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An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon

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article info abstract

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The objective of our research was to evaluate by sampling and field experiments the effects of the invasive intertidal reef-building polychaete Ficopomatus enigmaticus on the habitat use and foraging behavior of birds in Mar Chiquita coastal lagoon (37°40′S, 57°23′ W, Argentina). Nearby areas with and without reefs were selected to asses their use by birds. Focal observations during low tide showed that bird densities (migratory shorebirds $=$ Tringa melanoluca, T. flavipes, Calidris fuscicollis; non-migratory birds $=$ Phalacrocorax olivaceus, Larus dominicanus, L. maculipennis, Anas spp., Vanellus chilensis, Milvago chimango) were higher on reef surface compared with similar areas without reefs. Migratory shorebirds used reefs surface mainly for feeding, while local birds used it for resting. Foraging rates of T. melanoleuca and T. flavipes were higher on the reefs than in the bare sediment. Comparative sampling (10 core per site) showed that epifaunal organisms (amphipod Melita palmata, crab Cyrtograpsus angulatus and gastropod Heleobia spp.) were more abundant on reef surfaces, but the density of infaunal preys (the polychaetes Laeonereis acuta, Nepthys fluviatilis, and Neanthes succinea) were not different between areas. Bird exclosure experiment and control $(n= 10)$ showed no differences in density and size distribution between treatments for any benthic species analyzed. In conclusion, there was a positive effect of F. enigmaticus reefs on the habitat use of birds, because this area was preferred for feeding and resting, and there were more epifaunal preys which positively affected the foraging rates of shorebirds.

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1. Introduction

Bioinvasions are a threat for ecosystem integrity around the world [\(Pimentel et al., 2001\)](#page-6-0) probably resulting from globalization [\(Vitou](#page-7-0)[sek, 1990; Bright, 1999](#page-7-0)). Currently, invasions continue altering systems worldwide, especially coastal environments [\(Wasson et al.,](#page-7-0) [2001\)](#page-7-0). In the South Western Atlantic coastal ecosystems, several marine invading species have been reported (see [Orensanz et al.,](#page-6-0) [2002](#page-6-0)), affecting different environments such as intertidal rocky shores [\(Hidalgo et al., 2005; Rico and López Gappa, 2006\)](#page-6-0), shallow bays [\(Escapa et al., 2004](#page-6-0)) and coastal lagoons ([Schwindt and Iribarne,](#page-6-0) [1998; Muniz et al., 2005\)](#page-6-0). Some of them have caused important ecological and economic problems. The importance of the invader impact has been focalized on the negative effects on ecosystems, but little attention has been made on the positive effects they may have (but see [Escapa et al., 2004\)](#page-6-0). These effects have been described for several species (e.g., [Simberloff and Von Holle, 1999; Tecco et al.,](#page-6-0)

[2006; Escapa et al., 2004](#page-6-0)) but underemphasized in ecology, and tidal flats are not an exception.

Soft bottom intertidal contains scarce amount of three-dimensional abiotic features, however they host numerous biotic surface structures. In these tidal flats, ecosystem engineering plays a major role in the creation of habitats ([Jones et al., 1994; Gutierrez et al.,](#page-6-0) [2003](#page-6-0)). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials ([Jones et al., 1994](#page-6-0)). Bivalves (e.g. oysters, [Escapa et al., 2004](#page-6-0); mussels, [Crooks, 1998](#page-6-0); clams, [Gutierrez et al., 2003](#page-6-0)), seagrasses [\(Reusch, 1998](#page-6-0)), crabs [\(Botto](#page-6-0) [et al., 2006](#page-6-0)) and polychaete tube assemblages [\(Khaitov et al., 1999;](#page-6-0) [Zühlke, 2001](#page-6-0)) are some of the most conspicuous biogenic structures and a good example of substrate creators that directly or indirectly modify the intertidal flat creating a three dimensional relief bottom. These organisms enhance the spatial heterogeneity and the structure of habitat [\(Crooks and Khim, 1999; Escapa et al., 2004](#page-6-0)), and consequently increase the surface area for settlers of numerous invertebrate benthic species ([Crooks, 1998; Zühlke, 2001](#page-6-0)). They also elevate the bottom surface and offer refuges from predation or physical stress for associated fauna [\(Gutierrez et al., 2003](#page-6-0)). Thus, in flat muddy bottoms, ecosystem engineers often support higher

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densities of associated fauna than the surrounding flats. Associated fauna is a prey species for many birds, and constitutes an alternative food supply. Thus, migratory shorebirds may benefit from these biotic structures as important foraging and resting areas [\(Hilgerloh, 1997;](#page-6-0) [Petersen and Exo, 1999\)](#page-6-0).

