


ORIGINAL RESEARCH

The response of the natural and sewage-impacted intertidal epilithic community of the SW Atlantic to pulse (before/after summer) and chronic sewage discharges in the 1997-2014 period

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ABSTRACT. Until 2014 Mar del Plata city discharged its untreated sewage effluents to the intertidal sector. This city has a marked seasonality in the urban discharge, varying between 2.8 and 3.5 m³ s⁻¹ of effluents before/after summer. The effect on the intertidal benthic community was evaluated in both spatially, in sewage-impacted and reference sites, and temporarily in both the short term, before/after summer, and in long term along nine periods between 1997-2014. The bivalve *Brachidontes rodriguezii*, the ecosystem engineer, reach the maximum dominance and frequency in reference areas. Spatially the presence of opportunistic and tolerant species characterized the impacted areas, while in reference sites sensitive species were prevalent. The opportunistic polychaete species *Capitella 'capitata'* sp. and *Alitta succinea* were dominant near the sewage discharge in firsts periods. In other periods the indicator species were *Rhynchospio glutaea* or *Boccardia* spp. From 2008 the invader *Boccardia proboscidea* characterized the sewage-impacted sites building massive reefs. The crustaceans *Jassa falcata* and *Caprella* sp. were very abundant at intermediate distances from the sewage discharge, while *Monocorophium insidiosum* was very abundant in sewage-impacted areas. The tolerant and opportunistic species are favored after the summer due to the extra organic matter input. All community parameters showed lower values after the summer, and also a trend to diminish along the studied period.



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Key words: Epilithic community, macrobenthos, mussel bed, long term study, chronic and pulse disturbance, tendency, SW Atlantic.

La respuesta de la comunidad epilítica intermareal natural e impactada por las aguas residuales del Atlántico SO a pulsos (antes/después del verano) y descargas crónicas de aguas residuales en el período 1997-2014

RESUMEN. Hasta 2014 la ciudad de Mar del Plata descargaba sus efluentes cloacales sin tratamiento al sector intermareal. Esta ciudad tiene una marcada estacionalidad en sus descargas, variando el caudal entre 2,8 a 3,5 m³ s⁻¹ antes/después del verano. El efecto sobre la comunidad bentónica intermareal fue evaluado en la escala espacial, en sitios de referencia y sitios impactados, y también temporalmente en el corto período de tiempo, antes/después del verano, y a lo largo de nueve períodos entre 1997-2014. El bivalvo *Brachidontes rodriguezii*, el ingeniero ecosistémico, alcanza su máxima dominancia y frecuencia en áreas de referencia. Espacialmente la presencia de especies oportunistas y tolerantes caracterizó los sitios impactados, mientras que en sitios de referencia las

especies sensibles son prevalentes. En los primeros periodos el poliqueto oportunista *Capitella* “*capitata*” sp. fue dominante cerca de la descarga cloacal, y también *A. succinea*. En periodos posteriores las especies indicadoras fueron *Rhynchospio glutaea* o *Boccardia* spp. Desde 2008 el poliqueto invasor *Boccardia proboscidea* caracterizó los sitios impactados por la descarga por masivos arrecifes. Los crustáceos *Jassa falcata* y *Caprella* sp. fueron muy abundantes a distancias intermedias de la descarga, mientras que *Monocorophium insidiosum* fue muy abundante en el área impactada por la descarga cloacal. Las especies tolerantes u oportunistas se vieron favorecidas después del verano debido al aporte extra de materia orgánica. Todos los parámetros comunitarios mostraron valores menores después del verano, y también se observa una tendencia a disminuir a lo largo de los periodos estudiados.

Palabras clave: Comunidad epilítica, macrobentos, banco de bivalvos, estudio de largo plazo, disturbio crónico y de pulso, tendencia, Atlántico SO.

INTRODUCTION

Marine scientists have realized that the sea is not an inexhaustible sink. The coastal areas first and now huge ocean areas show that marine pollution is global. Increasingly more or larger dead zones deoxygenated seas and oceans due to the discharge of untreated wastewater, which affects marine ecosystems in an area of 245,000 km², with implications for fisheries, livelihoods and food chains (WWAP 2017). Coastal ecosystems are highly vulnerable to multiple environmental human stressors e.g. urban and agricultural runoff of pollutants and nutrients, habitat alteration, aquaculture, fishing, acidification, etc. (Fabry et al. 2008; Halpern et al. 2008).

The main source of organic pollution is associated with the discharge of sewage generated by domestic effluents, being considered the oldest form of pollution (Pearson and Rosenberg 1978; Bishop et al. 2002; Medeiros and Bicego 2004; Borja et al. 2006; Martins et al. 2008; Muniz et al. 2006, 2013). Domestic waters provide organic and inorganic substances, including nutrients (even those that have primary and secondary treatment) that produce eutrophication that leads to changes in structure and functioning of marine ecosystems (Clarke and Warwick 2001; Gray et al. 2002). Eutrophication, i.e. over-feeding the aquatic environment by substances that induce rapid algae growth (Nixon et al. 2009; Ferreira et al. 2011). Nutrient loading in coastal waters may

have direct or indirect effects on the environment. Some of the direct effects may be changes in chlorophyll levels, in primary production, in macro- and microalgae biomass and in the sedimentation of organic matter. Indirect effects include: changes in benthic biomass, benthic community structure, habitat quality, water transparency, increase in organically enriched sediments, changes in dissolved oxygen levels, mortality of aquatic organisms, changes in food chains, among others (Cloern 2001; Islam and Tanaka 2004; Díaz and Rosenberg 2008).

One of the main challenges in environmental impact assessment is to distinguish natural variability of natural communities of that variability induced by human activities. To assess the quality of the environment, and thus try to quantify the damage that man does to the ecosystem, several indices of environmental quality or ecological indices are calculated. Many of these indicators are based on benthic invertebrates because they have little or no mobility, they form associations that include species with a different degree of tolerance to stress, they respond to disturbances at supra-specific levels, such as genera, families and even classes, and finally because integrate the recent history of disturbance (Warwick 1993; Salas et al. 2006; Borja et al. 2008; Patricio et al. 2009; Dauvin et al. 2010; Muniz et al. 2013). The underlying idea that supports the concept of a biological indicator is that the selected organisms or groups provide, express or integrate information about their habitat. This can be shown through the condition, presence/absence, relative

abundance or biomass, reproductive event, association structure (that is, composition and diversity), community function (such as trophic structure, or functional diversity) or any other combination of these characteristics (Muniz et al. 2013).

The city of Mar del Plata (38° S-57° W), in the SW Atlantic, is the largest summer resort in Argentina, receiving about 3 million people in summer time (Bouvet et al. 2005). Although the city has a functional submarine outfall since 2014, sewage water with only a pretreatment was discharged directly into the coastline, 9 km from the city center, for more than 30 years at a mean rate of 2.8 m³ sec⁻¹ and up to 3.5 m³ sec⁻¹ in summer (Scagliola et al. 2006). Fisheries, factories fishmeal, tourism, restaurants and textile industries are the main industrial activity in the city and therefore are responsible for the supplement large amounts of fat (12 t day⁻¹ of industrial origin and 6 t day⁻¹ of domestic origin) to urban wastewater (Scagliola et al. 2006, 2011). The abundance of fecal indicators (*Enterococci* 100 ml⁻¹) showed risk to human health along 15 km of beaches popular use (Comino et al. 2008; 2011).

The scorched mussel *Brachidontes rodriguezii* (D'Orbigny, 1842), an ecosystem engineer inhabits the intertidal hard substrates in large areas of the SW Atlantic, including places with sewage discharges. It is a species that has the peculiarity of dominating natural rocky coasts (Adami et al. 2004). Its community structure has served as an indicator of sewage-impact in Mar del Plata (Vallarino 2002; Jaubet 2013; Sánchez 2013; Llanos 2018). Although the short-term response of polychaetes to increases in sewage discharge during summer is partially known (Elías et al. 2006), its temporal variation in relation to community, both in short and long term periods, is unknown. In this context, the present work describe the spatial-temporal dynamics of the intertidal community in the period 1997-2014, analyzing both impacted sites by sewage (chronic) disturbance by the sewer discharge and

reference sites (not impacted), as well as the community response to the events before/after the summer, in response to the increase of the sewage discharge (pulse disturbance).

MATERIALS AND METHODS

Study area

The coast of Mar del Plata city (Argentina 38° S-57° W) is dominated by sandy beaches, but occasionally there are quarzitic outcrops and horizontal abrasion platforms of consolidated loess formed by silica-cement sandstones (Teruggi 1959; Isla and Ferrante 1997). The tidal regime is regular and semidiurnal, with average heights of 60 cm in quadrature and up to 90 cm in high tides of syzygy, but very subjected to weather conditions. A strong littoral current (15 cm s⁻¹) run from South to North. During autumn-winter frequent storms from the S-SE constantly affect the coast (Manolidis and Alvarez 1994; Isla and Ferrante 1997). The climate is typically marine temperate with regular rains (850 mm year⁻¹). The area is influenced by derived on advected waters from the continental shelf (Subantarctic origin), with temperatures between 8 and 21° C and salinities between 33.3 and 33.8 (Guerrero and Piola 1997; Lucas et al. 2005). The present study was carried out on one of these horizontal platforms, which surrounds the sewage effluent of Mar del Plata city. Similar substrates with similar ecological conditions far from the influence of the sewage were used as reference (or control) sites.

Environmental quality

From the intertidal sewage discharge a gradient of environmental conditions was generated towards the south (sampling zone) by the flume dilution, which was function of the distance from the outfall. Vallarino and Elías (2006) revealed

that salinity was almost constant in the area (around 32-33), but occasionally in some seasons (i.e. autumn-winter) lower values (26-30) were recorded in closest sites to sewage discharge (200-50 m). Dissolved oxygen showed mean values of 10 mg l^{-1} in reference site, but less than 7 mg l^{-1} at 50 m from the effluent. Values of pH ranged 8.0 to 8.3 in reference site, but low near the discharge (7.7 to 8.0). Turbidity was constant in the reference site, reaching mean values of 50 NTU, while increasing to up to 300 NTU in sites under the influence of sewage discharge, particularly in the summer (see Vallarino and Elías 2006).

Total Organic Carbon (TOC) of the interstitial sediment was elevated in patches surrounding the effluent (1.5 to 2.0%), and decreased with distance and reference sites (mean of 0.5% at 1,000 m from the effluent and also in the Reference site). Sediment accumulated among mussels also showed an environmental gradient, being more abundant in intermediate distances ($20\text{-}50 \text{ kg m}^{-2}$) and lower in reference sites (between $20\text{-}30 \text{ kg m}^{-2}$), with a minimum in most near site to sewage site ($10\text{-}20 \text{ kg m}^{-2}$).

From 1989-2014 the city's sewage effluent was discharged with only a pre-treatment over the intertidal sector. The construction of the submarine outfall lasted from 2008 to 2014. This included a breakwater that alters the dynamics of the sea by slowing the flux of littoral waters and the rates of sedimentation around it. The intertidal sewer stops in December 2014, when the current submarine outfall was opened, which discharges the city's wastewater through 130 nozzles located in the last section of 500 m long (between 3.9 and 4.4 km offshore).

Sampling design

Monitoring was carried out in three intertidal areas with different distances from the sewage outfall. Each area includes a set of three sampling sites with different condition of organic contami-

nation (Figure 1). In the area called 1S, groups of samples (12 to 36 sampling units of 78 cm^2) were taken between 50 and 200 m from the point of discharge. In the area called 2S, groups of samples were taken between 1,000 and 1,200 m, both south from the point of discharge and the so-called Reference area (i.e. areas without sewage influence) and in different sites between 18,000 to 6,000 m north from the sewer discharge. Because differences between these 'References' were not statistically significant, values were averaged in one area. For more information, see Vallarino et al. (2002), Jaubet et al. (2013), and Sánchez et al. (2013).

