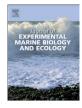
Contents lists available at ScienceDirect



Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe



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

Martín Bruschetti ^{a,c,*}, Cielo Bazterrica ^{a,c}, Tomás Luppi ^{b,c}, Oscar Iribarne ^{a,c}

^a Laboratorio de Ecología, Departamento de Biología, FCEyN, UNMdP, Argentina

^b Laboratorio de Invertebrados, Departamento de Biología, FCEyN, UNMdP, Argentina

^c Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

ARTICLE INFO

Article history: Received 15 January 2009 Received in revised form 15 May 2009 Accepted 18 May 2009

Keywords: Feeding behaviour Habitat use Invasive species Polychaete Shorebirds

ABSTRACT

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.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Bioinvasions are a threat for ecosystem integrity around the world (Pimentel et al., 2001) probably resulting from globalization (Vitousek, 1990; Bright, 1999). Currently, invasions continue altering systems worldwide, especially coastal environments (Wasson et al., 2001). In the South Western Atlantic coastal ecosystems, several marine invading species have been reported (see Orensanz et al., 2002), affecting different environments such as intertidal rocky shores (Hidalgo et al., 2005; Rico and López Gappa, 2006), shallow bays (Escapa et al., 2005). 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). These effects have been described for several species (e.g., Simberloff and Von Holle, 1999; Tecco et al.,

2006; Escapa et al., 2004) 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., 2003). 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). Bivalves (e.g. oysters, Escapa et al., 2004; mussels, Crooks, 1998; clams, Gutierrez et al., 2003), seagrasses (Reusch, 1998), crabs (Botto et al., 2006) and polychaete tube assemblages (Khaitov et al., 1999; Zühlke, 2001) 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), and consequently increase the surface area for settlers of numerous invertebrate benthic species (Crooks, 1998; Zühlke, 2001). They also elevate the bottom surface and offer refuges from predation or physical stress for associated fauna (Gutierrez et al., 2003). Thus, in flat muddy bottoms, ecosystem engineers often support higher

^{*} Corresponding author. Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina. Tel.: +54 223 475 3554.

E-mail address: mbrusche@mdp.edu.ar (M. Bruschetti).

^{0022-0981/\$ -} see front matter © 2009 Elsevier B.V. All rights reserved. doi:10.1016/j.jembe.2009.05.008

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; Petersen and Exo, 1999).

Tube-builder polychaetes as ecosystem engineers (Hutchings, 1998; Khaitov et al., 1999; Schwindt and Iribarne, 2000; Zühlke, 2001) 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, 2003; Dubois et al., 2006). 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 Iribarne, 2000; Schwindt et al., 2001). This polychaete is distributed in most brackish waters in temperate zones throughout the world (Ten Hove and Weerdenburg, 1978). It was recorded in Argentina in 1943 (Rioja, 1943) and before the seventies in the Mar Chiquita coastal lagoon (37°40′S, 57°23′ W: Orensanz and Estivariz, 1972). 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). 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), amphipods, gastropods, and free living polychaetes (Schwindt and Iribarne, 2000). They also modify the sedimentary patterns of the lagoon by increasing deposition (Schwindt et al., 2001) and have a strong topdown effect on the phytoplankton biomass of the lagoon (Bruschetti et al., 2008). 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). 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). 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) 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). 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). *Ficopomatus enigmaticus* reefs are located at the innermost zone of the lagoon (Schwindt et al., 2001). 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) and also several local species are present (non-migratory birds; Martinez, 2001).

2.2. Benthic prey availability

Reef-building organisms can affect infaunal communities and also, indirectly, their predators (Petersen and Exo, 1999). 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). Given that the gastropod Heleobia spp. was only found within the reefs (see Results), we only evaluated the hypothesis of no difference in density between depths (upper and lower) with a *t*-test (Zar, 1999). For every analysis, homogeneity of variances and normality were assessed using Levene and Shapiro-Wilks tests (Zar, 1999) respectively. Monotonic transformations were used when statistical assumptions were not satisfied (following Underwood, 1997).

