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Individual and reef growth of the invasive reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon

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The growth of the *Ficopomatus enigmaticus* reefs was measured throughout a coastal lagoon at different temporal and spatial scales (over 24 years, annually and monthly throughout the coastal lagoon). The results show that reef cover increased in the last 24 years, and many neighbouring reefs have coalesced into large platforms. Growth rate varies spatially and temporally. Small reefs grow faster than large ones. *Ficopomatus enigmaticus* polychaetes living in higher salinity areas show a lower biomass than those living in brackish water areas, and the same pattern was observed for the inter-ring distance measured on the tubes. The results also show that important environmental variables, including salinity, nutrient availability and environmental energy (measured as current speed and depth) may be the most important factors affecting the growth and spread of the reefs.

INTRODUCTION

The south-western Atlantic contains many marine coastal exotic species and one of the strongest ecological impacts is generated by the introduced polychaete *Ficopomatus enigmaticus* (Fauvel) (Schwindt, 2001). This polychaete is a reef-building species of unknown origin that has also been introduced in many sub-tropical brackish water areas worldwide (ten Hove, 1979). Reefs have variable shape and size (up to 7 m in diameter; Schwindt, 2001) and are formed by thousands of polychaetes. Each individual polychaete in the reefs lives in a calcareous tube that shows clear growth rings (Figure 1). The growth of this species can be affected by several environmental variables including temperature, salinity and nutrient availability (e.g. ten Hove, 1979; Bianchi & Morri, 1996; Thorp, 1997). Since the habitats invaded by *F. enigmaticus* worldwide have similar physical and ecological characteristics (ten Hove, 1979; Thorp, 1997), it might be possible to make comparisons among invaded regions and to predict where this species is likely to become a problem. In spite of this, few efforts have been directed to understand the environmental conditions where this species is spreading.

As in other areas of the world, the introduction of *Ficopomatus enigmaticus* in the Mar Chiquita coastal lagoon has generated ecological changes (Schwindt, 2001) such as an increase of the abundance of many benthic species (e.g. Bianchi & Morri, 1996; Schwindt, 2001). In addition, reefs are also known to alter the entire geomorphology of the system through effects on the hydrodynamic and sediment dynamics of the ecosystem (Schwindt et al., 2004). Despite all the environmental impacts of *F. enigmaticus*, the environmental variables that control the

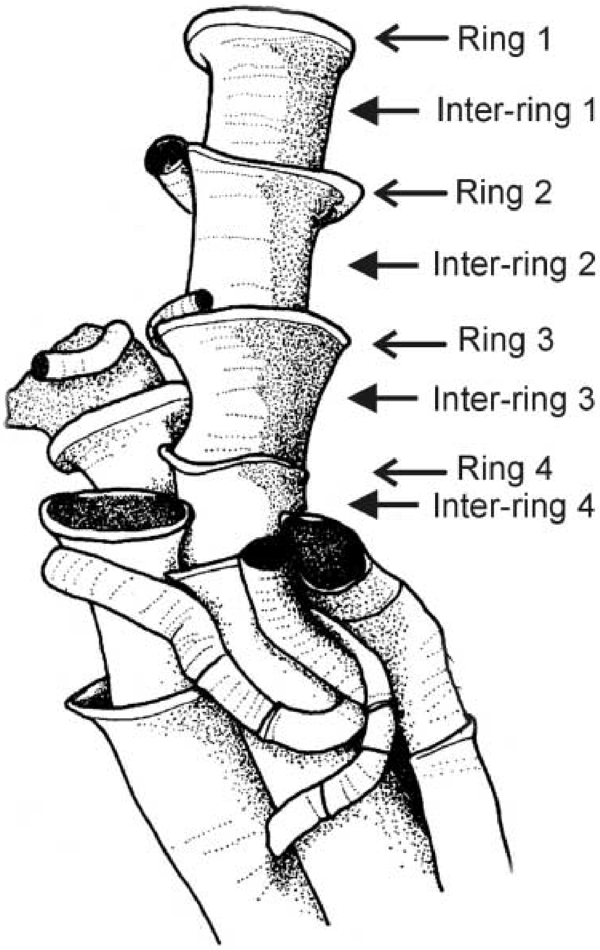

Figure 1. Drawing of the tubes of *Ficopomatus enigmaticus* showing the rings and inter-rings (modified from Bianchi, 1981).

