

Effects of an invasive reef-building polychaete on the biomass and composition of estuarine macroalgal assemblages

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Abstract Invasive species can transform ecological communities. Their profound effects may alter the sources and pathways of primary production. We investigated the effects of the reef forming polychaete *Ficopomatus enigmaticus* invasion on the biomass and distribution of estuarine macroalgae in a SW Atlantic coastal lagoon (Mar Chiquita, 37° 40'S, 57° 23'W, Argentina). Reefs built by this species serve as substrates for macroalgal development and furnish structures that modify physical and biological conditions for the surrounding benthos. We showed that (1) the red macroalga *Polysiphonia subtilissima* settles and grows almost exclusively on the surface of the reef, (2) the green macroalgae *Cladophora* sp. and *Enteromorpha intestinalis* are found almost exclusively in areas without reefs attached to mollusk shells and, (3) no macroalgae occur in the sediment between reefs. Manipulative experiments show that reefs provide a complex substrate for settlement and survival and therefore benefit red macroalga. These experiments also show that the invasive reef builder has negative

indirect effects on green macroalgae by increasing grazing and probably by increased sedimentation between reefs. Via these direct and indirect effects, reefs change the relative biomass contribution of each macroalgal species to the overall production in the lagoon. Knowledge of these processes is important not only for predicting net effects on primary production but also because changes in macroalgal species composition may produce effects that cascade through the food web.

Keywords Coastal lagoon · Macroalgae · Ecosystem engineer · Biological invasion

Introduction

Invasive species modify the distribution, abundance and composition of native species assemblages (Steneck and Carlton 2001). These effects can be more significant if the invasive organism is an ecosystem engineer (Crooks 2002). This is because ecosystem engineers can create, destroy or change the physical characteristics of the habitat (Jones et al. 1994). Therefore they regulate the availability of biotic and abiotic resources to other species (Jones et al. 1994) and exert positive and/or negative effects of varying intensity on local species (see Sousa et al. 2009). For example, they can create new accessible habitat (Ruesink et al. 2006), prevent recruitment of local species that might compete for space (see Lambrinos and Bando 2008), or increase their own

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reproductive success in the new environment (Cuddington and Hastings 2004). Thus, invasive ecosystem engineers can affect ecosystem processes as well as interactions between native species (e.g., Jones et al. 1997; Vitousek 1990). Moreover, non-native ecosystem engineers may facilitate the success of other non-native species (e.g., Heiman and Micheli 2010). Overall, the result of positive and negative effects will be changes in species composition, which can in turn influence ecosystem function.

Physical and biotic features may change when invasion of ecosystem engineers occurs (Crooks 2002), and in estuarine environments macroalgal assemblages usually respond rapidly to such changes (McClelland and Valiela 1998; Underwood and Krompkamp 1999). For example, invading macroalgae can displace the entire suite of native dominant macroalgae or modify the original macroalgal assemblage profoundly (Schaffelke and Hewitt 2007). Invaders that modify the substrate may exclude macroalgae or may expand their distribution (e.g., physically: Bertness 1984; chemically: Hecky et al. 2004). When invaders create substrate, they usually increase macroalgal biomass growing on them (e.g., bivalves, Gutierrez et al. 2003, Sousa et al. 2009). Understanding the intensity and direction of changes in macroalgal biomass due to invasion is important because several processes that structure natural communities and that are mediated by macroalgae may change. For example, the carbon fixation cycle and nutrient removal (Duarte and Cebrian 1996; Kamer et al. 2004) and the energy and biomass flux from basal levels to the trophic web (Riera and Hubas 2003; Hadwen and Arthington 2007). Changes in macroalgal biomass may also affect habitat availability to invertebrates (e.g., Wilson et al. 1990; Moreno 1995), to fishes (e.g., Laegdsgaard and Johnson 2001; Adams et al. 2004) and to other algae (Amsler et al. 1992).

The polychaete *Ficopomatus enigmaticus* Fauvel 1923, an invasive ecosystem engineering species, can potentially change the forms of primary production (see Crooks 2002), for example, by affecting macroalgae. This reef-forming species has been reported in estuaries of the eastern South Atlantic since the mid-19th century (Brankevich et al. 1988; Obenat and Pezzani 1994; Borthagaray et al. 2006). In its primary area of invasion, the Mar Chiquita coastal lagoon (37° 32' S, Argentina), it forms reef structures having a mean density of about 100 reefs ha⁻¹ (Schwindt et al.

2001, 2004a). Reefs may be up to 7 m in diameter and 0.5 m in height (Obenat and Pezzani 1994; Schwindt et al. 2001). Adjacent reefs can merge to form irregular platforms (Obenat and Pezzani 1994), but some areas are not occupied (Schwindt et al. 2001). Reefs produce a suite of positive and negative effects. They alter physical processes by increasing sedimentation rates, changing the bottom structure and decreasing the lagoon mean depth (Schwindt et al. 2004b).

Creation of reefs also has ecological effects. Reef structure is used as resting and feeding areas by birds (Bruschetti et al. 2009) thus increasing habitat for local and migratory species. The crab *Cyrtograpsus angulatus* Dana 1851 (Schwindt et al. 2001; Méndez Casariego et al. 2004) also uses reefs as a refuge and the local increase in crab density reduces the abundance of crab prey (Schwindt et al. 2001). Moreover, the filtering activity of the individuals generates a strong top-down control on phytoplankton (Bruschetti et al. 2008). In addition, the surfaces provide a hard substrate for macroalgae. Macroalgae grow on hard substrates as rocks, valves (Higgins et al. 2008) and living organisms (e.g., Firstater et al. 2008). Filamentous macroalgae turf grows on bivalve shells and on reefs in the lagoon (M.C. Bazterrica pers. obs.). As a newly available substrate, reefs may have a direct positive effect on macroalgal development. However, the increased sedimentation rate between reefs (Schwindt et al. 2004b) and the increased abundance of consumers (Schwindt et al. 2001) might also affect macroalgal biomass.