Studies lasted for almost 15 years, with different objectives and therefore different sampling designs. However, the constancy of sampling impacted and reference sites and before/after summer in 9 periods was maintained. The original database includes more periods and different seasonality (monthly, quarterly), but for the present study the nine periods that have a before/after summer were considered.

In each site, sampling units were taken in the intertidal benthic community from different and independent rocks. Each sample was fixed with 10% formalin. In laboratory the material was washed and sieved through a 1 mm mesh size and the retained biological material was identified to the lesser taxonomic level, quantified, and preserved in 70% ethanol solution.

Environmental variables

Three 10 g samples of sediments were taken in each site for determination of Total Organic Carbon (TOC) by the method of Walkley and Black (1965) and expressed as percentage.

Data analysis

Factors analyzed were Sites (1S, 2S, Reference), Event (before/after summer), and Periods (9).

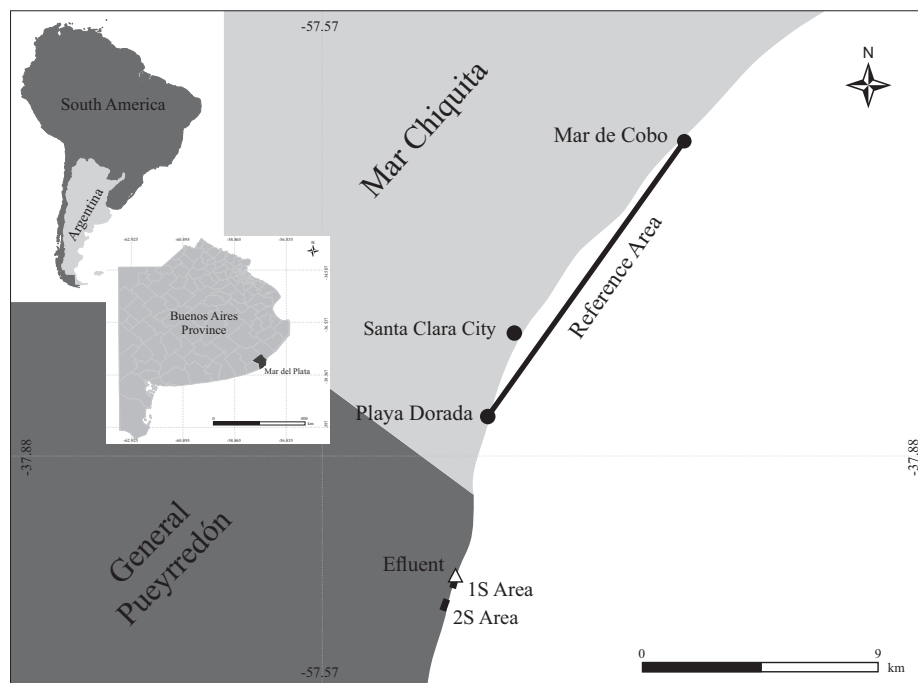


Figure 1. Sampling site. Area 1S is an average of sites located between 50-200 m south to the sewage effluent and Area 2S is an average of sites located between 1,000-1,200 m to the south of the point of discharge. The Reference Area corresponds to several reference sites (black circles). The white triangle is where the sewage discharges intertidally.

From the similarity matrix with square root transformation, a Permanova analysis was performed considering Sites, Event (before/after summer), and Periods (every before/after summer) as fixed factors. The Permanova analysis is a multivariate ‘semiparametric’ test which estimates parameters to adjust the distance matrix to a lineal model (Anderson 2001). Values of p are the result of permutations without normality suppositions, with characteristics of a free distribution test. Due to the existence of significant interactions in the Permanova analyses interpretation of results were conducted graphically.

The analysis of data included ordination by n-MDS and Cluster using a similarity matrix using the Bray-Curtis index with square root transformation to diminish the weight of dominant taxa. In the n-MDS ordination the three sites were discriminated by using different symbols. A cluster diagram was superimposed showing the groups

corresponding to the factor Event (before/after summer with different color). In the same graph, the spearman correlation between sites and species was added. Species were selected from a Similarity Percentage (SIMPER) analyses, and results for every group (Sites, Event) are presented in an Appendix. This graph was made for each of the 9 periods (with before/after sampling). For the trend analysis an oversimplification was made in a n-MDS by averaging the impacted sites (1S, 2S) in one, with averaged reference sites, resulting in 18 points (= samples) for impacted sites (9 before, 9 after) and 18 reference sites. This oversimplification was, however, of little use in clarifying the spatial and temporal behavior of the community. To improve the visualization a new graph was made showing the course of the impacted site and the reference site separately.

From the same matrix the following community parameters were calculated: Richness (S),

Abundance (N), Diversity (H') and Evenness (J'). These data were used to run a bi-factorial ANOVA (with Sites-Periods, and Sites-Events as fixed factors). Dominance was expressed as the abundance of the species over the total abundance, while Frequency was defined as percent of sample with the species over the total of samples.

RESULTS

Percentage of Total Organic Carbon showed significant differences among sites and periods (Table 1). Frequently the sewage-impacted sites showed the greatest values with a slight tendency to diminish. In the Period 2008-2009 a great peak of organic matter was evident in all sites, but in particular in sewage-impacted ones. Although values decrease, they remained higher compared to previous periods (Figure 2).

Table 1. ANOVA of Total Organic Carbon (%) by sites and periods. Data extended from November 1997 to March 2014.

| Effect | SC | df | MS | F | P |
|-------------|-------|----|-------|-------|--------|
| Site | 9.7 | 2 | 4.84 | 25.9 | 0.000* |
| Period | 403.9 | 10 | 40.39 | 216.4 | 0.000* |
| Site*Period | 51.0 | 20 | 2.55 | 13.7 | 0.000* |

Biological data

Total abundance, considering the 547 sampling units analyzed, was 459,437 individual, from 95 taxa of macroinvertebrates. Only a few species were constant and abundant (Appendix, Table A1). *Brachidontes rodriguezii*, the ecosystem engineer, reached maximum dominance (57%) and frequency (84.6%). Among polychaetes, *Syllis prolixa* Ehlers, 1901 was the most abundant

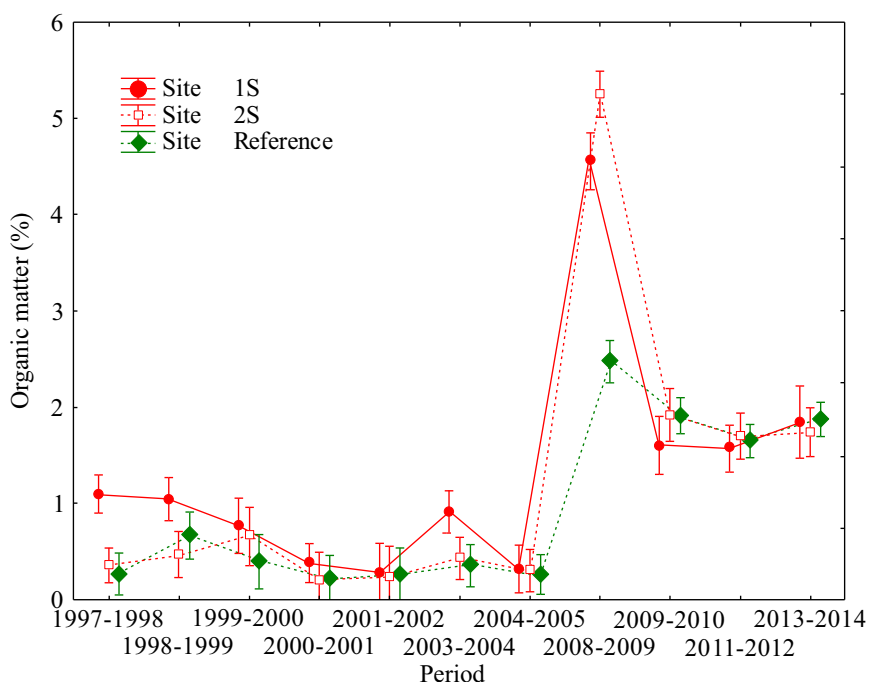


Figure 2. Organic matter from the three sampling Sites, from November 1977 to March 2014. Site 1S is the nearest to sewage (50 m) and 2S is the farthest (1,000 m). Reference sites were between 9 to 18 km north. Data modified from Llanos (2018).

species (4.5%), while in frequency *S. gracilis* Grube, 1840 and *S. proluxa* were both very frequent (76 and 70.9%, respectively). *Boccardia* spp. reached 19 and 15% in dominance and frequency, respectively, while *Boccardia proboscidea* Hartman, 1940, the invader species, was the second in dominance (19.2%) but with a low frequency (15.4%).

Multivariate analysis

A permutational analysis was carried out (999 permutations), considering fixed factors: Sites (1S, 2S, and Reference), Periods (9) and Event (before/after Summer nested in Periods) (Table 2). Due to the existence of significant interactions among all factors (Sites, Periods and Event), the analyses cannot be interpreted but can be analyzed graphically by n-MDS for each period.

Ordination period-event

Period 1997-1998

The n-MDS (Figure 3 A) showed the Reference sites separated from those sewage-impacted. Some sampling units of site 2S were grouped near the Reference sites, mostly before summer. The cluster (represented by the 59% similarity line in the n-MDS) grouped sampling units from before the summer at the top of the graph, while those from after the summer were at the bottom. Sampling units corresponding to the reference sites were grouped by their affinity for each other and kept at the top, unchanged by the summer. The Simper analysis of the percentage of similarity by Sites (Appendix, Table A2) showed *B. rodriguezii* been dominant and important in the Reference area, however decreased in 1S and 2S reaching the third place in these groups. The crustaceans *Jassa falcata* (Montagu, 1808) and *M. insidiosum* (Crawford, 1937) were more important in groups 1S and 2S, as well as the polychaete *C. 'capitata'* sp. On the other hand, the

Event (before/after summer) revealed higher abundances before summer, nevertheless *C. 'capitata'* sp. reached their maximum values after summer (Appendix, Table A3).

Period 1998-1999

The n-MDS (Figure 3 B) showed most Reference sites grouped, with some 2S sampling units, and most impacted sites (1S) and intermediate sampling units (2S) in the opposite side. Group before/after were grouped in the top and the bottom of the graph, respectively. The Simper analysis by sites (Appendix, Table A4) showed a great mean abundance of *B. rodriguezii* respect the precedent period and always remained dominant in the reference site. The polychaetes *Boccardia* spp., *Capitella 'capitata'* sp. and *S. proluxa* Grube, 1840 were dominant, the first two in sewage-impacted sites, while *Syllis* was in reference site.

Considering Events most species showed decreasing values after summer, except the most contributing species, *B. rodriguezii* and *Syllis proluxa* (Appendix, Table A5).

