Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment

Evangelina Schwindt[a,*], Oscar Osvaldo Iribarne[b,c],
Federico Ignacio Isla[c,d]

[a]*Maritime Studies Program, Williams College-Mystic Seaport, PO Box 6000, 75 Greenmanville Av, Mystic, CT 06355, USA*
[b]*Laboratorio de Ecología, FCEyN, Universidad Nacional de Mar del Plata, Argentina*
[c]*CONICET, Argentina*
[d]*Centro de Geología de Costas y del Cuaternario, Universidad Nacional de Mar del Plata, Argentina*

Abstract

Although the environmental impact of invasive species is variable, ecosystem engineers usually dramatically modify the ecosystem through different mechanisms. Here, we evaluated physical effects generated by *Ficopomatus enigmaticus*, an exotic and ecosystem engineer reef-building species, in one of the largest coastal lagoon of Argentina. To address this issue we analyzed aerial photographs covering 24 years of invasion and we performed short-term sampling and experiments. Our results show that the density and size of the reefs in the lagoon have increased reaching up to 370 reefs ha^{-1} and 7 m in diameter, respectively, in the last 24 years. At a local scale, we found that finest sediments settle on the top and leeward side of the reefs, whereas coarse sediments settle on the windward side. In addition, reefs altered both the bedload sediment transport and the relative water flow around them and these processes were related with both speed and direction of the wind. The results strongly suggest that the overall magnitude of the physical effects generated by this ecosystem engineer is much greater, considering that reefs invaded most of the lagoon.
© 2003 Elsevier Ltd. All rights reserved.

Keywords: exotic species; reefs; physical effect; ecosystem engineer; coastal lagoon; Argentina

1. Introduction

Biological invasions occur through either natural expansion in an organism's distributional range or by human-mediated introductions (Carlton, 1996). Transport mechanisms include fouling, aquaculture, fishing and ballast material of ships (Ruiz et al., 1997). Exotic species may affect native species through competition, predation and/or parasitism; however, habitat modification is one of the most important direct effects of non-indigenous species on native communities (Bertness, 1984; Simberloff, 1997). These species can modify habitats both ecologically (e.g. diversity and inter- and intra-specific interactions; Olenin and Leppäkoski, 1999) and physically (Ruiz et al., 1997; Hayward, 1997; Talley

et al., 2001). Some introduced species can directly or indirectly modulate the availability of resources (such as food or refuge) to other species, thereby modifying, maintaining and/or creating habitats (Jones et al., 1997). Organisms that can generate such changes have been called "ecosystem engineers" (Jones et al., 1997).

Several cases of ecosystem engineering by invasive species have been documented in aquatic systems (Bertness, 1984; Crooks, 1998; Strayer et al., 1999; Crooks and Khim, 1999; Talley et al., 2001). The reef-building polychaete *Ficopomatus enigmaticus* (Serpulidae) is an exotic species distributed in most brackish waters in temperate zones throughout the world (ten Hove and Weerdenburg, 1978). In Argentina, there is no evidence of the presence of its conspicuous reefs in Holocene deposits (Orensanz and Estivariz, 1972; Fasano et al., 1982), indicating that it is an exotic invader. *Ficopomatus enigmaticus* builds calcareous circular reefs up to 7 m in diameter by 0.5 m in height (Plate 1; Obenat

---

* Corresponding author.
E-mail address: schwindt44@hotmail.com (E. Schwindt).

Plate 1. Aerial photograph of the *Ficopomatus enigmaticus* reefs in Mar Chiquita coastal lagoon. The average size of the reefs is 2.5 m. Photo Credit: Alejandro Bortolus.

hydrodynamic in shallow areas are winds and tides (Emerson, 1991). In these environments, a combination of both intensity and direction of the wind would determine not only the amount of fauna and sediment transported but also the areas where they are deposited (Emerson, 1991; Arfi et al., 1993; Airoldi et al., 1996). For example, in the algal turf-dominated rocky shores of Livorno, Italy, during windy periods bottom sediments are resuspended, while during fair weather sediment deposition and movement are low (Airoldi et al., 1996).

The Mar Chiquita coastal lagoon (37°32′–37°45′S and 57°19′–57°26′W; Fig. 1), a MAB (man and the

and Pezzani, 1994; Schwindt, 2001a). This species is considered a physical ecosystem engineer since it can positively or negatively modify resources for other species (such as amphipods, gastropods, polychaetes, crabs and algae; Schwindt and Iribarne, 2000; Schwindt et al., 2001; Luppi et al., 2002).

Reefs can act as efficient traps for sediments (Bailey-Brock, 1979). Since reefs become obstacles to water movement, they generate topographic heterogeneity and ameliorate physical conditions by accumulating and stabilizing sediments (Bailey-Brock, 1979; Reusch and Williams, 1998; Crooks, 1998; Lenihan, 1999). Reefs indirectly and differentially modify the distribution and abundance of infaunal organisms (e.g. larvae and juveniles; Snelgrove and Butman, 1994), food supply (Abelson and Loya, 1995) and sediment transport (Jumars and Nowell, 1984). The intensity and duration of these hydrodynamic effects can vary at different distances and/or orientations from the reefs (Cusson and Bourget, 1997; Guichard et al., 2001). Through these biotic and physical processes, reefs can participate in several ecological processes (e.g. facilitation) with crucial roles for structuring benthic communities (Crooks and Khim, 1999; Schwindt et al., 2001). Among the principal factors that generate changes in the
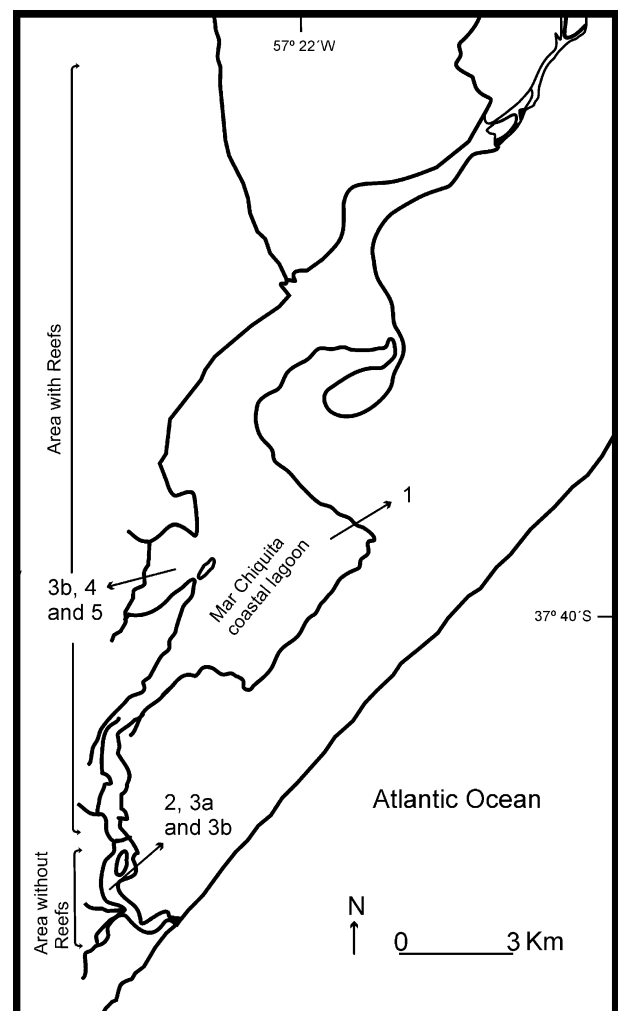