Given this background, the purpose of this study was to investigate changes in macroalgal biomass and distribution due to (1) reefs as substrate for macroalgae development, and (2) reefs as structures that modify the surrounding bottom. We hypothesize that *Ficopomatus enigmaticus* reefs have both direct and indirect effects on macroalgal biomass. They have a direct increase resulting from increased substrate and an indirect decrease resulting from the burial of bivalve shells by sediment and consumption by grazers that live under the reefs.

Methods

Study site

The study was performed at the SW Atlantic Argentinean Mar Chiquita Coastal Lagoon (37° 40'S, 57°

23°W), a UNESCO Man and the Biosphere Reserve. This body of brackish water (46 km²) is connected permanently to the sea. It has a wide salinity range (2–35 PSU; Schwindt et al. 2004a) and is affected by low amplitude tides (≤ 1 m) that decrease towards the main body of the lagoon (Isla 1997). The lagoon receives sediment and water from creeks and from artificial channels (Fasano et al. 1982). *Ficopomatus enigmaticus* reefs are found throughout the lagoon at varying densities and are more abundant toward the center (Fig. 1; Schwindt et al. 2004a). Experiments and observations were carried out in the lower intertidal zone of the central part of the lagoon at San Gabriel, approximately 6 km inland from the lagoon inlet (Fig. 1).

Patterns of macroalgal distribution on reef surfaces, in sediment between reefs and in sediment in areas lacking reefs

The low intertidal area in the Mar Chiquita lagoon is largely invaded by reefs (see Schwindt et al. 2004b).

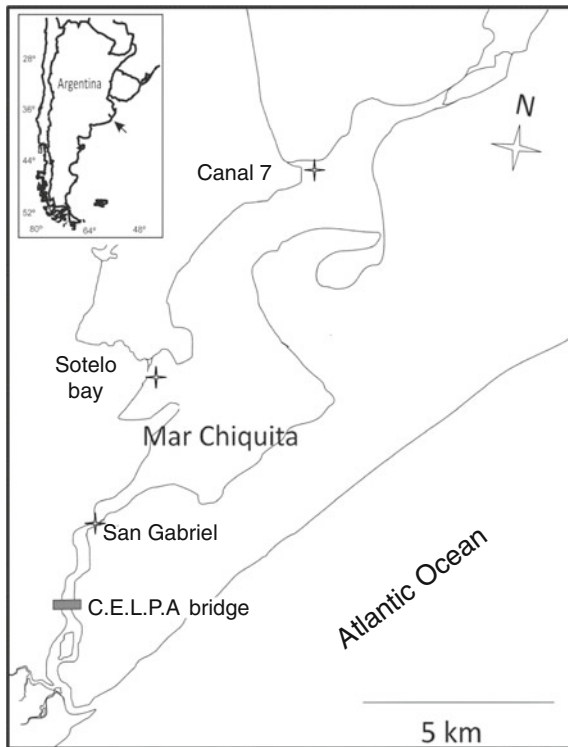


Fig. 1 Map of the Mar Chiquita coastal lagoon showing main channels and fishing sites. Reefs are present between C.E.L.P.A and Canal 7; most experiments were done in San Gabriel

However we identified an area (around 10 ha) not occupied by reefs with similar characteristic to the invaded areas in sediment type, tidal height and current flow. Although it is unknown why this area is devoid of reefs, we use this area as the best approximation to understand how macroalgae assemblages behave in the absence of reefs (hereafter “nonreef sediment”). For comparison, approximately 100 m away was an area of high density of reefs, in which we considered for analysis the surface of the reefs (hereafter “reef surface”) and sediment between reefs (hereafter “reef sediment”). We sampled macroalgal biomass (dry kg m⁻²) monthly from December 2005 to March 2008 in the three habitat types. Mean macroalgal biomass was estimated by taking core samples (area = 0.0075 m²) from the 1st cm of the reef or sediment. All samples were taken at the same tidal level, parallel to the coastline along a distance of 2 km. All macroalgae collected were manually cleaned, separated by species, dried at 60°C for 5 days and weighed to the nearest 0.0001 g. To compare macroalgal species composition across reef surface, reef sediment, and nonreef sediment areas, we used one-way ANOSIM analysis (Clarke and Warwick 2001). This analysis examined differences in macroalgal species biomass composition in terms of similarity matrices that were based on Bray-Curtis similarity statistics. These statistics were generated using the PRIMER (Version 5.2.2) statistical package for each year of sampling.

Monthly macroalgal biomass variation of the red alga *Polysiphonia subtilissima* Montagne 1840 and of green algae (*Cladophora* sp. and *Enteromorpha subtilissima* Linnaeus 1753) in areas in which each macroalgal group was well represented were also evaluated with one-way ANOVAs (Zar 1999) during both years: December 2005 to December 2006 (hereafter 2006) and December 2006 to December 2007 (hereafter 2007). We also estimated the contribution of reef surface, reef sediment and nonreef sediment to the total biomass production of the lagoon. To calculate this contribution, we first estimated the proportions of areas with and without reefs using satellite images (Google Earth Base Imagery; definition ~ 2.5 m) from randomly sampled quadrats (≈ 1 ha) from C.E.L.P.A to Canal 7 (Fig. 1). We used sampling quadrats that permitted the clear and unambiguous recognition of flat soft sediment and bottom with reefs (low tide; $n = 68$). We discarded all unclear images. This method may underestimate the area occupied by

reefs. Such underestimation should be considered when interpreting the data. Using previous estimates of the abundance and size of the reefs (Schwindt et al. 2001, 2004a), we then calculated the proportion of estimated reef area occupied by reef surface and the proportion occupied by reef sediment. We used Monte Carlo analysis to perform iterative recalculation ($n = 1,000 \text{ month}^{-1}$; 28 months) of the monthly biomass for each macroalgal species relative to the area of each substrate type in the lagoon. To carry out these calculations, we used the equation:

$$\text{Macroalgal species biomass} = (\text{biomass on reef surface} \times \text{reef surface area}) + (\text{biomass on sediment between reefs} \times \text{reef sediment surface area}) + (\text{biomass on non-reef sediment} \times \text{nonreef area}).$$

We calculated the monthly contribution by each macroalgal species to total biomass production and the mean annual biomass production for two cases: the environment with reefs and the hypothetical case in which no invasive events occurred and reefs were therefore absent.

