

Ecological impacts of two non-indigenous macroalgae on an urban rocky intertidal shore

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Abstract Non-indigenous marine species often change the abundance and diversity of native species in coastal ecosystems. On the SW Atlantic coast, the macroalgae *Ahnfeltiopsis* sp. (Rhodophyta, Phylloporaceae) and *Schizymenia dubyi* (Rhodophyta, Schizymeniaceae) have invaded the intertidal rocky shore of Mar del Plata, Argentina (38°S, 57°W). To study the spread and ecological associations of these invasive species, algal abundance, biomass and biodiversity of benthic assemblages at three different tidal levels were examined during five years. Sparse *Ahnfeltiopsis* sp. thalli (3 % cover) were detected in February 2007 at the three tidal levels. By January 2011, its cover had increased to 11 %, while its biomass showed a 27-fold increase. *S. dubyi* was detected at the lower intertidal level

in January 2010 with a cover of 2 %. By January 2011, it had increased to 5 % and spread to the other intertidal levels. The presence of these two non-indigenous algae modified the substrate and the structure and composition of the benthic assemblage. The constant increase in the algal biomass and presence along the intertidal suggest that the effect will be greater in the future. Moreover, the effects of these exotic algae could potentially displace *Brachidontes rodriguezii*—an important ecosystem engineer that creates microhabitat for a large number of organisms on these shores.

Introduction

Human activities have been impacting natural systems since the Holocene, when agriculture and urbanization began (Schmidt et al. 1998). In the marine realm, many activities that occur near the shore or in coastal waters add contaminants and nutrients to the ecosystem (Vitousek et al. 1997), decreasing the quality and availability of natural habitats (Gray 1997; Airoidi and Beck 2007). In addition, these activities can drastically alter local biodiversity through the introduction of non-indigenous marine species (NIMS) by two main sources. First, NIMS species can be accidentally introduced by means of transport and movement of vessels around the world (ballast waters, fouling on ships' hulls and other marine equipment), or can be introduced by intentional releases related to fisheries. More than 7000 species are transported in ballast water daily (Carlton 1999, Mineur et al. 2006). Also, commercial activities on land related to the sea can, intentionally or accidentally, introduce NIMS that have been moved around the world for the aquaculture and aquarium trade, and the use of algae and sea grass as packing material (Ruiz et al. 1997;

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Hewitt et al. 2007). Another source of NIMS introduction is climate change, since it has allowed the expansion of the geographic range of several species by increasing dispersal (Kinlan et al. 2005). Consequently, the current spatial distribution of species around the world is not only the result of ecological and evolutionary processes, but also of climate change and other anthropogenic impacts.

The introduction and establishment of NIMS has been showed to change the structure and composition of the receiving assemblages, depending on the characteristics of both invaded systems and introduced species (Stachowicz et al. 1999). In particular, ecosystem engineers, such as seaweeds, that provide habitat for benthic assemblages (Mann 1973) can become a dominant part of the assemblage and have a great impact on biodiversity and ecosystem processes in the coastal zone (Wikström and Kautsky 2004). For example, large Phaeophyta, such as *Undaria pinnatifida* (Harvey) Suringer (Hay 1990, Sanderson 1990, Meretta et al. 2012) and *Sargassum muticum*, can displace existing native species by overgrowing them (Critchley et al. 1990), changing not only algal species composition, but also habitat availability for epifaunal organisms and their trophic food webs (Sindermann 1991, Chambers and Prepas 1993).

In addition, ecosystem engineers can greatly modify the physical conditions of coastal and rocky shores (sensu Jones et al. 1994). Both canopy-forming and turf-forming macroalgae have the potential to substantially affect physical (light, sedimentation, water movement and desiccation) or biological parameters (recruitment, growth and survival of algal propagules, density and efficiency of predators) with different intensity and extent. For example, canopy-forming algae can have strong effects on light availability (Pearse and Hines 1979; Dayton et al. 1984), while turf-forming algae require very little light (Airoidi 2000) but accumulate significant amounts of sediment (Isaeus et al. 2004). In addition, non-indigenous ecosystem engineers that dominate the intertidal and subtidal rocky shore can have positive consequences for local biodiversity by providing new habitat for numerous species (Lohse 1993).