Fig. 1. Map of the Mar Chiquita coastal lagoon (Bs. As., Argentina) showing the areas populated with reefs and areas without them and the field sampling and experiment performed in both areas. Numbers from 1 to 5 correspond to the objectives studied, being (1) changes in density, size and distance over 24 years, (2) the effect of the reefs on sediment deposition, (3a) the effect of reefs on sediment deposition, (3b) suspended sediment concentration in areas with and without reefs, (4) the effect of reefs on bedload sediment and passive faunal transport, and (5) the effect of reefs on relative water flow.

biosphere site, UNESCO) is the largest coastal lagoon in Argentina which receives sediment and freshwater from a drainage basin of 10,000 km^2 (Fasano et al., 1982). Wind and local rains control variations in water level within the lagoon (Reta et al., 1997). Sediment transport in the lagoon can be caused by rainfall, river drainage, floods, and human activities (Isla, 1997). Little attention has been directed to exotic ecosystem engineer despite its invasion of 86% of the lagoon surface. Moreover, the invasion has caused a significant change in the benthic community and the geomorphology of the landscape (Schwindt et al., 2001). We hypothesized that the exotic *Ficopomatus* reefs affect sediment transport, as well as relative water flow, consequently increasing the sediment deposition near and on the reefs.

The objective of this study is to evaluate the physical effects of the invading reef-building *Ficopomatus enigmaticus* in an Argentinean estuarine environment. The specific aims are to evaluate: (1) changes in density, size and distance between reefs from 1975 to 1999; (2) the effect of the reefs on sediment deposition; (3) the relationship between the reefs and sediment deposition; (4) the effect of reefs on bedload sediment and passive faunal transport; and (5) the effect of reefs on relative water flow.

2. Materials and methods

The study was performed in Mar Chiquita coastal lagoon from December 1997 (late spring) to April 2000 (late summer). The lagoon is a body of brackish water (approximately 46 km^2) and from a hydrological point of view, may be divided into an innermost shallow zone where the tidal effect is insignificant and a zone around the mouth subjected to tidal action (tidal amplitude ≤1 m; Reta et al., 1997). The water level inside the lagoon fluctuates between 0.1 m and 0.5 m in depth depending on wind and local rains (Isla, 1997). *Ficopomatus enigmaticus* reefs are located at the innermost zone of the lagoon where the wind is the main mechanism to generate the movement of sediment and organisms (Schwindt et al., 2001). The lagoon is surrounded by *Spartina densiflora*-dominated salt marshes (Olivier et al., 1972). We performed mensurative and manipulative experiments (sensu Hurlbert, 1984, hereafter called experiments) to address the different objectives within the lagoon.

2.1. Changes in density, size and distance between reefs from 1975 to 1999

To evaluate changes in density of *Ficopomatus* reefs during the last two decades, aerial photographs from 1975, 1979 (1 : 5000 scale) and 1999 (1 : 2400 scale) were compared using the same area for all photographs (140 ha each). The photographs were digitized (Didger®, 1997) and, to evaluate changes in size of the reefs, 500 reefs were randomly selected from each photograph and the diameter of each was measured using a digital caliper with a precision of ±0.02 mm. These measurements in mm were then transformed, according to the scales of the photographs, to actual reef sizes. To evaluate the distance between reefs, 100 pairs of reefs from each photograph were randomly selected and the distance between them was measured with a digital caliper. The null hypotheses of no differences in the density, size and distance between reefs among years were evaluated separately with repeated measures of ANOVAs (Zar, 1999). A posteriori comparisons were made with a Tukey test (Zar, 1999). Data were transformed when assumptions of the analysis (normality and homoscedasticity) were violated following Zar (1999).

2.2. The effect of reefs on the sediment deposition

To evaluate if the reefs trap sediment between the individual worm tubes, 10 reefs ($x = 633$ cm^3, SE = 81.27) devoid of sediment were experimentally deployed in the field for one month. The experimental reefs were washed and oven-dried repeatedly to eliminate the inner sediment. The initial volume of each reef without sediment was estimated by measuring water displacement and then they were deployed at a distance of 4 m apart in an area without reefs. After one month (starting January 1999), the reefs were oven-dried and the final volume was again estimated by water displacement. The difference between the initial and final volumes was attributed to sediment trapping inside the reef structure and was transformed to kg of sediment m^{-3} of reef. Suspended sediment load in the environment was also quantified from water samples obtained every two days ($n = 12$ days, $n = 5$ each day, volume 240 cm^3 each sample) from the same area during the experiment.

To estimate the amount of sediment retained in the reefs of the entire lagoon, the area covered by reefs in the coastal lagoon was quantified from the most recent aerial photograph of the lagoon (1999, scale 1 : 2400) and also by using a map of the lagoon (scale 1 : 50 000; Instituto Geográfico Militar 1965). The map was divided in squares of 1000 × 1000 m and the area covered by reefs was calculated for each square. The average sediment weight per reef was calculated using the results described in the previous paragraph. From the photograph, the diameter (m) of 2185 reefs randomly chosen (in an area of 12 ha) was measured, and using their circular shape and their average height of 0.5 m (Obenat and Pezzani, 1994) the volume of each reef was estimated. The following equation was used to estimate the total amount of sediment retained by the reefs in the lagoon:

Sediment retained in the reefs in the lagoon

  = area covered by reefs (ha)

    × average sediment weight (kg) per reef (m^3)

    × average volume (m^3) of reefs per ha^{-1}

The estimation was performed with a computer iterative resampling procedure (Manly, 1997). The average amount of sediment per reef and the average volume of reefs per hectare were randomly resampled 10^3 times. The median and the 95% confidence limits for the estimates were obtained from the distribution of the resampling. This technique allowed an estimation of the sediment deposited in the reefs while retaining the variance of the multiplied variables. Since all the reefs have an approximately circular shape and are homogeneous in height (Obenat and Pezzani, 1994), we used the assumption that all reefs trap sediment in a similar way: between the individual worm tubes and on the top surface with no differences from the edge to the reef center. Two years of preliminary field sampling and observations support this assumption (Schwindt, 2001a).

2.3. Relationships between the reefs and sediment deposition

2.3.1. Effect of reefs on sediment deposition
To evaluate the effect of reefs on sediment grain size distributions deposited in different areas of the reefs and

around them, two reefs (0.5 m in diameter) were transplanted to an area without reefs and with unidirectional water flow. Transplanted reefs were deployed on the sediment in natural position fastened by four small wires and nylon thread. Because of the weight and fragility of larger reefs, it was not possible to transplant larger reefs. Control areas without reefs were established between the transplanted reefs, which were located 6 m from each other. After a year (January 1998–January 1999), sediment samples were obtained (150 g) from the windward side of the transplanted reefs (W), the control area (C), the leeward side of the reefs (L, at 0.2 m; Fig. 2) and on top of the reefs (T). In addition, samples from the same location were obtained from areas with existing reefs during a unidirectional wind period. Sediment samples were sieved through a series of screens with six different mesh openings ranging from 2000 to 62 μm (Carver, 1971).