Effects of the type and availability of hard substrate on macroalgal distribution

Ficopomatus enigmaticus tubes generated novel hard substrate within the lagoon, whereas the only available hard substrates in areas without reefs were empty shells of the bivalves *Maetra isabelleana* d'Orbigny 1846 and *Tagelus plebeius* Lingfoot 1785. We hypothesized that macroalgal distribution was influenced by its substrate preference. We designed a 2-factor experiment manipulating substrate type (*F. enigmaticus* tubes vs. bivalve shells) in two areas (reef vs. nonreef sediment), carried out during October and November 2007 ($n = 20$). Valves of *M. isabelleana* and *T. plebeius* without algae were randomly collected in the field in their natural relative abundances. To be supported on the sediment, valves were glued with epoxy putty on a grid square plastic base ($5 \times 5 \text{ cm}$) to prevent loss and burial. One valve was placed on each plastic base. Pieces of living reefs, without macroalgae, were cored (10 cm diameter, 10 cm depth) and glued with epoxy putty on the plastic bases described above. Plastic bases were anchored to the sediment with wire stakes. The experimental units were placed in the sediment at a distance greater than 0.5 m from any other experimental unit and from any reef in the case of areas with reefs. After 45 days, the

percent cover of macroalgae on the area of each experimental unit was calculated from digital pictures using an image analyzer (ImageJ 1.34). For *Polysiphonia subtilissima* and green macroalgae, we tested the hypothesis that mean percent cover did not differ between reefs and valves placed in reef and nonreef areas with a two-way ANOVA on range data (robust ANOVA to the lack of homogeneity of variances; Quinn and Keough 2002).

Valves and reefs differ in their structural complexity, whereas chemical composition is similar, as both are primarily calcium carbonate (Dame 1996; Vinn et al. 2008). To assess possible macroalgal preferences for reef structural characteristics, we manipulated reef structure. We transplanted cylindrical reef sections without macroalgae as detailed above. We used two treatments: high-complexity reef surface ("rugged") and low-complexity reef surface ("smooth"). The high-complexity treatment consisted of unmanipulated reef pieces (collected as described before) that preserved the structure formed by the tubes. The low-complexity treatments were similar pieces of reefs, with the top 4 cm of tubes cut off. The remaining material consisted of the inner part of the reef, where old dead tubes are compacted and generate a smooth surface lacking the original 3-dimensional structure. Like the rugged treatment, smooth pieces were 10 cm in diameter. Replicates of each treatment were transplanted at random to reef sediment areas and to nonreef sediment areas ($n = 18$) in October 2008. After 50 days, we evaluated the percent cover of macroalgae using digital photography as described above. We tested the hypothesis that the mean percent cover of algae did not differ between rugged and smooth reef surface in areas with reefs and nonreef areas with a two-way ANOVA (Zar 1999).

Effects of substrate availability

Reef surfaces clearly differ in availability between reef and nonreef areas, and bivalve shells, which provide the other major type of hard substrate in the lagoon, may also vary in density across habitats. To evaluate valve density, we counted the number of valves in randomly selected $40 \times 40 \text{ cm}$ plots of both types of habitat ($n = 45$) in December 2007. We tested the hypothesis that the mean number of available hard substrate items did not differ between areas using the Welch (tc) test (t test corrected for unequal variances;

Zar 1999). To evaluate colonization of valves, we determined the percentage of valves bearing macroalgae in both areas ($n = 200$ in reef sediment, $n = 430$ in nonreef sediment) in January 2008.

To assess macroalgal response to the availability of hard substrate, we collected bivalve shells without macroalgae as was described above. We then placed the valves in the sediment of areas with reefs at two distances from the reefs ("near" = 5 cm, "far" = 50 cm, $n = 18$) during January 2008. This design recognized that sedimentation rate varies slightly as a function of distance from the reef (see Schwindt et al. 2004b). Valves were placed on the sediment using plastic bases as was described above. The same procedure was followed in nonreef sediment in order to furnish a control. After 45 days, we recorded the percent cover of macroalgae on valves. Given that green algae only grew in nonreef sediment and given that red alga only grew in reef sediment, we solely compared differences in the red alga percent cover between the valves placed near and far from the reefs. To account for non-normal data, we used a Mann–Whitney U test (Conover 1999).

To assess macroalgal response to conditions within reef and nonreef areas, we transplanted shells containing macroalgae and recorded thallus size and survival. In February 2008, we randomly selected bivalve shells (*Macra isabelleana* and *Tagelus plebeius* in natural relative abundances) bearing macroalgae and placed them on reef and nonreef sediment ($n = 60$). Valves were attached to plastic bases and anchored to the sediment. After 4 days, we scored as living those algae having green thallus, and we scored as dead those algae having colorless thallus or absent. The proportions of living and dead macroalgae on the valves were compared for both areas using a Chi-squared test (Conover 1999). In a similar experiment ($n = 20$ valves) in February 2008, we assessed percent reduction of thallus size across habitats. To do so, we measured thallus size (cm) initially and at 1 and 4 days, with thallus loss calculated as the change in size. Thallus size was assessed using digital photography and estimated as the maximum thallus dimension exhibited by the macroalgal mats on each valve. We compared differences between reef and nonreef areas in the percent of thallus reduction on the 1 and 4 day (tc test).

