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Effect of the invader *Boccardia proboscidea* (Polychaeta: Spionidae) on richness, diversity and structure of SW Atlantic epilithic intertidal community



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ABSTRACT

In Mar del Plata (Argentine, SW Atlantic), a large seaside resort, the sewage discharges impact the littoral ecosystem. The invader polychaete *Boccardia proboscidea* has developed reefs since spring of 2008. The effect of this species on the richness, diversity and structure of epilithic intertidal community was assessed through an MBACI design in both sewage-impacted and reference sites, and Before/After the invasion. The presence of reefs of *B. proboscidea* since spring 2008 has caused a significant reduction of total individuals, total taxa and diversity in sewage-impacted sites regarding the reference ones. The species analyzed showed a high variable response because patterns were dominated by small-scale variability. Occasional peaks in abundance were observed on a single sampling site and time and a large variation among replicates. The associated fauna, formerly rich and diverse in impacted sites, shows a tendency to disappear as the ecosystem engineer *Brachidontes rodriguezii* is replaced by monocultures of *B. proboscidea*.

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1. Introduction

The presence of reef-building organisms increases richness and diversity by promoting habitat heterogeneity (Hewitt et al., 2005; McClain and Barry, 2010). It is widely accepted that an increase in habitat complexity will increase the diversity and/or abundance of the associated fauna (Crooks, 2002; Bouma et al., 2009). Coral reefs are the typical example of biogenic structures that most habitats create, but there are other organisms that can also create habitats allowing other organisms to live within or on. These organisms are often called ecosystem engineers. They regulate directly or indirectly the availability of resources to other species by changing the physical structure, complexity and heterogeneity of the environment (Jones et al., 1994, 1997; Gutiérrez et al., 2003). In Patagonian salt marshes, the richness and diversity of species were

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positively related to habitat complexity, while total density showed the opposite trend (Sueiro et al., 2011).

Intertidal mytilids ecosystem-engineers usually form multistratified complex matrices. Mussel beds in Southern latitudes are mainly monocultures of mytilids like *Mytilus*, *Brachidontes* or *Perumytilus*, whose heterogeneous structures are described as a secondary habitats for sessile and mobile organisms (Tsuchiya and Nishihira, 1985; 1986; Tsuchiya and Bellan-Santini, 1989; Suchanek, 1992; Seed and Suchanek, 1992; Tokeshi, 1995; Günther, 1996; Svane and Setyobudiandi 1996; Ragnarsson and Rafaelli, 1999; Vallarino et al., 2002; Adami et al., 2004; 2005; Borthagaray and Carranza, 2007). Thus, the presence of mussel beds increases the macrofaunal diversity over relative to that of adjacent bare areas (Günther, 1996).

The small mussel *Brachidontes rodriguezii* (d'Orbigny, 1846) forms beds on the SW Atlantic intertidal rocky shore, monopolizing the primary substrate and competitively excluding other sessile organisms (Adami, 2005). It is considered an ecosystem engineer (Borthagaray and Carranza, 2007).

In the argentine coast of the SW Atlantic, an unusual phenomenon is produced on the richness and diversity of the epilithic community. The intertidal community developed on abrasion

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platforms (hard substrate of stony rocks) was characterized by *B. rodriguezii* and had a relatively low number of associated macroinvertebrates (Vallarino et al., 2002). The natural area was characterized by the dominance of *B. rodriguezii* (between 82% and 91%), what produces low richness, diversity and evenness of the associated flora and fauna. By contrast, sewage-impacted areas presented higher richness and diversity in both temporal and spatial scale, with the organic contamination causing a decrease in mussel dominance and increasing the number of tolerant and opportunistic species, particularly closer to the effluent (Vallarino et al., 2002; Elias et al., 2006; Vallarino and Elías, 2006).

Since the spring of 2008, massive intertidal reefs have been developed in sewage-impacted areas. These reefs were constructed by an invader species, *Boccardia proboscidea* (Jaubet et al., 2011; Garaffo et al., 2012). The polychaete is native from British Columbia to Baja California as a solitary, not-reef builder (Hartman, 1941). The species have been mentioned as non-indigenous in 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 (Martínez et al., 2006). According to Kamel et al. (2010) it appears to have been introduced in all these places, inhabiting both hard (boring) and soft substrates, but only forming reefs in sewage-impacted areas of Argentine (see Jaubet et al., 2014 and reference therein).