2.3.2. Suspended sediment concentration in areas with and without reefs
To compare suspended sediment concentrations (SSC) in the water in areas with and without reefs, three samples from areas with reefs and three from areas without reefs were collected per day, during five randomly chosen days between January and February 2000 (*n* total = 30). At the same time, wind speed was recorded. Samples were filtered through a 0.7 μm pore mesh. Since the filters retain both organic matter and
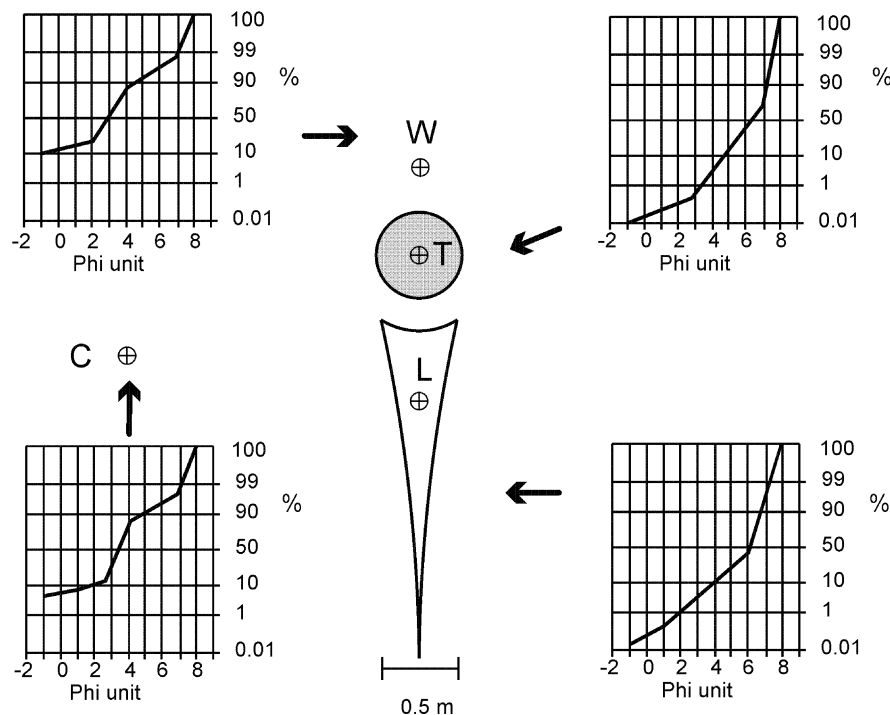

Fig. 2. Cumulative curves showing the grain size distribution plotted on a probability scale for control (C), windward (W), leeward (L) and top (T) plots one year after reefs were transplanted. Gray circle represents a reef and the triangle below it represents the shadow of the deposited sediment at the leeward side.

sediment, all filters were oven-dried at 100 °C for 24 h, weighed and combusted at 550 °C for 6 h to obtain the ash-free dry weights of SSC. The Wilcoxon paired sample test (Zar, 1999) was used to examine the differences in SSC and wind speed separately comparing areas with and without reefs.

2.4. Effect of reefs on bedload sediment and passive faunal transport

Since protruding structures generate changes in the hydrodynamic of the system (Nowell and Jumars, 1984), we expect that with a constant wind direction, reefs affect the bedload transport near them. To evaluate this hypothesis, sediment traps were deployed at three distances from the reefs (0.2 m, 2 m and 6 m), and in different directions (S, W, E and N). The sediment inside the traps after 24 h was collected for further analyses. This procedure was replicated in four randomly chosen days using four different reefs each day (n total = 16 reefs). We used 3-cm diameter and 60-cm long PVC pipes as traps with the bottom end closed. The top of the trap was flush with the sediment surface and no part of the trap was above the sediment. With these measures and design, the trap collects approximately the 90% of the saltating grains as well as organisms that have similar settling velocities to the transported sediment (for further technical information on the traps see Emerson, 1991). These traps avoid the resuspension and removal of the collected particles, even during periods of high flow and also prohibit the entry of large mobile macrofauna (Butman, 1986, 1989; Emerson, 1991). At the beginning of each day, the cylindrical traps were filled with filtered seawater (44 μm filter pore size). Each sampling period lasted 24 h and wind speed and direction were simultaneously monitored. After each day, a subsample of 10 cm^3 from each trap was taken to evaluate the density of organisms bedload transported. Organisms were sorted under a dissecting microscope (40×) and identified to the lowest taxonomic level possible. Trapped sediment of the whole sample was oven-dried at 100 °C for 24 h, weighed and combusted at 550 °C for 6 h to obtain ash-free dry weights. The null hypotheses of no effect in bedload transport of sediment and organisms in relation to distance and direction from the reefs were evaluated independently for each day with two-way ANOVAs (Zar, 1999). Data were transformed when assumptions of the analysis (normality and homoscedasticity) were not met following Zar (1999). Post hoc multiple comparisons were evaluated using a Tukey test (Zar, 1999). Correlation analyses were used to evaluate the relationship between the wind speed and the amount of sediment transported, as well as between wind speed and density of meiofaunal organisms (Zar, 1999).

2.5. Relationship between reefs and relative water flow

Water flow around the reefs was estimated indirectly by using the loss (i.e. dissolution) of standard plaster (plaster of Paris) cylinders (e.g. Petticrew and Kalff, 1991; Cusson and Bourget, 1997). These kind of plaster cylinders are good estimators of the relative flow within temperatures range of 3–25 °C, from 0 to 10 cm s^{-1} of current speed and within the 70 h of exposure (Petticrew and Kalff, 1991). In our study area, temperature and salinity were constant over all sites, and the normal current speed was less than 10 cm s^{-1} (Isla, 1997). The relative differences in current speed were estimated from the weight loss of the cylinders. The plaster cylinders were 3 cm in diameter and 5 cm in height. A 0.5-cm diameter stainless-steel rod was inserted through a hole along the longitudinal axis of each cylinder and both ends were protected with epoxy to ensure equal contact with the water. At each site, a cylinder was fixed 10 cm vertically above the bottom by driving the rod into the sediment. We deployed the cylinders for 24 h at three different distances from the reefs (0.2 m, 2 m and 6 m), and in four different directions (S, W, E and N). This design was replicated in five reefs randomly chosen within the study area. Plaster dissolution (weight loss in grams per exposure time) was calculated as the difference between oven-dried weights before and after deployment. The null hypothesis of no difference in weight loss between distances from the reefs and orientations was evaluated with a two-way fixed ANOVA and a posteriori Tukey test was used to identify the differences among means (Zar, 1999).

3. Results

3.1. Changes in density, size and distance between reefs from 1975 to 1999

From 1975 to 1999 the density of reefs increased significantly in 24.3% ($F_{2,278}$ = 12.8, MS = 11230.6, $p = 4.7 \times 10^{-6}$; Fig. 3A). In 1975 reef density was 71 reefs ha^{-1} (SE = 7.36), in 1979 the density increased to 84 reefs ha^{-1} (SE = 7.78) and in 1999 the density was 89 reefs ha^{-1} (SE = 7.41). Reef sizes showed significant differences among years ($F_{2,998}$ = 776.8, MS = 466.84, $p = 0.000$; Fig. 3B), which means an increase in 66.8% from 1975 to 1999. The distance between reefs decreased in 52% from 1975 to 1999 (square root transformed, $F_{2,198}$ = 91.16, MS = 45.75, $p = 0.000$; Fig. 3C).

