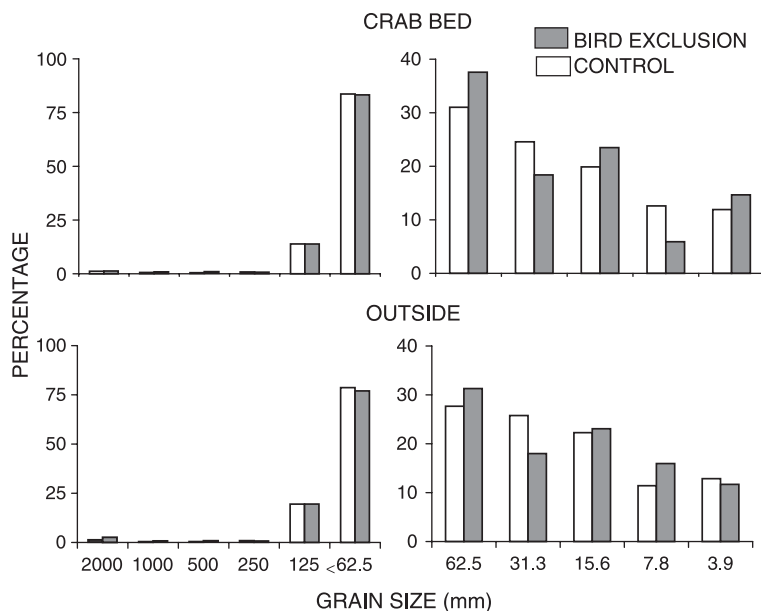


Fig. 7. Grain size distributions of bird exclusion and control plots outside and inside crab beds. Differences were not significant.

Size frequency distributions of polychaetes under roofs outside and inside crab beds were not different (Kolmogorov–Smirnov, $P > 0.10$) for all experiments independently (Fig. 5) except on December outside crab beds, where small polychaetes were more frequent under roofs (K-S test, $d_{\max} = 0.18$, $P < 0.05$).

There were no roofs effects on the sediment surface. Water content of the sediment under roofs did not differ significantly between treatments (Table 3, Fig. 6). Organic matter content decreased significantly outside crab beds, but there was no effect of roofs or interaction in both areas (two-way ANOVA, Table 3, Fig. 6). Surface sediments (5 cm) grain size distributions were not affected by roofs or by the presence of crab burrows (Kolmogorov–Smirnov two samples test, $P > 0.1$, Fig. 7).

5. Discussion

5.1. Prey availability

Polychaete densities and size frequency distributions show the same pattern inside and outside crab beds, with two recruitment events, in early summer (December), and the second in late summer. This pattern is expected in temperate estuaries, where recruitment often occurs in summer, when mild weather conditions enhance productivity (Kalejta, 1992b). The pattern of densities was also similar inside and outside crab beds, except in April when their density was higher inside crab beds. Similar differences were found in a

previous study (Botto and Iribarne, 1999) suggesting that when differences occur, polychaete density is higher inside crab beds. However, these differences may be due to different recruitment or mortality rate.

Most of the polychaetes live in the first 5 cm of sediment inside burrows always connected to the surface. This depth distribution exposed them to tactile predation (Pienkowski, 1983) equally in both sites. However, density or depth distribution does not accurately represent the actual availability for all shorebirds. Polychaetes in crab beds had more burrows with two connections with the surface (U-shaped burrows) and showed less surface activity. These changes in prey behavior could be important, since their appearance on the surface could increase visual predation risk.

For deposit feeders such as *L. acuta*, food acquisition determines their behavior because quality of mud is generally poor, and they have to ingest large volumes of sediment (Lopez and Levington, 1987). In crab beds, availability of food for polychaetes is higher and similar on the surface and below the surface (Botto and Iribarne, 2000). Thus, *L. acuta* could obtain the same amount of food below the surface. This has the advantage that food may be used for longer periods, and not restricted to periods when sediment is underwater or humid. Indeed the better body condition of polychaetes inside crab beds may be the result of these advantages. However, outside, the organic matter content is higher on the surface making it more profitable to be a surface deposit feeder, despite the increase of predation risk. This difference may be responsible for the higher surface activity of polychaetes outside crab beds. In any case, it is apparent that sediment homogenization by crab burrowing indirectly affects polychaete body condition, behavior and their susceptibility to predation.

Another way to escape predation is by fragmentation. Infaunal organisms often lose body parts exposed above the sediment surface to predators (de Vlas, 1979; Woodin, 1982). Although they survive this process, it negatively affects their growth (Peterson and Quammen, 1982), feeding activity (Lindsay et al., 1996) and sediment disturbance. *L. acuta* can indeed fragment their tail, which may help to escape predation. However, the proportion of individuals with their head pointing to the surface was much higher outside crab beds. This suggests that the likelihood of escaping predation by fragmentation is low in these habitats.