Because the reefs began as tubes among bivalves, and eventually became dominants, it is hypothesized that this polychaete has a significant effect on richness, diversity and in the mussel community structure. To assess the possible effect of the invader *B. proboscidea* on intertidal epilithic community a MBACI (Multiple Before–After Control–Impact), sampling design was performed. The analysis evaluate the structure and associated fauna in reference and sewage-impacted locations over two periods, one dominated by the mussel beds (before the arrival of the invader polychaete) and the other dominated by the polychaete reefs.

2. Material and methods

2.1. Study area

Mar del Plata (38°S, 57°W) is situated along a littoral fringe with by sandy beaches and outcrops of quartzite and stony rocks of consolidate loess, which forms almost horizontal abrasion platforms. The intertidal community studied develops on abrasion platforms both around Mar del Plata sewage outfall and reference sites.

Mar del Plata sewer discharge pre-treated material (trituration and sieving through 0.5 mm mesh) directly to intertidal fringe, with a mean volume of 2.8 m 3 s $^{-1}$ reaching up to 3.5 m 3 s $^{-1}$ during summer (Scagliola et al., 2006), when between 2 to 3 million people visit the city (Bouvet et al., 2005).

$2.2.\ Sampling\ design\ and\ field\ procedures$

The design used to evaluate the effects of *B. proboscidea* reefs on the structure of macrofaunal assemblages was based on the MBACI (Multiple Before–After Control–Impact) sampling strategy (Keough and Mapstone, 1997; Downes et al., 2002). This design is appropriate for impact assessment since it incorporates multiple sampling times, both before and after disturbance, in multiple control and impacted locations, ensuring appropriate temporal and spatial replication (Keough and Mapstone, 1997; Downes et al., 2002).

The locations impacted by *B. proboscidea* reef (induced by sewage-discharges) were at 50–200 m (Impacted 1) and 1000–1200 m south to the sewage effluent (Impacted 2). The reference locations (without polychaete reef) were place at 9000–8000 m north to the

sewage outfall (Control 1 and 2, respectively) (Fig. 1). In each location, we selected three stations 50 m-apart from each other at the high intertidal. In each station 4 sampling units were randomly collected from independent rocks of high intertidal by mean of a 10 cm-diameter corer (78 cm²), which was buried into the community matrix up to the basal rocky bottom. In order to simplify the linear model used in the analysis and also reduce the amount of information presented in graphs, data from the 4 sampling units were averaged and the three stations treated as replicates.

The samples were preserved in a 7% neutralized formalin in sea water solution. In the laboratory, each sampling unit was sieved trough a 0.5 mm mesh and the retained organisms were identified, counted and preserved in a 70% ethanol solution.

The reefs of *B. proboscidea* were first detected in the spring of 2008, and we collected samples Before (T1 = February 2008; T2 = April 2008; T3 = June 2008) and After (T1 = November 2008; T2 = January 2009; T3 = November 2009).

2.3. Data analyses

The total abundance of macrofauna, number of taxa, Shannon–Weaver diversity index and abundance of dominant taxa were analyzed separately using analysis of variance. The abundance of *Boccardia probocidea* was not used to calculate community structure descriptors, and its differences in abundance were tested separately. The linear model consisted of four factors with the following structure: Stress (two levels, fixed and crossed – control and impact), Period (two levels, fixed and crossed – before and after), Locations (two levels, random and nested within Stress) and Times (three levels, fixed and nested within Period).

Fitting a full ANOVA model containing all main effects and interactions (i.e. omnibus ANOVA) is a necessary step to correctly construct the planned comparisons to test specific hypothesis on treatments means. The omnibus ANOVA provided the appropriate mean square and degrees of freedom of the error term used for any subsequent planned comparison. In the MBACI design, the impact

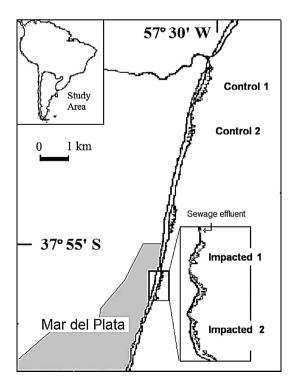


Fig. 1. Sampling locations in two impacted sites by *Boccardia proboscidea* reef (sewage-impacted), and two reference sites without reefs, SW Atlantic shore (Mar del Plata city).