Tube-builder polychaetes as ecosystem engineers [\(Hutchings, 1998;](#page-6-0) [Khaitov et al., 1999; Schwindt and Iribarne, 2000; Zühlke, 2001](#page-6-0)) usually increase the structural complexity of the habitat and the diversity and abundance of benthic species, changing the benthic community composition (e.g., [Zühlke, 2001; Callaway, 2003; Bolam and Fernandes,](#page-7-0) [2003; Dubois et al., 2006\)](#page-7-0). An exotic species capable to modify the physical habitat and create substrate for use by other organisms is the reef-forming polychaete Ficopomatus enigmaticus [\(Schwindt and Iri](#page-6-0)[barne, 2000; Schwindt et al., 2001\)](#page-6-0). This polychaete is distributed in most brackish waters in temperate zones throughout the world ([Ten](#page-7-0) [Hove and Weerdenburg, 1978](#page-7-0)). It was recorded in Argentina in 1943 [\(Rioja,1943\)](#page-6-0) and before the seventies in the Mar Chiquita coastal lagoon (37°40′S, 57°23′ W; [Orensanz and Estivariz, 1972](#page-6-0)). The reefs formed by the polychaete are circular, reaching up to 7 m in diameter and 0.5 m in height ([Schwindt et al., 2004](#page-6-0)). These reefs increase the number of refuges for many associated organisms that live between the tubes such as crabs [\(Luppi and Bas, 2002; Méndez Casariego et al., 2004](#page-6-0)), amphipods, gastropods, and free living polychaetes [\(Schwindt and](#page-6-0) [Iribarne, 2000](#page-6-0)). They also modify the sedimentary patterns of the lagoon by increasing deposition [\(Schwindt et al., 2001\)](#page-6-0) and have a strong top– down effect on the phytoplankton biomass of the lagoon [\(Bruschetti](#page-6-0) [et al., 2008\)](#page-6-0). During the last decades, F. enigmaticus reefs densities grew dramatically fast and occupied up to 80% of the benthos of the brackish portion of the lagoon ([Schwindt et al., 2004\)](#page-6-0). Thus, reefs have been combined forming large platforms of several meters of longitude. These areas occupied by F. enigmaticus reefs remain uncovered with medium and low tide and are frequently used by birds ([Martinez, 2001\)](#page-6-0). The Mar Chiquita coastal lagoon is an important stopover site for migratory birds (i.e., the greater yellowlegs Tringa melanoleuca, the lesser yellowlegs T. flavipes, the white-rumped sandpiper Calidris fuscicollis and the blackbellied plover Pluvialis squatarola; [Botto et al., 1998](#page-6-0)) and also for local breeding species (i.e., the Neotropical cormorant Phalacrocorax olivaceus, the kelp gull Larus dominicanus, the brown-hooded gull L. maculipennis, the South American stilt Himantopus melanurus, the Southern lapwing Vanellus chilensis, the black-necked swan Cygnus melanocoryphus, maguari store Ciconia maguari, and the chimango caracara Milvago chimango; [Martinez, 2001](#page-6-0)). However, little is known about the effects of the reef beds on the habitat use and foraging behaviour of these birds.

Therefore, the main objectives of our research were (1) to evaluate by sampling and field experiments the effects of the introduced reefbuilding polychaete F. enigmaticus on the habitat use and foraging behavior of birds in Mar Chiquita coastal lagoon, and (2) to evaluate the potential impact of bird predation on epifauna and infauna associated to reefs.

2. Materials and methods

2.1. Study area

The study was performed at the Mar Chiquita coastal lagoon (Buenos Aires, Argentina), a 46 $km²$ body of brackish water with an average depth of 0.6 m ([Fasano et al., 1982\)](#page-6-0). Ficopomatus enigmaticus reefs are located at the innermost zone of the lagoon [\(Schwindt et al.,](#page-6-0) [2001\)](#page-6-0). The main study site where we performed the experiments and observations was located in the central part of the lagoon (site named San Gabriel), about 6 km from the lagoon inlet, from November 2004 to March 2005, and from November 2005 to March 2006. These periods represented two entire migratory seasons for shorebirds (see [Myers and Myers, 1979](#page-6-0)) and also several local species are present (non-migratory birds; [Martinez, 2001](#page-6-0)).