Invasive algae and invertebrates can also show fast rates of growth in their introduced ranges, such as *Grateloupia turuturu* in the USA (Janiak and Whitlatch 2012), *Mytilus galloprovincialis* in South Africa (Robinson et al. 2005), *Ciona intestinalis* in USA (Blum et al. 2007) or *Undaria pinnatifida* on the Argentinean coast (Meretta et al. 2012). This is due, in part, to the unpalatability of invasive species and their escape from local grazing pressure (Scheibling and Anthony 2001; Engelen et al. 2011). Therefore, the impacts of non-indigenous ecosystem engineers on native assemblages are usually significant, with a high percentage

of negative effects impacting native seaweed abundance and diversity (Casas et al. 2004, Williams and Smith 2007). As the spread of NIMS is increasing (Sala et al. 2000; Orensanz et al. 2002; Wells et al. 2015), decisions on the conservation of biodiversity are more necessary than ever (Ojaveer et al. 2015). Managers need information about the extent of invasion and impacts of these NIMS on the natural systems to design control strategies.

Along the northern Argentinean coast, the native mussel *Brachidontes rodriguezii* covers up to 65 % of the mid- and upper mid-intertidal substratum, forming dense beds (Penchaszadeh et al. 2007) with many invertebrate species living within the matrix (Arribas et al. 2013). The algal habitat formers *Polysiphonia* sp., *Ceramium* sp., *Gymnogongrus* sp. and *Corallina officinalis* (Rhodophyta) extend in the adjacent areas (Olivier et al. 1966; Parma et al. 1987) along mid- and low intertidal zones. In the last years, the presence of two non-indigenous macroalgae, *Schyzymenia dubyi* (Rhodophyta, Schizymeniaceae; Ramirez et al. 2012) and an indeterminate species of the genus *Ahnfeltiopsis* (Rhodophyta, Phylloporaceae; Becherucci et al. 2014), have been detected around Mar del Plata city. The first record of *S. dubyi* on the Argentinean coast was 20 km south from the study site (Ramirez et al. 2012). Molecular analysis of the *rbcL* showed that specimens of *Schyzymenia dubyi* from Argentina formed a clade with the ones from France, Japan and the Pacific coast of the USA, which could indicate that one of them could be the origin of the invasion. However, the introduction vector is unknown (Ramirez et al. 2012). *Ahnfeltiopsis* sp. was recently identified as one of the most abundant algae on artificial structures in the area (breakwaters; Becherucci et al. 2014). This species may comprise a new kind of ecosystem engineer in the area (canopy algae), as it has different morphology than local algal species (turf algae) and therefore has the potential to impact the structure and composition of native assemblages. Based on the knowledge that the type of ecosystem engineer and morphology of algae can affect light, sedimentation, water flow, predation, settlement and post-settlement processes (Osman et al. 1992; Guichard and Bourget 1998; Goldberg and Foster 2002; Irving and Connell 2002), we predict that benthic assemblages inhabiting the algal NIMS *S. dubyi* and *Ahnfeltiopsis* sp. would differ from areas dominated by the native species the mussel *Brachidontes rodriguezii* and its accompanying algae, assuming that changes are due to the increase in invasive NIS.

The objectives of this study were to (1) investigate the spread in coverage and biomass of the non-indigenous macroalgae *Ahnfeltiopsis* sp. and *S. dubyi* on the intertidal rocky shore of Mar del Plata, Argentina (38°S, 57°W), during 5 years, and (2) compare the benthic assemblages

(sessile and epifaunal) between native mussel and the two NIMS algae.

Methods

Study site

Intertidal areas of Mar del Plata coast (38°01'15"S, 57°31'37"W) were sampled from 2007 to 2011. The intertidal rocky shore of Playa Chica, Mar del Plata, is an urban open coast with natural irregular quartz boulders, exposed to a long shore littoral current (south to north) and autumn storms (Mazzoni and Spalletti 1978). The littoral area forms a cliff, which receives heavy wave action (Penchaszadeh et al. 2007). The zone is characterized by a microtidal regime, with semidiurnal tides between 0.61 and 0.91 m (Isla and Ferrante 1997). The seawater temperature ranges from 8 °C in winter to 21 °C in summer, and the salinity varies between 33.5 and 33.8 psu (Guerrero and Piola 1997).

Sampling

To study the abundance and spread of NIMS, percentage cover was estimated following the standardized NaGISA protocol (see Rigby et al. 2007 for further details). Fifteen quadrats of 1 m² were randomly placed along transects positioned parallel to the waterline in the high, mid- and low intertidal zone in March 2009, January 2010, and January 2011. Percent cover using the point-intersection technique estimated abundance of macroalgae and sessile fauna. Most identification was performed in the field on living organisms, although occasional problematic specimens were collected for identification. All organisms were identified to low taxonomic level, which were genus or species.