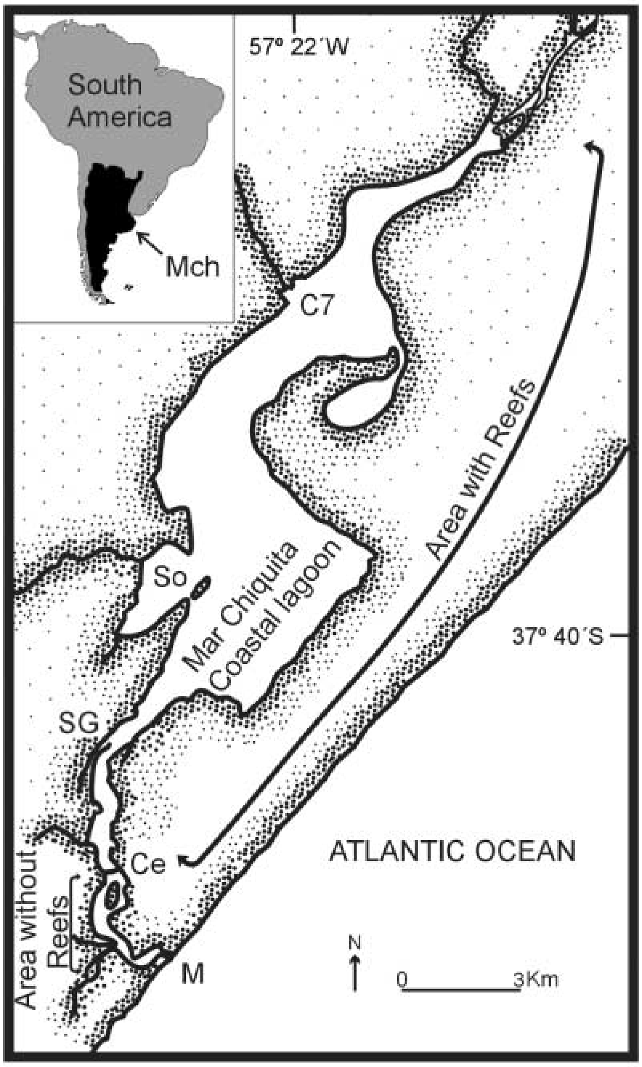

Figure 2. Map of the Mar Chiquita coastal lagoon showing the sampling sites and areas with and without reefs. M, Mouth; Ce, Celpa; SG, San Gabriel; So, Sotelo; C7, Canal 7.

growth and expansion of this species remain poorly understood in most areas of the world.

The main objective of this work was to evaluate the growth pattern of *Ficopomatus enigmaticus* and the relationship with the environmental variables in a south-western estuarine environment.

MATERIALS AND METHODS

Study area

The study was performed between 1999 and 2001 in the Mar Chiquita coastal lagoon (Argentina, 37°32′ to 37°45′S, and 57°19′ to 57°26′W; Figure 2). This lagoon is a body of brackish water of 46 km^2 and an average depth of 0.6 m. Sediment transport can be caused mainly by rainfall and river drainage (Isla, 1997). The lagoon may be divided into an innermost shallow zone where the tidal effect is insignificant and an estuarine zone subjected to tidal action (amplitude ⩽1 m). Wind and local rains control variations in water level within the lagoon but not in areas closer to the mouth. The bottom of the lagoon is composed primarily of silts and clays. Reefs occur everywhere within the lagoon occupying 86% of the surface with a mean density of 89 reefs ha^{-1} (Schwindt et al., 2004). Reefs are absent in the estuarine portion of the coastal lagoon.

What are the growth rates and growth patterns of Ficopomatus *reefs?*

The growth of the reefs was evaluated at four different temporal scales: (1) over 24 years; (2) three years; (3) annually, and (4) monthly. Since reefs increased in density and size over the last 24 years (Schwindt et al., 2004) an increase in reef cover during the same period is also expected. To measure changes in reef cover, aerial photographs obtained in 1975 and 1999 (1:5000 and 1:2400 scale respectively) were compared (older photographs were not available). From each photograph, 12 areas (1 ha each one) were randomly selected. Each reef from each area was measured in diameter with a digital caliper (precision ±0.02 mm) and transformed to actual size using the scale from the photographs. Then, with the size and the density of reefs, the cover of the reefs was calculated.