2.2. Benthic prey availability

Reef-building organisms can affect infaunal communities and also, indirectly, their predators [\(Petersen and Exo, 1999](#page-6-0)). To evaluate if there were differences in prey availability between the areas potentially used by birds (areas with reefs, and areas without reefs; Fig. 1A and B), we randomly collected ten cores (10 cm diameter, 10 cm depth) in each of the two areas: edges of F. enigmaticus reefs and soft sediment without reefs. We divided the samples in two layers: upper $(0-5$ cm) and lower $(5.1-10$ cm) to assess if there were some preferential vertical distribution of the organisms. Organisms retained were preserved in alcohol 70% and then identified, measured and quantified under a binocular scope (2×10) . Differences in abundance of individuals between areas and depths were evaluated with a twoway ANOVA (site and layer; [Zar, 1999\)](#page-7-0). Given that the gastropod Heleobia spp. was only found within the reefs (see [Results\)](#page-3-0), we only evaluated the hypothesis of no difference in density between depths (upper and lower) with a t-test [\(Zar, 1999](#page-7-0)). For every analysis, homogeneity of variances and normality were assessed using Levene and Shapiro–Wilks tests ([Zar, 1999](#page-7-0)) respectively. Monotonic transformations were used when statistical assumptions were not satisfied (following [Underwood, 1997\)](#page-7-0).

2.3. Shorebirds identification, abundances and habitat use

To evaluate bird habitat use of areas with and without reefs we compared the abundance and activity of the bird species observed in the study site. We separated the birds in two groups (see [Martinez,](#page-6-0) [2001\)](#page-6-0): migratory shorebirds (Tringa melanoleuca, T. flavipes, Calidris

Fig. 1. Photographs showing intertidal areas with reefs (A) and nearby intertidal areas without reefs (B).

fuscicollis and Pluvialis squatarola; hereafter migratory birds) and nonmigratory birds (Phalacrocorax olivaceus, Larus dominicanus, L. maculipennis, Himantopus melanurus, Vanellus chilensis, Cygnus melanocoryphus, Ciconia maguari, and Milvago chimango; hereafter nonmigratory birds).

Interspersed intertidal areas with ([Fig. 1A](#page-1-0)) and without reefs [\(Fig. 1B](#page-1-0)) of F. enigmaticus were selected. Areas were no longer than 150 meters, thus we could record comparable data in the moment of sampling (time of the day and weather conditions), and in the physical characteristics of the sites (slope, tidal level and sediment). Both areas are frequently used by birds (locals and migratory). To assess bird abundance, we made censuses of birds with binoculars (10×50) in each area during low tide, and recorded data with a portable tape recorder to identify species and count the number of individuals. Bird species were counted in a fixed area (2.1 ha) by an observer standing in a strategic point approximately 20 m from the study area. Taxonomic identification was carried out following the field guide of [Narosky and](#page-6-0) [Izurieta \(1987\)](#page-6-0). Each sampling unit was, at low tide, a strip of 300 m long and 70 m wide parallel to the coast. To assess bird activity, we identified and calculated the proportion of birds that were feeding or resting during the censuses. Abundances of each bird species were compared between sites with a test t [\(Zar, 1999\)](#page-7-0) or nonparametric Mann–Whitney test [\(Zar, 1999](#page-7-0)). Monotonic transformations were used when assumptions were not satisfied (following [Underwood,](#page-7-0) [1997](#page-7-0)).

To evaluate the habitat use by birds we tested the null hypothesis of no differences in the proportion of birds feeding or resting between areas by means of a two-way ANOVA (activity and area). When a significant interaction was found, main effects were not considered due to lack of independence between them ([Underwood, 1997](#page-7-0)). Tukey test ([Zar, 1999\)](#page-7-0) was performed for post hoc comparisons.