Period 1999-2000

The n-MDS (Figure 3 C) showed sites more or less separated according to sewage-impact,

Table 2. Results of Permanova. Si: Sites, Pe: Period, Ev: Event (nested in Period). In bold significant values.

| Source | fd | SS | MS | Pseudo F | P (perm) |
|-----------|-----|------------|--------|----------|----------|
| Si | 2 | 1.26E + 05 | 63186 | 77.208 | 0.001 |
| Pe | 8 | 2.61E + 05 | 32604 | 39.839 | 0.001 |
| Ev(Pe) | 9 | 96942 | 10771 | 13.162 | 0.001 |
| SixPe | 16 | 1.95E + 05 | 12186 | 14.89 | 0.001 |
| SixEv(Pe) | 18 | 68098 | 3783.2 | 4.6228 | 0.001 |
| Res | 491 | 4.02E + 05 | 818.39 | | |
| Total | 544 | 1.19E + 06 | | | |

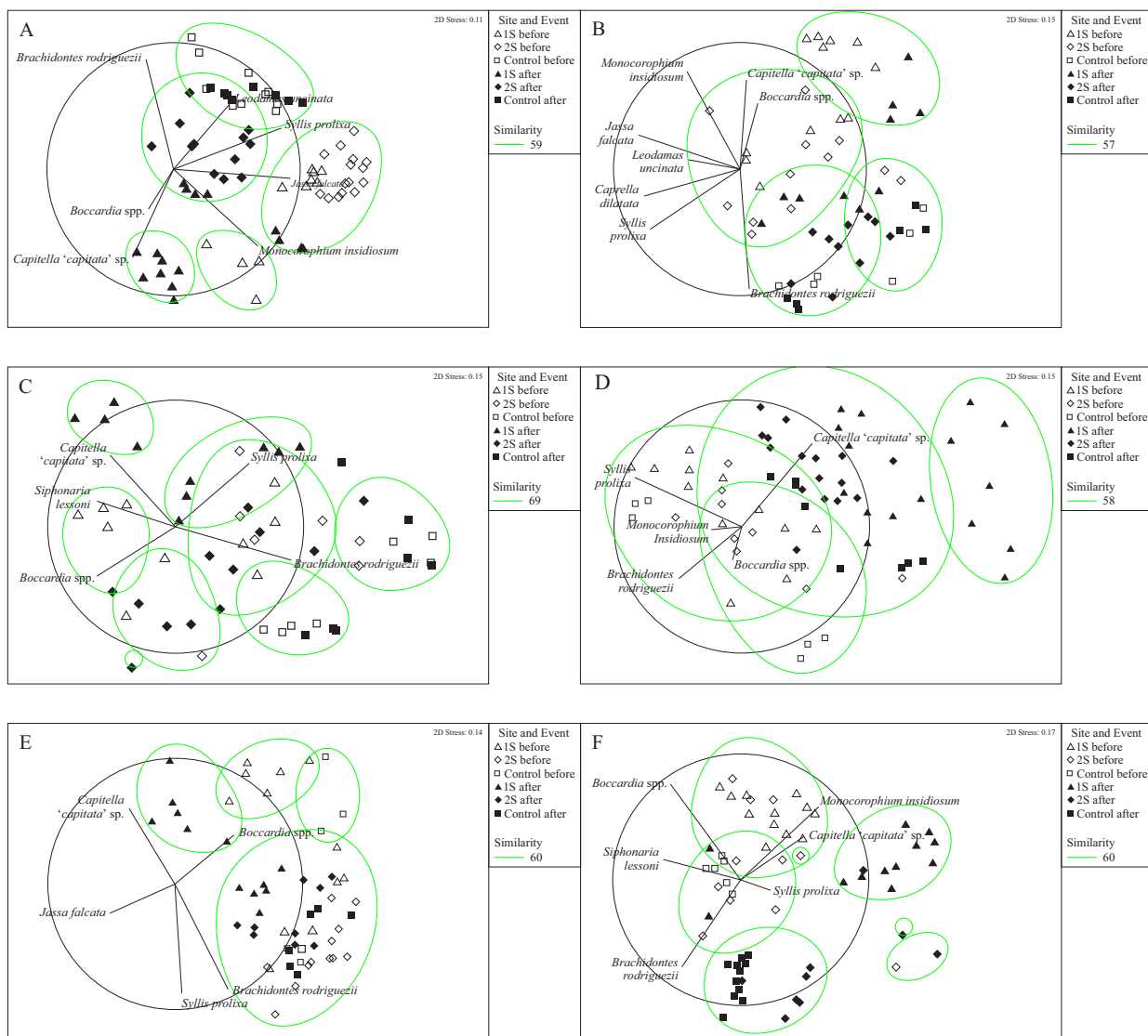


Figure 3. n-MDS showing sampling units for different periods, separated by sites (sewage-impacted, 1S and 2S, and reference site of before (white symbols) and after summer (black symbols)). Green line also represents the similarity aggrupation given by the cluster analysis as before/after summer response. Black circle and vectors correspond to the spearman correlation between species (given by SIMPER) and sampling units. A) n-MDS showing sampling units of period 1997-1998 separated by sites. Green line represents the 59% similarity aggrupation. B) n-MDS of sampling units by sites in the Period 1998-1999. Green line represents the 57% similarity aggrupation. C) n-MDS in the Period 1999-2000 showing reference site and sewage-impacted sites. Green line represents the 69% similarity aggrupation. D) n-MDS showing sampling units in the period 2000-2001. Green line represents the 58% similarity aggrupation. E) n-MDS showing sampling units in the period 2001-2002. Green line represents the 60% similarity aggrupation. F) n-MDS showing sampling units in the period 2002-2003. Green line represents the 60% similarity aggrupation. G) The n-MDS by sites in the Period 2005-2006. Green line represents the 60% similarity aggrupation. H) n-MDS by sites in the period 2008-2009. Green line represents the 60% similarity aggrupation. I) n-MDS by sites in the period 2013-2014 showed two groups of sampling units; one almost avoided of intertidal life in 1S (except to a few *Boccardia proboscidea*), and the rest of sampling units. Green line represents the 60% similarity aggrupation.

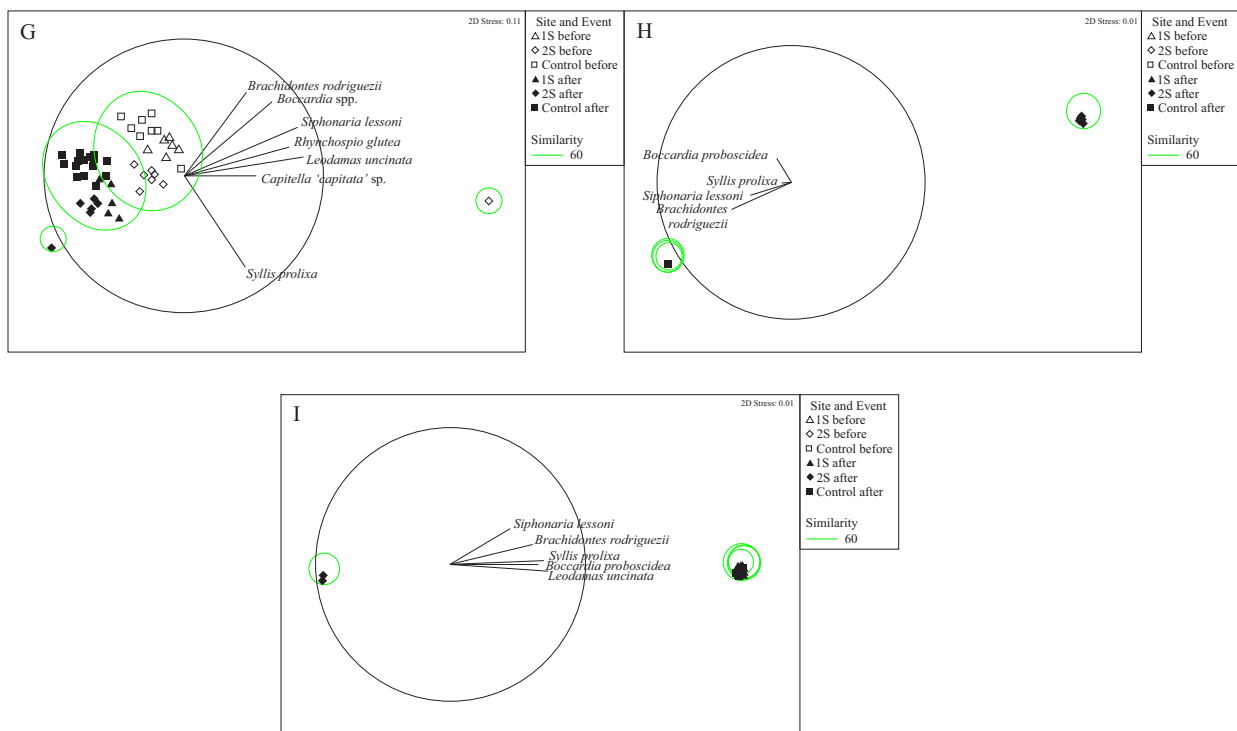


Figure 3. Continued.

except for 1S and 2S mixed, and the reference site units that are apart. The groups at the bottom of the graph represented those before summer, while the upper groups were after summer. The Simper analysis by Sites (Appendix, Table A6) showed *Brachidontes* as the main species contributing to differences among groups, with *Boccardia*, *Capitella* and *Siphonaria lessoni* Blainville, 1827 were dominant in sewage-impacted groups, while *S. prolixa* was dominant in the Reference site. In relation to factor Events most species showed decreasing values (Appendix, Table A7), except *C. 'capitata'* sp. and *S. gracilis*.

Period 2000-2001

The n-MDS (Figure 3 D) showed a mixed pattern of sampling units, without a clear pattern about the potential gradient of sewage impact. The pattern before/after is clearly observed in the

graph; sampling units before are in the left while sampling units after are in the right, related to high observed abundance of *C. 'capitata'* sp. The Simper analysis by Sites (Appendix, Table A8) showed the polychaetes *S. prolixa* and *C. 'capitata'* sp. as the most contributing species in sewage-impacted sites, whereas *B. rodriguezii* was in the Reference site. Respect Events most species showed decreasing values (Appendix, Table A9), but *C. 'capitata'* sp. and *S. gracilis*.

Period 2001-2002

The n-MDS did not show a clear pattern (Figure 3 E). The pattern before/after was also unclear, although the sampling units of 1S were separated in two groups, corresponding to before and after summer, and associate to them were the polychaetes *C. 'capitata'* sp. and *Boccardia* spp. The Simper by sites (Appendix, Table A10) revealed *B. rodriguezii* and *Caprella dilatata*

Krøyer, 1843 as dominant species in the Reference site while impacted sites are dominated by polychaetes like *Boccardia* and *Capitella*. In relation to Events most species showed decreasing values (Appendix, Table A11), except Nematode indet. and *Capitella* 'capitata' sp.

Period 2002-2003

The n-MDS showed well-grouped sampling units, with impacted Sites in one side and Reference sites in the other (Figure 3 F). Upper two clusters represent the before summer, and the others the after summer aggrupation. Indicator species *M. insidiosum* and *C. 'capitata'* sp. were associated with 1S site, the closest to sewage discharge. The Simper analysis (Appendix, Table A12) showed *Boccardia* spp. as the most important species in all sites, been particularly in sewage-impacted ones. *B. rodriguezii* was the second important species in the Reference site. About Events (Appendix, Table A13) several species increase their average abundances after the summer like *Mytilus platensis* d'Orbigny, 1846, *C. 'capitata'* sp. and *M. insidiosum*, whereas other decreases.

Period 2005-2006

The n-MDS (Figure 3 G) showed a crowded pack of sampling units, more or less separated into Reference and impacted sites, except sampling units 376 and 398 (2S). Sampling unit 376 was characterized by the absence of *B. rodriguezii* and a peak of almost 4,000 individual of *Rhynchospio glutaea* (Ehlers, 1897), while 398 had low values of all species. The group at the left represent the aggrupation before summer and the other the after summer samples units. The Simper analysis by sites in the Period 2005-2006 (Appendix, Table A14) showed higher values of *Boccardia* sp. and *Rhynchospio glutaea* in 1S and 2S, respectively. In addition, *Brachidontes* was the dominant species in Reference areas. All species showed decreasing values related to Event (Appendix, Table A15).

Period 2008-2009

The n-MDS showed a pattern of sampling units ruled by the demographic explosion of the invader polychaete *B. proboscidea* (Figure 3 H) resulting that dominated species were grouped to the right, while other sampling units were in the left. The Simper by sites (Appendix, Table A16) showed the dominance of *B. proboscidea* over *B. rodriguezii* in impacted areas. About Events the species showed also the impact of the invasion of *B. proboscidea* (Appendix, Table A17).