In addition, the extent of the invasion was evaluated using biomass. Macroalgal biomass was estimated by scraping 50 × 50 cm quadrats on five summer sampling dates (February 2007, March 2008, March 2009, January 2010 and January 2011) and three winter sampling dates (July 2008, July 2009 and July 2010). All macroalgae present inside the quadrats were sorted by species, and dry weight was determined (70 °C for 48 h).

To investigate whether the epifaunal assemblages differ in the habitats formed by *S. dubyi* from those in the *Ahnfeltiopsis* sp. areas and from the assemblage in the native mussel beds, eight cores were taken of each biogenic habitat in the mid-intertidal during November 2011. Each sample was obtained by scraping all the content inside a 10-cm-diameter core, preserved in 96 % alcohol and taken to the laboratory. The sediment was sieved through a 0.5-mm

mesh size, and the retained macrofauna were identified and counted. Macroalgae and mussels were dried at 70 °C. All organisms were identified to the lowest taxon possible, which was species in most cases. As sediment retention identifies different habitats and conditions for benthic infauna (Airoldi 1998), sediment retention in areas with *Schyzimonia dubyi*, *Ahnfeltiopsis* sp. patches and from the native species, i.e., the mytilid *Brachidontes rodriguezii*, were investigated. The sediments trapped in the cores were sieved, dried at 70 °C during 24 h and weighed to evaluate whether the differences in the macrofauna assemblages can be correlated with the trapped sediment. Grain-size parameters were determined in phi units ($-\log_2$ of particle diameter), and organic matter content in sediments was calculated after ignition at 500 °C for 8 h.

Data analysis

To evaluate the spread of the non-indigenous algae and the native mussel *B. rodriguezii* during the period studied, analysis of variance (ANOVA) was used to test the null hypotheses of no differences in percentage cover among years (random, 3 levels) and intertidal heights (fixed, 3 levels) for each species in the 1 × 1 m quadrats. Differences in biomass of algae among sampling dates and intertidal heights (as above) were also tested with ANOVA. A relationship of incidence of invasive algae along sampling dates was also explored. Data were previously tested for homogeneity of variances using Cochran's test and square root transformed in all the cases when needed to meet this assumption. Student–Newman–Keuls' (SNK) post hoc test was used to test for differences between factor levels after significant ANOVA.

The structure of the sessile assemblage associated with the non-indigenous species was evaluated during a three-factor permutational multivariate analyses of variance (PERMANOVA) on percentage cover of sessile organisms among years (random, 3 levels) and intertidal heights (fixed, 3 levels) in the 1 m × 1 m quadrates. In addition, biomass and presence/absence of algal species were evaluated. We tested the null hypotheses of no differences in biomass and presence/absence in algal assemblages among sampling dates (random, 8 levels) and intertidal heights (fixed, 3 levels) in the 50 × 50 quadrats. For these analyses, data were transformed using square root to reduce the effect of dominant species in the samples and Bray–Curtis similarity was used as resemblance measure. The analyses were performed with unrestricted permutation of raw data, and the number of permutations was 9999. In some situations in PERMANOVA, there are not enough possible permutations to get a reasonable test. When there are a large number of possible permutations, PERMANOVA *p* values and the Monte Carlo *p* values should be very close to one

another, but when the number of permutations is low, the p value associated with the permutation test may be quite different (case of the pair-wise tests in this study). Because of this limitation, in these cases (less than 100 permutations) we used the Monte Carlo p value (Anderson et al. 2005). When significant differences were found, taxa making the greatest contribution to these differences were detected using the SIMPER routine in PRIMER (PRIMER; Clarke 1993, Clarke and Warwick 2001).

To compare epifaunal assemblages among habitats (*B. rodriguezii*, *S. dubyi* and *Ahnfeltiopsis* sp.), a PERMANOVA analysis was performed (1 Factor: engineer, fixed, 3 levels). Data were transformed using square root, and Bray–Curtis similarity was used as resemblance measure as above. The analysis was performed with unrestricted permutation of raw data, and the number of permutations was 9999. The main species contributing to differences among assemblages were detected using the SIMPER routine. The t test (Zar 1984) was used to test for differences in sediment weight and organic matter content, between the two sediment-trapping engineers, the algae *Ahnfeltiopsis* sp and the mussel *Brachidontes rodriguezii*.