2.4. Foraging rates of migratory birds

Focal observations were performed to evaluate the effect of F. enigmaticus reef bed on foraging behavior of birds. As described before, feeding behavior of birds was evaluated comparing reef surfaces with sediment without reefs (bare sediment). Observations of feeding behavior were performed for two species: Tringa melanoleuca and T. flavipes, as they were the only ones frequently observed foraging in both areas (see [Results\)](#page-3-0). Observations were performed during low tides in the two more active moments of the day for birds: mid-morning and late afternoon. Each bird was observed for at least 3 min and no more than 5. Based on a previous sampling, a list of activities was defined to be recorded (walk, peck, capture of prey, and pause) that was maintained during the study to ensure standardized observations (following [Botto](#page-6-0) [et al., 1998\)](#page-6-0). The consumption rate (number of preys consumed per minute) and capture success (probes resulting in a successfully prey capture) in each zone were calculated and compared between areas.

Fig. 2. Mean abundance (ind/core; volume core = 785.4 cm⁻³) of infaunal and epifaunal preys inside reefs (Reef) and in sediment without reefs (Sedim) in lower (shaded bars) and upper layer (empty bars). Here and thereafter limits of the box represent 25 and 75 percentiles, vertical lines represent minimums and maximums and the line inside the boxes represent the median values.

Differences in capture success and consumption rates between areas were evaluated with t-tests [\(Zar, 1999\)](#page-7-0).

2.5. The effect of bird predation on infaunal prey species

The effect of bird predation on epifaunal species inhabiting polychaete reefs was evaluated with an exclusion experiment that consisted of bird exclosures (reefs with bird exclosures; $n = 10$) and controls (reefs without bird exclosures; $n = 10$). Shorebird exclosures were made with a 1 $m²$ plastic mesh ceiling (1 cm mesh size) raised 20 cm from the reef surface with four PVC stakes arranged in the corners (see [Botto et al., 1998\)](#page-6-0). The design of the ceilings excluded only birds and not other organisms such as crabs or fishes. During the study, exclosures were monitored to check if birds entered or fed from laterals. The exclosures, without walls, minimize factors that could affect infaunal organisms (e.g., alteration of water flow or sediment deposition; [Quammen, 1981](#page-6-0)). Experimental units were interspersed, separated by 5 m from each other, and located at the same tidal level in San Gabriel area ([Fig. 1](#page-1-0)A). At the end of the experiment (30 days), one core (diameter $= 10$ cm, depth $= 10$ cm) was extracted from the centre of each experimental unit. Organisms retained were preserved in alcohol 70% and then identified and quantified under a binocular scope (2×10) . The null hypothesis of no differences in abundance of each potential prey species among treatments (reefs with exclosure vs. reefs without exclosure) was evaluated with a t-test [\(Zar, 1999\)](#page-7-0). A Smirnov test ([Conover, 1980](#page-6-0)) was performed to evaluate the null hypothesis of no differences in the size frequency distribution of each species between areas.

3. Results

3.1. Benthic prey availability

The most common epifaunal species in the study area were the amphipod Melita palmata, the crab Cyrtograpsus angulatus and the gastropod Heleobia spp. The most abundant infaunal species were the free living polychaetes Laeonereis acuta, Nephtys fluviatilis and Neanthes succinea. Melita palmata densities were 600 times higher in the upper layer of reefs than in the lower layer or any layer in the bare sediment (log transformed data, interaction effect: $F_{1,36} = 165.3$, $MS = 16.1$, $P < 0.001$; [Fig. 2A](#page-2-0)). In a similar way, densities of the crab C. angulatus were at least 10 times higher in the upper layer than in lower layer of the reefs or in any layer of the bare sediment (log transformed data, interaction effect: $F_{1,36} = 5.35$, MS = 138.7, $P<0.001$; [Fig. 2](#page-2-0)B). The abundance of the polychaete L. acuta was similar between areas with and without reefs ($F_{1,36} = 0.04$, $P = 0.8$), but they were 10 times more abundant in the upper than in the lower layers (log transformed data, $F_{1,36} = 40.7$, MS = 6, P<0.001; [Fig. 2C](#page-2-0)). There were no differences in N. fluviatilis abundances between areas or depths (K–W test, $H = 6.2$, $n = 40$, $P = 0.1$; [Fig. 2D](#page-2-0)). Similarly, there were no differences for the free living polychaete N. succinea between areas ($F_{1,36}$ = 3.4, MS = 0.6, P = 0.07) or depths ($F_{1,36}$ = 1.2, MS = 0.2,

Fig. 3. Number of individuals of bird (ind/area) using intertidal areas with reefs (Reef) and nearby intertidal areas without reefs (Sedim).