Period 2013-2014

The n-MDS (Figure 3 I) showed two groups of sampling units. One characterized by absence of macrofaunal life (left) and the other with the rest of sampling units. The Simper by sites (Appendix, Table A18) showed site 1S avoided of the intertidal community, except a few endolithic *B. proboscidea*. This species has been described as an endolithic form (boring into the sedimentary rock), however in Argentine also develops a new types of habitat, as epilithic form, constructing tubes over the substrate. On the other hand, in the site 2S the invader polychaete is dominant over *B. rodriguezii*. In relation to Event most species showed decreasing values (Appendix, Table A19) but *Siphonaria lessoni* and *B. rodriguezii*.

Long-term trend

The n-MDS (Figure 4 A and B) produced by averaging abundances to made a single impacted or reference point (= sample) shows good stress (0.1), meaning good representation of two dimensional ordination of samples. However three Impacted samples in the upper part of the graph, far from the others due to high dissimilarity, corresponds to the high abundances of the polychaete *B. proboscidea* population (November 2008, February 2009, and November 2009). Large gap responds to the short-term effect (before/after summer, an again back to spring). The large effect of this invasive polychaete distorts the similarity

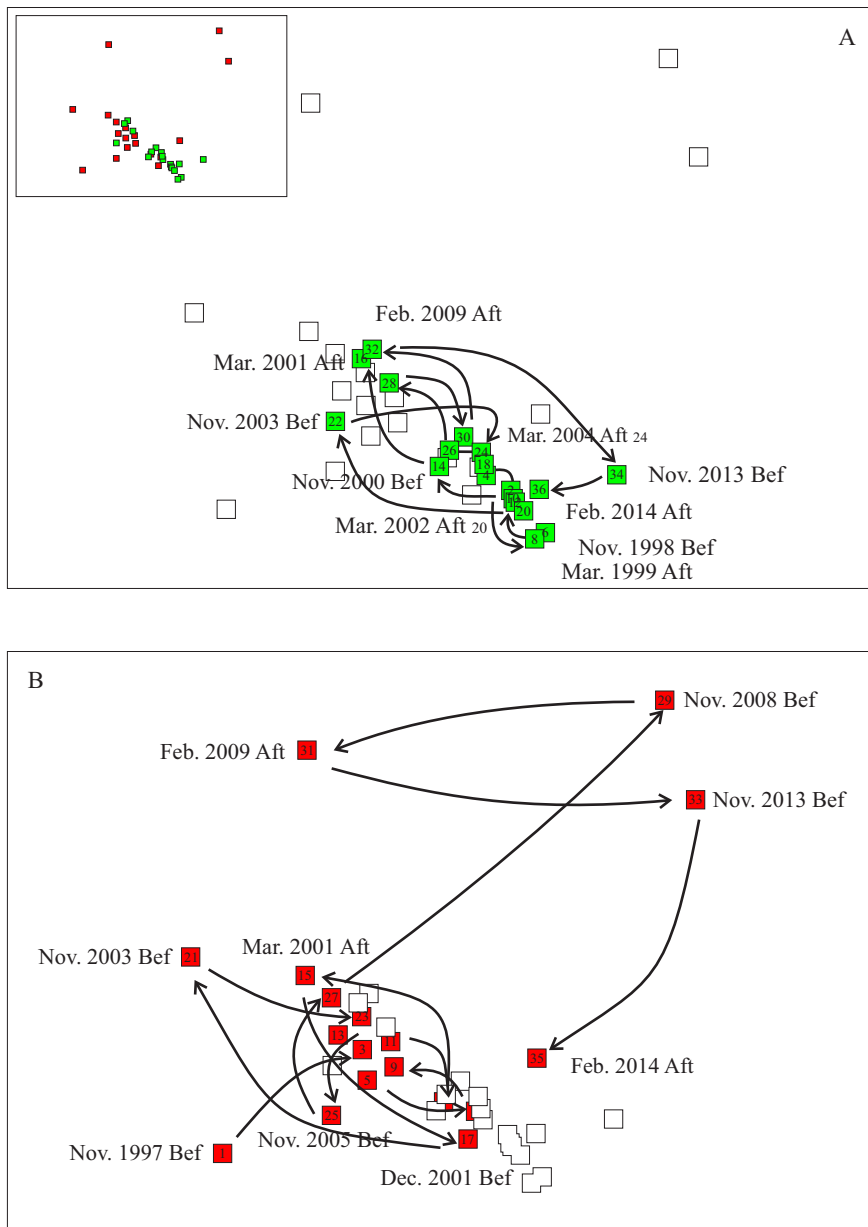


Figure 4. A) Reference site (green squares) with the general n-MDS inserted in the upper corner. B) Impacted sites (red squares). The arrows showed the drift of samples from November 1997 to March 2014. The stress is 0.1.

of the Reference and Impacted site samples. This is the reflection and consequence of the significant interactions of the Permanova that produces a confusing sampling path.

A basal group is mainly made up of samples

from Reference samples (Figure 4 A), and another group of samples located slightly above the previous group mainly made up of samples from Impacted sites (Figure 4 B), both with some inserted samples from the other location.

The basal group of Reference samples (Figure 4 A) is characterized by a great abundance of *B. rodriguezii* (1.100 average abundance) and *S. proluxa* (80), while in the above group *B. rodriguezii* mean abundance is low (385) as well as *S. proluxa* (14), but *Boccardia* spp. (28).

The basal group of Impacted samples (Figure 4 B) differs from the upper group of Impacted samples in the mean abundance of *Brachidontes*, twice in basal group than upper one (767 to 332), but more close to Reference basal samples (1.100). Indicator species are more abundant in Impacted samples, like *Boccardia* spp. (27-30), *R. glutaea* (27-0), *M. insidiosum* (14-6) and *C. 'capitata'* sp. (18-9).

Same samples were separated from these groups. For example, the first impacted sample corresponded to November 1997 (down left). It shows dominance of several crustaceans, like indicators *Jassa falcata* (302), *M. insidiosum* (169), and *Brachidontes* (216), *S. proluxa* (92), *Caprella* (52) and *S. gracilis* (29). The sample Impacted November 2003 before summer (left middle) showed a great abundance of *Boccardia* spp. (275) and low *Brachidontes* (148), and very low *Jassa* (4), *S. proluxa* (3), *Caprella* (0.1) and some *Monocorophium* (19).

The largest gaps between samples corresponded to the short-term change due to seasonal change (spring-end of summer) in Reference samples, and due to seasonal change and increasing sewage discharge in Impacted samples. Except for the gap between samples from November 2013 (before) to February 2014 (after) which in fact corresponded to the drastic reduction in the *B. proboscidea* abundance.

Community parameters

Community parameters (Richness (S), Abundance (N), Diversity (H') and Equitativity (J')) were studied in the three sites (1S and 2S in the sewage-impacted area, and Reference) along the nine periods (Figure 5). Data showed highly sig-

nificant differences in Reference versus sewage-impacted sites, in Periods and also interactions (Appendix, Table A20).

Mean abundance (Figure 5 A) showed the influence of the ecosystem engineer *B. rodriguezii* in the Reference Site, except in the period 2001-2002 due to the explosive increase in density of *R. glutaea* in 2S, and in the period 2008-2009 due to the demographic explosion of the invader *B. proboscidea*. On the other hand, mean richness (Figure 5 B) showed the opposite pattern, been higher in sewage-impacted sites 1S and 2S. It was observed a trend to diminish mean Richness along the studied periods, nevertheless a great increased was observed in the last one. In this last period, a peak in richness was due to the equilibrium between *B. proboscidea* and *B. rodriguezii*. Mean Diversity (Figure 5 C) and Evenness (Figure 5 D) showed a similar pattern, been higher in sewage-impacted sites rather than in Reference site, due to dominance of the ecosystem engineer in the later, and the presence of tolerant species in the first one.

The community parameters were also analyzed to Sites and Event (Figure 6). Data showed highly significant differences in Reference versus sewage-impacted sites in Event and interactions (Appendix, Table A21). All parameters showed lower values after the summer, and also a trend to decrease along the studied periods.

DISCUSSION

This was the first study in Argentina that analyzes the long-term response of the intertidal benthic community to the discharge of sewage without treatment directly to the intertidal sector. It was also the first study that analyzes the short-term response of the intertidal epilithic community before/after the summer. Due to the high seasonality of the sewage discharge, linked to the tourism peak in the summer months, the short-term variation induced by the pulse discharge was

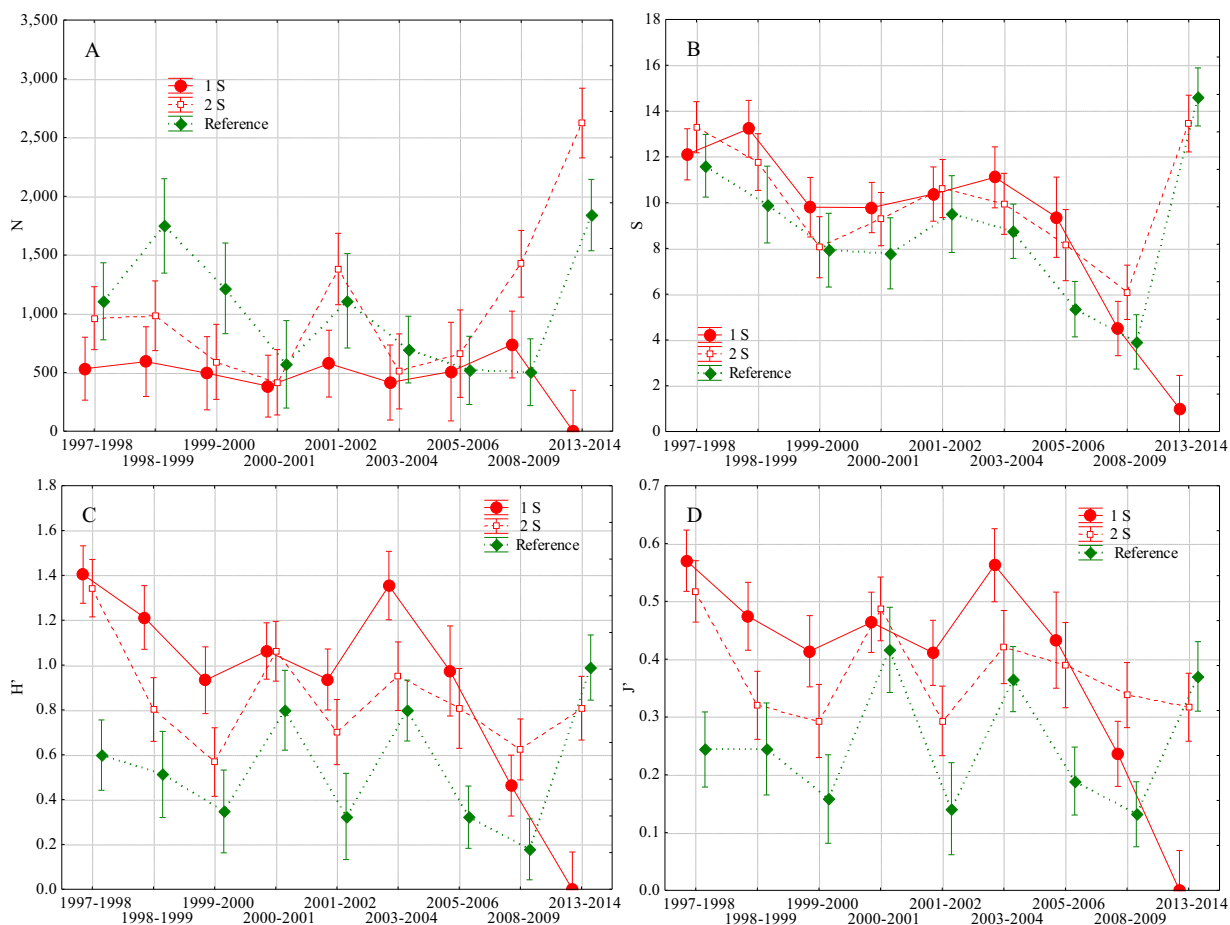


Figure 5. Mean values of Abundance (N) (A), Richness (S) (B), Diversity (H') (C), and Evenness (J') (D) in the three sites (1S, 2S in the impacted area in red lines, and Reference in green line) along the nine studied periods.

also analyzed, which in turn over-lapped with the chronic impact produced by the sewage discharge from Mar del Plata. In all cases, the study included the response of areas affected by sewers and reference areas.

