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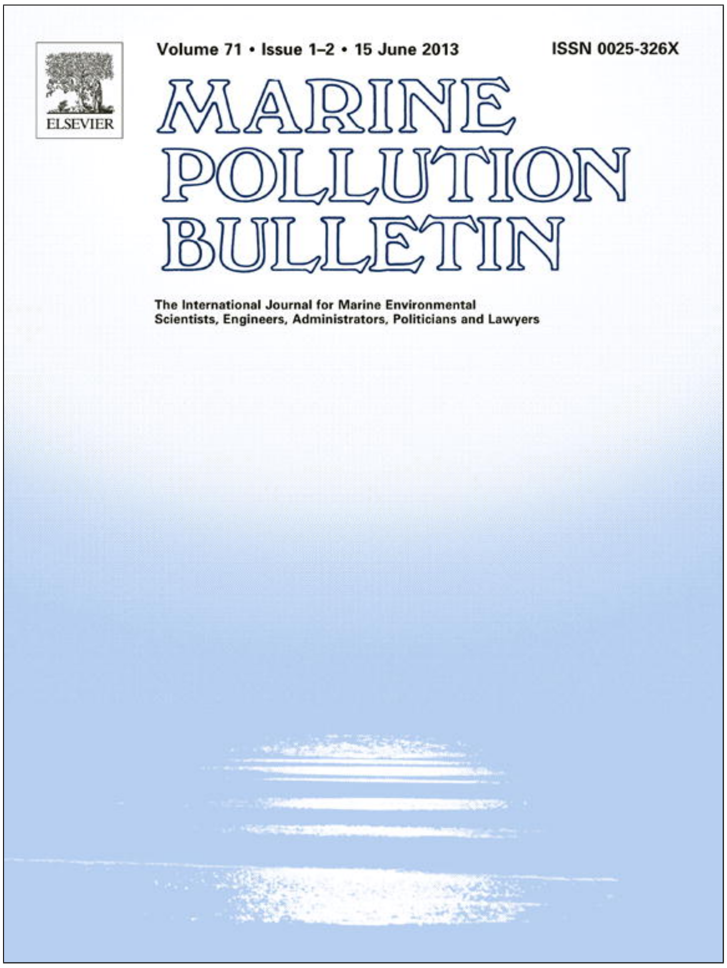

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Reef-forming polychaetes outcompetes ecosystem engineering mussels

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ABSTRACT

In order to understand changes in the functioning and the community structure of intertidal ecosystem in sewage-impacted sites, a long-term monitoring coverage study (2004–2011) was carried out on abrasion platforms of the SW Atlantic. The intertidal zone is characterized by the mytilid *Brachidontes rodriguezii*, an ecosystem engineer. Since the austral spring of 2008, a demographic explosion of an invader polychaetes, *Boccardia proboscidea,* has produced massive biogenic structures around the sewage discharge outfall. Cover percentage of this polychaete reached almost 100% in sewage-impacted sites but low or no coverage at all in Reference Sites. The density of *B. rodriguezii* declined due to the biogenic reefs stifles these mytilids. The massive settlement of *B. proboscidea* among mussels, the rapid growth and the tube construction smothers the mussels in sewage-impacted sites.

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1. Introduction

Biotic invasions are the result of a process that begins when certain organisms are transported from their native places to new environments (Baker, 1986). Invading species can displace native species through competition, predation or habitat alteration changing the dynamics and structure of benthic communities. Consequently, these species become the dominant species of the community and change the physical characteristics and productivity of ecosystems (Bertness, 1984; Vitousek, 1990).