Neighbouring reefs can coalesce with each other forming platforms several metres long (Obenat, 2002). Given the increase in size and density of reefs over time, the abundance of coalesced reefs may also have increased over time. To measure this, the number of coalesced pairs of reefs was counted in 23 ha on the same aerial photographs. Finally, to determine the size of each coalesced reef, the diameter of each reef was measured in the field from 31 pairs of randomly chosen reefs.

To determine if the net and relative growth rate differ among reefs of different sizes, and if the reefs grow at similar rates in all directions (i.e. north, south, east and west), different reefs were measured over time. Reefs in three size-categories were initially measured in diameter and marked with polyvinyl chloride pipes on the edges. Size-categories were: small (∼0.52 m), medium (∼1.73 m) and large (∼3 m). After three years the diameter of the same reefs was measured again, and both the relative and net growth rate were calculated between the initial and the final period. Since reefs have a circular shape (Obenat, 2002; Schwindt et al., 2004), they have been assumed to grow similarly in all directions (i.e. north, south, east, west). To evaluate this hypothesis, northern, southern, eastern, and western reef edges were marked (N=12 for each direction; total N=48) and the diameter was measured after three years and compared among directions. After this sampling, the mean reef diameter was calculated for the same reefs during a period of two years to measure the annual variability in the annual reef growth rate.

To determine the growth of the reefs at a shorter temporal scale, 70 additional reefs were marked (diameter ranging from 0.2 m to 6 m), and their diameters were measured every month from January 2000 to December 2000 and the mean monthly growth rate was estimated. During the same period, temperature, salinity and water depth were also measured (N=3 for each variable).

Does the growth of individual polychaetes vary throughout the estuarine gradient?

Since *Ficopomatus enigmaticus* usually lives in brackish water environments, we hypothesized that polychaetes living in higher salinity (i.e. near to the mouth of the lagoon) would grow less than those living in the innermost areas of the lagoon. To evaluate this prediction, the biomass of individual polychaetes and the length of the calcareous tubes were measured in different areas of the lagoon as measures of growth. First, the biomass of the polychaetes was obtained from four different areas homogenously distributed throughout the lagoon (Celpa [Ce], San Gabriel [SG], Sotelo [So] and Canal 7 [C7]; N=50 polychaetes from each area; see Figure 2). Each worm was separated from its calcareous tube, oven-dried at 70°C until reaching constant weight (digital balance ±0.0001 g). Simultaneously, the variation in polychaete biomass was evaluated through a reciprocal transplant of reefs between the brackish portion of the lagoon (So) and the most marine part of the lagoon (Ce) inhabited by *Ficopomatus*. Thus, the treatments were: (1) reciprocal transplant of reefs between Ce and So; (2) control: reefs randomly marked in both sites; and (3) manipulation control: reefs transplanted to the same areas where they were obtained (i.e. in So and Ce). There were 12 replicates for each treatment at each site (size of the transplants: 6300 cm^3). After a month, biomass was obtained as described above and compared among sites and treatments.

The length between adjacent growth rings (i.e. inter-ring; see Figure 1) on the calcareous tube of the polychaetes was used as an indicator of growth among areas. Six hundred polychaete tubes were randomly chosen from the same areas mentioned above and the last three penultimate inter-rings 2, 3 and 4 (N=200 for each inter-ring; Figure 1) were measured with a digital caliper (±0.02 mm) from different individuals. The first growth inter-ring was not utilized in this analysis since it may still be growing at the time of sampling.

Which environmental factors regulate the growth and expansion of the reefs?

Since the growth pattern of the polychaetes is not homogeneous throughout the lagoon gradient a sampling of the major environmental variables that may drive the growth was performed. The variables were: temperature (°C, T), salinity (psu, S), pH, depth (m, D), energy level (i.e. current speed, $\mathrm{m \cdot s^{-1}}$, CS), suspended sediment concentration ($\mathrm{g \cdot l^{-1}}$, SSC), nutrients (i.e. chlorophyll, $\mathrm{mg \cdot m^{-3}}$, C, and detritus concentration, $\mathrm{g \cdot l^{-1}}$, DC) and hard substrate (i.e. nuclei) availability. The variables were measured during November and December 2000, in the same areas described above and the mouth (M) of the lagoon was added as a contrasting area without reefs.