is identified by the interaction Stress \times Period ($S \times P$) indicating an overall difference between the impacted locations compared to controls from before to after the B. proboscidea invasion. The $S \times P$ interaction was examined using two planned comparisons testing for differences in each response variable between before and after sampling times at control and impact locations separately. Planned comparisons were tested over the $L(S) \times P$ interaction, which is the appropriate error term taken from the omnibus ANOVA (Keough and Mapstone, 1997; Downes et al., 2002).

Degrees of freedom, Mean Square Estimates and F-ratios for the MBACI model were calculated according to Keough and Mapstone (1997) and Downes et al. (2002) in the R environment (R Core Team, 2013). The homogeneity of variances was verified with the Bartlett's test and data were $\ln(x+1)$ transformed.

Differences among macrofaunal assemblages were tested by permutational multivariate analysis of variance (Anderson, 2001) using the same linear model from the univariate analyses through the PERMANOVA+ add-on package for PRIMER v6 (Clarke and Gorley, 2006; Anderson et al., 2008). A non-metric multidimensional scaling (nMDS) analysis was performed to visualize the main variation trends of assemblages between Stress and Period using vegan (Oksanen et al., 2013) package in the R environment (R Core Team, 2013). All multivariate analyses used the similarity coefficient of Bray-Curtis with ln(x+1) transformed data to downweighting the importance of the highly abundant species, so that the similarities depend not only on their values but also on those less common 'mid-range' species. The Similarity Percentage procedure (SIMPER) (Clarke, 1993) was used to determine the contributions of individual species to the Bray-Curtis dissimilarities between Before/After.

3. Results

Total number of individuals (excluding *B. proboscidea*) differs between Control and Impact treatments, as well as between Before and After the polychaete invasion. Impacted locations had low number of individuals, and after the polychaete invasion, the number was even lower, particularly in T3 (Fig. 2). Stress, Period, Time, Stress \times Period and Location(Stress) had a significant effect on the total number of macrofaunal individuals, while Locations(Stress) \times Times (Period) was significant (Table 1).

For Total number of taxa only differences in Times (Period) and the interaction $L(S) \times T(P)$ were significant. The general trend was to decrease after the polychaete invasion, and in particular for T3. The Shannon–Weaver index showed significant differences in Location(Stress), Times(Period) and Stress \times T(P). Values were greater for impacted sites rather than for reference sites, although the trend was decreasing from T1 to T3 (Fig. 2).

Patterns of dominant species were variable (Fig. 2). Part of this variability is due to variations in locations and patchy community distribution. The ecosystem engineer B. rodriguezii showed highly significant differences in Stress, as well as B. proboscidea. The mussels were abundant in reference sites (both Before and After) compared to the impacted sites, where abundances were even lower after the polychaete invasion, and almost zero in T3. B. proboscidea was exclusive from After the invasion, while Boccardia spp. was present only Before the invasion and absent After the invasion. In Location(Stress) Boccardia spp. showed significant differences, and Alitta succinea, Capitella sp. and Syllis gracilis showed highly significant differences. The polychaetes B. proboscidea and Boccardia spp. showed significant differences in Period, as well as B. rodriguezii. The interaction $S \times P$ was only highly significant for B. rodriguezii and significant for B. proboscidea. The interaction $S \times T(P)$ was significant only for *Boccardia* spp. (Table 1).

Of all taxa and community parameters analyzed, planned comparisons show that only total macrofaunal density and

densities of *Boccardia* spp. were consistently impacted by the invader polychaete (Table 2). Total density of macrofauna and density of *Boccardia* spp. were significantly lower at impact sites After the invasion rather than Before. However, they did not vary in reference sites (Table 2). Responses in Total number of taxa was lower at impact sites before the invasion than after the invasion and approached significance (P = 0.07). *B. proboscidea* and *B. rodriguezii* responses were significantly different Before the invasion in both reference and impact sites (Table 2).