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, 2001): 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) and without reefs (Fig. 1B) 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 Izurieta (1987). 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) or nonparametric Mann-Whitney test (Zar, 1999). Monotonic transformations were used when assumptions were not satisfied (following Underwood, 1997).

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). Tukey test (Zar, 1999) 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). 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 et al., 1998). 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.

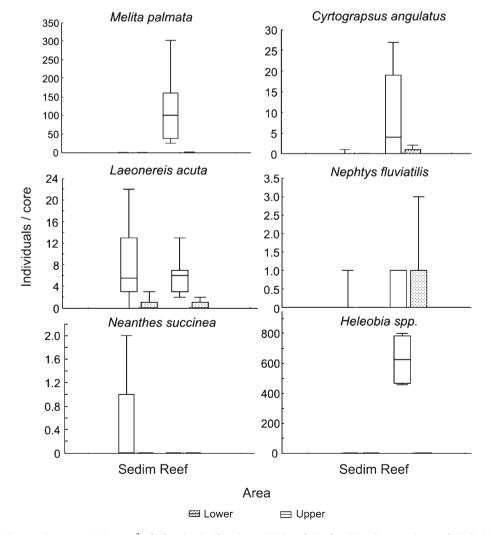


Fig. 2. Mean abundance (ind/core; volume core = 785.4 cm⁻³) of infaunal and epifaunal preys inside reefs (Reef) and in sediment without reefs (Sedim) in lower (shaded bars) and upper layer (empty bars). Here and thereafter limits of the box represent 25 and 75 percentiles, vertical lines represent minimums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

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 m^2 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). 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). Experimental units were interspersed, separated by 5 m from each other, and located at the same tidal level in San Gabriel area (Fig. 1A). 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). A Smirnov test (Conover, 1980) 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). 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. 2B). 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). 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). 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,

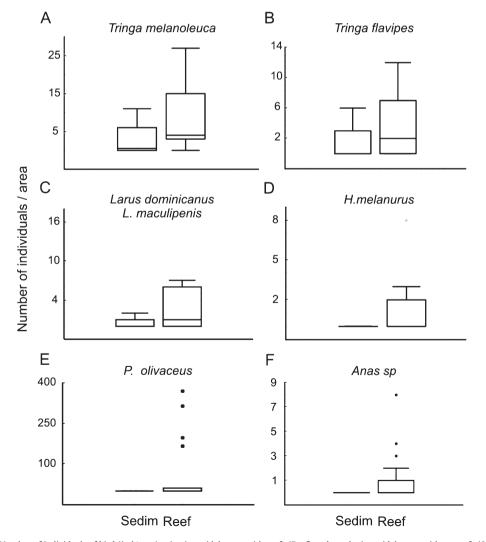


Fig. 3. Number of individuals of bird (ind/area) using intertidal areas with reefs (Reef) and nearby intertidal areas without reefs (Sedim).

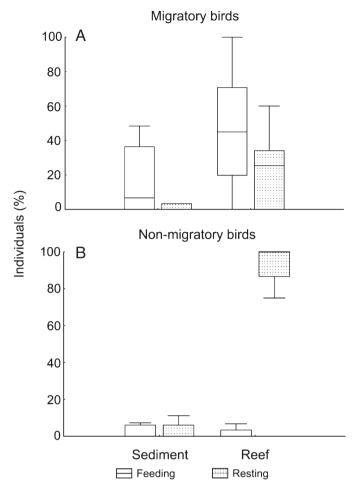


Fig. 4. Proportions of birds migratory (A) and non-migratory (B) foraging (shaded bars) and resting (empty bars) on intertidal areas with reefs (Reef) and nearby areas without reefs (Sedim).

P = 0.3; Fig. 2E). 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. 2F).

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%, SD = 0.74).

The density of *Tringa melanoleuca* (square root transformed data, t = -2.66, df = 34, P < 0.05; Fig. 3A), *Tringa flavipes* (square root transformed data, t = -2,05, df = 36, P < 0.05; Fig. 3B), *Larus dominicanus* and *L. maculipennis* (t = -2.05, df = 36, P < 0.05; Fig. 3C), 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) and *Ciconia maguari* (Mann–Whitney *U*-test: $Z_{adj} = -0.6$, $N_1 = 18$, $N_2 = 18$, P = 0.5). *Phalacrocorax olivaceus* (Fig. 3E), *Milvago chimango*, and *Anas spp.* (Fig. 3F) 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).