3.2. The effect of reefs on sediment deposition

The average weight of deposited sediment on our 10 experimental reefs after a month was 57.5 g (SE = 5.53),
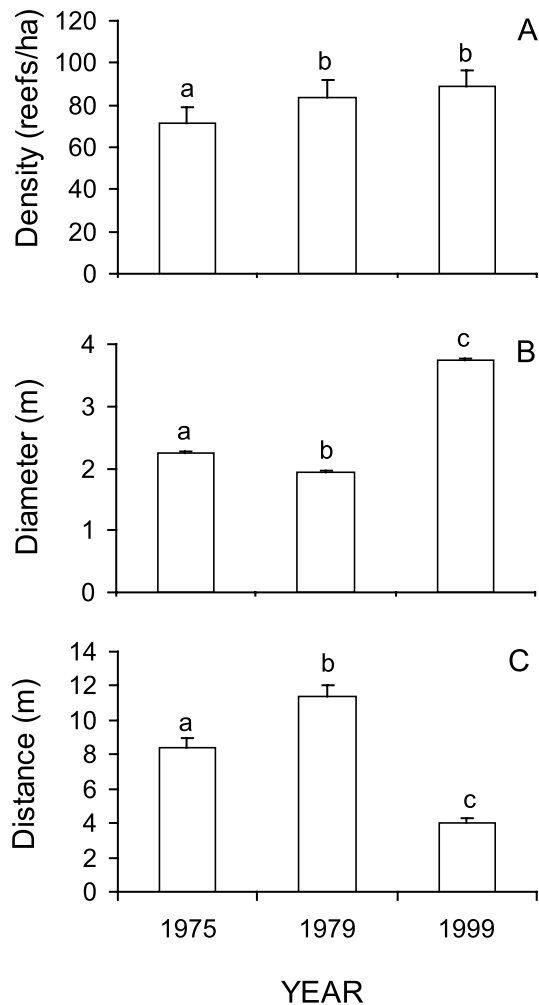
Fig. 3. Density (A), size (in diameter, B) and distance between reefs (C) among years. All bars show mean+SE. Same letters mean not significant differences.

Fig. 4. Variations in suspended sediment concentration (SSC, mean ± SE) in the water measured in the same period of the reef sediment deposition experiment.

which is equivalent to 107 kg m^{-3} of reef (SE = 19.3). The suspended sediment in the water samples collected during the same period varied between 8 g l^{-1} and 1 g l^{-1} (Fig. 4). The total amount of sediment deposited in the reefs in the lagoon was estimated as 339 tons (confidence interval: 221–517 tons).

3.3. Relationships between reefs and sediment deposition

3.3.1. Relationship between reefs and the sediment deposition

Sediment samples obtained from the bottom surrounding the reefs, which were transplanted in an area without previous reefs and with unidirectional flow, showed that the top of the reefs had the finest sediment grain size settling from suspension (Fig. 2). The leeward side of the reefs was also composed of coarse silt. The probab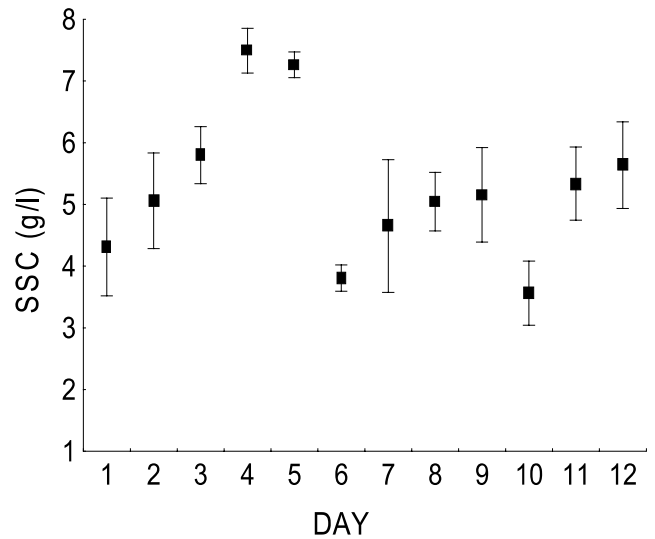ilistic curve indicated, however, that the coarse silt fraction was deposited from suspension and saltation (Table 1, Fig. 2). Control and windward side samples showed high percentages in coarse sediments in comparison with the samples of leeward side and top (Table 1, Fig. 2). Similar results were obtained from sediment samples of areas with reefs (Table 1).

3.3.2. Suspended sediment concentration in areas with and without reefs

Water samples obtained from areas with and without reefs showed that suspended sediment concentration was significantly 3.5 times higher in areas with reefs ($t = -6.8$, df = 14, $p = 7.6 \times 10^{-6}$; Fig. 5A), however, wind speed recorded during the same period showed no significant difference to suspended load between areas ($t = -0.78$, df = 4, $p = 0.47$; Fig. 5B).

3.4. Effect of reefs on bedload sediment and passive faunal transport

The amount of bedload sediment transported obtained from the traps showed no significant differences in relation to distance and orientations from the reefs (Fig. 6A and B, Table 2) in the first three days (days 1, 2

Table 1
Percentages of traction, saltation and suspension in samples of sediment at the top of the reefs (T), leeward (L), control (C) and windward (W) from the transplanted and existing (between brackets) reefs

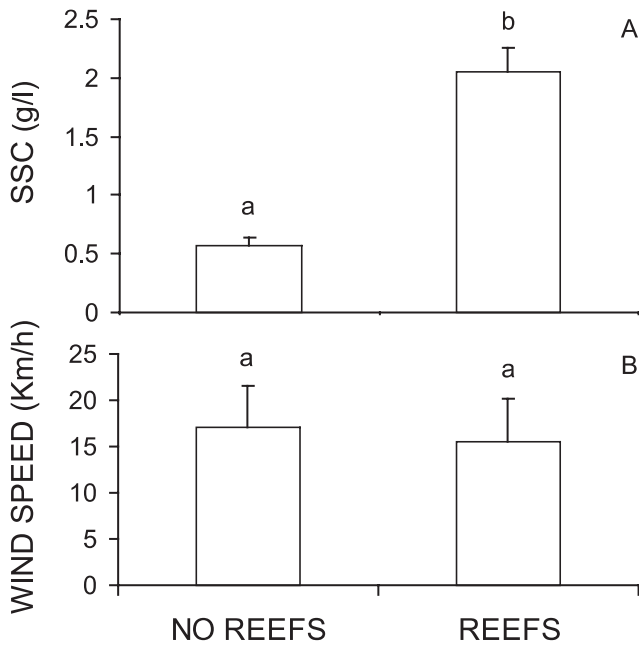|	T	L	C	W
% Traction	0.2 (3.2)	0.3 (2.3)	9	18 (26.2)
% Saltation	29.7 (24.5)	35 (32)	74	76 (64.8)
% Suspension	70 (72.3)	64.7 (65.7)	15	6 (9)