Despite a significant $L(S) \times T(P)$ interaction in PERMANOVA (Table 3), nMDS ordination has shown a clear difference in macrofaunal community Before the invasion compared with After polychaete invasion (Fig. 3). Differences in community structure between control and impact sites are more evident after the *B. proboscidea* invasion than before, which could be indicative of an impact.

The differences in multivariate analysis showed highly significant differences according to Stress, Locations (*S*), and in interactions between Locations, Period and Times (Table 3).

The differences between Before/After polychaete invasion were given mainly by the presence and abundance of two species: the mussel *B. rodriguezii* and the invader polychaete *B. proboscidea* (Table 4). The ecosystem engineer was responsible for more than 50% of dissimilarity due to the significant decrease. Note that the two other species that have mostly contributed to difference Before/After invasion periods were *B. proboscidea* (the invader) and the fading of the companion *Boccardia* spp. The total companion fauna was composed by 25 items (24 species, not shown), including empty shells of the ecosystem engineer *B. rodriguezii* (an indirect measures of mussel mortality), two times greater After the invasion. However, only 6 species account for the 98% of total individuals.

4. Discussion

The studied intertidal epilithic community has shown a significant shift in sewage-impacted sites. On one hand, the ecosystem engineer mussel *B. rodriguezii* has dominated and characterized this community through time (see Scelzo et al., 1996 and references therein), even in sewage-impacted sites (Vallarino et al., 2002, Vallarino and Elias, 2006). However, the increasing contamination nearby the sewage outfall caused a significant decrease in the mussel population (Jaubet et al., 2013; Vallarino et al., 2014). On the other hand, the sudden explosion of the *B. proboscidea* population, gave rise to the appearance of an polychaete-made reef, while this species had been previously reported as a not reefbuilding one (Jaubet et al., 2011; Garaffo et al., 2012).

There was a significant change in richness (Total taxa) in the epilithic intertidal community in stony rocks. Although there was a naturally fall in diversity and species richness in the epilithic intertidal community living on stony rocks, both descriptors were further reduced as a result of the invasion of the polychaete *B. proboscidea*, which have affected more drastically the impacted sites than the reference ones.

The epilithic intertidal community was unusual, because in reference sites there were very low richness and diversity, just the opposite of the ones in the sewage-impacted. This is due to the high dominance of mussels in reference sites, where *B. rodriguezii* reach between 70% and 90% of the total individuals. In reference sites, the richness of associate fauna and flora was low. High dominance and low richness produced low diversity. However, sites impacted by sewage had mussel population impoverished, and therefore low dominance. Furthermore, the presence of several opportunistic and tolerant species produced an increase of richness, thereby increasing the diversity. This was described as the

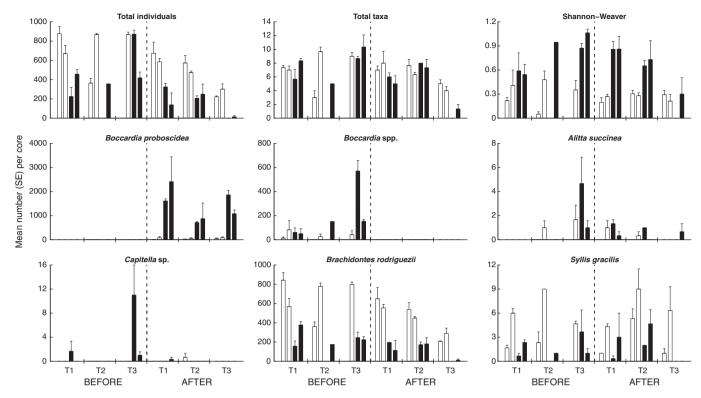


Fig. 2. Mean (SE, n = 4 cores, means of station averages) density of macrofauna, number of taxa, Shannon-Weaver diversity index and densities of dominant taxa in reference (empty bars) and sewage-impacted (full bars) sites from before (T1 = Feb.08; T2 = Apr.08; T3 = Jun.08) to after (T1 = Nov.08; T2 = Jan.09; T3 = Nov.09) the invasion of *Boccardia proboscidea*.

 Table 1

 Summary of Analysis of Variance of the MBACI model for total density of macrofauna, total number of taxa, Shannon-Weaver diversity index and densities of dominant taxa.