There was a positive tendency for species that tolerate organic contamination to prevail in the sites affected by the sewage discharge, i.e. the polychaetes *C. capitata* sp., the classic indicator of organic enrichment, and also the now-classic *B. proboscidea* species (Pearson and Rosenberg 1978, Dean 2008).

Recently, for all Latin American and Caribbean region the indicator species belonging to the

Capitella complex were widely mentioned and reaffirmed as an indicator polychaete, although the species identity remains to be determined in each region (Elías et al. 2021).

In some moments of the first periods *Neanthes* (= *Alitta*) *succinea* (Leuckart, 1847) was also the indicator species in agreement with classic literature (see Pearson and Rosenberg 1978; Dean 2008). In other periods the indicator species was *R. glutaea*, as well as *Boccardia* spp. (a pool of species). Firstly, the species was initially identified as *B. polybranchia* (Haswell, 1885), nevertheless through time seems to be several species. It was suspected that the invader *B. proboscidea*

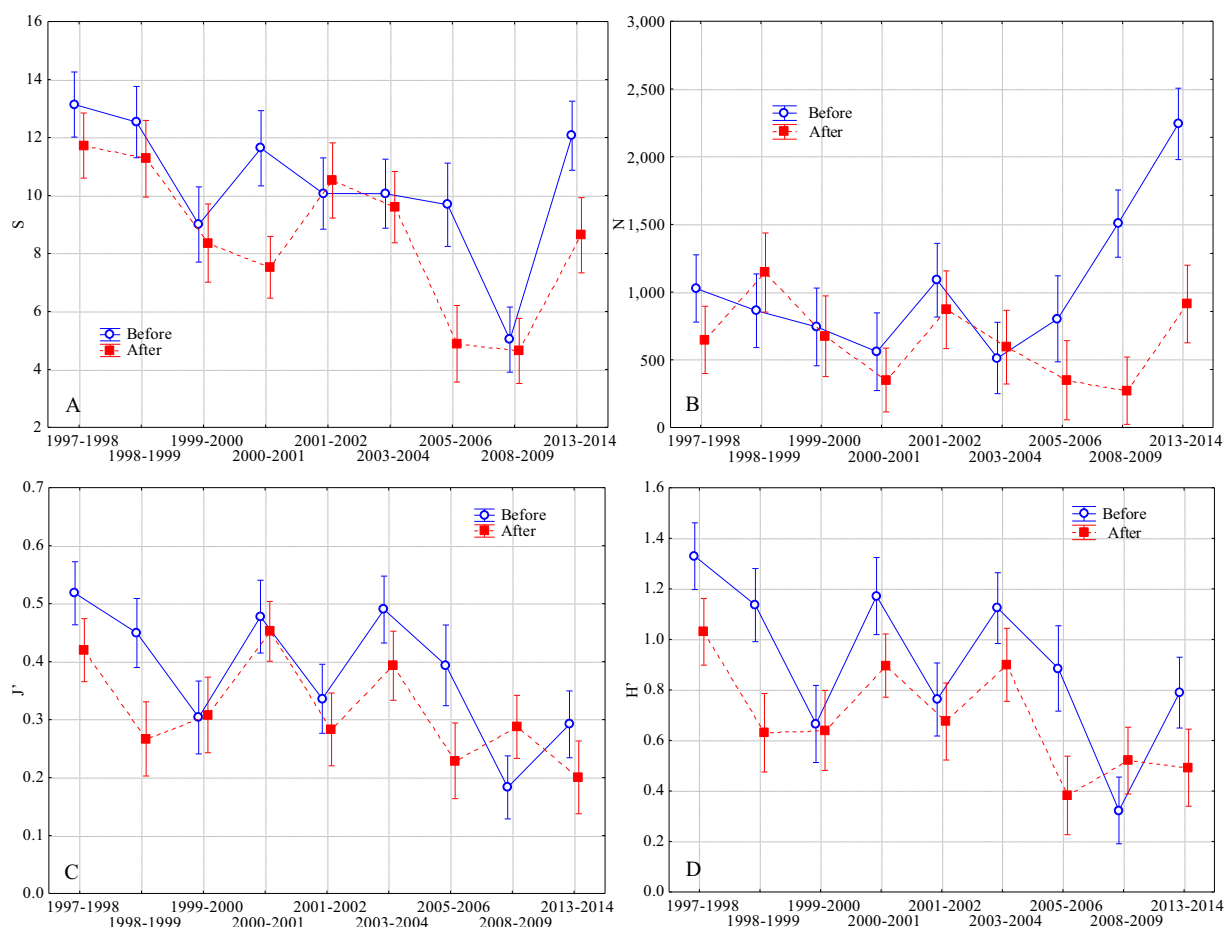


Figure 6. Mean values of Richness (S) (A), Abundance (N) (B), Evenness (J') (C), and Diversity (H') (D) in the Event before/after summer along the nine studied periods.

was present before the demographic explosion of 2008, and the present research showed that since 2006 the invader species is present as a companion species among the community.

Among the crustaceans, the tubicolous *M. insidiosum* was highly abundant in areas impacted by sewage discharge. Other crustacean indicators were also very abundant in areas located at intermediate distances from the sewage discharge (site 2S) such as *J. falcata* and *Caprella* sp. At the other extreme were the indicator species of good environmental quality, that was, sensitive or very sensitive species such as the polychaete *Leodamas tribulosus* (Ehlers, 1897), most Syllids

(see below) and the flatworm *Notoplana* sp. recently detected (Cuello et al. 2017).

The Syllidae in the area initially showed a classic behavior as sensitive species (Elías et al. 2003a, 2003b). However, long-term studies (Elías et al. 2006; Sánchez et al. 2013) showed erratic behavior. In some places and on some occasions they were very abundant at intermediate distances to the sewage discharge, exhibiting a high degree of tolerance to organic contamination. This could be because these species (*S. prolixa* and *S. gracilis*) are a complex of species, similar morphologically but with a different physiological response. The same can be said about *N. suc-*

cinea, ‘suspiciously cosmopolitan’ (Sánchez et al. 2013). Probably deeper and specific taxonomic studies must show the real identity of the syllids and nereidids indicator in the SW Atlantic.

The short-term effect (before/after the summer) showed that the chronic effect produced by the sewage discharge was compounded by an aggravated effect, since all the community parameters revealed significant reductions. Also, the analysis of similarity before/after the summer showed significant reduction of the average abundances of almost all the organisms of the intertidal community but the tolerant ones, which in many cases even increased after the summer. The fact that the sewer discharge increases significantly, and that during the summer the dominant winds came from the northern sector, pushing the discharge flow to the south towards the city and the sampling sites, (Vallarino et al. 2002) had an even greater negative impact on the intertidal benthic community.

Studies in the area, including this one, made possible to detect the presence of non-native species and the explosive development of some of them, giving rise to significant changes in the structure and functioning of the intertidal community. In fact, concerning the original description of this community, more than 50 years ago (Olivier et al. 1966), structural changes were detected due to the invasion of barnacles (Vallarino and Elías 1997). Other exotic species seem not to have had significant ecological impacts on native species, although specific studies are lacking, especially of macroalgae (Becherucci et al. 2016; Palomo et al. 2016). Subsequently, the demographic explosion of the invasive polychaete *B. proboscidea* dramatically altered the structure and function of the intertidal benthic community (Jaubet et al. 2011, 2013; Garaffo et al. 2012; Jaubet 2013; Elías et al. 2015; Llanos et al. 2019).

As a first result, a series of changes were observed in the arrangement of dominant species. One of the indicator species in the sewage-

impacted area were *Boccardia* spp. until year 2008. Since this year, the invader *B. proboscidea* exploded and monoculture biogenic reefs were built with extraordinary densities (Jaubet 2013; Jaubet et al. 2013). At the time no attempt to separate species was carried out, but it is suspected that the *B. proboscidea* was present with other species of the genus before the development of the reefs (2021 pers. comm. L Jaubet). Our research revealed the presence of the invader in March 2006. Most of the observed changes in the intertidal community in those periods were associated to the invasion of *B. proboscidea*, like mean values of Abundance, Richness, Diversity, and Evenness (see Elías et al. 2015). No other place in the world suffers large negative effects due to the invasion of this polychaete. In Australia and New Zealand the species has been declared ‘pest’ although densities are quite lower (one order of magnitude lesser respect our study area) (Hayes et al. 2005; Bradstock 2015).

The bivalve *B. rodriguezii* is the structuring organisms in the intertidal community because it provides shelter from waves and desiccation, and food for several associated species, i.e. an ecosystem engineer. On the other hand, the invasive polychaete *B. proboscidea* also build a tridimensional structure but for itself, been considered an auto-ecosystem engineer (Jaubet et al. 2013). However, *B. rodriguezii* had an unsuspected behavior about sewage-impact. Although it is the common and dominant organism of the natural community, it also shows a high level of tolerance to organic pollution. Its abundance oscillates in areas affected by the sewage discharge. In previous studies, Vallarino et al. (2002) indicated that *B. rodriguezii* was present even within 50 m from the sewage discharge in a pauperized community. However, at high and intermediate levels of organic contamination (i.e. at the sites closest to the sewage discharge, 1S and 2S) this species was competitively overcome by *B. proboscidea* (Jaubet et al. 2013; Elías et al. 2015; Llanos 2017; Llanos et al. 2018). Due to this behavior (toler-

ance) the calculation of ecological quality indexes was carried out with/without this mussel, been more representative the index without mussel abundance (Garaffo et al. 2017).

The organic matter underwent a jump-starting from 2005. Results from Jaubet et al. (2013) showed that from the year 2005 the value of the organic matter in the interstitial sediment of the bivalves doubled. This was probably due to the by-pass of the pre-treatment plant for sewage effluents. The maintenance of this plant (and therefore bypass) occurred twice a year, severely affecting benthic communities (Elías et al. 2009). The pre-treatment plant retained between 25 and 30 t per day of sewage sludge (Scagliola et al. 2011). The untreated wastes were released to the marine environment during bypass, aggravating the impact of the sewage on the ecosystem. It was possible that the observed increase of organic matter in the sediments could be the product of larger discharges due to the bypass.

Long-term trend

In the long term, the abundances of two species drive the changes in the epilithic intertidal community. In one hand the ecosystem engineer, *B. rodriguezii*, and in the other hand the ecosystem self-engineer, the polychaete *B. proboscidea*. While the former constructs a three-dimensional structure, which protrudes from the seafloor and allows other species to live among themselves and in the matrix they form (the definition of ecosystem engineer), the other constructs the same, but only *B. proboscidea* could live in their matrix acting as self-engineer ecosystem (Jaubet et al. 2013). In the Reference areas, the accompanying species were a few and were subject to seasonal changes, while the species of Impacted areas are mostly opportunistic or tolerant and change according to the discharge flow of the sewer of the Mar del Plata city.