Temperature, salinity and pH were measured with a Horiba U-10 water-quality analyser. The energy level was estimated by measuring the relative current speed using a neutrally buoyant sphere and calculating the time it took the sphere to move 5 m. These four variables (i.e. S, T, pH and energy level) were measured once a week (N=5 for each day) for four weeks during December 2000 within each area. Water depth was obtained every day of sampling with the same schedule as temperature. To measure SSC, water samples (1-l) were collected from each area and filtered (1.2-μm mesh size). Since the filters retain organic matter plus sediment, all filters were ovendried (100°C until reaching constant weight) and combusted at 550°C for 6 h in order to obtain the ash-free dry weight (AFDW) of the sample. Suspended sediment samples were taken once a week for four weeks (N=3 for each day). Nutrients at each station were estimated by measuring $\mathrm{mg \cdot m^{-3}}$, C and $\mathrm{g \cdot l^{-1}}$, DC in the water. To obtain chlorophyll levels, water samples were taken and maintained on ice until analysis (no more than two hours). Water was then filtered (1.2-μm mesh size) and analysed by the monochromatic method of Lorenzen (1967). Detritus concentration was obtained from the same samples of suspended sediment as described above (i.e. weight of the filters with organic matter and sediment minus the AFDW after combustion). For both variables samples were obtained once a week during December 2000 (N=3 at each sampling time).

Since larvae of *Ficopomatus enigmaticus* need a nucleus (i.e. hard substrate) to settle and initiate a new reef (Schwindt & Iribarne, 2000), transects were sampled in areas not yet colonized by reefs to estimate the availability of potential settlement substrates. Transects (80 m length × 6 m width; N=48; separated 50 m each one) ran parallel to the coastline from Ce to the lagoon's mouth along both coastlines of the lagoon. Possible nuclei (objects larger than 500 cm^3, such as bottles, pebbles and gastropods shells attached to the bottom; Schwindt & Iribarne, 2000) were quantified for each transect. Additionally, the number of species already living on the nuclei was quantified.

Statistical analysis

Differences in reef cover, abundance and size of the coalesced reefs were independently evaluated with a paired *t*-test. When assumptions of normality and homoscedasticity were not met, data were analysed with the Mann–Whitney test. One-way analyses of variance (ANOVAs) were used to evaluate differences in the net growth and the directions of growth of the reefs. The data were analysed with a Kruskal–Wallis test if the assumptions of normality and homoscedasticity were not met. Differences in relative growth of the reefs were analysed with a one-way ANOVA and proportions were arcsine transformed prior to statistical analysis. Patterns of polychaete biomass throughout the lagoon (Ce, SG, So and C7 sites) as well as in the reciprocal transplant (between Ce and So) were statistically analysed with one-way fixed ANOVAs. The same analysis was used to evaluate differences in length of the calcareous tubes of *Ficopomatus* among sites. *A posteriori* multiple comparisons were performed with a Tukey test (Zar, 1999). The environmental variables obtained throughout the coastal lagoon were analysed with a correlation-based principal component analysis (PCA). Prior to the analysis, some variables were square root transformed to comply with the assumption of normality and homogeneity of variances.

RESULTS

What are the growth rates and growth patterns of Ficopomatus *reefs?*

Reef cover in the lagoon increased from 1975 to 1999 by 24% ($t=-5.93$, df=23, $P<0.0001$). A similar but less dramatic increase was observed with the abundance of