Source	df	Total individuals		Total taxa		Shannon-Weaver	
		MS	F	MS	F	MS	F
Stress = S	1	14.93	33.718*	0.42	2171	0.64	9852
Locations(Stress) = L(S)	2	0.44	1076	0.19	3073	0.06	3.438*
Period = P	1	23.01	64.024*	1.01	3306	0.04	0.757
Times(Period) = T(P)	4	12.68	5.572*	2.14	7.303*	0.11	6.343*
$S \times P$	1	11.74	32.658*	0.78	2554	0.05	0.999
$S \times T(P)$	4	6.32	2777	0.83	2830	0.13	7.463*
$L(S) \times P$	2	0.36	0.158	0.30	1038	0.05	2954
$L(S) \times T(P)$	6	2.28	5.528***	0.29	4.636***	0.02	0.940
Residual	42	0.41		0.06		0.02	
Source	df	B. proboscidea		Boccardia spp.		A. succinea	
		MS	F	MS	F	MS	F
Stress = S	1	29.69	56.242*	20.36	5299	0.85	0.675
Locations(Stress) = L(S)	2	0.53	0.864	3.84	3.771*	1.26	9.603***
Period = P	1	245.41	464.927*	112.81	29.352*	0.60	2249
Times(Period) = T(P)	4	1.00	1426	1.58	2442	1.01	2616
$S \times P$	1	29.69	56.242*	20.36	5299	0.07	0.270
$S \times T(P)$	4	1.15	1641	4.12	6.358*	0.09	0.246
$L(S) \times P$	2	0.53	0.755	3.84	5.927*	0.27	0.696
$L(S) \times T(P)$	6	0.70	1144	0.65	0.636	0.39	2.949**
Residual	42	0.61		1.02		0.13	
Source	df	Capitella sp.		B. rodriguezii		S. gracilis	
		MS	F	MS	F	MS	F
Stress = S	1	2.49	1608	29.67	427.690**	3.25	0.907
Locations(Stress) = L(S)	2	1.55	13.695***	0.07	0.148	3.58	13.184*
Period = P	1	2.14	1155	15.51	328.017**	0.44	0.892
Times(Period) = T(P)	4	0.44	2291	12.33	8.454*	2.13	6.294*
$S \times P$	1	2.71	1466	6.76	142.977**	0.60	1200
$S \times T(P)$	4	0.46	2401	5.93	4065	0.19	0.568
$L(S) \times P$	2	1.85	9.653*	0.05	0.032	0.50	1471
$L(S) \times T(P)$	6	0.19	1693	1.46	3.102*	0.34	1245
Residual	42	0.11		0.47		0.27	

Significance codes: *P < 0.05; **P < 0.01; ***P < 0.001.

Table 2Planned comparisons for total density of macrofauna, total number of taxa, Shannon-Weaver diversity index and densities of dominant taxa contrasting temporal changes at control and impact sites.

Source	df	Total individuals		Total taxa		Shannon-Weaver	
		MS	P	MS	P	MS	P
Control (Before vs. After)	1	1764	0.157	0.051	0.723	0.004	0.812
Impact (Before vs. After)	1	41,626	0.009	3727	0.073	0.163	0.220
Error	2	0.359		0.305		0.052	
Source	df	B. proboscidea		Boccardia spp.		A. succinea	
		MS	P	MS	P	MS	P
Control (Before vs. After)	1	92,920	0.006	38,731	0.087	0.149	0.534
Impact (Before vs. After)	1	3,66,112	0.001	1,44,221	0.026	0.177	0.503
Error	2	0.528		3843		0.269	
Source	df	Capitella sp.		B. rodriguezii		S. gracilis	
		MS	P	MS	P	MS	P
Control (Before vs. After)	1	0.030	0.910	1547	0.029	0.134	0.656
Impact (Before vs. After)	1	4525	0.258	31,375	0.002	0.343	0.494
Error	2	1851		0.047		0.497	

Appropriate error terms were taken from omnibus ANOVA. Bold values are significant.

Table 3Summary of PERMANOVA (9999 permutations) of the MBACI model based on Bray-Curtis dissimilarities of ln(x+1) transformed macrofaunal densities.