Boccardia proboscidea Hartman, 1940 is a polychaete from the west Coast of North America, with a distribution extending from British Columbia to Baja California (Hartman, 1941). Today its range also includes Japan (Sato-Okoshi, 2000), southern Australia (Blake and Kudenov, 1978; Hewitt et al., 2004; Lleonart, 2001; Petch, 1995), South Africa (Robinson et al., 2005; Simon et al., 2010), Hawaii (Bailey-Brock, 2000), New Zealand (Read, 2004) and Spain (Martinez et al., 2006), all places where it appears to have been introduced (Kamel et al., 2010). Since the austral spring of 2008 the species has been detected in intertidal sewage-impacted sites in Mar del Plata (Argentina) forming massive reef-like structures. This is the first record of this species of the SW Atlantic (Jaubet et al., 2011).

The intertidal zone of Mar del Plata city (38°S, 57°W) is characterized by the presence of small mytilid *Brachidontes rodriguezii* (d'Orbigny, 1842) (Scelzo et al., 1996 and references therein), an ecosystem engineer. This species also inhabits areas moderately affected by sewage waters (Vallarino, 2002; Vallarino et al., 2002). This bivalve has formed dense mussel beds and has monopolized all intertidal hard space until the colonization of the introduced barnacle *Balanus glandula* Darwin, 1854 which led to a decrease in its coverage (Vallarino and Elías, 1997). Since the first record of the invader *B. proboscidea* in 2008, the coverage of *B. rodriguezii* has shrunk even further, and in sewage-impacted areas the species has practically disappeared.

Mar del Plata is the largest seaside resort of Argentina, and the wastewater of the city is discharged directly on the coast shoreline (Scagliola et al., 2006). Therefore, a fast and reliable method to measure sewage-induced pollution is needed. An effective method in intertidal rocky shore ecosystems is the cover (percentage) of the main macrobenthic organisms, as suggested by Ellis (2003). A monitoring program based on the cover method allows detecting the effects of the sewage pre-treatment when the plant stops for their maintenance (Elías et al., 2009). This program also allows the detection of polychaetes masses identified as *B. proboscidea* around sewage discharge.

The aim of this work was to show the progressive occupation of intertidal space by the invader polychaete *B. proboscidea* and the subsequent displacement of the mussel beds in sewage-impacted sites. A secondary goal was to describe briefly the *B. proboscidea* biogenic reef. Some hypotheses about the mechanisms of the competitive exclusion with the mussel beds were suggested and discussed.

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2. Materials and methods

2.1. Study site

The coast of Buenos Aires Province in the zone of Mar del Plata city is dominated by sandy beaches only interrupted by quartzite outcrops and almost horizontal abrasion platforms (geological formation of consolidated loess, limestone or stony rocks). The sewage outfall of Mar del Plata city is located to 9 km towards the north of the city center (N°11 route, km 507). This intertidal urban effluent discharges 241,920 m^3 of untreated sewage daily during winter season (flow average rate of 2.8 m^3 seg^{-1}) and 302,400 m^3 daily during summer ones (average of 3.5 m^3 seg^{-1}) into the coastal marine waters. Fishery, fish flour factories, tourism, restaurants and textile industries are the main industrial activity of the city and thus they are the responsible of supplying large amounts of grease (18 tons/day, 63% has industrial origin and the other 37% has domestic origin) to the urban wastewater (Scagliola et al., 2006, 2011).

Data obtained for several studies conducted by Mar del Plata Public Sanitations Works (OSSE) from 2000 to 2010 demonstrated that the sewage has a high content in organic matter and low levels of heavy metals (below the values required in national and international normative). The effluent pretreatment retains 20–25 tons (wet weight) of solids daily and the raw sludge contains 86% of organic mater. The annual average concentrations of the major constituents of the liquid effluent were: nitrogen total: 63.13 mg lt^{-1}; phosphorus total: 6.88 mg lt^{-1}; oil and grease: 67.11 mg lt^{-1} (Scagliola et al., 2006, 2011).