We evaluated sediment deposition in areas with and without reefs. We used plastic sedimentation platforms (10 cm diameter, 0.1 mm raised edge; $n = 5$ per

treatment) placed on sediment in reef (but at least 0.5 m from any reef) and nonreef areas. The low platforms facilitated collection of vertically deposited sediment. Platforms were placed and collected at low tide and then dried in the sun. Sediment was collected by surface scraping and then oven dried (70°C for 3 days) and weighed (precision 0.0001 g). The study was performed on 3 different days (January 5, 12 and 22, 2010). Because we found no differences among days, we combined the data for all days and compared sedimentation amounts (g m^{-2}) between areas (tc test).

Reefs augment the abundance of the herbivorous crab *Cyrtograpsus angulatus* (Schwindt et al. 2001). We investigated possible consumer effects on macroalgal development by means of a two factors experiment. In February 2008, we transplanted valves with macroalgae to reef and nonreef sediment and in each established three treatments ($n = 10$): exclusion, control, and no cage. Exclusion was achieved by using transparent plastic jars (0.12 m in diameter 0.13 m high). The sides of the plastic jars were replaced with a plastic net (mesh size = 2 mm) to allow water flow. Experimental controls were contained in transparent plastic jars open at the side. Biological controls were valves bearing macroalgae without jars. Bivalve shells were randomly collected, and initial thallus size was measured using digital photography as was described above. Shells were attached to plastic bases, assigned at random to treatments, and collected after 4 days as described above. For each experimental unit, we recorded the relative amount (percent) of thallus remaining as final thallus length (at 4 day) $\times 100/\text{initial thallus length}$. We tested for differences in the percentage of remaining thallus across treatments and across sites with a two-way ANOVA on ln transformed data to meet assumptions (Zar 1999).

Results

Patterns of macroalgal distribution on reef surfaces, in sediment between reefs and in sediment in areas lacking reefs

Our results show that different macroalgal species occurred in different areas. The red macroalga *Polysiphonia subtilissima* inhabited the reef surface while the green macroalgae (*Cladophora* sp. and *Enteromorpha*

intestinalis) inhabited the bivalve shells that are on the soft sediment in areas without reefs. Macroalgae were absent from the sediment between reefs. Macroalgal species biomass differed across areas (two-way ANOSIM; 2006: $R = 0.58$; 2007: $R = 0.56$; 2008: $R = 0.69$; $P < 0.05$). *P. subtilissima* (reef surface) and *Cladophora* sp. (nonreef sediment) were typical and characteristic macroalgae in their respective habitats (Fig. 2a, b). Macroalgae were rare and usually absent from reef sediments where they were present only in a few samples and in very low abundance (Fig. 3). *P. subtilissima* exhibited differences between months (2006: ANOVA, $F_{9; 193} = 5.63$, $P < 0.05$; 2007: ANOVA, $F_{11; 228} = 14.41$, $P < 0.05$). Growth

occurred primarily during summer (Tukey HSD tests, $P < 0.05$, both years; Fig. 2a). *Cladophora* sp. (2006: ANOVA, $F_{10; 100} = 5.22$, $P < 0.05$; 2007 ANOVA, $F_{10; 98} = 3.56$, $P < 0.05$) and *E. intestinalis* (2006: ANOVA, $F_{10; 100} = 2.08$, $P < 0.05$; 2007: ANOVA, $F_{11; 108} = 3.75$, $P < 0.05$) did not show any monthly pattern with different peaks along the months (Tukey HSD tests, $P < 0.05$; Fig. 2b). For the sampled areas (intertidal zone from C.E.L.P.A to Canal 7; Fig. 1), we estimated that nonreef sediment comprised 48.75% (SE = 5.40) of the lagoon bottom. Reefs occupied the remaining 51.25% (SE = 5.39) of the bottom. Within these areas, reef surfaces comprised 14.09% (SE = 1.48). Reef sediment accounted for the remaining