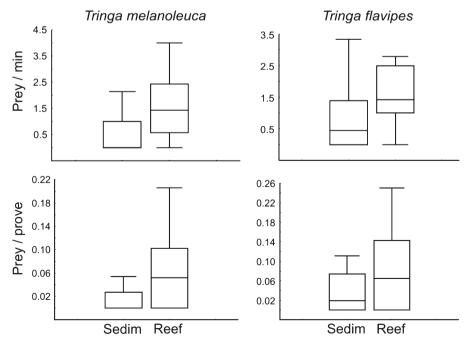


Fig. 5. Consumption rate (prey/min) and foraging efficiency (prey/prove) of sandpipers *Tringa melanoleuca* and *T. flavipes* in the reef surface (Reef) and the sediment without reefs (Sedim).

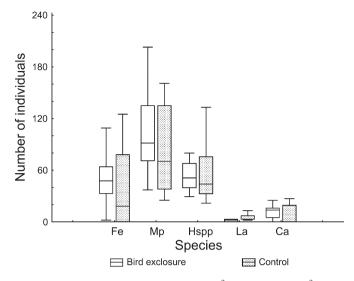


Fig. 6. Density of benthic organisms (ind. 0.07854 m^{-2}) in control plots (1 m^2) (empty bars) and exclosure plots (1 m^2 ; shaded bars). The number of individuals of the amphipods *Melita palmata* was divided by ten. Fe = *Ficopomatus enigmaticus*, Mp = *M. palmata*, Hspp = *Heleobia spp.*, La = *Laeonereis 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) 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). Sediments with biogenic structures differ physically, and support different infaunal communities than those from adjacent areas without structures (Trueblood, 1991). *Ficopomatus enigmaticus* is an autogenic ecosystem engineer (*sensu* Jones et al., 1994) whose reefs increase topographic complexity and benthic diversity in the Mar Chiquita coastal lagoon (Schwindt et al., 2001). 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., 2004). Similar to other structuring polychaete species (Terebellids polychaetes, Trueblood, 1991; *Polydora quadrilolobata*, Khaitov et al., 1999; *Lanice conchilega*, Zühlke, 2001; Callaway, 2003; *Pygospio elegans*, Bolam and Fernandes, 2003; *Sabellaria alveolata*, Dubois et al., 2006), the abundances of organisms is higher between *F. enigmaticus* tubes than in the surrounding habitats (e.g. crabs: Luppi and Bas, 2002; amphipods: Obenat et al., 2006; Schwindt et al., 2001; this work). *F. enigmaticus* tubes provide protection to *C. angulatus* crabs against predation (Luppi and Bas, 2002) and refuge (Méndez Casariego et al., 2004) 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., 2004), cord grass (Hedge and Kriwoken, 2000) and other macrophytes (Posev et al., 1993). The most important factor determining the quality of a feeding site is prey availability (Pienkowski, 1983). 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, 1991). 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 et al., 1998; Escapa et al., 2004) and, after F. enigmaticus invasion their densities have increased notably in this lagoon (see Luppi and Bas, 2002; De Francesco and Isla, 2003; Obenat et al., 2006). 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., 2004). In the European Wadden Sea, the replacement of native mussel beds by exotic oyster beds (Crassostrea gigas) caused a decrease in ovstercatcher Haematopus ostralegus populations (Wolff and Reise, 2002). 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). 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) and tidal level (Burger et al., 1977), influencing their foraging and roosting behaviors. Several shorebird species prefer to forage in shallow zones minor than 10 cm depth (Fredrickson and Reid, 1986). 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). The reefs of F. enigmaticus elevate the bottom of the Mar Chiquita lagoon (average height = 0.5 m, Obenat and Pezzani, 1994) 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, 1991). 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.