The incidence of wastewater discharge is about 5000 m to the north and 9900 m to the south, and the beaches in this sector do not fulfill the local compliance criteria. The criterion for the compliance level was the same one adopted by USEPA in 1986 for marine recreational waters, i.e. 35 *Enterococci* geometric mean per 100 ml. The impacted area (where the present work was conducted) is washed by waters with mean geometric values between more than 500 up to 7000 *Enterococci* NMP/100 ml and it had also the greatest counting for Total Coliforms and Termotolerant coliforms (Pérez Guzzi, 2003; Comino et al., 2011).

2.2. Sampling design

The study was carried out from 2004 to 2008 in three limestone sites: Impacted Site and South Impacted Site (50–200 m and 1000–1200 m south of the outfall, respectively) and Reference Site 1 (9000 m-north of the outfall). From 2008, a new reference site was added, Reference Site 2 (8000 m-north of the outfall) (Fig. 1). During the sampling period, all seasons were surveyed at least once. Although the cover of the entire community was measured, this study only shows the cover percentage of *B. rodriguezii* and *B. proboscidea*. Three separate stations 50 m apart were sampled in each site. A total of 10 sample units of 0.25 m^2-squares were taken in each station and averaged in a single value.

2.3. Data analysis

To analyse changes in the long term coverage, three repeated measures ANOVA were used considering the averaged value (3 data) for each site. The first ANOVA analysis included all sampling periods from 2004 to 2011 (without Reference Site 2) and was performed with coverage of *B. rodriguezii*. The others two ANOVA analyses included all sites (with Reference Site 2) but only from 2008 to 2011. These analyses were performed with coverage of *B. rodriguezii* and *B. proboscidea*, because the first appearance of *B. proboscidea* was from November 2008.

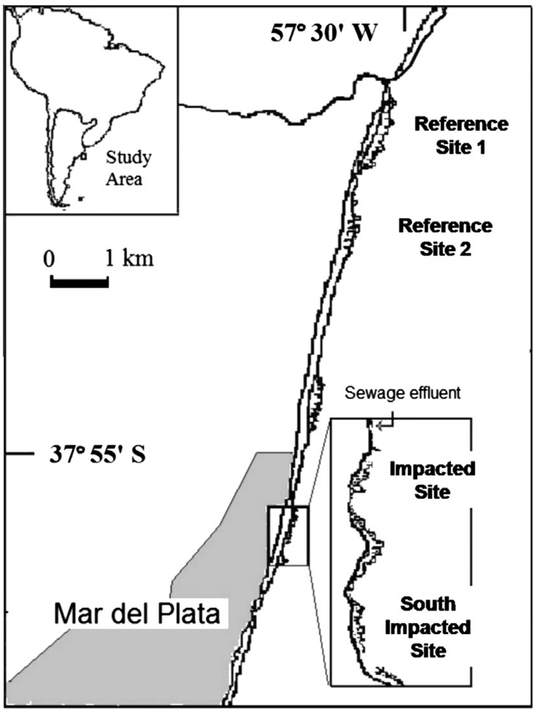

Fig. 1. Location of the four sites sampled around sewage discharge of the Mar del Plata city: Reference Site 1, Reference Site 2, Impacted Site and South Impacted Site, from 2004 to 2011. Position of the sewage effluent is shown.

3. Results and discussion

3.1. Long-term cover percentages

There are highly significant differences in coverage through time (years) and sites (Impacted versus Reference Sites), as well as interactions of *B. rodriguezii* (Table 1) considering the period 2004–2011 in the two Impacted Sites and the Reference Site 1. The analysis along 2008–2011 (including Reference Site 2) also shows highly significant differences in coverage between sites and interactions in the two species (Tables 2 and 3).

Due to the fact that there are significant interactions effects in the Analysis of Variance (ANOVA), the interpretation of the mains effects was performed graphically. The results of the long-term cover percentages in the different sites are presented in Fig. 2.