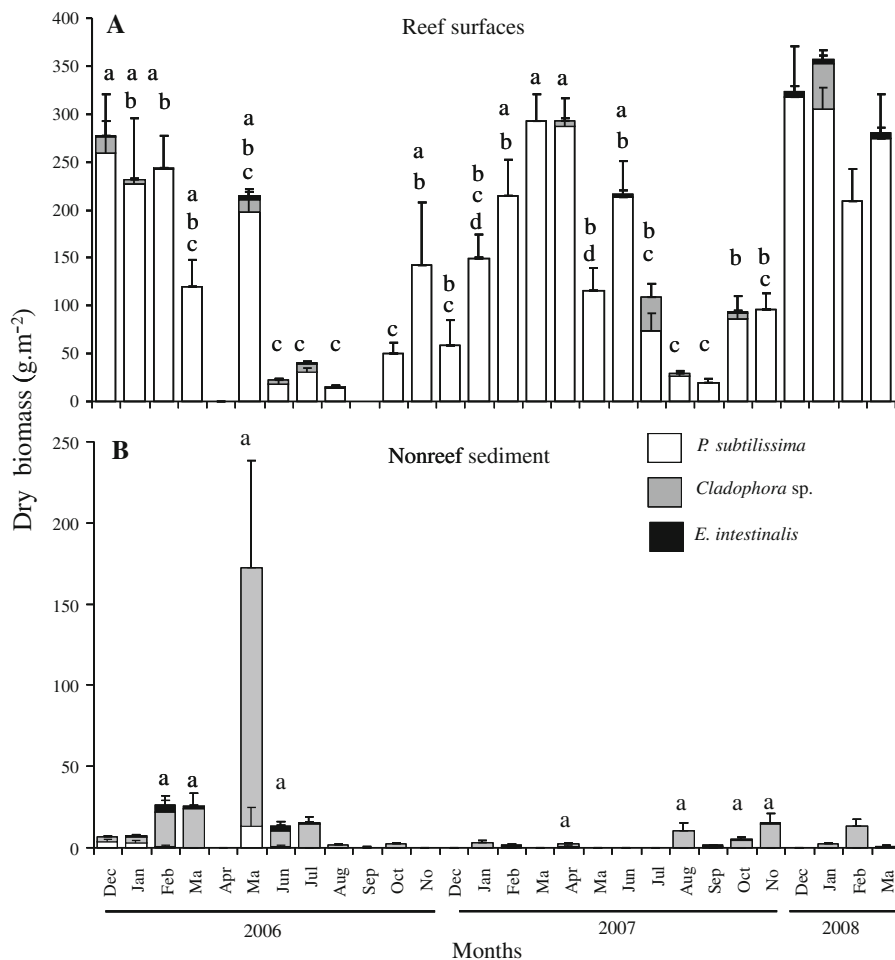
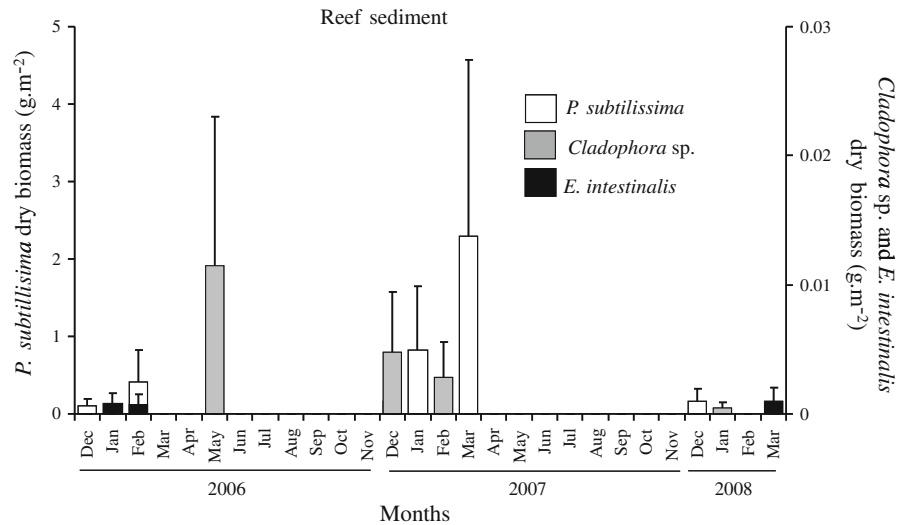


Fig. 2 *Polysiphonia subtilissima*, *Cladophora* sp. and *Enteromorpha intestinalis* monthly dry biomass on **a** “reef surface” and **b** “nonreef sediment” during the years sampled. Here and in Fig. 3 and 4, stacked columns compare the contribution of each species to the total across categories; every segment shows the

mean and 95 confidence interval of each dependent variable. Letters group months within each year when abundance was not statistically different (Tukey HSD $P > 0.05$). Letter **a** indicates the homogenous group with biggest biomass values; then, **b**, **c**, **d**, the following groups in decreasing mean biomass order

Fig. 3 *Polysiphonia subtilissima*, *Cladophora* sp. and *Enteromorpha intestinalis* monthly dry biomass on the “reef sediment” during the years sampled. *P. subtilissima* (red macroalga) appears on the left Y axis, while *Cladophora* sp. and *E. intestinalis* (green macroalgae) appear on the right Y axis due to the different magnitude order of the dry biomass measured in each macroalgae group



37.16% (SE = 3.91). We estimated that *P. subtilissima* accounted for almost 80% of total macroalgal biomass production at these sites (Fig. 4a). The results shown in Fig. 4b indicate what would happen in the hypothetical case of no reef invasion; there would be little red macroalga, and thus green macroalgae would be responsible for most of the biomass production.

Effects of the type and availability of hard substrate on macroalgal distribution

Polysiphonia subtilissima grew to higher cover on pieces of *Ficopomatus enigmaticus* reef than on bivalve shells, with no differences between reef and nonreef area and no interaction (two-way ANOVA on range transformed data, treatment: $F_{1, 73} = 80.19$, $P < 0.05$; area: $F_{1, 73} = 2.31$, $P > 0.05$; treatment \times area: $F_{1, 73} = 0.07$, $P > 0.05$; Fig. 5a). Green macroalgae had higher cover in nonreef than reef sediment (two-way ANOVA on range transformed data, area: $F_{1, 73} = 56.28$, $P < 0.05$; Fig. 5b), although cover was always low. Green macroalgal cover did not differ between substrate types or the area \times substrate interaction (two-way ANOVA on range transformed data, treatment: $F_{1, 73} = 0.01$, $P > 0.05$; area \times treatment: $F_{1, 73} = 1.63$, $P > 0.05$; Fig. 5b).

When reef surfaces were varied to furnish both high and low complexity, the red alga responded positively to the rough reef surfaces in both areas and grew more readily on the unmanipulated reef pieces than on the smooth inner reef material (two-way ANOVA, area \times treatment: $F_{1, 57} = 2.58$, $P > 0.05$; area:

$F_{1, 57} = 3.34$, $P > 0.05$; treatment: $F_{2, 57} = 26.32$, $P < 0.05$; Fig. 6).

Effects of substrate availability

The mean density of clam shells was smaller in reef sediment (24 valves m^{-2} , SE = 4) than in nonreef sediment (348 valves m^{-2} , SE = 22; tc test on square root transformed data, $tc_{38} = -16.42$, $P < 0.05$). Valves examined in situ had no macroalgae when were found in reef sediment but 70% had green macroalgae in nonreef sediment. In the experiment in which valves were transplanted into reef and nonreef sediment, green macroalgae grew only in nonreef sediment (mean cover = 17.92%, SE = 9.18). *Polysiphonia subtilissima* did not appear on valves in nonreefs areas, but occurred at low cover on valves placed in reef sediment, with no differences based on proximity to reefs ($U = 133.5$, $P > 0.05$; mean % cover: near = 0.5, SE = 0.33; far = 1.94, SE = 0.92).