Fig. 5. Suspended sediment concentration (SSC, A) and wind speed (B) within areas with and without reefs. All bars and symbols show mean + SE. Same letters mean not significant differences.
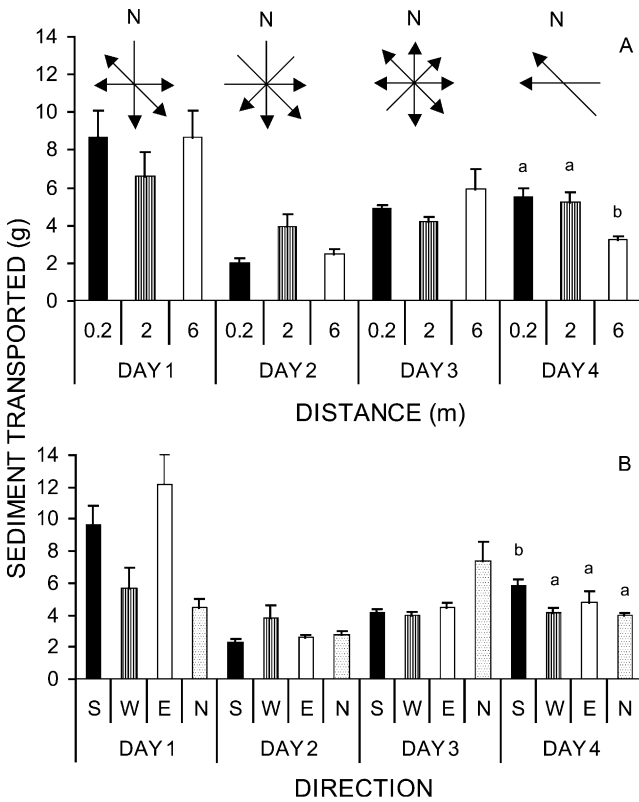

Fig. 6. Bedload sediment transported (g) at days 1, 2, 3 and 4, at three different distances (0.2, 2 and 6 m) from the reefs (A) and in four directions (S, W, E, N; B). Only day 4 showed significant differences in distance and direction. Same letters mean not significant differences. On the top of the figure are the variations in wind directions during each day. All bars are constructed with mean + SE.

Table 2
Summary of the two-way fixed factor ANOVA to test the amount of bedload sediment transport per day (1, 2, 3 and 4) at different distances and orientations from the reefs

Source of variation	Day	F (df effect, df error)	MS	p
Distance	1	0.75 (2, 36)	0.33	0.47
	2	0.75 (2, 36)	0.24	0.11
	3	0.55 (2, 36)	0.008	0.8
	4	4.46 (2, 36)	0.21	0.01
Orientation	1	2.28 (3, 36)	0.32	0.52
	2	0.51 (3, 36)	0.05	0.67
	3	1.86 (3, 36)	0.019	0.69
	4	2.88 (3, 36)	0.13	0.04
Distance × Orientation	1	0.22 (6, 36)	0.24	0.76
	2	0.48 (6, 36)	0.19	0.11
	3	1.29 (6, 36)	0.05	0.27
	4	0.99 (6, 36)	0.047	0.43

Data were log-transformed.

and 3). However, the amount of sediment transported showed significant differences in relation to distance and direction from the reefs (Table 2, Fig. 6A and B), while there were no differences in the interaction term (Table 2). Higher amounts of sediment were transported at 0.2 m ($p = 0.009$) and 2 m ($p = 0.01$) than at 6 m from the reefs (Fig. 6A). Also, the sediment transported to the south was two times higher than to the west ($p = 0.0001$), east ($p = 0.0001$) and north ($p = 0.0002$; Fig. 6B). During this sampling day, the direction of the wind mainly came from east-southeast (Fig. 6).

Subsamples of meiofauna transported from the same traps showed that the density of ostracodes and nematodes transported increased significantly from 0.2 to 6 m from the reefs on day 2 (Table 3, Fig. 7A and B). No other differences in density were found with distance, direction from the reefs or with the interaction term on any date (Table 3, Fig. 7A–D). The density of harpacticoid copepods transported showed no significant differences in relation to the interaction term, distances and orientations from the reefs on days 1 and 4 (Table 3). The density of copepods on days 2 and 3 was low and they were not statistically analyzed (Table 4). Other organisms were observed in the traps, such as cladocerans, ciliates, polychaetes juveniles (nereids), the amphipod *Corophium insidiosum*, and the gastropod *Heleobia conexa*, but they were in low densities and they were not statistically analyzed (Table 4).

The mean bedload transport of sediment was high with high wind speed ($r = 0.97$, $n = 4$, $p = 0.02$; Fig. 8A), but there was no relationship between the amount of meiofaunal organisms transported and the wind speed ($r = 0.82$, $n = 4$, $p = 0.17$; Fig. 8A). There was not a predominant direction of the wind during the first three days and the wind speed was very variable along the same day (Figs. 6 and 8B, respectively).

Table 3
Summary of the two-way fixed factor ANOVA to test the density of ostracodes (O), nematodes (N) and harpacticoid copepods (C) at different distances (D) and orientations (Or) from the reefs

Source of variation	Day	O			N			C		
		F	MS	p	F	MS	p	F	MS	p
Distance	1[a]	0.16	0.16	0.84	1.02	0.98	0.36	0.76	0.59	0.47
	2[a]	6.76	1.25	**0.003**	8.83	1.33	**0.0008**			
	3[a]	0.19	0.08	0.82	1.56	0.32	0.21			
	4[b]	2.23	28.63	0.11	0.24	3.24	0.78	2.93	28.79	0.06
Orientation	1[a]	0.62	0.61	0.6	0.49	0.47	0.68	0.37	0.28	0.77
	2[a]	2.2	0.41	0.1	1.69	0.25	0.18			
	3[a]	2.79	1.27	0.05	0.32	0.06	0.8			
	4[b]	1.62	20.79	0.19	0.21	2.78	0.88	0.36	3.55	0.78
Distance × Orientation	1[a]	1.06	1.04	0.4	0.95	0.21	0.96	0.98	0.75	0.44
	2[a]	1.14	0.21	0.36	0.46	0.06	0.83			
	3[a]	0.78	0.35	0.58	0.32	0.06	0.92			
	4[b]	1.15	14.77	0.34	1.47	19.29	0.2	0.9	8.85	0.5

Copepods at days 2 and 3 were not found. Significant p-values were highlighted. Df effect values for distance, orientation and interaction term were always 2, 3, and 6, respectively. Df error value in all cases was 36.

[a] Log-transformed data.
[b] Square root transformed data.

3.5. Relationship between reefs and relative water flow

The weight loss of plaster cylinders found after 24 h of exposure did show significant differences relative to the direction from the reefs ($F_{3,48} = 4.42$, MS = 10.2, $n = 60$, $p = 0.008$; Fig. 9B) but did not differ significantly in the interaction term (distance × orientation; $F_{6,48} = 0.9$, MS = 2.09, $n = 60$, $p = 0.49$) or in distances from the reefs ($F_{2,48} = 0.98$, MS = 2.27, $n = 60$, $p = 0.38$; Fig. 9A). The east showed the highest weight loss in relation to north ($p = 0.003$), W ($p = 0.007$) and south ($p = 0.004$). This coincides with the main wind direction recorded at a mean speed of 10.96 km h^{-1} (SE = 0.92) that came from east.

4. Discussion

Our results suggest that the introduced *Ficopomatus* reefs play an important role in the hydrodynamics of the Mar Chiquita coastal lagoon by affecting the bedload transport and deposition of the sediment entering the system. Moreover, these effects would be magnified by the increase in density and size of the reefs that increased over time.