Acknowledgements

We acknowledge J. Alberti and D. Montemayor for their helpful comments on the manuscript. We thank A. Mendez Casariego for field help. Support for this project was provided by Universidad Nacional de Mar del Plata, CONICET (Argentina, PIP 5669) and ANPCyT (Argentina, PICT-13527) all granted to O. Iribarne. M. Bruschetti and C. Bazterrica were supported by doctoral scholarships from CONICET (Argentina).**[SS]**

References

- Baker, M.C., 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). Oikos 33, 121–126.
- Bolam, S.G., Fernandes, T.F., 2003. Dense aggregations of Pygospio elegans (Claparède): effect on macrofaunal community structure and sediments. J. Sea Res. 49, 171–185.
- Botto, F., Iribarne, O.O., Martinez, 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., Iribarne, O.O., Gutierrez, J., Bava, J., Gagliardini, A., Valiela, I., 2006. Ecological importance of passive deposition of organic matter into burrows of the SW Atlantic crab *Chasmagnathus granulata*. Mar. Ecol. Prog. Ser. 312, 201–210.
- Bright, C., 1999. Invasive species: pathogens of globalization. Foreign Policy 116, 50–64. Bruschetti, C.M., Fanjul, E., Rosenthal, A., Luppi, T.A., Iribarne, O., 2008. Grazing effect of the invasive reef-forming polychaete *Ficopomatus enigmaticus* (Fauvel) on phytoplankton biomass in a SW Atlantic coastal lagoon. J. Exp. Mar. Biol. Ecol. 354, 212–219.
- Burger, J., Howe, M.A., Hahn, D.C., Chase, J., 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrant shorebirds. Auk 94, 743–758.
- Callaway, R., 2003. Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. J. Exp. Mar. Biol. Ecol. 283, 115–132.
- Canepuccia, A.D., Isacch, J.P., Gagliardini, D.A., 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.
- Castel, J., Labourg, P.J., Escaravage, V., Auby, I., Garcia, M.E., 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuar. Coast. Shelf Sci. 28, 71–85.
- Commito, J.A., Rusignuolo, B.R., 2000. Structural complexity in mussel beds: the fractal geometry of surface topography. J. Exp. Mar. Biol. Ecol. 225, 133–152.
- Conover, W.J., 1980. Practical nonparametric statistics, Second edition. John Wiley and Sons, Inc., New York.
- Crooks, J.A., 1998. Habitat alteration and community-level effects of an exotic mussel, Musculista senhousia. Mar. Ecol. Prog. Ser. 162, 137–152.
- Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153–166.
- Crooks, J.A., Khim, H.S., 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. J. Exp. Mar. Biol. Ecol. 240, 53–75.
- De Francesco, C.G., Isla, F.I., 2003. Distribution and abundance of hydrobiid snails in a mixed estuary and a coastal lagoon. Argentina, Estuaries 26, 790–797.
- Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on Sabellaria alveolata (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. Estuar. Coast. Shelf Sci. 68, 635–646.
- Escapa, M., Isacch, J.P., Daleo, P., Alberti, J., Iribarne, O.O., Borges, M., Dos Santos, E.P., Gagliardini, D.A., Lasta, M., 2004. The distribution and ecological effects of the introduced pacific oyster *Crassostrea gigas* (Thunberg, 1793) in Northern Patagonia. J. Shellfish Res. 23, 765–772.
- Fasano, J.L., Hernández, M.A., Isla, F.I., Schnack, E.J., 1982. Aspectos evolutivos y ambientales de la laguna Mar Chiquita (Provincia de Buenos Aires, Argentina). Oceanol. Acta [Spec Publ] 285–292.