Source	df	MS	Pseudo-F
Stress = S	1	5789.7	4.689***
Locations(Stress) = L(S)	2	1450.6	3.405***
Period = P	1	7992.8	8493
Times(Period) = T(P)	4	3209.9	3.01*
$S \times P$	1	3016.3	3205
$S \times T(P)$	4	2612.4	2.446*
$L(S) \times P$	2	1078.4	2.532**
$L(S) \times T(P)$	6	1150.8	2.702***
Residual	42	425.9	

Significance codes: *P < 0.05; **P < 0.01; ***P < 0.001.

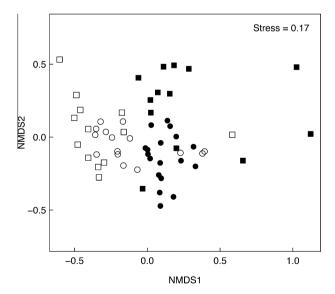


Fig. 3. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix of $\ln(x+1)$ transformed data comparing macrofaunal assemblages between reference and sewage-impacted sites from before (Control = \bigcirc ; Impact = \blacksquare) to after (Control = \bullet ; Impact = \blacksquare) the *Boccardia proboscidea* invasion. Stress = 0.17

paradox of epilitic intertidal community, i.e. low richness and diversity in areas of reference and high richness and diversity in sewage-impacted sites (Vallarino and Elias, 2006). However, the invasion of *B. proboscidea* produced an acute effect in total number of taxa, diversity, and the abundances of the species. Vallarino

(2002) mentioned 43 companion species, but 98% of individual belongs to only 13 species. In the present study, only 6 species were responsible for the 98% of individuals.

The reef formations, resulting from the bloom of *Boccardia proboscidea*, cover almost entirely the sewage-impacted sites, from 50 to 1200 m south to outfall when this study was developed (Jaubet et al., 2013). Nowadays, the intertidal area shows patches of mussel community alternating with polychaetes reefs. Reefs are also present in reference sites (8000–9000 m to north), but they are in patches with low coverage, alternating with the epilithic intertidal community of mussel beds, bare space and algae (Jaubet et al., 2011; 2013).

Mar del Plata reefs cannot be compared with any other reefformation associated to sewage-impacted sites because, to the best of our knowledge, the present one is the only report of such a phenomenon. *B. proboscidea* mentioned in high densities (>160,000 ind m⁻²) were reported from an intertidal substrate affected by secondary treated sewage discharge in Australia (Dorsey, 1982). However, in Mar del Plata this polychaete reached densities greater than 1,600,000 ind m⁻² (Jaubet, 2013; Jaubet et al., 2013). This extraordinary density leads to build reefs formations more than 30 cm high, which were strong enough to support a person walking up. Probably, the grease released with the sewage allows blinding the sediment and giving a high resistance to the reefs (Jaubet, 2013).

Although some small-scale variations occurred, the monoculture of *B. proboscidea* had a significant effect on community structure. The associate fauna and flora living on and within the mussel beds disappeared. Formerly, rich and diverse fauna living among mussel had no place to live, because the invader polychaete filled in all available space. Epilithic algae, also rich and diverse in both reference and sewage-impacted sites (Santiago, 2009) were also excluded. Some algae (*Bryopsis*, for example) made patches over polychaete reef. However, the algal attachment was buried by the growing reef, causing the rot and, finally the algal death (Elias, personal observations).

The structure of the intertidal community has been severely affected by the introduction of the polychaete *B. proboscidea*. Since 2008, the population of this polychaete exploded. It was suspected that the species was present as companion fauna in the mussel beds, together with *B. polybranchia*, and other tolerant polychaete species (see Elías et al. 2003; 2006). The reasons to explain the explosive development of *B. proboscidea* are unknown, but they could be triggered by the high organic matter content in the

Table 4SIMPER. Species that most contributes to dissimilarity between Before and After *Boccardia proboscidea* invasion. Average abundance is log(X+1) transformation.