From 2004 to 2008, the intertidal benthic community of hard substrate around Mar del Plata was dominated by the mytilid *B. rodriguezii* in both References and Impacted Sites. *B. rodriguezii* percent cover reached high values in the Reference Site 1 (up to 80%), whereas in the Impacted Sites the values were significantly lower. In the same period, the polychaete *Boccardia* spp. (cited previously as *B. polybranchia* in Elías et al., 2003; 2006) appeared between the mussel beds but without forming large patches enough to be identified in the cover method. In June 2008, *B. proboscidea* was found in mussel beds in sewage-impacted sites, forming visible incipient masses, without being considered reefs.

In November 2008, the density of *B. proboscidea* increased dramatically, result of the formation of solid biogenic structures named reefs. These reefs covered about 70% of the sampled area at the South Impacted Site (Fig. 2, event 1). In February 2009 *B. proboscidea* covered almost 100% of the substrata at the Impacted Sites. Argentina is the only place in the world where this species has built such structures (Jaubet et al., 2011).

In January 2009, the coverage of *B. proboscidea* reached 30% in the Reference Site 1. This was due to a strong storm that broke

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Table 1
Results of ANOVA analysis testing the percent cover of *Brachidontes rodriguezii* versus sites (South Impacted Site, Impacted Site and Reference Site 1) from 2004 to 2011.

	df Effect	MS effect	df Error	MS error	F	*p*-Level
Site	2	17419.32	6	988.9915	17.61322	0.003083
Time	22	982.79	132	250.5590	3.92240	0.000000
Site * Time	44	668.91	132	250.5590	2.66965	0.000009

Table 2
Results of ANOVA analysis testing the percent cover of *Brachidontes rodriguezii* versus sites (South Impacted Site, Impacted Site, Reference Site 1 and Reference Site 2) from 2004 to 2011.

	df Effect	MS effect	df Error	MS error	F	*p*-Level
Site	3	23328.24	8	243.7063	95.72274	0.000001
Time	12	344.79	96	177.4488	1.94302	0.038333
Site * Time	36	412.29	96	177.4488	2.32344	0.000593

Table 3
Results of ANOVA analysis testing the percent cover of *Boccardia proboscidea* versus sites (South Impacted Site, Impacted Site, Reference Site 1 and Reference Site 2) from 2008 to 2011.

	df Effect	MS effect	df Error	MS error	F	*p*-Level
Site	3	18956.7	8	254.1	74.6117	0.000003
Time	11	3430.9	88	141.6	24.2313	0.000000
Site * Time	33	1098.5	88	141.6	7.7580	0.000000

the reefs in the Impacted Site and moved its debris to the north to the Reference Site in December 2008 (Fig. 2, event 2). Several studies demonstrated that polychaetes reefs have been affected by cycles of storm-destruction and rapid rebuilding (Bolam and Fernandes, 2002; Jaubet et al., 2011; Garaffo et al., 2012). As regards *B. rodrigueziii,* the cover percent in the Reference Site 1 decreased to 50% whereas in the Reference Site 2 the values increased. However, the coverage at the Impacted Sites was almost 0%.

In February 2009, the cover percent of both *B. proboscidea* and *B. rodriguezii* decreased in the Impacted Site (Fig. 2, event 3). The disappearance of both reefs and mussel beds was due to the chlorination process. The local water authorities started to chlorinate the untreated sewage effluent in an attempt to lower microbiological indicators. The chlorination started between January 23 and 27th 2009, adding 7–10 ppm of sodium hypochlorite for 40 h to the untreated raw sewage (Comino et al., 2010). Furthermore, the chlorinated water and its by-products were released to the environment without any prior dechlorination process. This produced the death

