



Effect of biodeposition of an invasive polychaete on organic matter content and productivity of the sediment in a coastal lagoon

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ABSTRACT

The reef-forming polychaete *Ficopomatus enigmaticus* is the main benthic suspension-feeding species of the Mar Chiquita lagoon (37° 40' S, 57° 23' W; Argentina) and exerts a strong top-down control on phytoplankton biomass. A large portion of the ingested material is rejected as faeces, and a fraction of the material filtered is packed and discarded as pseudofaeces, which could be deposited on the sediment or horizontally displaced by water flow. In this work we evaluate the effect of this biodeposition on the organic matter (OM) content and productivity of the sediment between reefs. Laboratory experiments show that the OM from biodeposition was 21 times higher than the sediment between reefs and with low C per mg matter/N per mg matter. Sediment traps underneath live reefs showed higher OM content compared to traps underneath dead reefs but only in areas with low water currents, suggesting the importance of hydrodynamic conditions for this process. *In situ* mesocosms showed that *F. enigmaticus* decreased up to 45% the phytoplankton biomass, up to 50% the turbidity and up to 20% the particulate OM of the water column and, consequently enhanced up to 50% the OM deposited on the bottom. But there were no differences in the OM of sediment with increased distance from the reefs. Sediment gross primary production was lower in the sediment closer to reefs, but when adults of the high-density local crab that live underneath reefs were excluded, the productivity increased, suggesting that the activity of the crabs could be counteracting the reef effect on sediment. In summary, biodeposits of *F. enigmaticus* can enrich the sediment, but crab activity and water currents can disperse the suspended and/or deposited material, decreasing the OM content of sediment close to the reefs. However, these effects (suspension feeding and biodeposition) are linked, and could increase flux of particles from water column to the bottom of the lagoon, increasing the benthic–pelagic coupling.

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1. Introduction

Suspension-feeder benthic animals remove large amounts of suspended matter from the water column and are thus often important species in shallow coastal ecosystems (e.g., Alpine and Cloern, 1992; Hily, 1991; Riisgård et al., 2004). Most of the material ingested by suspension-feeding species is rejected as faeces, and a large part of the material filtered is packed and discarded as pseudofaeces. Both fractions end up deposited on the nearby sediment surface, or carried horizontally by the water column (Wotton and Malmqvist, 2001). The faeces and pseudofaeces (hereafter referred to as “biodeposits”) ejected by suspension-feeders are mucus-bound aggregates, and settle down up to 40 times faster than non-aggregated particles from which they are formed (e.g., bivalves: Giles and Pilditch, 2004; Widdows et al., 1998; polychaetes:

Wotton and Malmqvist, 2001; Wotton et al., 1998). Biodeposits of suspension-feeders can be rich in carbon and nitrogen, which may produce a continuous organic enrichment of surrounding sediments (Kautsky and Evans, 1987) providing an energy-rich food source potentially available to benthic organisms (Newell et al., 1982; Zhou et al., 2006). Thus suspension-feeders can mediate the flux of particles and increase of nutrients from the water column to the benthos, increasing the benthic–pelagic coupling (Kautsky and Evans, 1987). Moreover, the enrichment of the sediment with nitrogen and phosphorus may stimulate the growth of micro-phytobenthos (Miller et al., 1996).

Polychaetes and bivalves are major groups of marine fauna that produce biodeposits as a result of their suspension-feeding (see Murray et al., 2002), and are also widely distributed in most environments (estuaries, coastal waters, freshwaters, deep sea; Dame, 1996; Fauchald and Jumars, 1979). Some species of these groups form dense benthic aggregations and are often dominant components of the macrobenthos, both in terms of number of individuals and biomass (e.g., Sabellarids: Dubois et al., 2006; Posey et al., 1984; Serpulids: Schwindt et al., 2001). Effects of biodeposition

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by bivalves on sediment (Cranford et al., 2009; Hartstein and Rowden, 2004; Newell et al., 2002, 2004) and benthic macrofauna assemblage (Hartstein and Rowden, 2004; Levin and Gage, 1998) have been widely studied, but much less is known about polychaetes (but see, Cavallo et al., 2007), although these are very abundant and diverse in estuarine environments.

Ficopomatus enigmaticus is a reef-building polychaete species possibly introduced from Australia (Allen, 1953) that has successfully invaded several estuaries and coastal systems of the world (e.g., USA: Jewett et al., 2005; Italy: Bianchi and Morri, 2001; England: Thorp, 1994; New Zealand: Read and Gordon, 1991; Argentina: Orensanz and Estivariz, 1972; Uruguay: Muniz et al., 2005) however its origin has not been satisfactorily elucidated. It is a fouling species which affects ships and harbor structures and, possibly was introduced in Argentina in the ballast water of ships (Rioja, 1943). *F. enigmaticus* has successfully invaded the SW Atlantic Mar Chiquita lagoon (37° 40' S, 57° 23' W; Argentina) since the 1970s (Orensanz and Estivariz, 1972; Schwindt et al., 2004). They form reefs and have variable sizes reaching more than 7 m of diameter (mean diameter = 2.5 m) and up to 0.5 m in height (Obenat and Pezzani, 1994; Schwindt et al., 2001). The shape of the reefs can differ depending on location, the kind of substratum, the water depth and direction of water flow (Fornós et al., 1997; Obenat, 2002). However, the form most frequently found in Mar Chiquita coastal lagoon is circular (shallow waters), and they grow in the same proportion in all directions, reaching a mean distance between reefs of 4 m in 1999 (Schwindt et al., 2004). Their reef structure adds topographic complexity and high levels of biodiversity compared to soft bottom environments (Schwindt and Iribarne, 2000).

Ficopomatus enigmaticus is the main suspension-feeder in this lagoon and feeds on phytoplankton and suspended particles (Bruschetti et al., 2008). Reefs of *F. enigmaticus* reduce the phytoplankton biomass and water turbidity, and their grazing effect has been postulated as control of primary producers in an estuary of South Africa (Davies et al., 1989) and in South America (Bruschetti et al., 2008). The reefs (up to 370 reefs ha⁻¹; Schwindt et al., 2004) negatively affect overall estuarine primary production and the planktonic and benthic carbon sources to higher trophic levels (Bruschetti et al., 2008). A constant production of faeces and pseudofaeces is generated by their filtering activity and is released on top of the tubes of worms (M. Bruschetti pers. obs.) and deposited on the nearby sediment surface, or carried horizontally by the water. This differs to the faeces and pseudofaeces of the reefs/beds built up by oysters or blue mussels where they are deposited underneath the organisms (see Dame, 1996).