In this same community, a study more limited in time but including seasonal analyzes (Elías and

Vallarino 2006) showed that the great changes in similarity occur between spring-summer in impacted areas, but between winter-spring in reference areas. These changes were associated to seasonality but to sewage-induced stress in sites close to discharge. The Control site behaved in a cyclic way and in counter clock wise, but the impacted stations showed no clear pattern.

The decreasing in ‘defender species’ allowed the introduction of exotic species that finally become invasive species. An altered environment creates a potentially favorable environment for the establishment of introduced or non-indigenous species (Dukes and Mooney 1999). Non-indigenous species are favored in places and at times when stress is negatively affecting native flora and fauna, resulting in vacant niches available for colonization (Occhipinti-Ambrogi and Savini 2003; Piola and Johnson 2008). When several environmental quality indices were calculated, it was necessary to exclude *B. rodriguezii* from these calculations, since it induced the homogenization of sites of high index value with sites with low values (Garaffo et al. 2017).

During the 2013-2014 period, the presence of the polychaete *B. proboscidea* was observed in greater abundance at the site near the point of discharge of the sewage effluent (site 2S) but without generating the impressive reefs recorded during the years 2008-2009. However, after the demographic explosion, the population of *B. proboscidea* decreased and did not completely displace *B. rodriguezii* near the sewage discharge, giving a coexistence of both species. In this way, being the organic pollution lesser, it may on the one hand have favored the growth and development of *B. rodriguezii*. On the other hand, the smaller amount of food available for *B. proboscidea* (a polychaete that feeds by filtration or facultative by superficial deposit), would tend to diminish the reproduction rates and densities previously registered. This ‘balance’ could be the reason why these two species, an ecosystem engineer and the other an invasive polychaete, could

coexist in this environment. Because this, the community has been described as an example of the 'bloom and bust' dynamics (Strayer et al. 2017) since the bloom of the invading *B. proboscidea* was followed by a decrease in the abundance of this polychaete (the bust) and the coexistence with the ecosystem engineer *B. rodriguezii* in areas still affected by sewage discharges (Llanos et al. 2021). Although the values of total organic matter decreased since 2008-2009, they were still almost four times higher than those recorded by Vallarino (2002) that ranged between 1 and 0.4% in site 1. This decrease in the amount of organic matter allowed *B. rodriguezii* to coexist with *B. proboscidea* because *B. rodriguezii* can tolerate average concentrations of organic matter (Vallarino et al. 2002; Vallarino and Elías 2006).

Regulation trend

What is the underlying mechanism that explains the community structure and dynamics of intertidal epilithic mussel beds? The community was described as lacking the barnacle belt, as well as lygiid isopods, littorinids snails, echinoderms and a top predatory (Olivier et al. 1966; Adami et al. 2004, 2008; Bertness et al. 2006; Hidalgo et al. 2007). Most macrophytes were seasonal, and their cycles do not significantly affect the availability of the substrate and there are also no herbivores that significantly regulate the algal cover as shown Penchaszadeh (1973). Space competition has been pointed out as the major biological structuring force in the 2-4 years period, while later successional stages were characterized by space monopolization (Nugent 1986). The regulation and stability of the intertidal community of the Mar del Plata rocky shore is also influenced by the degree and frequency of disturbance, as well as by the population dynamics of both mussels and introduced barnacles (Vallarino and Elías 1997). Therefore the top-down mechanism could not be the prevalent one. Is it a bottom-up effect?

The particulate matter from sewage discharge could be an extra supply, a bottom-up factor, but their effect is limited to the influence of the flume. Vallarino and Elías (2006) and the present work has shown great changes in sewage-impacted sites due to the short term effect before/after the summer when sewage discharge increased 60% and wind flow from the north. On the other hand, the detritus supply from subtidal macrophytes could be a structuring factor, but it was only present near the study site because there are hard substrates in the subtidal around Mar del Plata city. However, the extended distribution of *Brachidontes* beds were far away from detritus supply, because in all the distribution there were not extended subtidal macrophytes due to sand bottoms. Nevertheless, *Perumytilus* beds are distributed in southern cold-temperate regions (Patagonia), where submersed macrophytes are abundant. In here, macrophytes detritus would be present (but it was not quantified), but top-down forces (herbivory) are weak, due to environmental hardness because the evaporation pressure induced by the wind and the dryness of the air (see Bertness et al. 2006; Hidalgo et al. 2007). In South Africa, Bustamante and Branch (1996) observed that the *in situ* productivity was insufficient to support the high biomass of filter-feeders on exposed shores, suggesting dependence on external subsidies, and isotope analyses showed 60-85% of the food of filter-feeders came from particulate subtidal kelp.

Bottom-up processes can have important effects on rocky intertidal community structure. Oceanographic effects could generate large ecological variability in the basal levels, increasing the input of phytoplankton, detritus, and/or larvae, and through upward-flowing food chain effects, lead to variation in top-down trophic effects. Under these conditions the invertebrates can dominate the structure and dynamics of rocky intertidal communities (Menge 2000). In this context, the continuous recruitment of *Brachidontes* (Torroglosa 2015) could be a bottom-up

factor, as mentioned by Menge (2000). Other bottom-up effect was observed by Montoya et al. (2021) by showing high concentrations of *Cl_a* in the period studied for the two localities near the study area (Santa Teresita and Villa Gesell), varies from 4.71 to 65.67 $\mu\text{g l}^{-1}$ and from 0.10 to 33.73 $\mu\text{g l}^{-1}$ (respectively), due to high input of nutrients in the Buenos Aires intertidal region (although with marked temporal variability).

The dominant covered of mussels mono-cultures suggests that predators did not have a strong impact in the mid intertidal, perhaps due to their small size or due to the phylogeographic history of the Patagonian region (Hidalgo et al. 2007). As a general phenomenon, physical factors appear been the dominating structuring force in these communities and were likely to be evolutionarily and ecologically responsible for weakening the effects of consumers (Bertness et al. 2006).

Ultimately the changes that take place in the intertidal community of impacted areas are changes within the same community, in response to organic contamination induced by the sewage discharge. This basically corresponds to what is stated by Pearson and Rosenberg (1978). The intertidal epilithic community dominated by the mussel *B. rodriguezii* shown a great capacity to absorb a disturbance, and back to revert to a pre-disturbance situation, to finally reach again the initial state. This mean resistance, recovery and reversibility, was defined as ecological resilience (see review by Gollner et al. 2017).

Although the sewage discharge of the Mar del Plata city no longer occurs in the coastal zone, studies of the intertidal community are still valid. Although Mar del Plata has a submarine outfall functionally since the beginning of 2014, practically all of Argentina's coastal towns discharge their sewage without treatment directly into the coastal marine environment. This situation should stopped as soon as possible, and for this, this study and the preceding ones will be of great value to evaluate the environmental impact and take eventual mitigation measures. As previously

mentioned, both in Europe and in the United States, guidelines were drafted to improve the quality of recreational waters and monitor and evaluate their quality (Water Framework Directive and the Clean Water Act, respectively). The Republic of Argentina and eventually all Latin America countries should direct its attention to the environmental quality of its waters and draft its water act.

We do not predict how climate change, sea level, and acidification could affect intertidal rocky shores in the SW Atlantic. Community assemblages are expected to change in response to ocean acidification because of relative shifts in abundance between ecological winners and losers (Fabry et al. 2008). This work could be a baseline study of how the benthic epilithic community responds in both sewage-impacted and reference sites during a long term time period.

CONCLUSIONS

- The intertidal benthic community structure response to natural changes at non-impacted sites and to changes induced by organic pollution at sewage discharge sites.
- The structural changes in the community parameters and in the multivariate abundance of the benthic species showed significant changes in both the spatial and the temporal scale.
- The temporal change was reflected in both the short-term (before/after the summer) and the long-term (15 years from November 1997 to March 2014). Unexpected quickly benthic response occurs between spring and summer (three months) in relation to sewage increase and wind direction.
- Spatially the areas affected by sewage discharges showed the ecosystem engineer *B. rodriguezii* pauperized, as well as all the sensitive species, while tolerant and opportunistic

species increased, as a consequence the richness and diversity were high respect natural-low diversity areas.

- Indicator species change from period to period, tolerant/opportunistic polychaete species were *C. 'capitata' sp.*, *A. succinea*, *R. glutaea*, *Boccardia spp.*, and *B. proboscidea*; while among the crustaceans were *Monocorophium insidiosum* and *J. falcata*; sensitive species were *Nemerteans*, *Syllids*, *L. tribulosus*, and recently the flatworm *Notoplana sp.*
- The abundance of organic matter in the sediments trapped by the bivalve matrix showed increasing values near the sewage discharge, and a temporal pattern of increasing values throughout the period studied, resulting in increasing environmental degradation.
- The major impact to the community was the bloom of the invader polychaete *B. proboscidea*. This community has been described as an example of the 'bloom and bust' dynamics since the bloom of the invading *B. proboscidea* was followed by a decrease in the abundance of this polychaete (the bust) and the coexistence with the ecosystem engineer *B. rodriguezii*.
- The intertidal community dominated by the mussel *B. rodriguezii* shows resistance, recovery and reversibility, i.e. resilience.

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APPENDIX

Table A1. Ranking of dominance (abundance/total abundance) and frequency (%) of all recorded species in the period 1997-2014. MOL: Mollusca, POL: Polychaeta, CRU: Crustacea, NMER: Nemertean, NEMA: Nematoda, QUIR: Quironomidae (Insecta), TUR: Turbellaria, OLIG: Oligochaeta, TAN: Tanaidacea (CRU), ANEM: Anemone, PIC: Pictogonida, SIPUN: Sipuncula, NUD: Nudibranchia (MOL), ASC: Ascidea, INS: Insecta, PRIA: Priapulida, OPHIU: Ophiura (Echinoderma).

| Species | Group | Dominance | Frequency (%) |
|---|-------|-----------|---------------|
| <i>Brachidontes rodriguezii</i> | MOL | 57.08 | 84.6 |
| <i>Boccardia proboscidea</i> | POL | 19.25 | 15.4 |
| <i>Syllis proluxa</i> | POL | 4.50 | 70.9 |
| <i>Boccardia</i> spp. | POL | 3.27 | 47.2 |
| <i>Jassa falcata</i> | CRU | 2.55 | 33.1 |
| <i>Monocorophium insidiosum</i> | CRU | 2.09 | 32.0 |
| <i>Rhynchospio glutaea</i> | POL | 2.02 | 18.1 |
| <i>Siphonaria lessoni</i> | MOL | 1.38 | 59.4 |
| <i>Leodamas tribulosus</i> | POL | 1.36 | 43.5 |
| <i>Syllis gracilis</i> | POL | 1.11 | 76.2 |
| <i>Capitella 'capitata'</i> sp. | POL | 1.05 | 34.0 |
| <i>Caprella dilatata</i> | CRU | 0.81 | 19.9 |
| <i>Mytilus platensis</i> d'Orbigny, 1842 | MOL | 0.72 | 51.2 |
| Nemertina indet. | NMER | 0.42 | 38.4 |
| Nematode indet. | NEMA | 0.39 | 23.8 |
| <i>Hyale grandicornis</i> (Krøyer, 1845) | CRU | 0.28 | 28.7 |
| Quironomidae indet. | QUIR | 0.22 | 16.6 |
| <i>Protocirrinieris angelicollatio</i> Elías y Rivero, 2009 | POL | 0.16 | 21.8 |
| <i>Caulleriella bremecae</i> Elías y Rivero, 2009 | POL | 0.15 | 12.4 |
| <i>Idotea balthica</i> (Pallas, 1772) | CRU | 0.14 | 13.3 |
| <i>Balanus</i> sp. | CRU | 0.13 | 12.2 |
| <i>Alitta succinea</i> | POL | 0.11 | 25.4 |
| <i>Sphaeroma serratum</i> (Fabricius, 1787) | CRU | 0.09 | 13.3 |
| Copepoda sp. 1 | CRU | 0.07 | 2.2 |
| <i>Halicarcinus planatus</i> (Fabricius, 1775) | CRU | 0.04 | 4.2 |
| <i>Lineus bonaerensis</i> Moretto, 1971 | NMER | 0.04 | 5.5 |
| Nereididae indet. | POL | 0.04 | 5.3 |
| <i>Notoplana</i> sp. | TUR | 0.03 | 4.6 |
| Spionidae indet. 1 | POL | 0.03 | 1.8 |
| <i>Pachycheles haigae</i> Rodrigues da Costa, 1960 | CRU | 0.02 | 2.2 |
| Zoeas | CRU | 0.02 | 6.2 |