5.2. Effect of shorebirds

Shorebirds censuses showed that the two most abundant species, White-rumped Sandpiper and Two-banded Plover, arrived at the lagoon in January and departed by May. The White-rumped Sandpiper was more abundant outside crab beds, while the Two-banded Plover was more common in crab beds (Botto et al., 2000). Experimental exclusion of shorebirds showed that they influenced crab bed and non-crab bed areas differently. Densities of polychaetes decreased in control plots outside crab beds in February and April. The predation by shorebirds was in general non-selective, given that the distribution of polychaete size was different between treatments only outside crab beds in December. However, no effect was ever found inside crab beds. If roofs treatments were compared between January and February in both areas, it is evident that there is an increase on polychaetes density in February in roofs plots outside crab beds that did not

occur inside crab beds. This pattern is the result of a recruitment event, but shorebirds significantly decreased the survival of those newly recruited polychaetes outside crab beds. Thus, in general our results show that shorebirds were able to affect polychaete density and size frequency distribution only outside crab beds.

The White-rumped Sandpiper is a tactile feeder (Pienkowski, 1981) and was more abundant outside crab beds. For tactile foragers, areas with crab burrows could be disadvantageous, since they have to avoid them. This species is known to consume the same amount of polychaetes outside than inside crab beds. However, their efficiency is higher outside given that they have to probe more times in crab beds to find a worm (Botto et al., 2000). Moreover, this species seems to have a more visual tactic outside (Botto et al., 2000) probably due to the different polychaete behavior explained before. The higher abundance of White-rumped Sandpipers outside crab beds suggests that they were responsible for the decrease in polychaete densities. The strength of the interaction could change depending on several factors. Predation can be weak when physical disturbance or low prey productivity occurs (Menge et al., 1994). If productivity decreases, and consequently the abundance of preys also decrease, the low prey density could act as a refuge from predation, decreasing the feeding efficiency (Seitz et al., 2001). Our results show that when polychaete abundance was low (January and February), the effect of predation was not significant. However, when polychaete abundance outside was high (February and April), the effect of predation was significant. Therefore, it is likely that the reduction of prey densities reduces prey encounter rates and leads to a decrease in foraging efficiency or predators move to more profitable patches leading to a decrease in the effect of predation (Seitz et al., 2001).

The Two-banded Plover is a visual feeder and was more frequently observed inside crab beds, where they are more successful and showed higher capture rates (Botto et al., 2000). Therefore, at least for this species, the more frequent surface appearance of polychaetes does not increase their predation efficiency outside crab beds. This species is less affected by crab burrows (Botto et al., 2000). Capture rates of these shorebirds inside crab beds (0.6 pol min^{-1}) are similar to the White-rumped Sandpiper capture rates outside crab beds (0.5 pol min^{-1} ; Botto et al., 2000). However, our experiments did not show an effect of shorebirds inside crab beds. It is interesting because the interaction occurs, even when it is not detected by the experiment. Other experiments have also failed to show a predation effect although high capture rates occurs (Kalejta, 1992b, 1993). However, in our case the results do not appear to be an artifact of the exclusion experiment. These experiments have been criticized (Hall et al., 1990), mainly because sediment composition may change due to the hydrodynamic effect of roofs (see Hall et al., 1990; Sewell, 1996) and migration of prey (Kalejta, 1993; Sewell, 1996). However, in our case sediment organic matter, grain size and water content was not affected by the experiment, and migration is unlikely to occur given the permanent burrows of *L. acuta*. Thus, all evidences suggests that the interaction between shorebird and polychaetes is stronger (i.e. higher magnitude of their effect) outside than inside crab beds. The magnitude of the effect, considering the same capture rates and densities of predators, could be diminished by decreasing the duration of predation or increasing the area of predation. In this case, crab beds are known to increase the area of predation for shorebirds, by increasing the humidity along the intertidal during ebbing tides (Botto and Iribarne, 2000).

In summary, these results suggest that the strength of the predator–prey interaction between shorebird and polychaetes varies depending on the presence of burrowing crabs. Like any other environment, in soft-sediment communities, predation intensity ranged from strong to weak (Wilson, 1991). Both intensities could significantly alter natural communities and depend on factors such as environmental gradients (Menge et al., 1994). However, indirect effects may also be responsible of changing the strength of interactions. Indeed, indirect effects could be larger and of greater magnitude than direct effects (Strong, 1997). In some cases, the relative importance of indirect effects was similar to that of direct effects (Menge, 1997). In our case, the burrowing crabs *C. granulatus* modify the environment by the construction and maintenance of burrows (Botto and Iribarne, 2000). This alteration, influences the habitat use of shorebirds (Botto et al., 2000, our results), and also the behavior (and availability) of their benthic polychaete prey. Thus, our results show that the SW Atlantic burrowing crab *C. granulatus* affects the strength of predator–prey interactions between shorebirds and polychaetes. This is evidence for changes in interaction strength due to an indirect effect.

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