Macroalgal survival on transplanted valves was very low on reef sediment relative to nonreef sediment ($\chi^2_1 = 84.18$, $P < 0.05$). The percent reduction of maximum thallus size in 1 and 4 days was greater on reef sediment than on nonreef sediment (tc tests for percent of thallus reduction between areas: 1 day after, $tc_{76} = -7.9$, $P < 0.05$; 4 days after, $tc_{76} = -9.73$, $P < 0.05$; Fig. 7). The amount of sediment deposited in reef sediment was higher (197.53 $g m^{-2}$, SE = 19.15) than in nonreef sediment (37.92 $g m^{-2}$, SE = 4.81; tc test on ln transformed data, $tc_{28} = -10.86$, $P < 0.05$). In the exclusion experiment, the

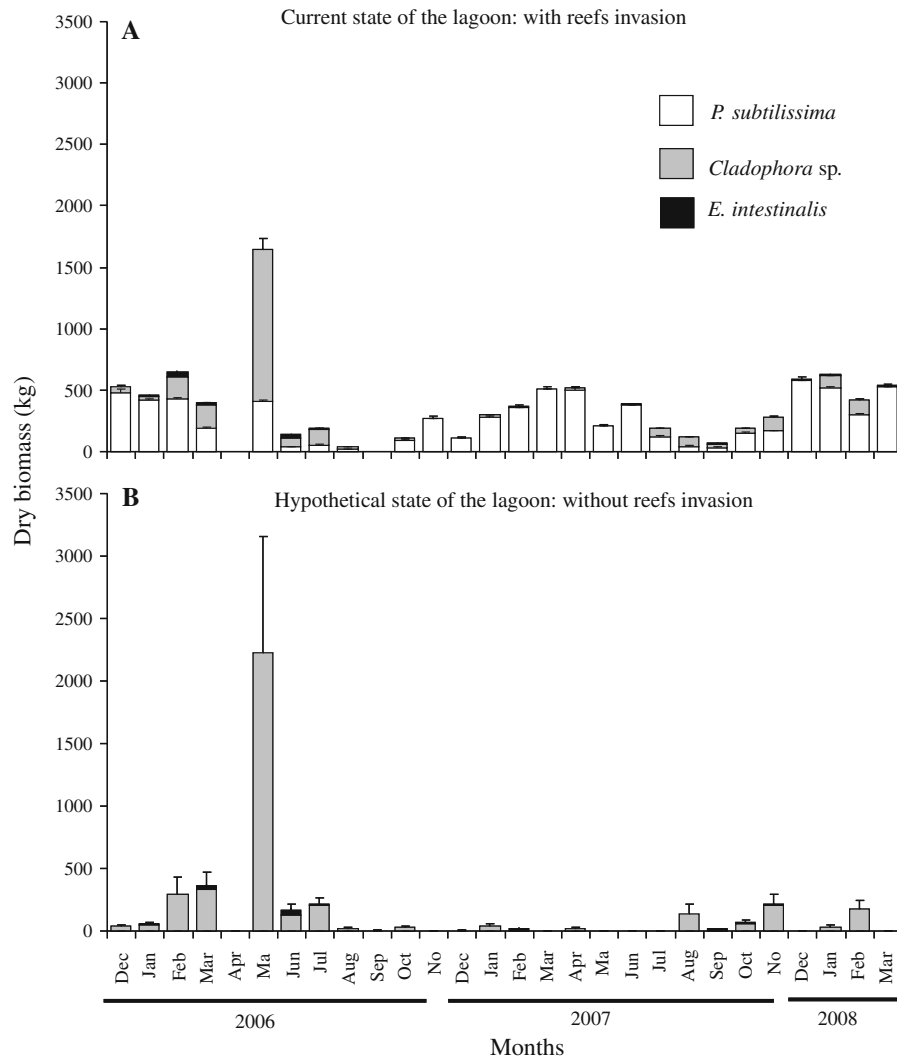


Fig. 4 *Polysiphonia subtilissima*, *Cladophora* sp. and *Enteromorpha intestinalis* monthly dry biomass estimated: **a** for the years sampled in relation to the proportion in which every area

(“reef surface”, “reef sediment” and “nonreef sediment”) is represented in the coastal lagoon and **b** for the hypothetical state without reefs

area \times treatment interaction showed that the percent of thallus remaining was smaller in control and control cages only in reef sediment (two-way ANOVA on ln transformed data, area \times treatment: $F_{2,54} = 4.66$, $P < 0.05$; area: $F_{1,54} = 13.43$, $P < 0.05$; treatment: $F_{2,54} = 3.94$, $P < 0.05$; Fig. 8).

Discussion

Green macroalgae (*Cladophora* sp. and *Enteromorpha intestinalis*) inhabited soft sediment in areas without

reefs and attained their highest biomass during different months across the study period. *Ficopomatus enigmaticus* reefs directly enhanced the biomass of the red macroalga *Polysiphonia subtilissima*. Reefs had an indirect effect on green macroalgae, which are excluded from the sediment between reefs. In this habitat, some red alga developed on reef fragments and on the few available valves.