Fig. 4. Proportions of birds migratory (A) and non-migratory (B) foraging (shaded bars) and resting (empty bars) on intertidal areas with reefs (Reef) and nearby areas without reefs (Sedim).

 $P= 0.3$; [Fig. 2E](#page-2-0)). The gastropod Heleobia spp. was only present in reefs, with abundances 200 times higher in the upper than in the lower layer (log transformated data; $t = 22.3$, df = 18, P<0.001; [Fig. 2](#page-2-0)F).

3.2. Shorebirds identification, abundances and habitat use

The most abundant migratory birds present in the study area (reefs and sediment without reefs) were Tringa melanoleuca (34.9%, $SD = 28.3$), T. flavipes (15.7%, $SD = 25.4$) and Phalacrocorax olivaceus $(21.12\%$, SD = 37.35). Low abundances were found for Calidris fuscicollis (6.1%, SD = 18.9), Charadrius falklandicus (1.33%, SD = 4.17) and Pluvialis squatarola (1.27%, $SD = 4.42$). The non-migratory birds present in the study site were Larus dominicanus and L. maculipennis (6.3%, SD= 11.3), Anas spp. (2.98%, SD= 7.35), Cygnus melanocoryphus $(4.79\% , SD = 12.15)$, Himantopus melanurus (3.86%, SD = 6.42), Vanellus chilensis (0.35%, SD = 1.28), Milvago chimango (0.95%, SD = 1.9), and Ciconia maguari $(0.19\% \text{ SD} = 0.74)$.

The density of Tringa melanoleuca (square root transformed data, $t=-2.66$, df= 34, P<0.05; [Fig. 3A](#page-3-0)), Tringa flavipes (square root transformed data, $t=-2.05$, df= 36, P<0.05; [Fig. 3B](#page-3-0)), Larus dominicanus and L. maculipennis ($t=-2.05$, df=36, P<0.05; [Fig. 3](#page-3-0)C), was higher in the reef surface than in the sediment without reefs, but there were no differences for Himantopus melanurus ($t=-1.08$, $df = 36$, $P = 0.3$; [Fig. 3D](#page-3-0)) and Ciconia maguari (Mann–Whitney U-test: Z_{adi} = −0.6, N₁ = 18, N₂ = 18, P = 0.5). Phalacrocorax olivaceus ([Fig. 3](#page-3-0)E), Milvago chimango, and Anas spp. [\(Fig. 3F](#page-3-0)) were only found on the reef surface.

Regarding the activity of the birds, the one seen feeding most frequently were the migratory sandpipers Tringa melanoleuca and T. flavipes, while the non-migratory birds were found resting. The proportion of migratory sandpipers was two times higher in the reef than in the sediment (two-way ANOVA, $F_{1,99} = 21.4$, MS = 13540.7, $P_{0.01}$, Fig. 4A), and the proportion of sandpipers feeding was also more than two times higher than resting in both sites ($F_{1,99}$ = 16.9, $MS = 10667.2$, $P < 0.01$). The proportion of non-migratory birds resting was 8 times higher in the reefs than in bare sediments and than the proportion of them feeding in either area (interaction effect: $F_{1.98} = 64.4$, MS = 12.3, P<0.01; Fig. 4B).

Fig. 5. Consumption rate (prey/min) and foraging efficiency (prey/prove) of sandpipers Tringa melanoleuca and T. flavipes in the reef surface (Reef) and the sediment without reefs (Sedim).

Fig. 6. Density of benthic organisms (ind. 0.07854 m $-$ ²) in control plots (1 m²) (empty bars) and exclosure plots (1 m^2 ; shaded bars). The number of individuals of the amphipods Melita palmata was divided by ten. Fe $=$ Ficopomatus enigmaticus, Mp $=$ M. palmata, $Hsp = Heleobia$ spp., La = Laeonereis acuta, Ca = Cyrtograpsus angulatus.