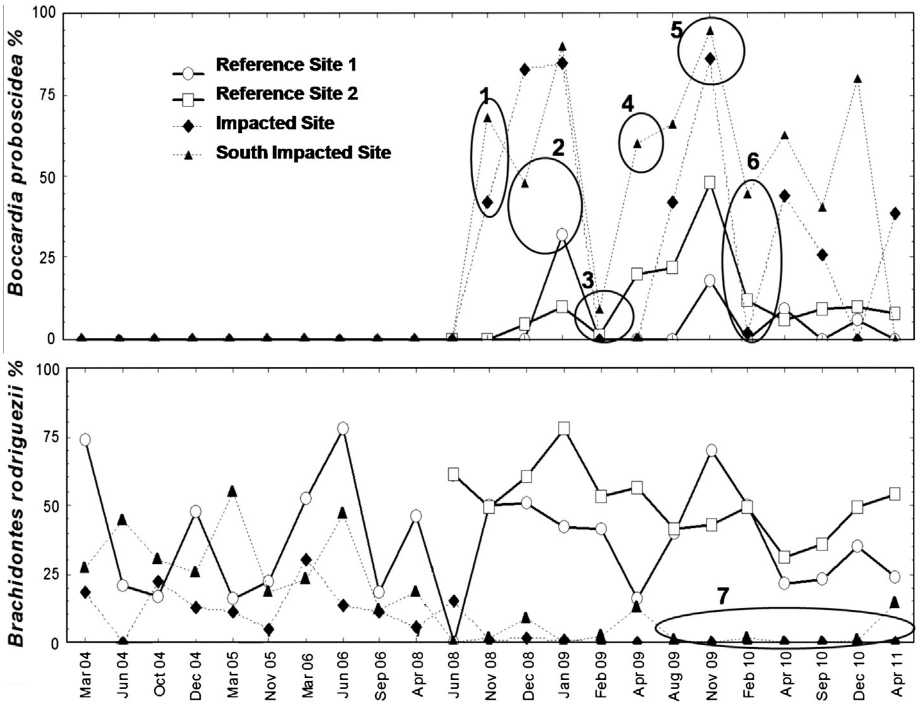

Fig. 2. Changes in the coverage percentage of *Boccardia proboscidea* and *Brachidontes rodriguezii* in the four sampling sites from 2004 to 2011 (without Reference Site 2 from 2004 to 2008). Important ecological events are marked with black circles and listed chronologically. Point 1: indicate the first appearance of *B. proboscidea* biogenic reefs in Impacted Sites (November 2008); point 2: indicate the destruction of the *B. proboscidea* biogenic reefs in South Impacted Site due to a storm (December 2008) and appearance of new biogenic reefs in the Reference Site 1 (January 2009); point 3: indicate the disappearance of *B. proboscidea* biogenic reefs in Impacted Sites due to a chlorination process (February 2009); points 4 and 5: indicates reefs rebuilding (April 2009) and further reef development (November 2009) in Impacted Sites; point 6: indicate the decrease of *B. proboscidea* cover percent in South Impacted Site and reefs disappearance in Impacted Site due to a new chlorination process (February 2010); and point 7: shows the *Brachidontes rodriguezii* competitive exclusion (August 2009–April 2011) .

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of all macro organisms from the area within a radius of 3 km. The effects of chlorination are sewage-dependent because the depletion of the flora and fauna occurs only around the sewage discharge, the point source of the by-products of chlorination.

For several months no macroorganism colonized the sites affected by the sewage water chlorination. However, in April 2009 new biogenic reefs of *B. proboscidea* appeared in the South Impacted Site (Fig. 2, event 4). In November 2009, these reefs reached the maximum cover (Fig. 2, event 5 and Fig. 3). In December 2009–March 2010, another chlorination process affected the Impacted Sites. This led into the reef depletion in the Impacted Site and a decrease in the South Impacted (Fig. 2, event 6). Between August 2009 and December 2010, *B. rodriguezii* was displaced from the Impacted Sites due to the competition with *B. proboscidea* (Fig. 2, event 7). In April 2011, the reef disappeared due to a storm and the mussel beds recolonized the South Impacted Site partially.