Substrate type can regulate macroalgal development (Bertness 1984; Vadas et al. 1991; Fletcher and Callow 1992; Abelson and Denny 1997) and general condition (Piazzi et al. 2001). Substrate characteristics could be

responsible for the conspicuous association between red macroalgae and reefs. The specific mechanisms linking higher structural heterogeneity of reef surfaces to red macroalgal distribution could involve particular features of sexual reproduction in *P. subtilissima* (Vadas et al. 1991). These considerations seem particularly important in algae with non-motile spores such as Rhodophyta (Clayton 1992). For example, the three-dimensional structure of *Ficopomatus enigmaticus* tubes could reduce water velocity (see Abelson and Denny 1997) and may increase fertilization probability by a decrease in gamete dilution and a corresponding increase in male gamete retention around female fronds (Brawley and Johnson 1992). Substrate colonization could increase when large red algal spores and fertile

fragments of broken thallus are trapped between reef tubes (Fletcher and Callow 1992). Also, reduced water motion could decrease detachment and thallus damage. Structural complexity can improve settlement, attachment and survival of propagules, with mechanisms that include refuge from grazers, and decreased desiccation at low tide (Vadas et al. 1991). Although no specific

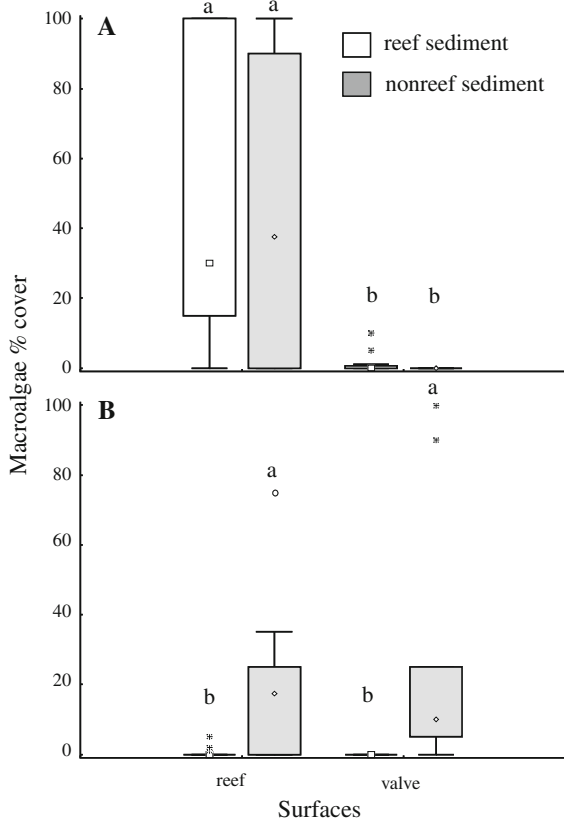


Fig. 5 **a** Red macroalgae and **b** green macroalgae recruitment as percent cover on initially bare surfaces of high complexity (reefs) and low complexity (valves) in “nonreef sediment” and in “reef sediment”. Here and after, central markers indicate the median; *box* indicates 25, 75% percentiles; *whiskers* indicate non-outlier Min and Max; *circles* indicate outliers; *asterisks* indicate extremes. *Different letters* show differences between substrate types for red macroalgae, and between sites for green macroalgae (Tukey HSD test, $P < 0.05$)

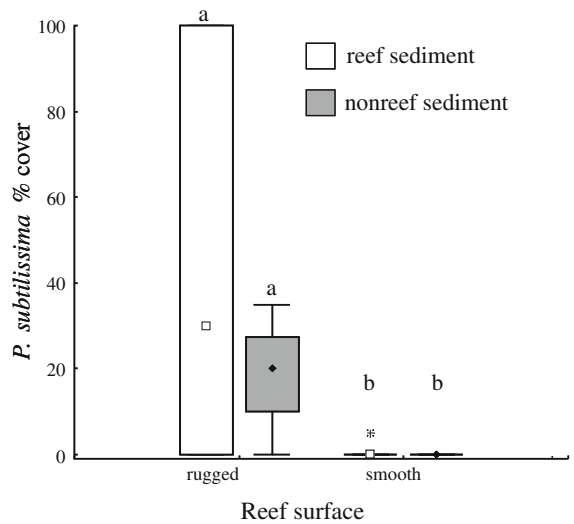


Fig. 6 *Polysiphonia subtilissima* percent cover on rugged and experimental smooth reef surfaces in sediment with and without reefs. *Different letters* show differences between substrate types in each area (Tukey HSD test, $P < 0.05$)

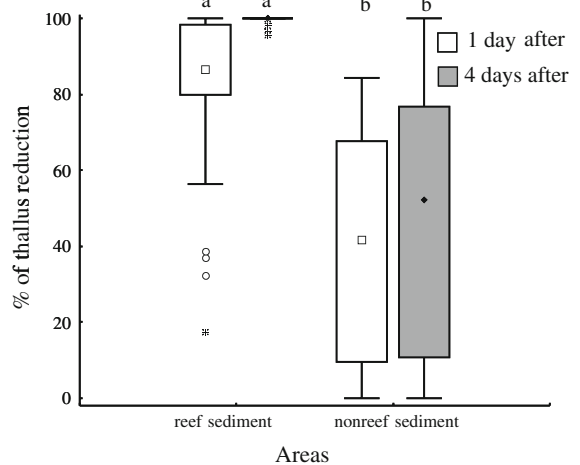


Fig. 7 Percent of thallus size reduction 1 and 4 days after the valves were transplanted in “reef sediment” and “nonreef sediment”. *Different letters* show differences (tc test, $P < 0.05$) between areas 1 and 4 days after the experiment started