- Fredrickson, L.H., Reid, F.A., 1986. Wetland and riparian habitats: a nongame management overview. In: Hale, J.B., Best, L.B., Clawson, R.L. (Eds.), Management of nongame wildlife in the Midwest: a developing art. The Wildlife Society, Grand Rapids, Michigan, pp. 59–96.
- Goss-Custard, J.D., Moser, M.E., 1988. Rates of change in numbers of Dunlin, *Calidris alpina*, wintering in British estuaries in relation to the spread of *Spartina anglica*. J. Appl. Ecol. 25, 95–109.
- Gutierrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90. Hedge, P., Kriwoken, L.K., 2000. Evidence for effects of *Spartina anglica* invasion on
- Hedge, P., Kriwoken, L.K., 2000. Evidence for effects of Spartina anglica invasion on benthic macrofauna in Little Swanport Estuary, Tasmania. Austral Ecol. 25, 150–159.
- Hidalgo, F., Barón, P., Orensanz, J., 2005. A prediction comes true: the green crab invades the Patagonian coast. Biol. Invasions 7, 547–552.
 Hilgerloh, G., 1997. Predation by birds on blue mussel *Mytilus edulis* beds of the tidal
- flats of Spiekeroog (southern North Sea). Mar. Ecol. Prog. Ser. 146, 61–72. Hutchings, P., 1998. Biodiversity and functioning of polychaetes in benthic sediments.
- Biodivers. Conserv. 7, 1133–1145. Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos
- 689, 373–386. Khaitov, V.M., Fokin, M.V., Nicolaeva, M.A., 1999. Structure of communities associated with dense assemblages of the tube-dwelling polychaete *Polydora quadrilobata*
- Jacobi (Spionidae) in the White Sea. Hydrobiology 393, 221–226. Luppi, T., Bas, C., 2002. Role of reefs of the invasive polychaete *Ficopomatus enigmaticus* Fauvel 1923 (Polychaeta: Serpulidae) in the recruitment of *Cyrtograpsus angulatus* Dana 1851 (Brachyura: Grapsidae), in the Mar Chiquita coastal lagoon, Argentina. Cienc. Mar. 28, 319–330.
- Martinez, M.M., 2001. Avifauna de Mar Chiquita. In: Iribarne, O.O. (Ed.), Reserva de biosfera Mar Chiquita: Características físicas, biológicas y ecológicas. Martin, Mar del Plata, pp. 227–250.
- Méndez Casariego, A., Schwindt, E., Iribarne, O., 2004. Evidence of habitat structuregenerated bottleneck in the recruitment process of the SW Atlantic crab Cyrtograpsus angulatus. Mar. Biol. 145, 259–264.
- Muniz, P., Clemente, J., Brugnoli, E., 2005. Benthic invasive pests in Uruguay: a new problem or an old one recently perceived? Mar. Pollut. Bull. 50, 993–1018.
- Myers, J.P., Myers, L., 1979. Shorebirds of coastal Buenos Aires Province, Argentina. Ibis 121, 186–200.
- Narosky, T., Izurieta, D., 1987. Aves de Argentina y Uruguay. Guía de campo. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Obenat, S.M., Pezzani, S.E., 1994. Life cycle and population structure of the polychaete *Ficopomatus enigmaticus* (Serpulidae) in Mar Chiquita Coastal Lagoon, Argentina. Estuaries 17, 263–270.
- Obenat, S., Spivak, E., Garrido, L., 2006. Life history and reproductive biology of the invasive amphipod *Melita palmata* (Amphipoda: Melitidae) in the Mar Chiquita coastal lagoon, Argentina. J. Mar. Biol. Assoc. U.K. 86, 1381–1387.
- Orensanz, J.M., Estivariz, M.C., 1972. Los anélidos poliquetos de aguas salobres de la Provincia de Buenos Aires: Revista del Museo La Plata, Universidad Nacional de La Plata, vol 11, pp. 95–112.
- Orensanz, J.M., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elías, R., López Gappa, J.J., Obenat, S., Pascual, M., Penchaszadeh, P., Piriz, M.L., Scarabino, F., Spivak, E.D., Vallarino, E.A., 2002. No longer a pristine confine of the world ocean: a survey of exotic marine species in the Southwestern Atlantic. Biol. Invasions 4, 115–143.
- Petersen, B., Exo, K.M., 1999. Predation of waders and gulls on *Lanice conchilega* tidal flats in the Wadden Sea. Mar. Ecol. Prog. Ser. 178, 229–240.
- Pienkowski, M.W., 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. Mar. Ecol. Prog. Ser. 11, 141–150.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., Tsomondo, T., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agric. Ecosyst. Environ. 84, 1–20.
- Posey, M.H., Wigand, C., Stevenson, J.C., 1993. Effects of an introduced aquatic plant, *Hydrilla erticillata*, on benthic communities in the upper Chesapeake Bay. Estuar. Coast. Shelf Sci. 37, 539–555.
- Quammen, M.L., 1981. Use of exclosures in studies of predation by shorebirds on intertidal mudflats. Auk 82, 812–817.
- Reusch, T.B.H., 1998. Differing effects of eelgrass Zostera marina on recruitment and growth of associated blue mussels Mytilus edulis. Mar. Ecol. Prog. Ser. 167, 149–153.
- Rico, A., López Gappa, J., 2006. Intertidal and subtidal fouling assemblages in a Patagonian harbour (Argentina, Southwest Atlantic). Hydrobiologia 563, 9–18.
- Rioja, 1943. Estudios Anelidiológicos IX. La presencia de la Mercierella enigmatica Fauvel, en las costas argentinas. An. Inst. Biol. (Méx.) 14, 547–551.
- Schwindt, E., Iribarne, O., 1998. Reef of *Ficopomatus enigmaticus* (Polychaeta; Serpulidae) in the Mar Chiquita coastal lagoon, Argentina. Boll. Soc. Hist. Nat. Balears 41, 35–40.
- Schwindt, E., Iribarne, O.O., 2000. Settlements sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. Bull. Mar. Sci. 67, 73–82.
- Schwindt, E., Bortolus, A., Iribarne, O.O., 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biol. Invasions 3, 137–149.
- Schwindt, E., De Francesco, C.G., Iribarne, O.O., 2004. Individual and reef growth of the introduced reef building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon. J. Mar. Biol. Assoc. U.K. 84, 987–993.
- Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown. Biol. Invasions 1, 21–32.
- Stralberg, D., Toniolo, V., Page, G.W., Stenzel, L.E., 2004. Potential impacts of non-native Spartina spread on shorebird populations in South San Francisco Bay. PRBO report