Results

Spread of NIMS and a native ecological engineer

The presence of the non-indigenous algal species in samples (incidence) within all three levels showed a positive relationship along sampling dates. *Ahnfeltiopsis* sp. increased its presence in the samples from February 2007 to November 2011, from 15 % to 80 % of the samples. *S. dubyi* appeared for the first time in our samples in 2010 and increase from 20 % in January 2010 to 70 % in November

2011 (Fig. 1). Meanwhile, the presence of the mussel *B. rodriguezii* remained constant and was the most abundant species along years and intertidal heights (Fig. 1). The abundance of *B. rodriguezii* did not change among years (ANOVA test, $F_{(2, 36)} = 0.21$, $p > 0.05$) or among intertidal heights (ANOVA test, $F_{(2, 36)} = 1.76$, $p > 0.05$). The percentage cover of *B. rodriguezii* along intertidal heights and years was between 36 and 68 %, presenting considerable variability among samples (Fig. 2a). The non-indigenous macroalgae *Ahnfeltiopsis* sp. and *Schyzimonia dubyi* had a mean percentage cover between 3 and 20 % and 0.4 and 7.6 %, respectively (Fig. 2a). The abundance of *Ahnfeltiopsis* sp. was different among intertidal heights, with a higher percentage cover in the low intertidal in all years (ANOVA test, $F_{(2, 36)} = 6.67$, $p < 0.01$, SNK test: High = Mid < *Low, Fig. 2a). The abundance of *S. dubyi* was low in 2010 and increased in 2011 (ANOVA test, $F_{(1, 24)} = 17.58$, $p < 0.001$, Fig. 2), and no differences were found between intertidal heights.

A different pattern was observed when analyzing biomass. The two non-indigenous species, *Ahnfeltiopsis* sp. and *S. dubyi*, differed in biomass among years and intertidal levels. *Ahnfeltiopsis* sp. appeared in all sampling dates, from 2007 to 2011 and at the three intertidal heights, but showed a pattern to move higher in the intertidal zone through time (Fig. 2b). It increased in biomass at the low intertidal in July 2009, at the low and mid-intertidal in January 2010, and at the mid-intertidal in July 2011 (significant interaction between sampling date and intertidal height, ANOVA test, $F_{(14, 96)} = 3.39$, $p < 0.001$, Fig. 2b). *S. dubyi* appeared in 2010 at the low intertidal level and expanded its distribution to the other two levels in 2011, having higher abundance in the low intertidal (ANOVA test, $F_{(2, 36)} = 7.14$, $p < 0.01$, SNK: High = Mid < **Low, Fig. 2b).

Fig. 1 Percentage of presence (incidence) of mussels (*Brachidontes rodriguezii*) and NIS algae (*Schyzimonia dubyi* and *Ahnfeltiopsis* sp.) ($n = 15$ for each species per sampling date) for each sampling dates