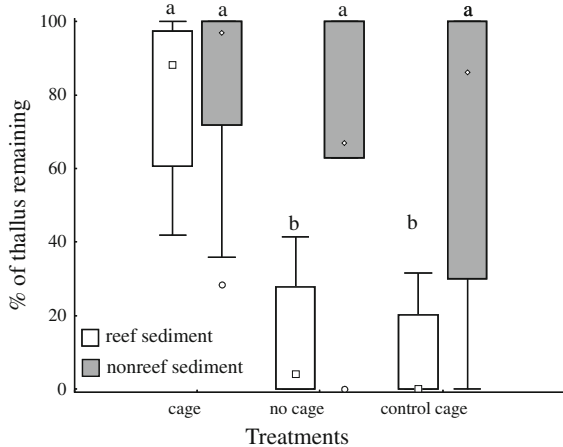


Fig. 8 Percent of remaining thallus at 4 day across exclusion treatments in “reef sediment” and “nonreef sediment”. Different letters indicate differences between treatments (Tukey HSD test, $P < 0.05$)

mechanisms were investigated in this study, our results show that reefs furnish a favorable substrate, especially for red macroalga. Despite the increase of possible consumers inhabiting the reefs (Schwindt et al. 2001; Heiman and Micheli 2010), the overall effect on red alga is positive, particularly in the season of greatest abundance.

Green macroalgae mainly occur in sediments where reefs are absent. However, we found that macroalgae, including red macroalga, did not occur in the sediment between reefs. This absence may be due to enhanced consumer abundance on *Ficopomatus enigmaticus* reefs, for instance, the herbivorous crab *Cyrtograpsus angulatus* (Schwindt et al. 2001). However, sedimentation rate might be an additional important factor (Schwindt et al. 2004b). The reduction of shell availability in areas with reefs does not explain the absence of macroalgae since we found no green macroalgal development or survival on experimentally transplanted valves. Indeed, macroalgal survival was extremely low (<2 days). Our experimental study excluding consumers indicates that consumer pressure is stronger in reef habitats than in areas without reefs. Moreover, other factors, possibly sedimentation, negatively affect macroalgae growing near reefs. It is well known that consumers (Lubchenco and Gaines 1981; Vadas et al. 1991) and sediment dynamics may influence benthic macroalgal distribution patterns (Chapman and Fletcher 2002). Our results suggest that in areas with reefs both, consumption and

sedimentation, limit the development of macroalgae. Their relative importance may differ across life history stages. Before spores settle, high sedimentation could reduce substrate availability, spore attachment and germination (*sensu* Vadas et al. 1991). After spores settle, plants are subject to grazing, and high sedimentation may cover plants and/or inflict mechanical damage on thallus (*sensu* Piazzini et al. 2001).

These changes in macroalgal biomass and distribution alter the relative contribution of each macroalgal species to the overall biomass of macroalgae in the lagoon. The total system production estimated for an environment without reefs was in general lower than that estimated for the actual situation. However, calculations of system productivity without reefs must be viewed with caution. The actual state of the lagoon without reefs is not known. In particular, we lack information on (1) the availability of shells or other hard substrate to settling spores, (2) nutrient concentration or turbidity of the water column, currently regulated by *Ficopomatus enigmaticus* (Bruschetti et al. 2008) and (3) the abundance of consumers and the pressures they would exert on the resources they consume. Ecological consequences of the observed changes on the abundances of the different macroalgal groups must also be taken into account. *Cladophora* sp. and *Polysiphonia subtilissima* are morphologically similar (lightly corticated and delicately branched) hence display similar productivities (Littler and Arnold 1982). However, macroalgae productivity is affected by macroalgal assemblage richness and by biomass accumulation (Bruno et al. 2005). *Enteromorpha intestinalis* is in the most productive morphological group (thin tubular structure, Littler and Arnold 1982) but is generally less abundant than *Cladophora* sp. In all likelihood, it would not increase the overall productivity of the green macroalgae significantly. Nevertheless, changes in species composition from green to red macroalga may represent a decrease in food quality (Montgomery and Gerking 1980). The resulting changes in abundance of preferred foods and in their availability to herbivores could then cascade through the entire trophic web. Such cascade effects are not always buffered (Strong 1992). Finally, green algae appear on the reefs only when they peak in biomass. When they are present they grow between red macroalga. This pattern suggests that additional factors could regulate the development of green algae. For example, weather

events could produce blooms of green macroalgae. Rains enhance nutrient inputs from surrounding fields (Marcovecchio et al. 2006) that could be correlated with the peaks of green macroalgal growth (e.g., McClelland and Valiela 1998).

Our results also exemplify certain processes that mediate ecosystem engineer invasions and that should be taken into account in their interpretation. For example, as the response of red macroalga to reef surface characteristics demonstrates, the impact of habitat alteration on native communities (see Crooks 1998) is modulated by the particular susceptibility and response capability of the local species (Crooks 2002). Engineering also has negative indirect effects. An example of such negative indirect effects is our finding that reefs produce both abiotic (sedimentation) and biotic (consumer) changes (*sensu* Jones et al. 1994). These processes are especially evident in the habitat we studied, in which reefs represent discrete units with abundant red alga that are surrounded by sediment without macroalgae and can be compared informatively with areas that lack reefs but support abundant green macroalgae. The invasion of *Ficopomatus enigmaticus* in Mar Chiquita coastal lagoon has global relevance. This species is invading many additional sites worldwide (North America: Cohen and Carlton 1995; Europe: Thorp 1994; Bianchi and Morri 1996; Fornós et al. 1997; Bianchi and Morri 2001; Africa: Davies et al. 1989; Asia: Kazanci et al. 2003; and Oceania: Read and Gordon 1991). At least in the SW Atlantic region (Brankevich et al. 1988; Borthagaray et al. 2006), this invasive reef builder may produce changes similar to those described here. Knowledge of the mechanisms by which this invasive engineer species exerts both positive and negative effects on macroalgae is important. Such knowledge may make it possible to predict net effects on primary production. Moreover, changes in macroalgal species composition may have cascading effects on the food web. *F. enigmaticus* exerts top down control through its effects on plankton grazing (Bruschetti et al. 2008) and our results suggest that it further produces bottom up control by changing the trophic subsidies of macroalgal production.

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