Ficopomatus has generated changes in the bed load sediment transport via modification of flow and the sedimentation patterns (Schwindt et al., 2004), and in the native benthic community structure for the creation of refuges for the macrofauna (e.g., crabs, Luppi and Bas, 2002; Schwindt et al., 2001). For these reasons, *Ficopomatus* is considered as an ecosystem engineer (Schwindt et al., 2001). Large amounts of adult native crabs *Cyrtograpsus angulatus* live underneath the reefs (average 42 ind reef⁻¹, Schwindt et al., 2001), while the individuals showed larger densities than in the nearby open mudflats (<0.5 crab m⁻²; Schwindt and Iribarne, 2000). The crabs feed on benthic micro-algae (Botto et al., 2005; Martinetto et al., 2007) and free-living polychaetes in the adjacent sediment (Schwindt et al., 2001) and, therefore feeding and bioturbation activities can both decrease the organic matter content of the sediment close to the reefs. Thus, *F. enigmaticus* reefs appear to be indirectly affecting the organic matter (OM) and sediment microalgae by providing refuge to the omnivorous crabs.

Consequently, we expected a strong supply of biodeposit production to the benthic organic matter content. Thus, we hypothesize that due to the effect of biodeposition, *F. enigmaticus* enhances the OM content and productivity of the sediment between reefs. Additionally,

we investigate if adults of *C.angulatus* crabs that live under the reefs can modify this possible effect of added OM.

2. Materials and methods

2.1. Study area

The experiments were performed at the brackish portion of the Mar Chiquita coastal lagoon. The lagoon, located along the northern Argentinean Atlantic coast is a body of brackish water (area = 46 km², average depth = 0.6 m; Fasano et al., 1982) affected by a semidiurnal tidal regime (<1 m) and characterized by mud flats and a large surrounding cord grass areas (*Spartina densiflora*; Iribarne et al., 1997). The experiments and samplings were performed during warm southern seasons in two different areas, site A: San Gabriel and site B: Sotelo bay (see Fig. 1). Sotelo is a shallow zone (mean depth = 21 cm; Bortolus et al., 1998) with a lower hydrodynamic exchange. Freshwater influence is more important than that of seawater and its main input is the continental drainage (Lanfredi et al., 1987). In this site, the width of the lagoon is 4370 m. San Gabriel is located close to the lagoon inlet (approx. 6 Km) with high marine influence. The distance of coast to coast is ten times less than Sotelo (approx. 450 m.) and therefore has more intense water currents (40 cm s⁻¹; Lanfredi et al., 1987).

2.2. Organic matter and nutrient content of the biodeposits of *F. enigmaticus*

To evaluate if *F. enigmaticus* can affect the OM content of the sediment we compared the OM of biodeposits and the sediment between reefs. In addition, we also evaluated the total N and total C of the biodeposit. To determine the OM of faeces and pseudofaeces, pieces of reefs (20 × 20 × 20 cm) with live organisms were collected from San Gabriel and transported to the laboratory into buckets (vol = 10 l) with lagoon water during January of 2008. Individual organisms with their tubes (n = 45) were obtained from each reef and placed in 15 test tubes (three polychaetes per tube) of 20 ml during 2 h with water from the lagoon filtered through Whatman GF/C filters. After 2 h, faeces and pseudofaeces of each tube were collected using a Pasteur pipette and placed in 15 filters previously incinerated (550 °C for 4 h). Five filters were then randomly assigned for nutrient content and ten for OM content analyses. The OM of the collected material was calculated by the difference in weight following ashing in a furnace (AFDW; 550 °C for 4 h). The percentages of C and N in biodeposits were evaluated with a mass spectrometer in the Stable Isotope Facility of the University of California Davis. Filters were dried at 70 °C, weighed, and loaded into capsules. Additionally, 10 cores of sediment (diameter = 5 cm, depth = 3 cm) were obtained for analysis of sediment OM content in San Gabriel (Fig. 1). Differences in OM between the biodeposit and sediment samples were evaluated with a *t*-test (Zar, 1999).

2.3. Organic matter in traps of sedimentation

In the field, traps of sedimentation (n = 8) were used to estimate the OM content of biodeposits generated by the reefs of *Ficopomatus*. Because hydrodynamic conditions (e.g. current speed) can determine the extent to which biodeposits modify the sediments (Giles and Pilditch, 2004), the amount of material deposited, the rate of assimilation of the benthos and the degree of the impact (Chamberlain et al., 2001; Hayakawa et al., 2001), the experiments were performed in Sotelo bay (current velocity >10 cm s⁻¹; Isla, 1997) and San Gabriel (current velocity 40 cm s⁻¹ approx; Lanfredi et al., 1987) in an area without reefs during March of 2007 (Fig. 1). The two sites were selected because both have easy access and different hydrodynamic features (current velocities) which allowed to evaluate the proposed hypothesis.