3.3. Foraging rates of migratory birds

Foraging rates (prey min $^{-1}$) were two times higher on the reefs than on the bare sediment for Tringa melanoleuca ($t=-3.2$, df = 44, P<0.01; [Fig. 5](#page-4-0)) and T. flavipes (t = −2.1, df = 66, P<0.05; Fig. 5). Foraging efficiency (prey probe-1) was higher in the reefs for T. melanoleuca ($t=-2.11$, df = 44, P<0.05), but there were no differences between sites for T. flavipes ($t = -0.51$, df = 66, P = 0.6).

3.4. The effect of bird predation on infaunal prey species

There were more individuals of the free living polychaete Laeonereis acuta in the control treatments than in bird exclosures ($t=-2.83$, df = 18, $P<0.05$; Fig. 6). However, the excluding birds did not affect the density of the amphipod Melita palmata ($t=-0.19$, df=18, P=0.9), the crab Cyrtograpsus angulatus ($t=0.74$, df = 18, P = 0.5), the polychaete Ficopomatus enigmaticus (t = 0.56, df = 18, $P=0.6$) and the gastropod Heleobia spp. $(t=-0.12, df=18, P=0.9; Fig. 6)$. No differences were also found in the size frequency distribution between treatments for any species (K–S, Cytograpsus angulatus: Max dif = 0.09, X_1 = 51.3 mm, X_2 = 49 mm; Melita palmata: Max dif=0.04, X_1 =3.58 mm, X_2 =3.56 mm; Heleobia spp.: Max dif = 0.07, X_1 = 3.18 mm, X_2 = 3.17 mm).

4. Discussion

Focal observations showed that birds prefer areas with reefs of Ficopomatus enigmaticus. Migratory and non-migratory birds showed differences in the use of the reefs. The former used reef surface mainly for foraging, while non-migratory birds used it for resting. Foraging rate of the most frequently observed migratory birds T. melanoleuca and T. flavipes was higher on reef surface than in the sediment. Higher abundances of epifaunal preys in this site could modify habitat use by birds, positively affecting the feeding rates of migratory shorebirds.

Epibenthic biogenic structures built by ecosystem engineers such as polychaetes, corals and bivalves provide habitat for several benthic organisms and, considerably modify their physical environment (e.g., [Crooks, 2002; Commito and Rusignuolo, 2000; Dubois et al., 2006](#page-6-0)). Sediments with biogenic structures differ physically, and support different infaunal communities than those from adjacent areas without structures [\(Trueblood, 1991\)](#page-7-0). Ficopomatus enigmaticus is an autogenic ecosystem engineer (sensu [Jones et al., 1994\)](#page-6-0) whose reefs increase topographic complexity and benthic diversity in the Mar Chiquita coastal lagoon [\(Schwindt et al., 2001\)](#page-6-0). This invasive species is highly gregarious and probably it is in continuous expansion, invading a large fraction of the brackish portion of the lagoon (up to 80%; [Schwindt et al.,](#page-6-0) [2004\)](#page-6-0). Similar to other structuring polychaete species (Terebellids polychaetes, [Trueblood, 1991;](#page-7-0) Polydora quadrilolobata, [Khaitov et al.,](#page-6-0) [1999;](#page-6-0) Lanice conchilega, [Zühlke, 2001; Callaway, 2003](#page-7-0); Pygospio elegans, [Bolam and Fernandes, 2003;](#page-6-0) Sabellaria alveolata, [Dubois et al., 2006](#page-6-0)), the abundances of organisms is higher between F. enigmaticus tubes than in the surrounding habitats (e.g. crabs: [Luppi and Bas, 2002](#page-6-0); amphipods: [Obenat et al., 2006; Schwindt et al., 2001;](#page-6-0) this work). F. enigmaticus tubes provide protection to C. angulatus crabs against predation ([Luppi](#page-6-0) [and Bas, 2002\)](#page-6-0) and refuge [\(Méndez Casariego et al., 2004\)](#page-6-0) that buffers harsh physical conditions and/or predation.