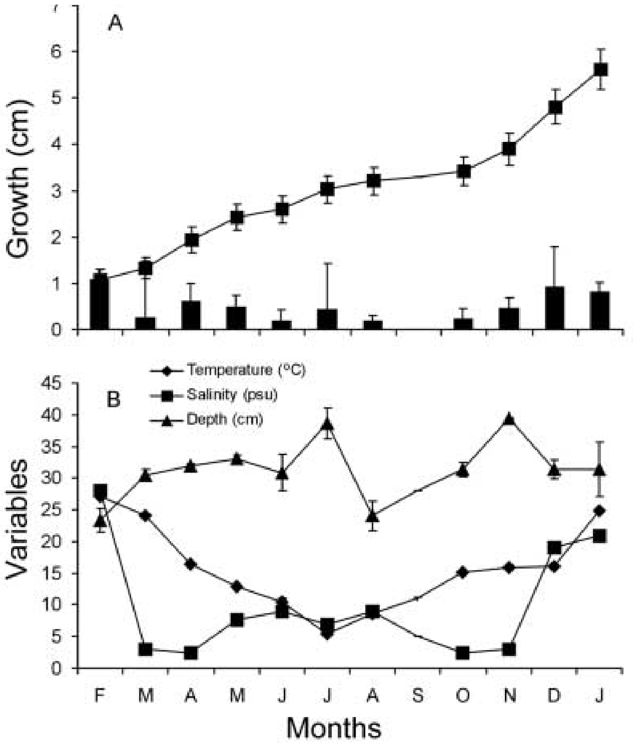

Figure 3. (A) Cumulative (squares) and monthly (bars) growth (cm) of the reefs from February 2000 to January 2001 and (B) variations in salinity (psu), temperature (C) and depth (cm) during the same period. The scale is the same for the three variables. Symbols and bars are means ±SE. Due to weather conditions, data are not available for September.

coalesced reefs (12.5%, Mann–Whitney *U*-test: U=27.5, Z=−5.2, N=23, $P<0.01$), although the size of these reefs was similar between the two sampling dates (t=0.48, df=30, $P>0.05$).

Reefs did not show significant differences in net growth in diameter for the different sizes (small: x=49.5 cm, SD=7.76; medium: x=52.27 cm, SD=6.21; large: x=48.31 cm, SD=8.71; F=0.78, df=2, $P>0.05$). Smaller reefs, however, showed higher relative growth rate than the larger ones (small: x=64%, SD=35; medium: x=30%, SD=4.5; large: x=16%, SD=3; arcsine transformed, Kruskal–Wallis: H=16.36, $P<0.05$). All reefs grew homogenously in all directions (W: x=24.36 cm, SD=3.15; N: x=24.2 cm, SD=4.16; E: x=26.55 cm, SD=2.62; S: x=24.13 cm, SD=4; F=1.29, df=3, $P>0.05$). The annual growth rate was 7.9 cm (SD=7, N=20) for 1999–2000 and 9.45 cm (SD=9.35, N=20) for 2000–2001, while in the same period reefs grow at a rate of 1.6 cm·month^{-1} (SD=1.27). Monthly growth of the reefs showed the highest values in summer (February x=1 cm, SD=1.85) and the lowest values in winter (June: x=0.17 cm, SD=0.57; August: x=0.17 cm, SD=0.41; Figure 3A). Water temperature and salinity showed the highest values during summer (January, 30°C and 49.6 psu respectively) whereas depth showed the lowest value (6.3 cm) during the same period. These variables showed the opposite pattern in winter (temperature x=5.5°C, SD=0.5; salinity x=7 psu, SD=0; depth x=38.6 cm, SD=4; Figure 3B). Due to weather conditions the measurement could not be taken in September.