Table A1. Continued.

| Species | Group | DominanceFrequency (%) | |
|--|-------|------------------------|-----|
| <i>Barnea lamelosa</i> (d'Orbigny, 1841) | MOL | 0.02 | 9.1 |
| Copepodo harpac. indet. | CRU | 0.02 | 5.9 |
| <i>Polydora</i> sp. | POL | 0.02 | 2.2 |
| <i>Lyonsia</i> sp. | MOL | 0.01 | 2.9 |
| Capitellidae indet. | POL | 0.01 | 2.9 |
| Polychaeta indet. 2 | POL | 0.01 | 3.1 |
| Lumbrinellidae indet. | POL | 0.01 | 3.1 |
| Oligochaeta sp. 4 | OLIG | 0.01 | 2.9 |
| Oligochaeta sp. 1 | OLIG | 0.01 | 1.8 |
| <i>Lumbrineris tetraura</i> (Schmarda, 1861) | POL | 0.01 | 5.1 |
| Polychaeta indet. 1 | POL | 0.001 | 4.2 |
| <i>Cyrtograpsus affinis</i> (Dana, 1851) | CRU | 0.001 | 2.6 |
| <i>Hemigrapsus crenulatus</i> (H. Milne Edwards, 1837) | MOL | 0.001 | 4.9 |
| <i>Cyrtograpsus angulatus</i> Dana, 1851 | CRU | 0.001 | 2.9 |
| <i>Dodecaceria meridiana</i> Elías y Rivero, 2009 | POL | 0.001 | 1.6 |
| Tanaidacea | TAN | 0.001 | 2.0 |
| <i>Syllis</i> sp. | POL | 0.001 | 3.1 |
| <i>Stenothoe</i> sp. | CRU | < 0.001 | 1.6 |
| Polynoidae indet. | POL | < 0.001 | 2.9 |
| <i>Erichtonius brasiliensis</i> Dana, 1853 | CRU | < 0.001 | 0.5 |
| <i>Joeropsis</i> sp. | CRU | 0.004 | 2.0 |
| Syllidae indet. | POL | < 0.001 | 0.9 |
| Anemona indet. 1 | ANEM | < 0.001 | 2.2 |
| Phyllodocidae indet. | POL | < 0.001 | 0.7 |
| <i>Phyllodoce</i> sp. | POL | < 0.001 | 2.0 |
| Isopoda Valvifera | CRU | < 0.001 | 0.7 |
| <i>Cyrtograpsus altimanus</i> Rathbun, 1914 | CRU | < 0.001 | 0.5 |
| Isopoda indet. | CRU | < 0.001 | 0.9 |
| Oligochaeta sp. 2 | OLIG | < 0.001 | 0.9 |
| Polychaeta sp. 3 | POL | < 0.001 | 1.5 |
| Bivalvia indet. 1 | MOL | < 0.001 | 1.5 |
| Pignogonida indet. | PIC | < 0.001 | 1.1 |
| Sipunculida indet. | SIPUN | < 0.001 | 0.9 |
| Anphipoda indet. | CRU | < 0.001 | 0.7 |
| Nudibranchia indet. | NUD | < 0.001 | 0.7 |
| Ascidea indet. | ASC | < 0.001 | 0.4 |
| Insecta indet. | INS | < 0.001 | 0.7 |
| Priapulida indet. | PRIA | < 0.001 | 0.5 |

Table A1. Continued.

| Species | Group | Dominance | Frequency (%) |
|--|-------|-----------|---------------|
| <i>Pachycheles laevidactylus</i> Ortmann, 1892 | CRU | < 0.001 | 0.2 |
| Isopoda Flabellifera | CRU | < 0.001 | 0.5 |
| <i>Crepidula</i> sp. | MOL | < 0.001 | 0.7 |
| Hesionidae indet. | POL | < 0.001 | 0.2 |
| Polychaeta indet. | POL | < 0.001 | 0.5 |
| Oligochaeta sp. 3 | OLIG | < 0.001 | 0.5 |
| Bivalvia indet. 2 | MOL | < 0.001 | 0.5 |
| <i>Halosydnella australis</i> (Kinberg, 1856) | POL | < 0.001 | 0.4 |
| Nemertina sp. 2 | NMER | < 0.001 | 0.4 |
| <i>Glycera americana</i> Leidy, 1855 | POL | < 0.001 | 0.4 |
| Spionidae indet. 3 | POL | < 0.001 | 0.2 |
| Oeonidae indet. | POL | < 0.001 | 0.4 |
| Hyperida indet. | CRU | < 0.001 | 0.2 |
| <i>Heteromastus similis</i> Southern, 1921 | POL | < 0.001 | 0.2 |
| <i>Corbula</i> sp. | MOL | < 0.001 | 0.4 |
| Anemona indet. 2 | ANEM | < 0.001 | 0.4 |
| <i>Elasmopus marplatensis</i> Alonso de Pina, 1997 | CRU | < 0.001 | 0.5 |
| Ostracoda indet. | CRU | < 0.001 | 0.2 |
| Crysopetallidae indet. | POL | < 0.001 | 0.2 |
| Terebellidae indet. | POL | < 0.001 | 0.2 |
| Sabellaridae indet. | POL | < 0.001 | 0.2 |
| Onuphidae indet. | POL | < 0.001 | 0.2 |
| Ophiuroidea indet. | OPHIU | < 0.001 | 0.2 |
| <i>Lumbrineriopsis mucronata</i> (Ehlers, 1908) | POL | < 0.001 | 0.2 |
| Acari | INS | < 0.001 | 0.2 |

Table A2. Species that most contributed to the differences among Sites in the Period 1997-1998. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before, but the order follows the first comparison.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Jassa falcata</i> | 5.54 | 12.43 | 15.25 | 2.73 | 15.38 |
| <i>Monocorophium insidiosum</i> | 9.23 | 9.95 | 10.35 | 1.06 | 13.14 |
| <i>Brachidontes rodriguezii</i> | 14.14 | 17.95 | 9.61 | 30.66 | 19.42 |
| <i>Syllis prolixa</i> | 4.08 | 6.94 | 8.15 | 6.99 | 7.5 |
| <i>Caprella dilatata</i> | 0.3 | 5.31 | 7.09 | 1.35 | 7.06 |
| <i>Capitella 'capitata' sp.</i> | 4.12 | 0.21 | 6.54 | 0 | 6.55 |
| Nemertina indet. | 0.33 | 3.23 | 5 | 1.38 | 4.35 |
| <i>Syllis gracilis</i> | 2.24 | 4.97 | 4.89 | 4.14 | 3.63 |
| <i>Leodamas tribulosus</i> | 0.55 | 1.95 | 2.61 | 2.86 | 3.4 |

Table A3. Species that most contributed to the differences between before/after summer in the Period 1997-1998.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Jassa falcata</i> | 12.74 | 2.1 | 15.88 |
| <i>Brachidontes rodriguezii</i> | 19.35 | 20.05 | 14.05 |
| <i>Monocorophium insidiosum</i> | 9.53 | 5.38 | 11.39 |
| <i>Syllis prolixa</i> | 7.95 | 3.82 | 8.32 |
| <i>Caprella dilatata</i> | 4.42 | 0.46 | 5.84 |
| <i>Capitella 'capitata' sp.</i> | 0.71 | 2.53 | 4.37 |
| <i>Syllis gracilis</i> | 4.66 | 2.82 | 4.22 |

Table A4. Species that most contributed to the differences among Sites in the Period 1998-1999. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Brachidontes rodriguezii</i> | 393.68 | 774.82 | 57.69 | 1475 | 68.26 |
| <i>Boccardia</i> spp. | 36 | 37.23 | 7.85 | 39.08 | 5.99 |
| <i>Syllis prolixa</i> | 27.36 | 47.64 | 6.28 | 128 | 10.12 |
| <i>Caprella dilatata</i> | 6 | 36.73 | 4.78 | 8.85 | 3.61 |
| <i>Capitella 'capitata' sp.</i> | 19.55 | 2.95 | 2.91 | 0 | 0 |
| <i>Syllis gracilis</i> | 26.69 | 3.77 | 1.59 | 26.69 | 2.09 |

Table A5. Species that most contributed to the differences between before/after summer in the Period 1998-1999.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Brachidontes rodriguezii</i> | 22.82 | 30.09 | 21 |
| <i>Syllis prolixa</i> | 4.95 | 5.78 | 9.46 |
| <i>Boccardia</i> spp. | 5.46 | 2.93 | 8.7 |
| <i>Leodamas tribulosus</i> | 3.1 | 0.34 | 4.97 |
| <i>Jassa falcata</i> | 3.09 | 0.56 | 4.84 |
| <i>Monocorophium insidiosum</i> | 2.97 | 1.13 | 4.69 |
| <i>Caprella dilatata</i> | 2.71 | 0.79 | 4.5 |
| <i>Capitella 'capitata' sp.</i> | 1.88 | 1.65 | 4.4 |

Table A6. Species that most contributed to the differences among Sites in the Period 1999-2000. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Brachidontes rodriguezii</i> | 18.00 | 21.67 | 17.11 | 32.5 | 31.23 |
| <i>Boccardia</i> spp. | 4.52 | 4.08 | 15.17 | 1.56 | 8.16 |
| <i>Capitella 'capitata'</i> sp. | 5.6 | 1.22 | 14.49 | 0 | 11.61 |
| <i>Siphonaria lessoni</i> | 4.67 | 2.15 | 10.28 | 1.8 | 3.67 |
| <i>Syllis prolixa</i> | 3.15 | 3.75 | 10.24 | 7.35 | 14.46 |
| <i>Leodamas tribulosus</i> | 0.78 | 1.8 | 5.37 | 0.5 | 1.9 |

Table A7. Species that most contributed to the differences between before/after summer in the Period 1999-2000.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Syllis prolixa</i> | 8.25 | 5.33 | 12.97 |
| <i>Brachidontes rodriguezii</i> | 18.12 | 14.5 | 11.78 |
| <i>Capitella 'capitata'</i> sp. | 0.04 | 3.91 | 8.65 |
| <i>Rhynchospio glutaea</i> | 3.35 | 0 | 7.01 |
| <i>Leodamas tribulosus</i> | 2.68 | 0.08 | 5.97 |
| <i>Syllis gracilis</i> | 3 | 3.51 | 5.64 |
| <i>Jassa falcata</i> | 2.74 | 0.03 | 5.5 |
| <i>Boccardia</i> spp. | 1.98 | 1.12 | 5.46 |