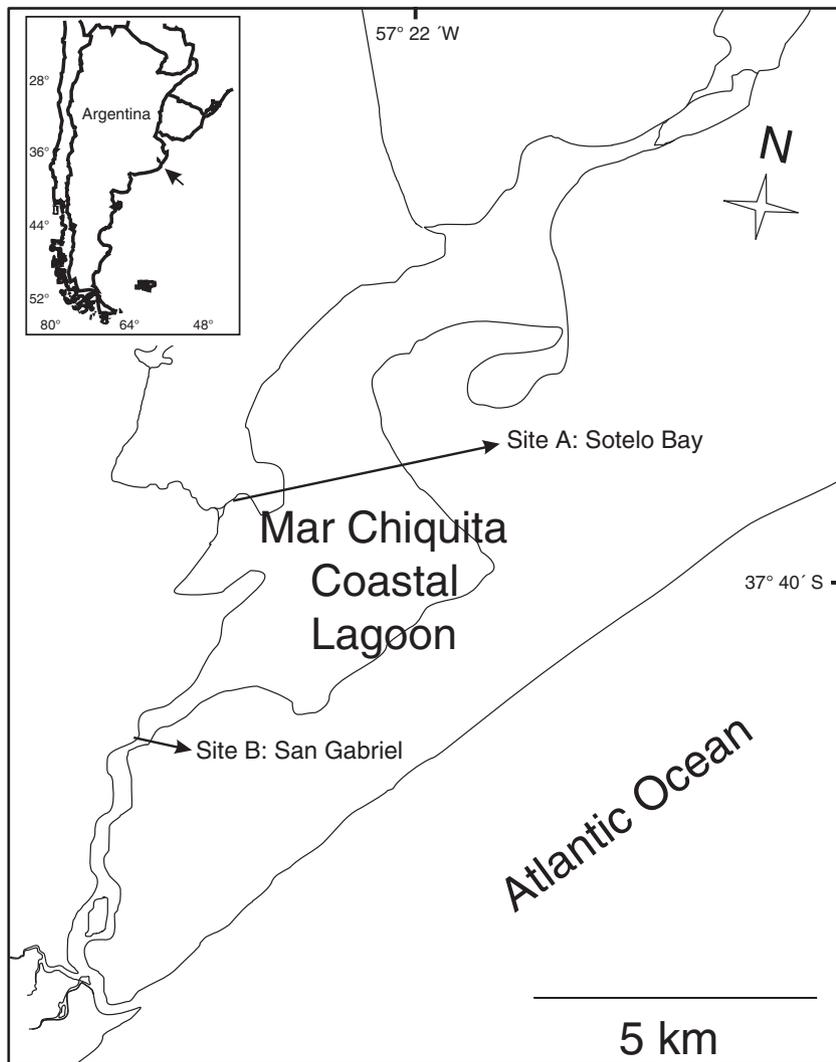


Fig. 1. Map of the Mar Chiquita coastal lagoon showing the sites of study.

Sediment traps consisted of plastic funnels (mouth diameter = 19 cm, depth = 20 cm, $n = 20$; Fig. 2A) located perpendicular to the dominant tidal flow at 15 cm from the sediment surface, where they were attached. In the mouth of each funnel, we placed one core (depth = 10 cm, diameter = 10 cm) of either live ($n = 10$) or dead reef ($n = 10$; used as controls). The treatment consisting of dead reef addressed the effect of the structure on sediment deposition. After 7 days the biodeposition and trapped sediment was transferred to buckets and a sub-sample (100 g) per replicate was collected to determine OM content of the sediment. Differences in sediment OM content between funnels with live and dead reefs were evaluated using a *t*-test (Zar, 1999).

2.4. Organic matter content of sediment between reefs

To determine if there was a relationship between distance from the *F. enigmaticus* reefs and the sediment OM, ten sediment cores (depth = 3 cm, diameter = 5 cm) were collected at four different distances from the edge of the reef during January of 2007. In Mar Chiquita, the mean distance between reefs is 4 m (see Schwindt et al., 2004), thus the maximum distance without overlap between neighboring reefs was 2 m. This distance was divided into 4 sampling sites (0, 50, 100 and 200 cm; following Schwindt and Iribarne, 2000). The sediment OM content was determined using described methods. The reefs were randomly chosen among those between 2.5 and 3 m in

diameter at the San Gabriel site (Fig. 1). Considering that the wind speed and direction can affect the bed-load sediment transport around the reef (Schwindt et al., 2004) and they are very variable in this lagoon, the directions of sampling were randomly chosen.

The null hypothesis of no differences in OM content between distances was evaluated with a one-way ANOVA test (Zar, 1999).

2.5. Mesocosm experiments

To evaluate if the reefs of *F. enigmaticus* increased the OM content of the sediment, *in situ* mesocosm experiments were performed in San Gabriel (Fig. 1) during October of 2009. The experiments consisted of 14 cylindrical plastic buckets with their bottoms (diameter = 20 cm, height = 40 cm, volume = 12 l; Fig. 2B) buried 15 cm into the sediment at the shore of the lagoon. The upper and open end was kept at about 20 cm above the maximum water level in order to avoid mixing of water from inside and outside the bucket. The experimental design consisted of two treatments, with reefs and without reefs, with 7 replicates each and run over 24 h. Mesocosms without reefs (empty buckets; hereafter “no reef-treatment”) served as controls. A treatment consisting of reefs without worms (dead reef) to control for the hydrodynamic effects of reefs was not considered because water flow is negligible inside buckets. Mesocosms were randomly located at the same tidal level and at similar distances to the coast (approximately 2 m) in an area where *F. enigmaticus* reefs naturally

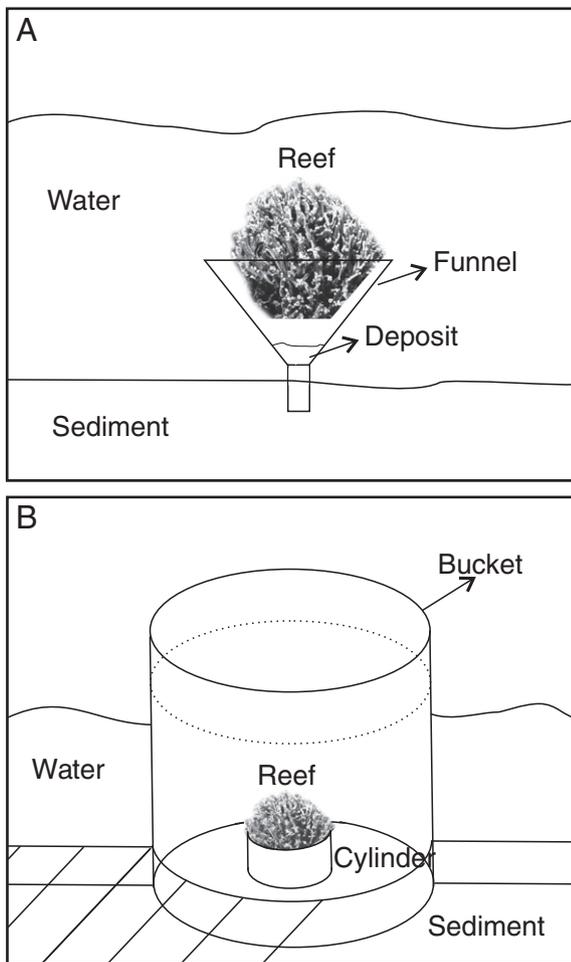


Fig. 2. Schematic diagram of a trap of sedimentation (A) and a mesocosm (B).