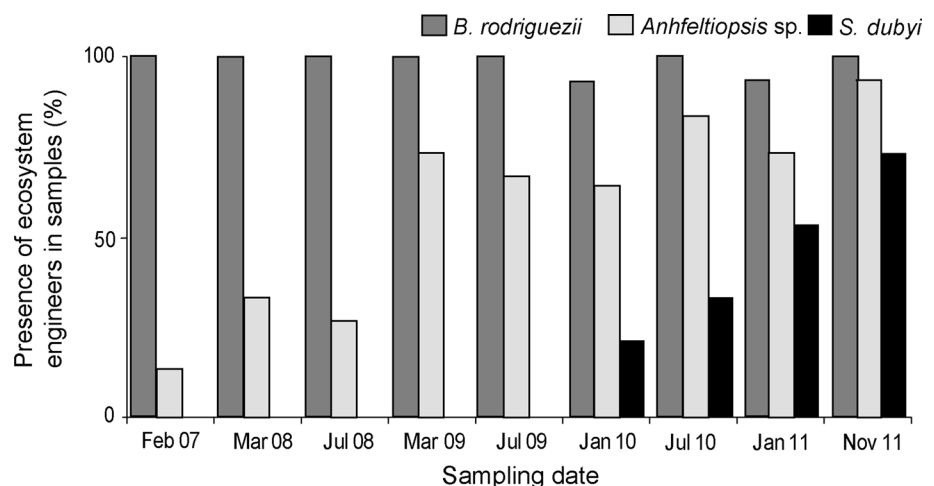
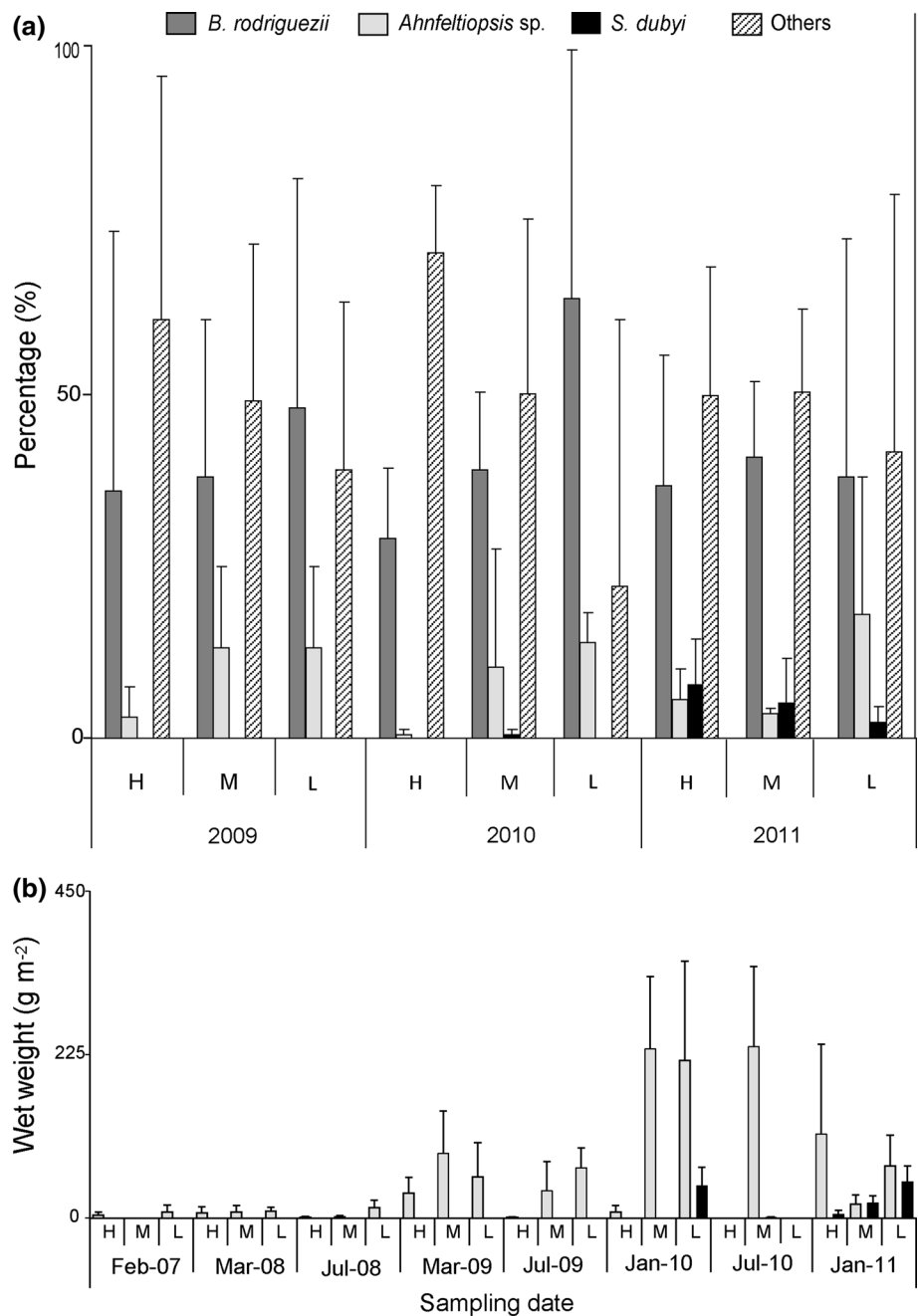


Fig. 2 a Coverage percentage (mean + SD) in 1 m × 1 m quadrates and b. Biomass (g m⁻²) in 1 m² quadrates showing ecosystems engineers (*Brachidontes rodriguezii*, *Ahnfeltiopsis* sp. *Schyzimena dubyi* and other species) in the different intertidal heights (*H* high, *M* mid, and *L* low) sampled for 3 years in Mar del Plata shore



Sessile assemblage along years and intertidal heights

The sessile assemblage in the area comprised 15 native algal species (Table 1), the cirripedian *Balanus glandula*, three different species of sea anemones and the mussel *Mytilus edulis*. However, the sessile fauna was in very low cover (e.g., 2 % *Mytilus* sp., 2.37 % *Balanus glandula*). The percentage cover of the most representative native algae was between 5 and 48 % for *Polysiphonia* sp. and between 2.4 and 35 % for *Ulva lactuca*.