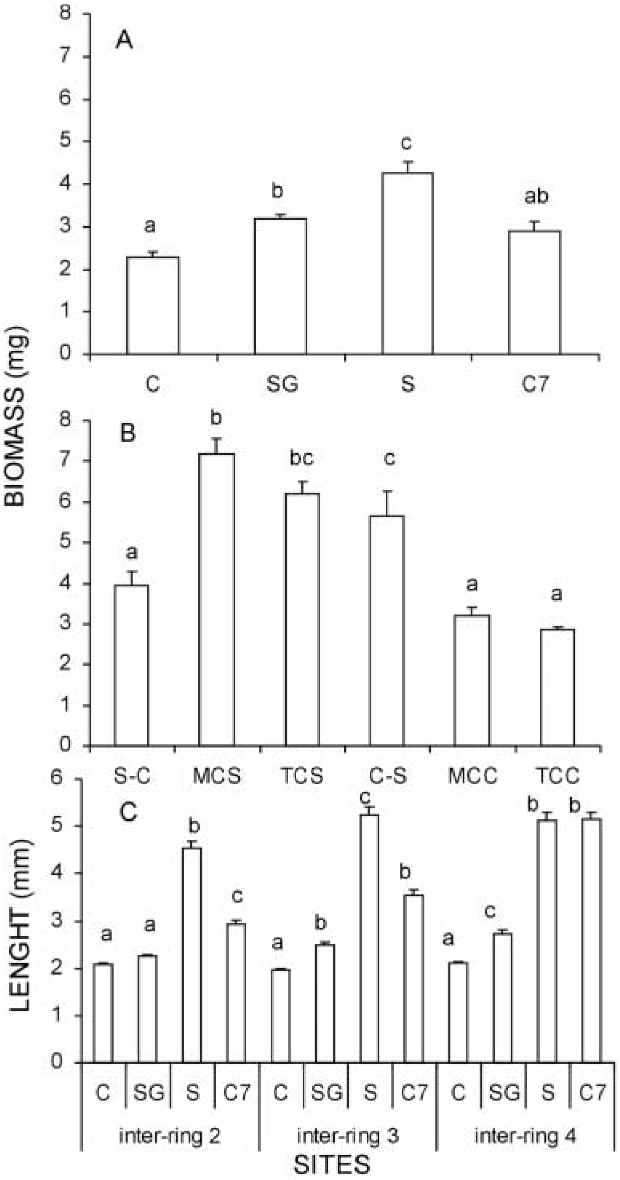

Figure 4. (A) Biomass (mg) of individual *Ficopomatus enigmaticus* obtained from Celpa (C), San Gabriel (SG), Sotelo (S) and Canal 7 (C7); (B) biomass (mg) of individual *Ficopomatus enigmaticus* obtained from the reciprocal transplant of reefs from Sotelo to Celpa (S–C), manipulation control in Sotelo (MCS), total control in Sotelo (TCS), transplant from Celpa to Sotelo (C–S), manipulation control in Celpa (MCC) and total control in Celpa (TCC) and (C) length of inter-rings (mm) 2, 3 and 4 from the same areas of the lagoon as in A. All bars are means ±SE. Identical letters indicate no statistically significant differences.

Does the growth of individual polychaetes vary throughout the estuarine gradient?

The biomass of individual polychaetes in So was two times higher than the biomass of individuals from Ce (F=18.95, df=3, $P<0.01$, Figure 4A). The biomass of individuals in the reciprocally transplanted reefs was consistent with the pattern observed. The biomass of polychaetes transplanted from Ce to So increased significantly, while the biomass of the polychaetes transplanted from So to Ce decreased (F=29.2, df=5, $P<0.05$, Figure 4B). No manipulation effect was detected ($P>0.05$, Figure

Table 1. *Principal component analysis (PCA) of the environmental variables measured along the coastal lagoon showing the contribution of each variable to the first three PCA axes.*

Variables	Axis I	Axis II	Axis III
PH	0.515	−0.78	−0.119
Temperature	0.463	−0.822	−0.38
Salinity	−0.697	−0.263	0.546
Current speed	−0.839	−0.193	0.162
Depth	−0.954	−0.07	−0.191
Suspended sediment concentration	0.893	0.06	0.391
Chlorophyll concentration	0.812	0.174	−0.252
Detritus concentration	0.908	0.185	0.296