Anthropogenic disturbances facilitate the introduction of exotic species throughout the world, and estuaries are one of the most impacted environments (Ruiz et al., 1999). Reefs of the exotic polychaete *Ficopomatus* are currently populating the 86% of Mar Chiquita coastal lagoon (Plate 1; Schwindt et al., 2001). Our results show that during the last 24 years, both reef size and reef density have increased while the distance between them has decreased. Consequently, reefs are

being combined and forming big platforms of several meters of longitude (Obenat and Pezzani, 1994; Schwindt, 2001a). The rate of spread seems to have slowed since 1979; may be due to reduced availability of the preferred nuclei for the settlement (the fossil shell of the gastropod *Adelomelon brasiliana*; Schwindt and Iribarne, 2000). Most of the reefs (more than 70%) were found to use these shells as nuclei, however, these shells presently occur in a very low density within the lagoon (∼1 shells 20 m^{-2}; Schwindt and Iribarne, 2000). However, since water sports and fishing have increased in the lagoon together with the amount of thrash such as bottles and cans, which are eventually used as settlement sites by *Ficopomatus* (Iribarne et al., 2000; Schwindt, 2001a,b), human activities may have played a significant role in the success of this invader magnifying its effects on the ecosystem.

Reefs are known to influence the hydrodynamics near seabeds (Nowell and Jumars, 1984; Lenihan, 1999; Guichard et al., 2001). As was observed with other polychaete reefs (Bailey-Brock, 1979) our results show that during days with a constant wind direction, the relative water flow and the bedload sediment transport are higher on the windward side than on any other side of the reefs. Especially in shallow water ecosystems, the wind is an important factor to be considered when sediment transport is studied (Arfi et al., 1993; Airoldi et al., 1996). For example, if the wind comes from the south, the flow and sediment transport are higher on the southern part of the reefs than in the northern part. As a result of the wind variation, most days the windward side can switch with changes in wind direction. In our study, the wind was not constant in direction in three of four days, causing all bedload traps to contain the same
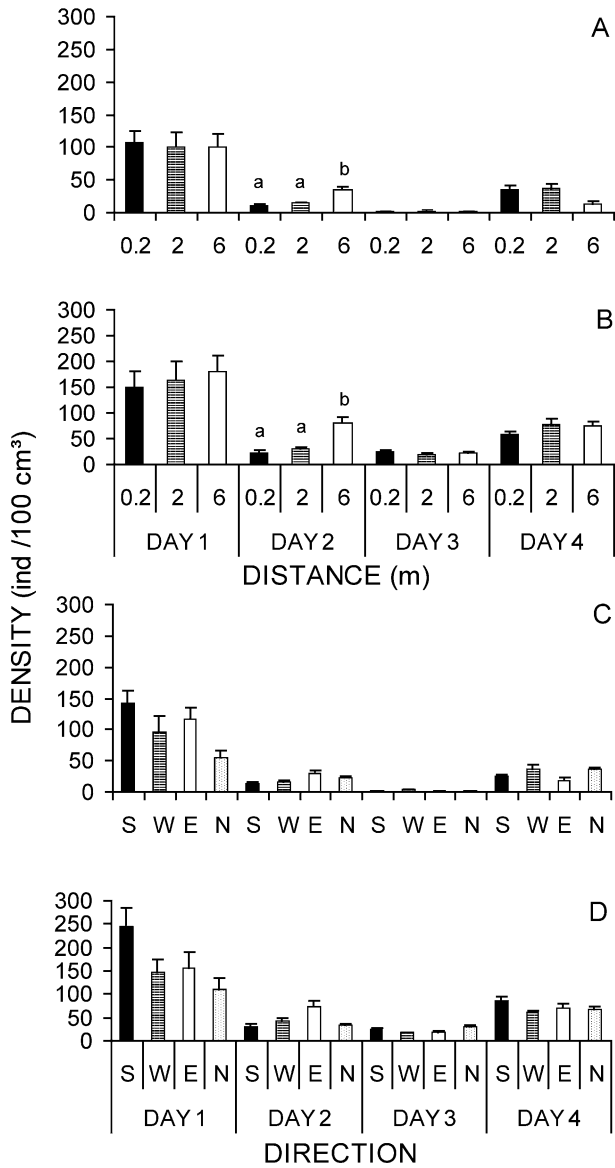
Fig. 7. Density of ostracodes (A and C) and nematodes (B and D) bedload transported at days 1, 2, 3 and 4, at three different distances (0.2, 2 and 6 m) from the reefs (A and B) and in four directions (S, W, E, N; C and D). Only the day 2 showed significant differences in distances. Same letters mean not significant differences. All bars are constructed with mean + SE.

Table 4
Average density of meiofaunal organisms (ind 100 cm^{-3}) bedload transported during the four days of sampling

	Day 1	Day 2	Day 3	Day 4
Cladocerans	4.85 (2.8)	0.06 (0.03)	Nf	Nf
Palaeomonetes argentinus	0.25 (0.14)	Nf	Nf	Nf
Ciliates	14.25 (3.18)	2.09 (0.49)	Nf	0.33 (0.26)
Nereids juveniles	1.67 (4)	0.22 (0.13)	2.14 (0.44)	7.66 (1.82)
Corophium insidiosum	1.03 (0.43)	0.17 (0.08)	0.97 (0.43)	1.66 (0.71)
Hirudineans	0.2 (0.2)	Nf	Nf	Nf
Heleobia conexa	0.44 (0.25)	0.07 (0.05)	Nf	0.33 (0.37)
Harpacticoid copepods	16.09 (3.81)	3.07 (0.51)	2.32 (0.45)	34.3 (4)
Hydra sp.	0.33 (0.19)	0.04 (0.04)	Nf	0.83 (0.48)

The error standard is in brackets. Nf = not found.

In shallow water estuarine systems, calm periods are generally associated with low sediment transport and high sedimentation rates (Arfi et al., 1993). In turn, windy periods generate waves and increase the sediment transport (McManus, 1998; Airoldi et al., 1996). Our results show that at high wind speed there is a higher bedload sediment transport. However, areas with reefs always have more suspended sediment concentration than areas without reefs, regardless of the wind. Thus,
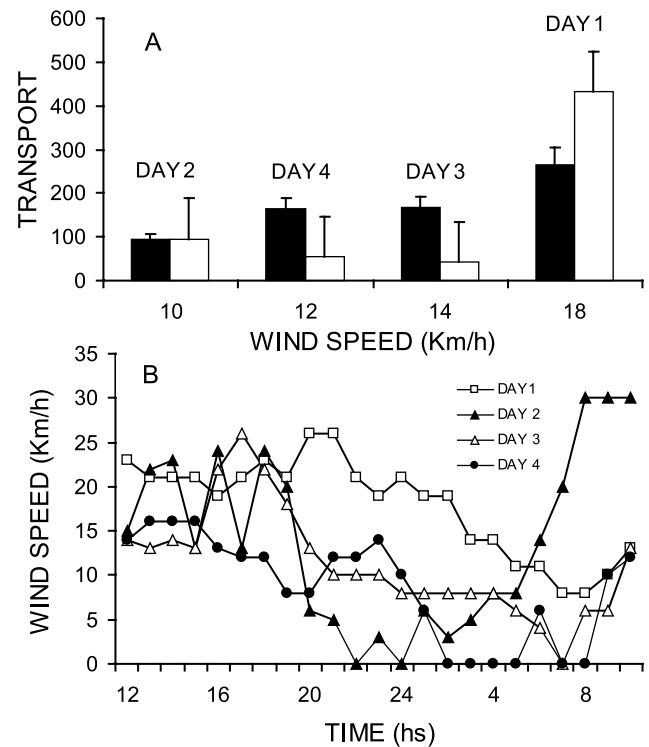
amount of sediment. Thus, since the estuarine environment has wind conditions very variable during the same day (i.e. in intensity and direction), further investigations at larger temporal scale is needed to completely understand the hydrodynamic effects of the reefs. However, the wind variation over time suggests that the net movement of sediment to the outside of the lagoon may be very low. This low-energy process is likely to combine with the dense reef formations favoring the retention of the entering sediments more than discharging them out of the lagoon (Isla, 1997).