The formation and growth of dense masses of *Boccardia* tubes around mussel beds smothered the bivalves (Fig. 4). In sewage-impacted areas, the supply of organic matter is enough to sustain a population of *Boccardia*. However, this amount of organic matter brings about deleterious consequences to mussels which then decrease in abundance and exhibit poor biological condition (Vallarino, 2002; Vallarino et al., 2002). The introduction of *B. proboscidea* probably occurred several years ago without ecological consequences, coexisting with the other spionids species and the mussels in the intertidal community. The increase of the *B. proboscidea* population is probably caused by the increase of the sewage-contamination. The organic matter content in sewage-impacted sites increased from 0.5% to 1% (previous to 2008) to more than 2% in 2008, in agreement with the development of *B. proboscidea* reefs (Sánchez et al., 2011). This, together with the weakness of the mussels caused by sewage contamination, enabled the explosive development of the polychaete population and led to decrease of the mussel beds in sewage-impacted sites. Previous works in both *B. rodriguezii* population (Vallarino et al., 2012) and the community (Vallarino et al., 2002; Vallarino and Elías, 2006) show the declination of mussels in the sewage-impacted area. The temporal trend shows that the reference sites are affected by seasonal variability, whereas in sewage-impacted sites the changes on the intertidal benthic community are forced by the sewage discharges (Vallarino and Elías, 2006). The invader polychaetes outcompetes the local intertidal species displacing the ecosystem engineer *B. rodriguezii* as structuring species due to a combination of weakness of the mussels and competitive exclusion for space.

Reefs found in the South Impacted Site on November 2008 were spherically or irregularly shaped, covering the rocks completely under the influence of sewage. Reefs have been found even on vertical walls of rocks. These biogenic reefs are built by aggregations of thousands of cohesive and hard *B. proboscidea* tubes strong enough to walk over. In longitudinal internal view, the tubes showed mostly parallel and vertical orientation (Jaubet et al., 2011, unpublished data). The sediment grains of each tube are bound by mucus secreted by large paired gland present in some body's chaetigers of the worm (Simon et al., 2010), linked to a thinner inner organic layer. Simon et al. (2010) described the species as secondary borer in abalone shells. However, in Argentina, the species is a primary borer. This is in agreement with Hartman (1940) and Woodwick (1963). This species was also recorded in Patagonia, inhabiting both stony rocks and sand beaches. Stony rocks are almost destroyed by the boring activity of *B. proboscidea* (E. Diez and V. Radashevsky, personal communications); however tube building in sandy beaches is only possible due to sheltered habitat. In Mar del Plata, it is suspected that these spionids settle primarily in stony rocks, boring among mussel beds. However, high rates of sedimentation of both inorganic and organic particles from the sewage effluent force the worms to build a tube in order to avoid be buried. The tube-building is then a secondary adaptation.

In their natural habitat, Pacific area, *B. proboscidea* reached densities no greater than 164,000 ind m^{-2} under a secondary treated sewage discharge (Dorsey et al., 1983). In Mar del Plata, densities of this species in the reefs reached 1,465,000 ind m^{-2} (Garaffo et al., 2012) and even 2,340,000 ind m^{-2} (unpublished data) under an untreated sewage discharge.

Polydorid worms, like *B. proboscidea*, display both r-selected (high fecundity, fast maturation rates, a semi-continuous supply of larvae and rapid population growth) and k-selected (encapsulation of eggs which are brooded within the maternal burrow) traits (Simon et al., 2005). In addition, they also produce larvae that are either planktonic or benthic (Blake and Arnofsky, 1999), with aseasonal recruitment periods (Simon and Booth, 2007). Some spionids, like as *Polydora cornuta*, can growth very fast reaching up to 60% $.day^{-1}$ of their body-volume under moderated experimental currents (Hentschel and Harper, 2006). *B. proboscidea* growth could be even greater because of the strong longshore current (15 cm s^{-1}, Isla and Ferrante, 1997) and the large supply of food through sewage. This could explain the fast building of the massive biological formations by *B. proboscidea*. In order to estimate the change of surface and volume reached of the reefs, the spherical cup formula

Fig. 3. Photo showing the South Impacted Site (located 1000–1200 m south of the sewage discharge of Mar del Plata city) covered completely by *Boccardia proboscidea* biogenic reefs. The person shown in the photo has an approximate height of 1.65 m.