occur. Cores (diameter = 10 cm, height = 10 cm) of reefs with live polychaetes were obtained in San Gabriel (Fig. 1). To prevent the sediment within the reefs from transferring during the experiment (and ensure only worm depositions were measured), we placed the reef fragments into plastic chambers (diameter = 12 cm, height = 9 cm; see Fig. 2B). Prior to use, the reef cores were thoroughly washed with lagoon water to remove macro and meiofaunal organisms, and any adhered sediment. All buckets were filled with 10 l of lagoon water, the reef fragments were then introduced (hereafter “reef treatment”; see Fig. 2B). The addition of living worms would also add extra organic matter from their gut contents at the time the experiment starting. Therefore, for the first 24 h of the experiment the gut contents of the polychaetes were purged in the buckets with water from the sampling site. The water was then renewed with lagoon water from the study area. In shallow coastal lagoons, due to action of wind and tidally induced currents, the resuspension of sedimentary material, causing variations in inorganic particles, may affect the organic concentration of seston available to suspension-feeders (Dubois et al., 2009). Therefore, the water in the buckets was not mixed to avoid resuspension of deposited particles. After 24 h the biodeposits and the sedimented material from the reef-treatment and no reef-treatment respectively were collected from the bottom of the buckets using a Pasteur pipette and placed in bottles. OM content was calculated as explained before (see Section 2.2). In order to confirm the filtration activity of polychaetes, the *in vivo* chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) and turbidity of the water (Nephelometric Turbidity Units) were determined in each mesocosm with an Aquafuor handheld Fluorometer (Turner Design, Model 8000–01. Detection range: 0.05–

$300 \mu\text{g Chl a l}^{-1}$ and 0.5–150 NTU). Also, a sample of water (500 ml) of each mesocosm was obtained and filtered through GF/C Whatman filters (diameter = 47 mm, pore size = $1.7 \mu\text{m}$) and the particulate organic matter (POM) content of the water (phytoplankton and other seston) was calculated as described in the Section 2.3 for OM content.

Differences in the OM content of the sedimented material between treatments were evaluated with a *t*-test (Zar, 1999). The differences in turbidity, *in vivo* Chl *a* concentration and in POM of the water inside buckets between treatments were also analyzed with a *t*-test (Zar, 1999). Monotonic transformations were used when statistical assumptions were not satisfied (following Underwood, 1997).

2.6. Metabolism of sediment between reefs

If the biodeposit generated by the reef of *F. enigmaticus* produces an increment of the OM of the sediment between reefs, we also expect an increase in sediment metabolism. To evaluate this prediction, we recorded changes in dissolved oxygen concentration in water inside transparent and obscured cylindrical chambers (following Stutes et al., 2006) placed over the sediment surface ($n=8$, diameter = 12 cm, height = 9 cm, volume = 1 l) at three distances from the edge of the reef (0, 50 and 100 cm). Incubation time was between 1 and 2 h. Half of the transparent chambers were darkened with black tape, producing obscured chambers. One transparent and one obscured chamber were placed as a pair at each distance from the reef ($n=5$) with only the top 7 cm of the chamber exposed above the sediment surface. All incubations were in sunny conditions and at noon (depth of water = 40 cm approximately) at the San Gabriel site (Fig. 1) during December 2007. The water enclosed in the benthic chambers was not mixed during the incubation time. Before starting the incubations, measurements of initial oxygen concentration were taken in the chambers (initial concentration). At the end of the incubations, samples of water were collected from the chambers through a 1 cm hole at the top of the chambers with a 60 ml syringe. After collection, the water was transferred to a bottle (60 ml) and the oxygen concentration read with portable oxygen probe (Hach® SensION6™ Waterproof Dissolved Oxygen Meter; concentration range: 0–20 mg/l, accuracy: $\pm 1\%$). We measured changes in dissolved oxygen concentration in water (final minus initial) in each of the chambers during incubation, where the sediment net production (SNP) correspond to the differences in the transparent chamber, and sediment respiration (SR) to the differences in the dark chambers. The SNP and SR were determined using the equations (from Stutes et al., 2006):

$$\text{SNP} = [(f-i) / t] \times C \times H \times P_{\text{con}}$$

$$\text{SR} = [(f-i) / t] \times C \times H \times R$$

where f and i are the final and initial dissolved oxygen concentrations (mg l^{-1}), t is the incubation time (h), C is the conversion factor of liters to m^3 , H is the height of the water column in the chamber (0.09 m), P_{con} is the oxygen/carbon conversion factor for sediment net production ($0.344 \text{ mg C mg}^{-1}$ oxygen; based on a photosynthetic quotient of 1.2 and a respiratory quotient of 1; Strickland and Parsons, 1972), and R is the oxygen/carbon conversion factor for sediment respiration ($0.375 \text{ mg C mg}^{-1}$ oxygen; based on a respiratory quotient of 1; Strickland and Parsons, 1972).

Finally, sediment gross production (SGP, in mg C m^{-2} sediment h^{-1}) was calculated as the difference between SNP and SR. Differences in SNP, SR and SGP between distances from reefs were evaluated with a one-way ANOVA (Zar, 1999). Common monotonic transformations were used to remove heterogeneity of variances when needed (Underwood, 1997).

2.6.1. Effect of the benthic crabs on sediment metabolism

Adult individuals of the crab *C. angulatus* inhabit underneath the reefs (Schwindt and Iribarne, 2000; see Fig. 3) and feed on benthic

micro-algae (Botto et al., 2005; Martinetto et al., 2007), and therefore can affect the benthic primary production of the sediment between reefs. If this were the case, it may counteract the effect of added OM due to biodeposition. Consequently, a crab exclusion experiment was performed in order to detect their impact on benthic primary production in San Gabriel site (Fig. 1) during March of 2008. The experiment consisted of the following treatments (n = 9 per treatment): (a) cages that excluded crabs (hereafter cage), (b) a control cages that were located 5 cm above the surface, permitting the free movement of crabs but with the same structure to detect potential artifacts of the cage (hereafter control), and (c) an open control without cage (hereafter out). Crab exclusion and cage control treatments were performed using a plastic mesh (35 cm height, 110 cm length, 30 width and 1 cm mesh size). The cages were placed radially, from the edge of the reef to outside and they were supported using four PVC stakes (50 cm height) in each corner. After 20 days, the cages were removed and the productivity of the sediment was measured by analyzing changes in dissolved oxygen concentration inside transparent and obscure chambers, and at different distances from the reefs in each treatment as described in the previous section.