Similar patterns of increased abundances and species richness have been seen for a variety of other species that provide structural complexity, including invasive species such as oysters [\(Escapa et al.,](#page-6-0) [2004](#page-6-0)), cord grass ([Hedge and Kriwoken, 2000\)](#page-6-0) and other macrophytes [\(Posey et al., 1993](#page-6-0)). The most important factor determining the quality of a feeding site is prey availability ([Pienkowski, 1983](#page-6-0)). However, the increase of environmental heterogeneity can negatively affect the settlement of species due to predation by established recruits or hydrodynamic effects (e.g., [Castel et al., 1989; Trueblood,](#page-6-0) [1991\)](#page-6-0). In this work, epifaunal species were more abundant inside the reefs as Melita palmata, juvenile of C. angulatus, and Heleobia spp. as occurred at higher densities into the reefs than in bare sediments. Even though the identification of preys was not possible through focal observation, we can infer that the migratory sandpipers fed on organisms associated to reefs. The mentioned epifaunal and infaunal species are potential prey items for sandpipers [\(Martinez, 2001; Botto](#page-6-0) [et al., 1998; Escapa et al., 2004](#page-6-0)) and, after F. enigmaticus invasion their densities have increased notably in this lagoon (see [Luppi and Bas,](#page-6-0) [2002; De Francesco and Isla, 2003; Obenat et al., 2006\)](#page-6-0). Therefore, the intertidal reefs of the polychaete F. enigmaticus generate a new profitable habitat for migratory shorebirds with higher availability of food resources.

Non-indigenous ecosystem engineer species can act modifying their physical habitat positively for some populations or communities, and negatively for others. For example, in San Francisco Bay the non-native cordgrass Spartina alterniflora and hybrids, and S. anglica in the British coast, have occupied large mudflat areas decreasing the available area where shorebirds can feed, and hence, bird numbers declined due to the loss of feeding habitat [\(Goss-Custard and Moser, 1988; Stralberg et al.,](#page-6-0) [2004\)](#page-6-0). In the European Wadden Sea, the replacement of native mussel beds by exotic oyster beds (Crassostrea gigas) caused a decrease in oystercatcher Haematopus ostralegus populations [\(Wolff and Reise,](#page-7-0) [2002\)](#page-7-0). Even though theoretically predicted, examples of marine nonindigenous species that positively affect the habitat use by birds are scarce (e.g., [Crooks, 2002; Escapa et al., 2004\)](#page-6-0). In this context, our work shows that the invasive reef-forming polychaete F. enigmaticus can create suitable structures on bare sediments positively affecting the habitat use by providing more food resources and substrate.

In addition, shorebirds with morphological limitations (e.g., short legs, necks and beak) are more affected by the increase in water depth [\(Baker, 1979\)](#page-6-0) and tidal level ([Burger et al., 1977\)](#page-6-0), influencing their foraging and roosting behaviors. Several shorebird species prefer to forage in shallow zones minor than 10 cm depth ([Fredrickson and Reid,](#page-6-0) [1986\)](#page-6-0). This pattern has been reported from Mar Chiquita coastal lagoon, where habitat use by migratory shorebirds is affected by the increase in precipitations with the associated water level, resulting in higher shorebird diversity and abundance when the water level of the lagoon is lower ([Canepuccia et al., 2007](#page-6-0)). The reefs of F. enigmaticus elevate the bottom of the Mar Chiquita lagoon (average height $=0.5$ m, [Obenat and](#page-6-0) [Pezzani,1994](#page-6-0)) and therefore generate an exposed surface without water for more time compared to the sediment without reefs. At the landscape scale, the reefs increased habitat diversity by generating a mosaic of mudflats and F. enigmaticus reefs, suitable for feeding and resting by birds.

Shorebirds have been shown to be important predators of invertebrate organisms in intertidal soft-bottom communities [\(Wilson,](#page-7-0) [1991](#page-7-0)). In this study we tried to determinate the predation role of shorebirds on the structure and abundance of the community of invertebrates in the reefs. Shorebird exclusion experiments did not show an increase in the abundance of infaunal and epifaunal species. Only the free living polychaete Laeonereis acuta showed higher abundances in the control treatment. Therefore, the consumption rates or the abundance of birds were not large enough to reduce the abundance of invertebrate organisms on the reefs.

In summary, we have shown that there is a positive effect of the reefs on habitat use by birds because the reef surface was preferred as a feeding and a roosting area. At a small scale, the increase in food availability could play a major role in the preference of those areas for migratory birds. At the lagoon scale and considering the magnitude of the area invaded by F. enigmaticus, the existence of suitable resting and feeding areas could be the main factors determining the distribution and habitat use by shorebirds in this environment.

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