Fig. 8. (A) Relationship between the wind speed and both the amount of sediment (in g m^{-1}, black boxes) and density of meiofauna (in 100 cm^3, empty boxes) bedload transported during four randomly chosen days. All bars are constructed with mean + SE; (B) variation of the wind speed during the same four days of sampling.
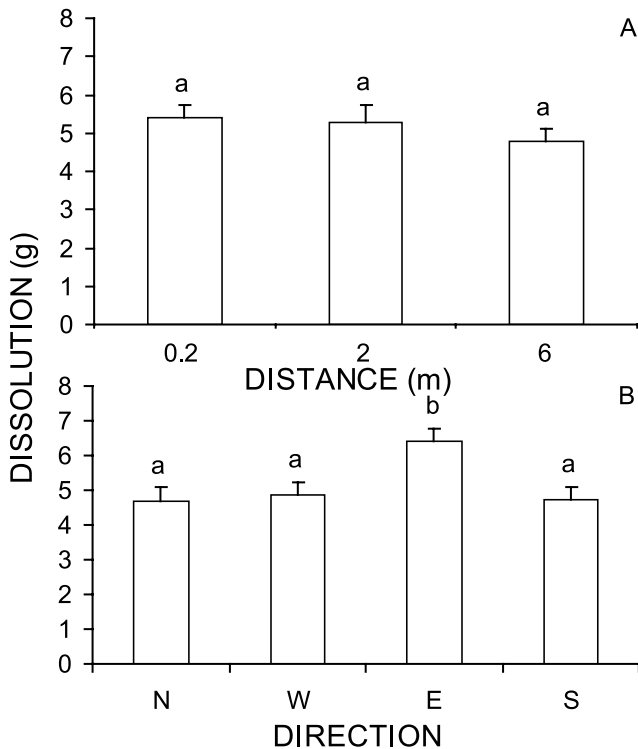
Fig. 9. Plaster dissolution (g) after 24 h for each distance (A) and direction (B) from the reefs. All bars show mean + SE. Same letters mean not significant differences.

reef-populated areas have always sediment ready for deposition, even more under strong wind conditions but different sediment grain sizes are deposited in different areas on the reefs and around them. Similar to seagrasses (Fonseca and Cahalan, 1992) and marsh plants (Wood et al., 1989; Bruno, 2000), reefs and other biogenic structures (Bailey-Brock, 1979) are known to trap sediment, enhancing settlement of fine-grained suspended sediments (Loya, 1976; Crooks and Khim, 1999). When reefs were transplanted to areas without neighboring reefs and with unidirectional water flow, sediment samples from the top of the reef and from the different surrounding areas showed different grain size fractions. The top of the reefs and the leeward side concentrated on the most fine-grained sediments (i.e. fine sand, silt and clay), while the windward side and areas without reefs (i.e. control areas) had coarse sediments (i.e. coarse sands). These results seem to agree with the pattern described from areas populated by reefs (see Table 1). Even though we analyzed a small number of sediment samples from the experimental reefs, the similarity between pattern and experimental results suggests that *Ficopomatus* reefs are able to strongly alter these physical characteristics in the invaded environment (Schwindt et al., 2001).

The different organisms found in the traps may have different meaning. The shrimp *Palaeomonetes argentinus*

and the amphipod *Corophium insidiosum* are organisms able to swim inside and outside the traps. Also, *Hydra* sp., hirudineans, *P. argentinus* and cladocerans came from freshwater areas during previous rainfalls (E. S. pers. obs.). Only juvenile nereids, ostracodes, nematodes, harpacticoid copepods, and the gastropod *Heleobia conexa* are typical brackish organisms found in the lagoon throughout the year (Schwindt, 2001a). The most abundant organisms in the traps were ostracodes and nematodes, showing lower densities near the reefs during a different day observed for the sediment transported. This difference in days may come from the highest wind speed (up to 30 km h^{-1}) observed during the day when nematodes and ostracodes showed a significant transport (see Fig. 8b). This evidence suggests that both the direction and intensity of the wind are important variables for the transport of sediment and organisms. However, smaller temporal scale than the studied (i.e. 24 h) would contribute to evaluate the movement of the dominant meiofauna in the sediment. Even though total bedload organism transport is not related to wind speed, reefs affected the transport of the organisms (i.e. nematodes and ostracodes) and this may be an evidence for how changes in depositional and transport processes can affect the local distribution of organisms (Cusson and Bourget, 1997).

After the link between an organism's activities and the ecosystem emerged under the concept of ecosystem engineering (Jones et al., 1994, 1997), the role of species in structuring ecosystems was recognized in terrestrial (e.g. Reichman and Seabloom, 2002) and aquatic (e.g. Coleman and Williams, 2002) systems. This concept is especially interesting when the ecosystem engineers studied are invasive species (e.g. Crooks and Khim, 1999; Reusch and Williams, 1998; Posey, 1988) because their impact may be magnified at large spatial scale while spreading. The exotic ecosystem engineer *Ficopomatus enigmaticus* builds reefs that are known to create refuge for other organisms such as amphipods, crabs and gastropods (Schwindt et al., 2001). In this work we show that *F. enigmaticus* also physically modified the estuarine ecosystem where it was introduced by altering sediment dynamics. In so doing, reefs favor the sediment deposition around them and may generate resources (e.g. refuge) for several native soft-bottom organisms. Considering that 86% of the estuarine environment is already populated by reefs (Schwindt et al., 2001), and they are increasing over time, they may completely alter the entire environment in the long term. Our results agree with the hypothesis that this exotic ecosystem engineer is favoring the filling in of the estuarine environment and may eventually change the landscape in the long term (Isla and Gaido, 2001), but further investigation is needed in order to make predictions. Since this species has been recorded invading many estuarine environments worldwide with

similar characteristics to those reported here (e.g. Italy, Bianchi and Morri, 1996; Spain, Fornós et al., 1997), our conclusions should be evaluated for those other systems in order to improve our understanding of its global impact.

References

Abelson, A., Loya, Y., 1995. Cross-scale patterns of particulate food acquisition in marine benthic environments. American Naturalist 145, 848–854.

Airoldi, L., Fabiano, M., Cinelli, F., 1996. Sediment deposition and movement over a turf assemblage in a shallow rocky coastal area of the Ligurian Sea. Marine Ecology Progress Series 133, 241–251.

Arfi, R., Guiral, D., Bouvy, M., 1993. Wind induced resuspension in a shallow tropical lagoon. Estuarine, Coastal and Shelf Science 36, 587–604.

Bailey-Brock, J.H., 1979. Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. Journal of Marine Research 37, 643–656.

Bertness, M.D., 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65, 370–381.

Bianchi, C.N., Morri, C., 1996. *Ficopomatus* 'reefs' in the Po River Delta (Northern Adriatic): their constructional dynamics, biology, and influences on the brackish-water biota. Pubblicazione della Stazione Zoologica di Napoli I: Marine Ecology 17, 51–66.