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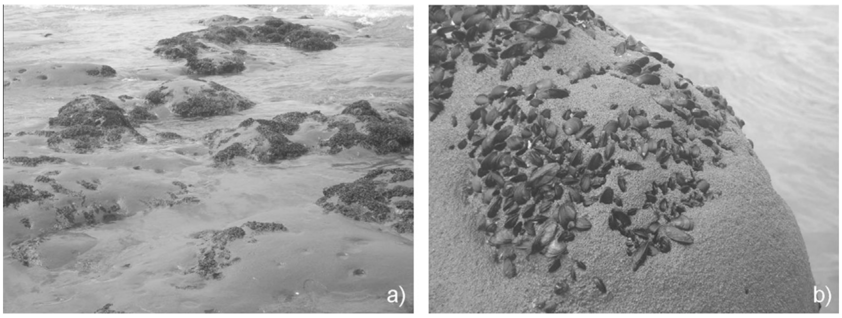

Fig. 4. Suffocation dynamics of *Brachidontes rodriguezii* ecosystem engineer by *Boccardia proboscidea* invasive polychaetes: (a) *B. rodriguezii* mussel beds being smothered by fast growth *Boccardia proboscidea* reef; and (b) photo showing a detail of the suffocation process of mussels.

was calculated. The surface and volume of a 1 m diameter reef vary from initial stages (1 cm height), from 31.42 m^2 and 0.004 m^3 to 34.24 m^2 and 3.5 m^3 in their maximum development (30 cm height). Due to sewage discharge, the high rate of sedimentation forces the worms to build their tubes very fast, increasing the reef volume dramatically. The recoveries of reefs after small scale disturbance take less than 5 days (Garaffo et al., 2012). This, together with the fast body growth, could explain the smothering of mussel beds. Macroalgae (*Bryopsis*, *Polysiphonia*, *Ulvacea*) that could attach to some hard surfaces ends up dying because they also get buried and covered by reef development. The lack of physical space among mass tubes as well as the anoxic condition could explain the impossibility of any other organisms to inhabit this reef. Due to the phenomenon described in this study and its effect in the environments, *B. proboscidea* could be considered as auto-ecosystem engineer since the organisms made a tridimensional habitat but only for it selves. Coral reefs are characterized to provide spatial heterogeneity and increase biodiversity; however the *B. proboscidea* biogenic reefs constitute a monoculture that excludes all flora and fauna associated with intertidal community (Jaubet et al., 2011; Garaffo et al., 2012).

The development of *B. proboscidea* reef is a sewage-dependent phenomenon because it is limited to the areas surrounding the outfall. However, in non-impacted sites, *B. proboscidea* and *B. rodriguezii* coexist in patches of variable size. This might be due to the low organic matter supply.

4. Conclusion

Untreated sewage discharge in intertidal stony rocks induced the explosive development of a *B. proboscidea* population inhabiting among ecosystem engineer mussels. Fast individual growth, high reproduction rates and large supplies of organic matter allows the development of biogenic structures reefs-like. These reefs smothered and excluded the mussel beds in sewage-impacted sites. When reefs are fully developed, they cover the entire surface of rocks avoiding the mussel settlement. The process is coupled to the pauperization of individual mussels exhibiting poor biological condition due to sewage pollution. The outcompeting of *B. rodriguezii* mussel by *B. proboscidea* polychaetes is a sewage-dependent process.

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