Species	Before	After					
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%	
Brachidontes rodriguezii	3.45	3.94	14.93	1.06	53.65	53.65	
Boccardia proboscidea	0	3.23	10.17	0.81	26.87	80.52	
Boccardia spp.	1.54	0	5.66	1	10.12	90.64	
Empty shells of B. rodriguezii	0.95	1.71	5.36	0.94	3.05	93.70	
Pachysiphonarialessoni	0.72	1.03	4.35	1.02	2.49	96.18	
Syllis prolixa	0.82	0.86	4.24	1.02	0.94	97.13	
Syllis gracilis	0.70	0.89	3.73	1.03	0.76	97.89	
Lineus bonaerensis	0.28	0.43	2.23	0.73	0.4	98.28	
Leodamasuncinata	0.04	0.43	2.21	0.88	0.31	98.59	
Syllidaeindet	0.65	0.01	1.76	0.76	0.26	98.85	
Capitella sp.	0.20	0.06	1.75	0.63	0.23	99.09	

mussel matrix from 2008 (Jaubet et al., 2013). The growing of Mar del Plata city, together with the increase in fish flour production could be the reason for the increasing organic pollution. Fishery, fish flour factories, tourism, restaurants, and textile industry are the main industrial activity of Mar del Plata. They supply about 18 tons of grease by day (63% has industrial origin and the other 37% has domestic origin) to the urban wastewater (Scagliola et al., 2006; 2011).

Only the amphipod *Monocorophium* sp. was able to inhabit the reef build by *B. proboscidea*, living among the polychaete tubes with direct contact to the water interface, but not inside the reef (Sanchez, 2014), where the conditions were unfavorable due to anoxia. The only infaunal organism living inside the reef was *A. succinea*. Visual observation of reefs showed trials of black (anoxic) sediment in the surface produce by *A. succinea* (Elias, pers. obs.). Perhaps the ondulatory behavior of nereidids allowed this species to tolerate anoxic conditions within the reef. All other infaunal organisms, formerly present among mussels were excluded.

A positive correlation between reef mass and infaunal biomass, density and diversity was found in the reefs made by the invader polychaete *Ficopomatus enigmaticus* in South Africa (McQuaid and Griffiths, 2014). This species was also an ecosystem engineer by providing habitat complexity, food, and shelter to its associated fauna (Schwindt et al., 2001, 2004). The underlying hypothesis is that the greater the structure, the greater will be the available resources, habitats, and niches (Connor and McCoy, 2001). However, in Mar del Plata a square meter of substrate becomes 3.5 m³ of reef of *B. proboscidea* (Jaubet et al., 2013), a massive structure which does not provide habitat complexity. Accordingly *B. proboscidea* could be considered an auto-ecosystem engineer, with its massive, protruding reefs are not heterogeneous and, thus, are virtually self-inhabited.

Native and non-native species components are expected to respond differently to environmental impacts. In Australia, an increasing pollution exposure caused a decrease in native species diversity on hard-substrates by between 33% and 50% (Piola and Johnston, 2008).

Despite the fact that the process of competitive exclusion cannot be fully demonstrated, we hypothesized that the growth of spionids patches among the mussel beds could be responsible of the smothering and depletion of mussels. Intermediate sucessional stages of the epilithiic intertidal community in sewage-impacted sites show mussels in vertical position, trying to avoid been smothered by the increasing presence of *B. proboscidea* tubes (Jaubet et al., 2013). In Mar del Plata sewer, this polychaete reached more than one million of ind m⁻² in less than 5 days after a small scale disturbance (Garaffo et al., 2012). Opportunistic species, as opposed to equilibrium species, are those which respond rapidly to environmental changes by changes of population size. The rate of change, which is the major distinction between species

tending toward opportunism and those tending toward equilibrium, is in turn dependent on both generation time and innate capacity for increase (King, 1964 in: Osman and Whitlatch, 2000).

The principle of competitive exclusion states that stable coexistence cannot result when two co-occurring species have the same ecological requirements. The exclusion may result in either the local extinction of the species having the reproductive disadvantage and that the intrinsic rate of increase r is strongly related in an inverse manner to the size of the individual. B. proboscidea, like other polydorids, 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 (Gibson, 1997; 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). B. proboscidea, is not an exception, having a continuous reproduction period, and brooded eggs with both benthonic and planktonic larvae, being thus able to proliferate in an environment plenty of sewagemediated food (laubet, 2013).

The accommodation of the introduced polychaete *B. proboscidea* to an environment impacted by untreated sewage resulted in a shift in the epilithic intertidal community structure. The boring worm become an invader, tube-building reef forming, facilitated by the pauperization of the original epilithic assemblage and, particularly, by an increasing mortality of the population of the mussel *B. rodriguezii*, ecosystem engineer.

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