Bruno, J.F., 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. Ecology 81, 1179–1192.

Butman, C.A., 1986. Sediment trap biases in turbulent flows: results from a laboratory flume study. Journal of Marine Research 44, 645–693.

Butman, C.A., 1989. Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. Journal of Experimental Marine Biology and Ecology 134, 37–88.

Carver, R.E., 1971. Procedures in Sedimentary Petrology. Wiley Interscience, New York, 653 pp.

Carlton, J.T., 1996. Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78, 97–106.

Coleman, F.C., Williams, S.L., 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution 17, 40–44.

Crooks, J.A., 1998. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Marine Ecology Progress Series 162, 137–152.

Crooks, J.A., Khim, H.S., 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. Journal of Experimental Marine Biology and Ecology 240, 53–75.

Cusson, M., Bourget, E., 1997. Influence of topographic heterogeneity and spatial scales on the structure of the neighbouring intertidal endobenthic macrofaunal community. Marine Ecology Progress Series 150, 181–193.

Didger®, 1997. The Golden Software Inc., Colorado, USA.

Emerson, C.W., 1991. A method for the measurement of bedload sediment transport and passive faunal transport on intertidal sandflats. Estuaries 14, 361–371.

Fasano, J.L., Hernández, M.A., Isla, F., Schnack, E.J., 1982. Aspectos evolutivos y ambientales de la laguna Mar Chiquita (Provincia de Buenos Aires, Argentina). Oceanologica Acta (special number), 285–292.

Fonseca, M.S., Cahalan, J.A., 1992. A preliminary evaluation of wave attenuation by four species of seagrasses. Estuarine, Coastal and Shelf Science 35, 565–576.

Fornós, J.J., Forteza, V., Martínez Taberner, A., 1997. Modern polychaete reefs in Western Mediterranean lagoons: *Ficopomatus enigmaticus* (Fauvel) in the Albufera of Menorca, Balearic Islands. Palaeogeography, Palaeoclimatology and Palaeoecology 128, 175–186.

Guichard, F., Bourget, E., Robert, J.L., 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternate trajectories mediated by hydrodynamics and shading. Marine Ecology Progress Series 217, 27–41.

Hayward, B.W., 1997. Introduced marine organisms in New Zealand and their impact in the Waitemata Harbour, Auckland. Tane 36, 197–223.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187–211.

Iribarne, O., Botto, F., Martinetto, P., Gutierrez, J.L., 2000. The role of burrows of the SW Atlantic intertidal crab *Chasmagnathus granulata* in trapping debris. Marine Pollution Bulletin 40, 1057–1062.

Isla, F.I., 1997. Seasonal behavior of Mar Chiquita tidal inlet in relation to adjacent beaches, Argentina. Journal of Coastal Research 13, 1221–1232.

Gaido, E.S., 2001. Evolucion geologica de la laguna Mar Chiquita. In: Iribarne, O.O. (Ed.), Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas, Editorial Martín, Mar del Plata, Argentina, pp. 19–30.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical engineers. Ecology 78, 1946–1957.

Jumars, P.E., Nowell, A.R.M., 1984. Fluid and sediment dynamic effects on marine benthic community structure. American Zoologist 24, 45–55.

Lenihan, H.S., 1999. Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69, 251–275.

Loya, Y., 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. Bulletin of Marine Science 26, 450–466.

Luppi, T.A., Spivak, E.D., Anger, K., Valero, J.L., 2002. Patterns and processes of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae) recruitment in Mar Chiquita Coastal lagoon, Argentina. Estuarine, Coastal and Shelf Science 55, 287–297. (doi: 10.1006/ecss.2001.0904).

Manly, B.F.J., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, second ed., Chapman & Hall, London, 399 pp.

McManus, J., 1998. Temporal and spatial variations in estuarine sedimentation. Estuaries 21, 622–634.

Nowell, A.R.M., Jumars, P.E., 1984. Flow environments of aquatic benthos. Annual Review of Ecology and Systematics 15, 303–328.

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.

Olenin, S., Leppäkoski, E., 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia 393, 233–243.

Olivier, S.R., Escofet, A., Penchaszadeh, P., Orensanz, J.M., 1972. Estudios ecológicos de la región estuarial de Mar Chiquita. 1. Las comunidades bentónicas. Anales de la Sociedad Científica Argentina 193, 237–262.

Orensanz, J.M., Estivariz, M.C., 1972. Los Anélidos Poliquetos de aguas salobres de la Provincia de Buenos Aires, Argentina. Revista del Museo de La Plata (Argentina) 11, 95–112.

Petticrew, E.L., Kalff, J., 1991. Calibration of a gypsum source for freshwater flow measurements. Canadian Journal of Fisheries and Aquatic Sciences 48, 1244–1249.

Posey, M.H., 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology 69, 974–983.

Reichman, O.J., Seabloom, E.W., 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17, 44–49.

Reta, R., Martos, P., Piccolo, M.C., Perillo, G.M.E., Ferrante, A., 1997. Características de la marea en la laguna costera Mar Chiquita, Argentina, VII Congreso Latinoamericano de Ciencias del Mar. Santos, Brasil 2, 330–332.

Reusch, T.B.H., Williams, S.L., 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia 113, 428–441.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H., 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. American Zoologist 37, 621–632.

Ruiz, G.M., Fofonoff, P., Hines, A.H., Grosholz, E.D., 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography 44, 950–972.

Schwindt, E., 2001a. Efectos de una especie exótica formadora de arrecifes *Ficopomatus enigmaticus* en la laguna costera Mar Chiquita. Doctoral thesis, Universidad Nacional de Mar del Plata, Argentina.

Schwindt, E., 2001b. Impacto de un poliqueto exótico y formador de arrecifes. In: Iribarne, O.O. (Ed.), Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas. Editorial Martín, Mar del Plata, Argentina, pp. 109–113.

Schwindt, E., Iribarne, O., 2000. Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. Bulletin of Marine Science 67, 73–82.

Schwindt, E., Bortolus, A., Iribarne, O., 2001. Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biological Invasions 3, 137–149.

Simberloff, D., 1997. The biology of invasions. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise. Island Press, Washington, DC, pp. 3–17.

Snelgrove, P.V.R., Butman, C.A., 1994. Animal–sediment relationship revisited: cause versus effect. Oceanography and Marine Biology Annual Review 32, 111–117.

Strayer, D.L., Caraco, N.F., Cole, J.J., Findlay, S., Pace, M.L., 1999. Transformation of freshwater ecosystems by bivalves. Bioscience 49, 19–27.

Talley, T.S., Crooks, J.A., Levin, L.A., 2001. Habitat utilization and alteration by the invasive burrowing isopod *Sphaeroma quoyanum*, in California salt marshes. Marine Biology 138, 561–573.

ten Hove, H.A., Weerdenburg, J.C.A., 1978. A generic revision of the brackish-water serpulid *Ficopomatus* Southern 1921 (Polychaeta: Serpulidae), including *Mercierella* Fauvel 1923, *Sphaeropomatus* Treadwell 1934, *Mercierellopsis* Rioja 1954, and *Neopomatus* Pillai 1960. Biological Bulletin 154, 96–120.

Wood, M.E., Kelley, J.T., Belknap, D.F., 1989. Patterns of sediment accumulation in the tidal marshes of Maine. Estuaries 12, 237–246.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, NJ, 931 pp.