Differences in SNP, SR and SGP between treatments and distances from reefs were evaluated with two-way ANOVA for randomized block design (Zar, 1999), with reefs treated as blocks and distance and treatment as fixed factors. The Tukey test for non-additivity was used to exclude interactions between factors (treatments and blocks; Zar, 1999). Levene's test was used to evaluate the homogeneity of variances. Plots of residuals were also examined to evaluate deviations from normality (Zar, 1999).

3. Results

3.1. Organic matter and nutrient content of the biodeposit of *F. enigmaticus*

The percentage of the OM in biodeposits of *F. enigmaticus* ($x = 43.9\%$, $SD = 1.3$) was 21 times higher than the sediment between reefs ($x = 2.05\%$, $SD = 0.3$; $t = -218$, $df = 18$, $n = 10$, $P < 0.001$). The nitrogen and carbon content of the biodeposit was $6.93 \mu\text{g N mg of matter}^{-1}$ ($SD = 1.99$) and $53 \mu\text{g C mg of matter}^{-1}$ ($SD = 12.01$) respectively. The C per mg matter/N per mg matter ratio was 7.8 ($SD = 0.8$).

3.2. Organic matter in traps of sedimentation

In Sotelo bay, an area of low energy, the percentage of OM in the deposited material in the treatment with live reef was 18% higher

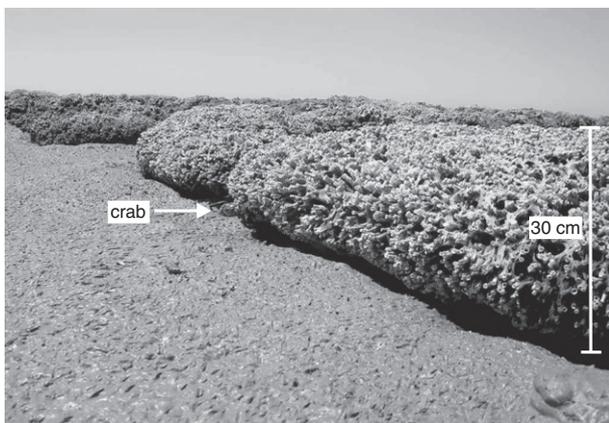


Fig. 3. Photograph showing the reefs of *F. enigmaticus* with very low tide in San Gabriel. Adult crabs of *C. angulatus* lives at the sediment under the reef (white arrow).

than in dead reef treatment ($t = -2.42$, $df = 14$, $n = 8$, $P < 0.05$, Fig. 4). However, in San Gabriel, the area of relatively higher energy, the percentage of OM was not different between treatments ($t = 0.8$, $df = 14$, $n = 8$, $P = 0.43$, Fig. 4).

3.3. Organic matter content of sediment between reefs

No differences were found in the percentage of OM in sediment between distances from the edge of the reefs (ANOVA: $F_{3,36} = 1$, $MS = 0.08$, $P = 0.4$). The average OM in the sediment was 2.15% ($SD = 0.41$), 2.1% ($SD = 0.3$), 1.97% ($SD = 0.22$) and 1.97% ($SD = 0.15$) at 0 cm, 50 cm, 100 cm and 200 cm from the edge of the reef, respectively.

3.4. Mesocosm experiments

After 24 h, the food (phytoplankton) was not completely depleted for the polychaetes (Fig. 5). *In vivo* Chl *a* concentration in the mesocosms with reefs was less than in the mesocosms without reefs (log transformed data: $t = -7.65$, $df = 12$, $P < 0.001$). Similarly, water turbidity (log transformed data: $t = -6.2$, $df = 12$, $P < 0.001$) and POM of the water ($t = -7.84$, $df = 12$, $P < 0.01$) was lower when polychaetes were present (Fig. 5). However, the percentage of OM deposited on the bottom of the buckets with reefs was higher than deposited on buckets without reefs (log transformed data $t = -3.45$, $df = 12$, $P < 0.01$; Fig. 5).

3.5. Metabolism of sediment between reefs

Sediment net production (SNP) was augmented with increased distance from the edge of the reefs ($F_{2,15} = 6.06$, $n = 6$, $MS = 308.1$, $P < 0.05$; Fig. 6). At 100 cm from the reef edge, SNP was about seven

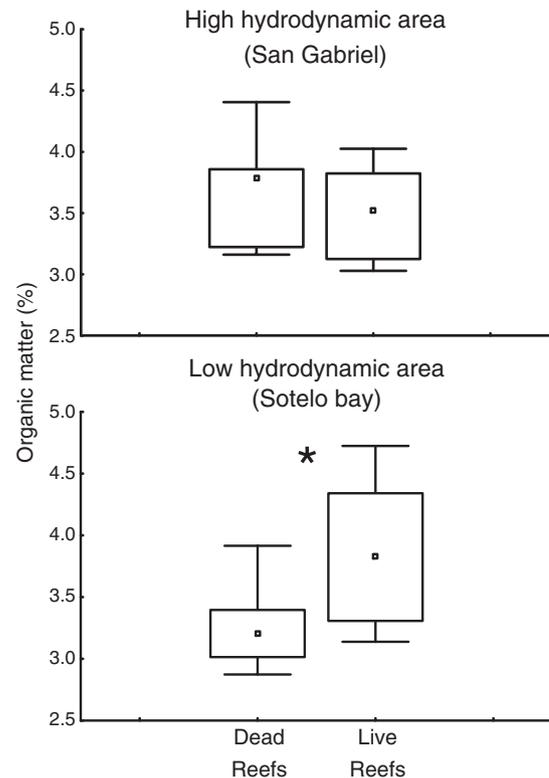


Fig. 4. Organic matter (%) in sediment traps (funnels) with dead and live reefs in a high hydrodynamic area (San Gabriel) and a low hydrodynamic area (Sotelo bay). Asterisks indicate significant differences between treatments. Here and thereafter limits of the box represent 25 and 75 percentiles, vertical lines represent minimums and maximums and the circles inside the boxes represent the median values.