Table A8. Species that most contributed to the differences among Sites in the Period 2000-2001. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Syllis prolixa</i> | 5.56 | 7.76 | 14.69 | 6.17 | 14.15 |
| <i>Capitella 'capitata' sp.</i> | 4.32 | 1.45 | 11.94 | 0 | 11 |
| <i>Brachidontes rodriguezii</i> | 14.06 | 15.93 | 10.16 | 19.82 | 15.71 |
| <i>Syllis gracilis</i> | 2.35 | 4.54 | 7.75 | 3 | 6.17 |
| <i>Siphonaria lessoni</i> | 1.91 | 2.31 | 6.73 | 2.28 | 4.59 |
| <i>Boccardia spp.</i> | 1.8 | 1.52 | 6.31 | 0.69 | 4.47 |
| <i>Rhynchospio glutaea</i> | 1.19 | 1.42 | 5.2 | 1.55 | 4.11 |
| <i>Jassa falcata</i> | 1.72 | 0.46 | 4.24 | 1.1 | 4.25 |

Table A9. Species that most contributed to the differences between before/after summer in the Period 2000-2001.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Syllis prolixa</i> | 8.25 | 5.33 | 12.97 |
| <i>Brachidontes rodriguezii</i> | 18.12 | 14.5 | 11.78 |
| <i>Capitella 'capitata' sp.</i> | 0.04 | 3.9 | 8.65 |
| <i>Rhynchospio glutaea</i> | 3.35 | 0 | 7.01 |
| <i>Leodamas tribulosus</i> | 2.68 | 0.08 | 5.97 |
| <i>Syllis gracilis</i> | 3 | 3.51 | 5.64 |
| <i>Jassa falcata</i> | 2.74 | 0.03 | 5.5 |
| <i>Boccardia spp.</i> | 1.98 | 1.12 | 5.46 |

Table A10. Species that most contributed to the differences among Sites in the Period 2001-2002. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Brachidontes rodriguezii</i> | 19.33 | 32.69 | 25.34 | 30.92 | 28.18 |
| <i>Syllis prolixa</i> | 3.41 | 8.81 | 13.21 | 5 | 10.25 |
| <i>Boccardia</i> spp. | 4.23 | 4.25 | 8.95 | 0.84 | 8.15 |
| <i>Jassa falcata</i> | 3.85 | 3.95 | 7.56 | 1.22 | 6.49 |
| <i>Caprella dilatata</i> | 0.81 | 3.35 | 5.09 | 1.8 | 3.48 |
| <i>Capitella 'capitata' sp.</i> | 3.15 | 0.77 | 4.91 | 0.08 | 6.74 |
| <i>Leodamas tribulosus</i> | 0.64 | 2.81 | 4.79 | 0.74 | 2.15 |

Table A11. Species that most contributed to the differences between before/after summer in the Period 2001-2002.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Brachidontes rodriguezii</i> | 27.31 | 26.00 | 21.51 |
| <i>Syllis prolixa</i> | 7.36 | 3.92 | 12.59 |
| <i>Boccardia</i> spp. | 4.54 | 2.39 | 9.27 |
| <i>Jassa falcata</i> | 3.55 | 3.09 | 7.45 |
| Nematode indet. | 1.24 | 2.95 | 5.07 |
| <i>Leodamas tribulosus</i> | 2.78 | 0 | 4.97 |
| <i>Caprella dilatata</i> | 2.48 | 1.37 | 4.78 |
| <i>Capitella 'capitata' sp.</i> | 1.45 | 1.82 | 4.65 |

Table A12. Species that most contributed to the differences among Sites in the Period 2002-2003. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Boccardia</i> spp. | 9.14 | 5.96 | 19.36 | 5.71 | 16.13 |
| <i>Brachidontes rodriguezii</i> | 13.11 | 16.3 | 12.5 | 22.25 | 18.66 |
| <i>Monocorophium insidiosum</i> | 4.99 | 0.93 | 9.68 | 0.08 | 9.71 |
| <i>Mytilus platensis</i> | 1.91 | 3.13 | 6.15 | 0.14 | 3.62 |
| <i>Syllis proluxa</i> | 1.22 | 3.28 | 5.62 | 0.45 | 3.03 |
| <i>Siphonaria lessoni</i> | 3.34 | 2.12 | 5.32 | 5.19 | 6.17 |
| <i>Capitella</i> 'capitata' sp. | 2.38 | 0.55 | 5.11 | 0.08 | 4.7 |

Table A13. Species that most contributed to the differences between before/after summer in the Period 2002-2003.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Boccardia</i> spp. | 12.12 | 1.83 | 21.46 |
| <i>Brachidontes rodriguezii</i> | 13.67 | 19.03 | 14.86 |
| <i>Monocorophium insidiosum</i> | 1.87 | 3.11 | 6.9 |
| <i>Siphonaria lessoni</i> | 4.16 | 2.3 | 5.94 |
| <i>Leodamas tribulosus</i> | 2.98 | 0.36 | 5.62 |
| <i>Mytilus platensis</i> | 1.87 | 2.12 | 5.12 |
| <i>Syllis proluxa</i> | 0.96 | 2.77 | 4.65 |
| <i>Capitella</i> 'capitata' sp. | 0.46 | 2.07 | 4.2 |

Table A14. Species that most contributed to the differences among Sites in the Period 2005-2006. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Boccardia</i> spp. | 7.14 | 1.24 | 16.74 | 3.23 | 16.67 |
| <i>Brachidontes rodriguezii</i> | 18.64 | 15.62 | 11.03 | 21.07 | 13.2 |
| <i>Rhynchospio glutaea</i> | 1.36 | 4.89 | 10.44 | 0.22 | 3.94 |
| <i>Leodamas tribulosus</i> | 2.5 | 4.16 | 10.33 | 0.96 | 7.59 |
| <i>Siphonaria lessoni</i> | 3.63 | 2.32 | 9.06 | 1.58 | 10.38 |
| <i>Capitella 'capitata' sp.</i> | 3.41 | 0.49 | 7.84 | 0.36 | 9.51 |
| <i>Syllis proluxa</i> | 3.08 | 4.99 | 6.33 | 0.8 | 8 |

Table A15. Species that most contributed to the differences between before/after summer in the Period 2005-2006.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Brachidontes rodriguezii</i> | 20.49 | 17.59 | 14.51 |
| <i>Boccardia</i> spp. | 6.11 | 1.38 | 13.9 |
| <i>Siphonaria lessoni</i> | 4.8 | 0.12 | 12.58 |
| <i>Leodamas tribulosus</i> | 4.91 | 0 | 12.53 |
| <i>Rhynchospio glutaea</i> | 4.02 | 0 | 7.82 |
| <i>Syllis proluxa</i> | 3.26 | 1.94 | 7.42 |

Table A16. Species that most contributed to the differences among Sites in the Period 2008-2009. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Boccardia proboscidea</i> | 16.75 | 28.59 | 52.18 | 1.5 | 25.11 |
| <i>Brachidontes rodriguezii</i> | 6.89 | 9.51 | 19.85 | 21.3 | 50.61 |
| <i>Syllis prolixa</i> | 2.15 | 1.26 | 4.4 | 0.48 | 3.86 |
| <i>Siphonaria lessoni</i> | 0.6 | 1.78 | 4.38 | 1.28 | 3.41 |

Table A17. Species that most contributed to the differences between before/after summer in the Period 2008-2009.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Boccardia proboscidea</i> | 24.55 | 6.67 | 44.81 |
| <i>Brachidontes rodriguezii</i> | 14.01 | 11.12 | 29.21 |
| <i>Siphonaria lessoni</i> | 1.18 | 1.26 | 3.85 |
| <i>Syllis prolixa</i> | 1.12 | 1.47 | 3.79 |

Table A18. Species that most contributed to the differences among Sites in the Period 2013-2014. The species are given in the order shown by the Simper analysis in the comparison between sewage-impacted sites, 1S and 2S with their contribution percentage. Reference site was added before.

| Species | 1S | 2S | Contrib% | Reference | |
|---------------------------------|-------------------|-------------------|----------|-------------------|----------|
| | Average abundance | Average abundance | | Average abundance | Contrib% |
| <i>Boccardia proboscidea</i> | 0.1 | 33.12 | 30.56 | 9.26 | 10.06 |
| <i>Brachidontes rodriguezii</i> | 0 | 22.92 | 29.59 | 33.45 | 37.86 |
| <i>Syllis prolixa</i> | 0 | 5.6 | 6.67 | 3.61 | 3.52 |
| <i>Leodamas tribulosus</i> | 0 | 6.91 | 6.62 | 5.45 | 4.94 |
| <i>Siphonaria lessoni</i> | 0 | 2.84 | 3.89 | 8.08 | 9.86 |

Table A19. Species that most contributed to the differences between before/after summer in the Period 2013-2014.

| Species | Before | After | Contrib% |
|---------------------------------|-------------------|-------------------|----------|
| | Average abundance | Average abundance | |
| <i>Brachidontes rodriguezii</i> | 19.59 | 21.47 | 24.67 |
| <i>Boccardia proboscidea</i> | 22.45 | 7.64 | 22.77 |
| <i>Leodamas tribulosus</i> | 8.07 | 0.31 | 8.09 |
| <i>Siphonaria lessoni</i> | 3.56 | 4.37 | 6.38 |
| <i>Rhynchospio glutaea</i> | 5.86 | 0.11 | 5.43 |
| <i>Syllis prolixa</i> | 3.82 | 2.85 | 4.72 |

Table A20. Results of ANOVA between Sites and Periods. In all cases there were highly significant differences between factors and interactions.

| Effect | SS | df | MS | F | p |
|-------------|------------|----|------------|-------|--------|
| Evenness | | | | | |
| Site | 1.934 | 2 | 0.967 | 49.11 | 0.00* |
| Period | 4.113 | 8 | 0.514 | 26.1 | 0.00* |
| Site*Period | 3.825 | 16 | 0.239 | 12.14 | 0.00* |
| Diversity | | | | | |
| Site | 13.23 | 2 | 6.615 | 57.55 | 0.00* |
| Period | 27.87 | 8 | 3.484 | 30.31 | 0.00* |
| Site*Period | 25.02 | 16 | 1.564 | 13.61 | 0.00* |
| Richness | | | | | |
| Site | 157 | 2 | 78.7 | 8.99 | 0.000* |
| Period | 2589 | 8 | 323.6 | 36.98 | 0.000* |
| Site*Period | 2323 | 16 | 145.2 | 16.59 | 0.000* |
| Abundance | | | | | |
| Site | 3.88E + 07 | 2 | 1.94E + 07 | 38.62 | 0.000* |
| Period | 4.80E + 07 | 8 | 6.00E + 06 | 11.94 | 0.000* |
| Site*Period | 6.84E + 07 | 16 | 4.28E + 06 | 8.52 | 0.000* |

Table A21. Results of ANOVA between Event and Periods. In all cases, there were highly significant differences between factors and interactions.

| Effect | SS | df | MS | F | p |
|--------------|------------|----|------------|-------|--------|
| Evenness | | | | | |
| Event | 0.596 | 1 | 0.596 | 21.6 | 0.000* |
| Period | 4.231 | 8 | 0.529 | 19.17 | 0.000* |
| Event*Period | 0.959 | 8 | 0.12 | 4.34 | 0.000* |
| Diversity | | | | | |
| Event | 6.69 | 1 | 6.692 | 41.13 | 0.000* |
| Period | 31.67 | 8 | 3.959 | 24.34 | 0.000* |
| Event*Period | 6.21 | 8 | 0.776 | 4.77 | 0.000* |
| Richness | | | | | |
| Event | 423 | 1 | 423.2 | 35.94 | 0.000* |
| Period | 2861 | 8 | 357.6 | 30.37 | 0.000* |
| Event*Period | 391 | 8 | 48.8 | 4.15 | 0.000* |
| Abundance | | | | | |
| Event | 2.05E + 07 | 1 | 2.05E + 07 | 35.56 | 0.000* |
| Period | 5.34E + 07 | 8 | 6.68E + 06 | 11.6 | 0.000* |
| Event*Period | 3.77E + 07 | 8 | 4.72E + 06 | 8.2 | 0.000* |