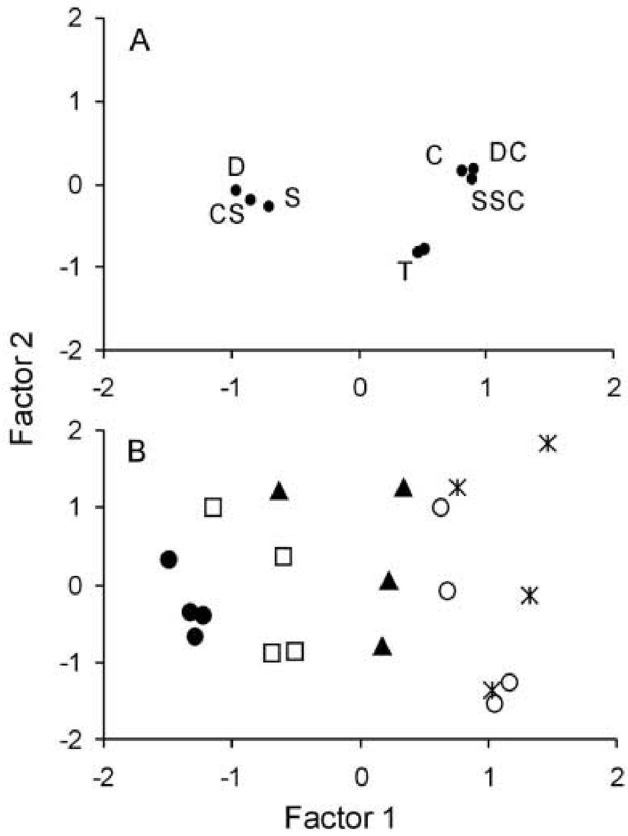

Figure 5. Principal component analysis of the environmental variables measured along the estuarine gradient. (A) Temperature, (T), salinity (S), depth (D), pH, suspended sediment concentration (SSC), current speed (CS), detritus (DC) and chlorophyll (C) concentration for factor 1 and 2; and (B) factor 1 and 2 for the Mouth (●), Celpa (□), San Gabriel (▲), Sotelo (○) and Canal 7 (∗).

4B). The same pattern along the lagoon was obtained for the length of the three inter-rings (inter-ring 2: F=51.6, df=3, $P<0.01$; inter-ring 3: F=77.16, df=3, $P<0.01$; inter-ring 4: F=61.97, df=3, $P<0.01$, Figure 4C).

Which environmental factors regulate the growth and expansion of the reefs?

In PCA analysis the first and second axes explained together 79.19% of the total variance (axis I: 60.85%, axis II: 18.34%; Table 1). Ordination of the environmental variables on the first two axes is shown in Figure 5A. Since axis III explained just 8.51% of the variance, and showed no strong correlation with any of the variables, it is not considered here. Concentration of suspended sediment, chlorophyll and detritus showed positive and high contributions to axis I (maximum−minimum=3.68–0.0086 $g\cdot l^{-1}$, 167.32–1.52 $mg\cdot m^{-3}$, 2.94–0.0034 $g\cdot l^{-1}$, respectively), while salinity, depth and current speed showed negative and high contributions to the same axis (maximum−minimum=35–0.3 psu, 2–0.2 m, 0.4–0.025 $m\cdot s^{-1}$, respectively). Temperature and pH showed positive but low contributions to axis I and high and negative contributions to axis II (maximum−minimum=21.5–12.6°C, 8.96–7.59, respectively). Figure 5A shows a clear estuarine gradient where nutrients (C and DC) and SSC are higher in the inner areas of the lagoon than in the M, and CS, S and D shows the opposite pattern. Figure 5B shows the variation of variables among sites, where M, Ce and SG are well separated and both So and C7 are very similar.

The most abundant nuclei found within transects in areas without reefs were shells of the gastropod *Adelomelon brasiliana* (x=0.48 shells·100 m^{-2}, SD=0.42). Artificial nuclei such as bottles and medium-size pebbles were also found (x=0.3 nuclei·100 m^{-2}, SD=0.51). Only 10% of the nuclei (N total=321) had colonizers growing on them, *Ficopomatus enigmaticus* tubes and *Balanus improvisus* being the least (0.3%) and most abundant (0.8%) respectively. The former was only observed on small pebbles close to Ce, but the tubes were empty.

DISCUSSION

Ficopomatus enigmaticus was introduced in Argentina more than 60 years ago and has rapidly increased in both reef density (24.3%) and size (66.8%; Schwindt et al., 2004). Consequently, reef cover is presently much higher than in the past and reefs of similar size coalesce to form platforms several metres long.