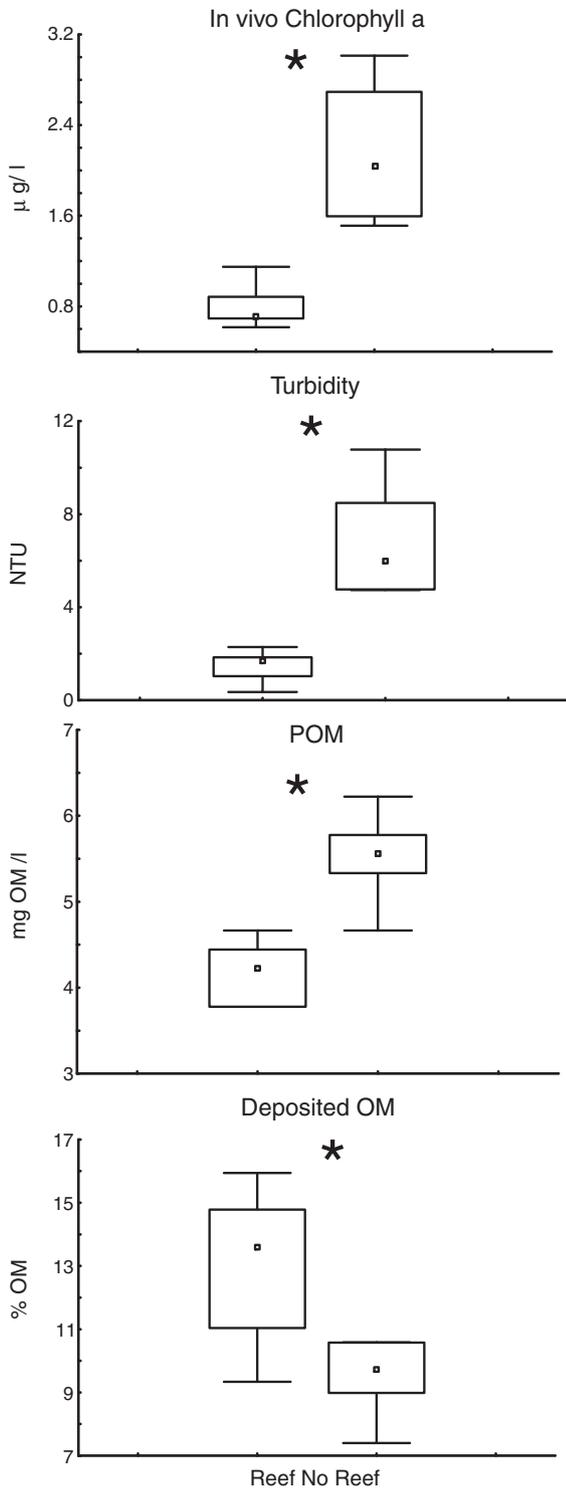


Fig. 5. *In vivo* Chlorophyll *a* ($\mu\text{g l}^{-1}$) and turbidity (NTU) of the water of the buckets, and OM deposited on the bottom (SOM; g m^{-2}) in the treatments with and without reef. Asterisks indicate significant differences between treatments for a given dependent variable.

times higher than at 50 cm or at reef edge. Sediment respiration (SR) did not vary between distances from the reefs (ANOVA, $F_{2,15} = 0.75$, $n = 6$, $MS = 79.9$, $P = 0.49$; Fig. 6). Similarly to SNP, sediment gross primary production (SGP) increased from the edge of the reefs reaching their highest values at 100 cm from the reefs (square root

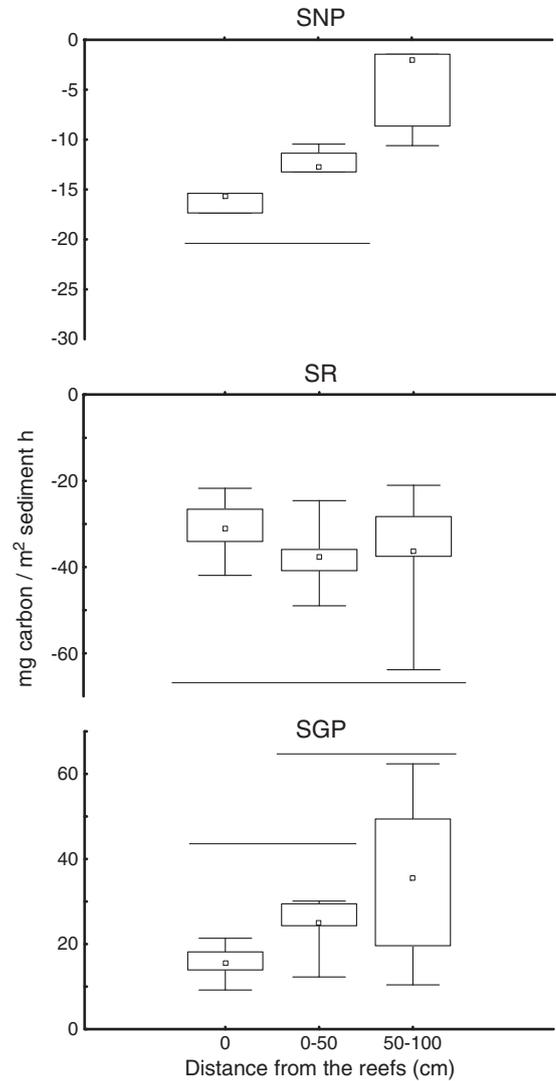


Fig. 6. Net primary production (SNP), Respiration (SR) and gross primary production (SGP) of sediment at three different distances (0, 50 and 100 cm) from the reefs. Horizontal lines indicate no significant differences ($P > 0.05$, ANOVA).

transformed data: ANOVA, $F_{2,15} = 4.03$, $n = 6$, $MS = 4.9$, $P < 0.05$; Fig. 6). The SGP at 100 cm was more than twice higher than at the edge of the reefs.

3.5.1. Effect of the benthic crabs on sediment metabolism

Sediment gross primary production (SGP) varied among treatments and distances, as indicated by significant interactive effects between variables (ANOVA, $F_{4,24} = 3.25$, $MS = 469.27$, $P < 0.05$; Fig. 7). Caging artifacts were not detected (Fig. 7). At the reef edge, the SGP was three times higher in the sediment without crabs than in control cages and sediment with crabs. At 50 and 100 cm from the reefs, there were no treatment effects on sediment SGP.

Sediment respiration (SR) varied among distances (ANOVA, $F_{2,24} = 6.62$, $MS = 873.5$, $P < 0.01$, Fig. 7), but no differences were found between treatments (ANOVA, $F_{2,24} = 2.91$, $MS = 384.6$, $P = 0.07$). Sediment respiration close to the reefs was lower than at 100 cm. No differences in sediment respiration were found between 50 and 100 cm (Fig. 7).