to California Coastal Conservancy (contract #02-212). InPRBO Conservation Science, Stinson Beach, CA.

- Tecco, P.A., Gurvich, D.E., Diaz, S., Pérez-Harguindeguy, N., Cabido, M., 2006. Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. Austral Ecol. 31, 293–300.
- Ten Hove, H.A., Weerdenburg, J.C.A., 1978. A generic revision of the brackish-water serpulid *Ficopomatus* southern 1921 (Polychaeta: Serpilinae), including *Mercierella* Fauvel 1923, *Sphaeropomatus* Treadwell 1934, *Mercierellopsis* Rioja 1945 and *Neopomatus* Pillai 1960. Biol. Bull. 154, 96–120.
 Trueblood, D.D., 1991. Spatial and temporal effects of terebellid polychaete tubes on
- Trueblood, D.D., 1991. Spatial and temporal effects of terebellid polychaete tubes on soft-bottom community structure in Phosphorescent Bay, Puerto Rico. J. Exp. Mar. Biol. Ecol. 149, 139–159.
- Underwood, A.J., 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.
- Vitousek, P.M., 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57, 7–13.

- Wasson, K.C.J., Zabin, L., Bedinger, M.C., Diaz, Pearce, J.S., 2001. Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol. Conserv. 102, 143–153.
- Wilson, W.H., 1991. The foraging ecology of migratory shorebirds in marine softsediment communities: the effects of episodic predation on prey populations. Am. Zool. 31, 840–848.
- Wolff, W.J., Reise, K., 2002. Oyster imports as a vector for the introduction of alien species into Northern and Western European coastal waters. In: Leppakoski, E., Gollasch, S., Olenin (Eds.), Invasive aquatic species of Europe. InKluwer Academic Publishers, Dordrecht, Netherlands.
- Zar, J.H., 1999. Biostatistical analysis, 4th edition. Prentice-Hall, Upper saddle River, NJ, E.E.U.U.
- Zühlke, R., 2001. Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. J. Sea Res. 46, 261–272.