The morphology of *Ficopomatus enigmaticus* reefs may vary among environments according to water depth, type of substrate and direction of water flow (Fornós et al., 1997; Obenat, 2002). In shallow water areas where the water flow is multidirectional—e.g. in the innermost area of the Mar Chiquita coastal lagoon—reefs have a circular shape, and they grow in the same proportion in all directions as we expected. While the shape of the reefs is elongated forming fringing reefs where the water flow is unidirectional (Obenat, 2002), they build cauliflower-like forms reaching up to 3 m in height in deep water areas (Albufera of Menorca, Spain; Fornós et al., 1997). The growth rate of individual *F. enigmaticus* has been studied in several environments (e.g. Bianchi & Morri, 1996, 2001), but less known is the growth rate of entire reefs. If a single polychaete can grow up to 2 $cm\cdot month^{-1}$ (Bianchi & Morri, 2001), the growth of entire reefs reported here (1.6 $cm\cdot month^{-1}$), which are formed by thousands of polychaetes, is not unusual. In addition, as reported for juvenile individual worms (ten Hove & van der Hurk, 1993), the results show that smaller reefs grow faster than larger ones. These differences in growth may be a result of differences in available space for recruitment or to destructive or erosive processes (e.g. reefs tubes may be attacked by boring fungi, algae, sponges, crabs, fish and polychaetes; ten Hove & van der Hurk, 1993; Bianchi & Morri, 1996).

Reef growth varied in both space and time. As in other polychaetes (Kupriyanova et al., 2001), the results show that reefs grow faster in summer, when the temperature is higher. Along the estuarine gradient, lower biomass values were found for polychaetes living in higher salinities (i.e. near the mouth of the lagoon) in comparison with those living in brackish water, indicating that there are spatial differences in growth rates. Since this organism is primarily a brackish water species (ten Hove, 1979), the permanent contact with seawater seems to be negatively affecting its biomass, which may explain the different growth of polychaetes located near the mouth of the lagoon in comparison with those located in the inner part of the lagoon. In addition, *Ficopomatus enigmaticus* may be damaged by waves because its tubes are biomechanically weak (Bianchi & Morri, 2001). Thus, harsh environmental conditions near the mouth of the lagoon may reduce growth and increase erosion relative to the innermost areas of the lagoon. However, even near the mouth of the Mar Chiquita coastal lagoon where environmental conditions may be harsh for the polychaetes, these organisms show a biomass twice as high than the biomass reported (Bianchi & Morri, 1996). These results strongly suggest that invasions by this exotic species may not be limited to brackish water environments.

Several environmental conditions can be related to the spatio-temporal variations in the growth of serpulid worms (Kupriyanova et al., 2001 and references therein). In the innermost areas of the lagoon, where the polychaetes are larger and grow faster, the concentrations of suspended sediment and nutrients were high and salinity and current speed were low relative to the outer lagoon. In addition, the inner lagoon is shallower than the outer lagoon, probably because of the low rain and high evaporation (Isla, 1997). Finally, environmental conditions were more variable in the inner lagoon as compared with the relatively temporally constant areas near the lagoon's mouth.

Suspended sediment concentration is higher where polychaetes show higher biomass and growth (i.e. in the innermost part of the lagoon), suggesting that high-suspended sediment concentration does not adversely affect the development of the polychaetes. Thus, this variable may not be a useful parameter to prevent the spread of this exotic species. However, higher nutrient concentration, lower salinity and lower current speeds in the innermost part of the lagoon suggest that these conditions might improve the reproduction and growth of *Ficopomatus enigmaticus*. Similar conclusions were found in England (Thorp, 1997), suggesting that these environmental variables are important to the success of this exotic species worldwide. Another key variable that may control the spread of the reefs is the availability of nuclei, since nuclei are necessary for the establishment of a new reef (Schwindt & Iribarne, 2000). Even though the areas without reefs have a high abundance of nuclei, the results show that *Ficopomatus* does not survive for long on them, suggesting that other environmental variables are more critical rather than the availability of nuclei. There is little evidence (either in this estuary or elsewhere) to suggest that predation and competition are important processes controlling this species, however these processes should be evaluated (Schwindt, 2001).

In summary, the exotic polychaete *Ficopomatus enigmaticus* is now a dominant component of the Mar Chiquita coastal lagoon ecosystem. As a consequence of high reef density and size, the abundance of coalesced reefs has increased over time. Both the growth rate and growth pattern vary spatially and temporally, and several environmental variables can be related to these differences. The results suggest that the most important variables that control the spread of this exotic species in invaded habitats may be salinity, nutrients and environmental energy (e.g. current speed and depth). Given that most of the habitats invaded by *F. enigmaticus* are remarkably similar in their physical, chemical and biological characteristics; global comparisons among sites should be done to improve the management and control of this species.

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