Sediment net primary production (SNP) differed between treatments (ANOVA, $F_{2,24} = 5.24$, $MS = 595.8$, $P < 0.05$) and distances (ANOVA, $F_{2,24} = 4.3$, $MS = 485.6$, $P < 0.05$; Fig. 7). SNP was 50% higher without crabs than with the presence of crabs. No differences were

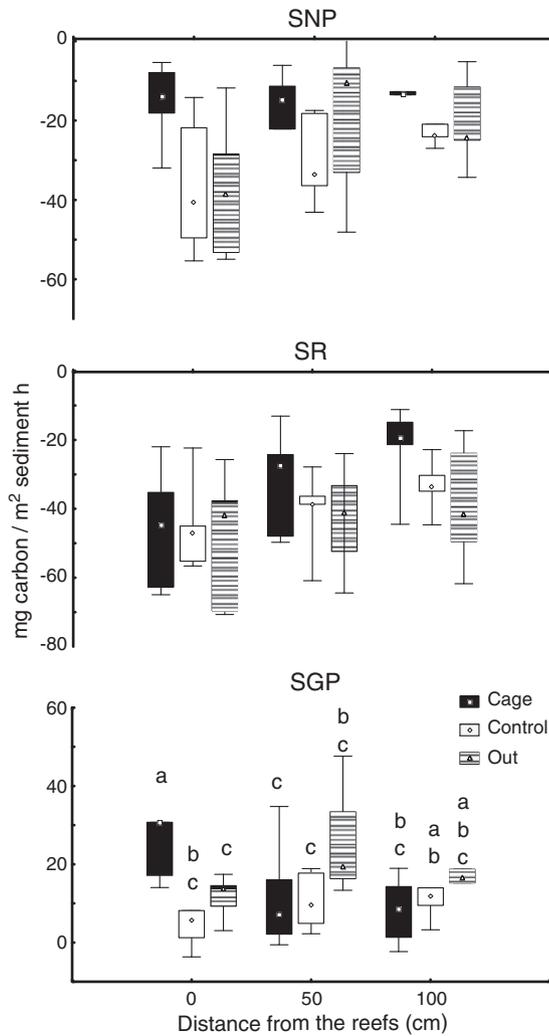


Fig. 7. Effects of crab exclusion on net primary production (SNP), respiration (SR) and gross primary production (SGP) of sediment at three different distances (0, 50 and 100 cm) from the reefs. Different letters indicate significant differences ($P > 0.05$, ANOVA for randomized block design).

found between out and control cage treatments. SNP close to the reefs was 50% lower than at 50 cm and at 100 cm from the reefs.

4. Discussion

Ficopomatus enigmaticus is the main benthic suspension feeder of the Mar Chiquita coastal lagoon, and their filtration activity strongly decreases the seston level (i.e., phytoplankton and turbidity; Bruschetti et al., 2008) and consequently increases the OM on the sediment by biodeposition. Laboratory experiments show that OM content of *F. enigmaticus* biodeposits is higher than OM in the sediment between reefs. Sediment samples around the reefs showed that material is not accumulating in their surrounding area, and therefore is possibly being transported by the currents and deposited elsewhere or is affected by the crabs that live underneath. Sediment traps with live reefs showed higher OM content compared to traps with dead reefs in an area with low water currents, and therefore suggest the importance of hydrodynamic conditions in the deposition of the particles. Feeding on microalgae and bioturbation activities by the dominant crabs *C. angulatus* can both impact on the stabilizing effect of microbial mats on sediment close to the reefs. Therefore they could counteract the effect of the reefs on the productivity of the sediment. Both effects (crab activity and water transport) can

diminish the effect of biodeposit on the sediment close to the reefs, and therefore would be playing a major role in the OM content by modulating its availability in these areas.

Organic matter enrichment can change the composition of sediments and benthic communities (van Es, 1982). The quality and quantity of the biodeposits generated by suspension-feeder animals and the physical and chemical characteristics of the existing sediments determine to what extent the sediment can be altered (Giles and Pilditch, 2004). Typically, suspension-feeders produce large numbers of faecal pellets, and it is their abundance and filtering rates that make them such significant transformers of OM. Material with a C/N ratio of 5.5 are considered typical of bacteria, and near 8 indicates phytoplankton, faecal pellets and other easily degraded material (Fenchel and Blackburn, 1979; Kautsky and Evans, 1987). Our results show that OM content of biodeposit was 20 times higher than the OM content of the sediment between reefs with a C/N ratio of biodeposits of 8. Thus may be classified as material of high content of nutrients compared to OM usually found in marine sediments (see Kautsky and Evans, 1987).

Organic matter deposited as faeces and pseudofaeces represent a significant proportion of the energy and nutrients potentially available to invertebrate consumers as a food resource (Stuart et al., 1982; Zhou et al., 2006), and to submerged aquatic vegetation (Peterson and Heck, 1999). Because of their high energetic content, biodeposits are important nutritious resources to benthic macrofaunal species (Roditi et al., 1997) and, additionally can stimulate the benthic micro-algae production (Miller et al., 1996). The high abundance of detritivorous organisms that live within *Ficopomatus* reefs, suggests that the communities of associated organisms rely on accumulation of organic matter for food (see Heiman et al., 2008). Within reefs of Mar Chiquita lagoon the more abundant organisms are juvenile crabs, amphipods and free living polychaetes (i.e., detritivores and herbivores; Bruschetti et al., 2009; Schwindt and Iribarne, 2000) and may be the result of enhanced local availability of OM through sediment entrapment (107 kg sediment m^{-3} reef; Schwindt et al., 2004), but also by accumulation of pseudofaeces and faeces. However, further study to evaluate the quality and origin of the OM of the mud between tubes of *Ficopomatus* is needed to understand how organisms use this resource.

In this work, contrary to our hypothesis, the benthic chambers showed a decrease in gross primary production of the sediment at the areas closest to the reefs. However, these areas are also closest to large densities of *C. angulatus* (up to 40 ind reef $^{-1}$, Schwindt et al., 2001; carapace width range = 20 mm to 50 mm, Spivak et al., 1994) living under the *F. enigmaticus* reefs. Stomach content analysis (Martinetto et al., 2007; Schwindt et al., 2001) and stable isotope analysis (Botto et al., 2005) showed that benthic microalgae are the main food source for this crab. When *Ficopomatus* reefs together with *Cyrtograpsus* were experimentally introduced, most of the infaunal organisms (deposit feeders) decreased in density compared with control areas (Schwindt et al., 2001). Our results showed lower productivity of the sediment at 0 m from the reefs, but when we excluded the crabs the productivity was higher than at other distances (Fig. 7). Therefore, *Ficopomatus* reefs directly and positively increase the density of the crabs by giving them shelter, but they also indirectly and negatively affect the infaunal organisms (which are preyed upon by crabs; Schwindt et al., 2001) and the productivity of the sediment near the reefs (our results, Fig. 6). This background, coupled with our results, reveals that the presence of crabs can generate a decrease in SGP at the areas closest to the reefs. This result can be a direct consequence of *C. angulatus* foraging activity on the benthic microalgae (microphytobenthos) or an indirect bioturbation effect on the sediment due to their activities. Other factors such as flow acceleration around the reef, scour at the base of the reef or even a shadow cast by the reef structure itself could be affecting the productivity in the sediment between reefs. However, water flow around the reefs was estimated indirectly by using the loss (i.e., dissolution) of standard plaster cylinders, and did not differ

significantly in distances (0.2 m, 2 m and 6 m) from the reefs (see Schwindt et al., 2004). Whatever the cause, the removal of crabs in exclusion experiments generated an increase of SGP at the edge of the reefs. This result shows that the reefs promote productivity in the sediment between reefs (<50 cm) but with a more indirect negative effect because reefs facilitate the establishment of crabs (Schwindt and Iribarne, 2000) that reduce sediment productivity. However, the methods utilized to measure sediment primary production have limitations; these limitations should not affect our conclusions significantly. For example, the water enclosed in the chambers was not mixed during the incubation time, and this could have led to reduced oxygen exchange between the sediment and the overlying 7 cm water column in the chamber. Thus, there would be an underestimation of sediment primary productivity and respiration. These limitations were common to all our experimental treatments, and thus the differences observed between our experimental treatments should be indicative of the true impact of the reefs and the crabs on the variables measured.

Hydrodynamic conditions also determine the extent to which biodeposits modify the existing sediments (Giles and Pilditch, 2004). Faeces and pseudofaeces of bivalves are resuspended at currents speeds that reach up to 25 cm s^{-1} and 15 cm s^{-1} respectively, and with flows below these thresholds biodeposits tend to accumulate on the bottom (Widdows and Navarro, 2007). At San Gabriel, where water current velocity is high enough to resuspend or disperse faeces and pseudofaeces, the presence of live reefs did not affect the OM content of the deposited sediment. In contrast, at the Sotelo Bay where water current is lower and hydrological regime is more stable (see Lanfredi et al., 1987), the OM content of the material deposited by *F. enigmaticus* was higher than OM of the dead reef treatment, suggesting the importance of hydrodynamic conditions (currents) for removal and dispersion of the particulate material. Therefore, if biodeposits settle, the sediment between reefs should be enriched (compared with sediment without reefs) and this enrichment should decrease with increasing distance from reefs. Nevertheless, we did not find differences in sediment OM content between different distances from reefs (see also Schwindt et al., 2001) at San Gabriel. Therefore the biodeposits are either not being deposited close to the reefs, or they are being removed after deposition (e.g., degradation, predation, bioturbation, resuspension) in this place.

In situ mesocosm experiments showed that without the influence of water currents, *F. enigmaticus* decreased considerably the phytoplankton biomass (up to 45% per day), the turbidity (up to 50%) and the POM (up to 20%) of the water and, consequently enhanced the OM deposited on the bottom (up to 50%). OM of the sediment collected at mesocosms with reefs was two times higher than those collected without reefs. Therefore, in San Gabriel, the material (biodeposit) expelled by *F. enigmaticus* reefs could be dispersed by the water and then deposited somewhere else. In shallow-water ecosystems, the action of wind and tides may generate resuspension of sedimentary material (inorganic particles), causing variations in organic concentration and nutritional value of seston available to suspension-feeders (see Dubois et al., 2009). Studies on the effects of seston on polychaete clearance rates remain very scarce in the literature. For example the clearance rates of *Sabellaria alveolata* (Polychaete: Sabellariidae; Dubois et al., 2009), *Ditrupa arietina* and *Euchone papillosa* (Polychaeta: Sabellidae; Riisgård et al., 2002) were negatively affected by an increase of seston available. Consequently the biodeposition rates can also be affected. In this work, the mesocosm experiments were performed without tidal and current influence, and therefore amount of deposited OM on the bottom may have been overestimate compared to natural conditions. However, our result of grazing effect of *Ficopomatus* on primary producers is similar to previously reported work (average decrease in chlorophyll a due to the reef-treatment was 56% in summer; see Bruschetti et al., 2008). Our *in situ* mesocosms cannot provide complete characterization of how reefs

affect chlorophyll concentration and biodeposition of OM, but it represents an important approach to evaluate the proposed hypothesis. Both laboratory and field approaches will be needed to get at the range of combinations of physical and biological factors that affect seston concentration as water flows and deposition rates over reef beds. Others field and experimental studies (Bruschetti et al., 2008; Davies et al., 1989) confirmed the substantial filtration capabilities of *Ficopomatus* reefs, and the present study shows the potential of this invasive species to transfer the pelagic production to the benthos.

Similar results have been observed in a number of other invasive aquatic ecosystem engineers, such as the mussel *Dreissena polymorpha* (MacIsaac et al., 1999), the Asian clam *Corbicula fluminea* (Sousa et al., 2008) and the bivalve *Limnoperna fortunei* (Sylvester et al., 2007). These species decrease the phytoplankton biomass and the turbidity and, increase the sedimentation rates in the column water via filter feeding (e.g., Karatayev et al., 1997; Phelps, 1994; Prokopovich, 1969). While invasive bivalves have been widely studied (see references above), much less is known about invasive polychaetes. Comparing with bivalves and considering the high abundance of *Ficopomatus* (86% of the brackish portion of the lagoon is currently covered by reefs; Schwindt et al., 2004), this invasive species can potentially having analogous ecosystem-level effects.

In summary, the results presented indicate that biodeposition loadings of the polychaete *F. enigmaticus* could be significant. As, *F. enigmaticus* occurs at high densities in this lagoon, it is therefore reasonable to expect that biodeposits will form a significant component of the OM of the water column. In addition, activity of native crabs (bioturbation and/or feeding) that live underneath of reefs and currents water may counteract reef effects on OM content of sediment. Processes of filtering and production of biodeposits in filter feeders are linked, resulting in an increased flux of particles from the water column to the bottom of the lagoon, increasing the benthic–pelagic coupling.

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