When evaluating the algal assemblage in the invaded area, there was an interaction between year and intertidal height on the percentage cover of the algae assemblage (PERMANOVA, MS = 3205.5, $F_{4,36} = 2.26$, p (permutation) <0.01). SIMPER analysis showed that in 2010, the high intertidal was characterized by *Ralfsia* sp. and *U. lactuca*, the mid-intertidal by *U. lactuca* and the low intertidal by *Ahnfeltiopsis* sp. and *Polysiphonia fucoides* (with contributions higher than 20 % in all cases). Biomass and presence/absence of algal species showed an

Table 1 Algal species found in the study site (Mar del Plata, Argentina)

Species	Taxa	Intertidal heights	Origins	Morphology	Source
<i>Ahnfeltiopsis</i> sp.	R	H M L	NIMS	T	Becherucci et al. (2014)
<i>Bryopsis</i> sp.	C	H M L	N	T	Olivier et al. (1966), Casas et al. (2004)
<i>Ceramium</i> sp.	CC	H M L	N	T	Olivier et al. (1966), Ramirez et al. (2012)
<i>Chaetomorpha aerea</i>	C	H M L	N	T	Olivier et al. (1966)
<i>Cladophora</i> sp.	C	H	N	T	Casas et al. (2004)
<i>Corallina officinalis</i>	R	H M L	N	T	Olivier et al. (1966)
<i>Enteromorpha</i> sp.	C	M L	N	C	Olivier et al. (1966)
<i>Gymnogongrus</i> sp.	R	H M L	N	T	Becherucci et al. (2014)
<i>Hildenbrandia</i> sp.	R	H M	N	E	Olivier et al. (1966)
<i>Jania</i> sp.	R	H M L	N	T	Ramirez et al. (2012)
<i>Nemalion elminthoides</i>	R	H M	N	T	Olivier et al. (1966)
<i>Polysiphonia fucoides</i>	CR	H M L	N	T	Ramirez et al. (2012)
<i>Polysiphonia</i> sp.	CR	H M L	N	T	Olivier et al. (1966), Ramirez et al. (2012)
<i>Porphyra</i> sp.	R	H M L	N	C	Olivier et al. (1966)
<i>Ralfsia</i> sp.	P	H M	N	E	Becherucci et al. (2014)
<i>Schizymenia dubyi</i>	R	H M L	NIMS	C	Ramirez et al. (2012)
<i>Ulva lactuca</i>	C	H M L	N	C	Olivier et al. (1966)

Origins were assigned based on bibliography: non-indigenous marine species (NIMS); species not mentioned in the literature as non-indigenous species and cited in local studies of over 40 years are considered native (N)

Abbreviations. *Taxon:* Chlorophyceae (C), Phaeophyceae (P), Rhodophyceae (R). *Intertidal levels:* high level (HL), mid-level (ML) and low level (LL). *Morphology:* canopy-forming algae (C), turf-forming macroalgae (T) and encrusting algae (E)

interaction between sampling date and intertidal height (PERMANOVA, biomass $MS = 3418.2$, $F_{13, 84} = 1.70$, p (permutation) < 0.001 ; presence/absence $MS = 2388.6$, $F_{13, 84} = 1.98$, p (permutation) < 0.01 , Fig. 3). Pair-wise comparisons for biomass data showed that there were differences mainly between sampling dates in the mid-intertidal (Supplementary Material Table 1). SIMPER analysis showed *Ulva lactuca* and *Polysiphonia* sp. contributed the most to the similarities within each sampling date in most cases (both with biomass and presence/absence data).

The native mussel and the NIS algae as habitats for the benthic assemblage

Eleven invertebrate species were found within *Brachiodontes rodriguezii* habitat, while 10 were found within *S. dubyi* and 12 within *Ahnfeltiopsis* sp. habitats (Supplementary Material, Table 2). Specifically, two native species (*Pachycheles laevidactylus* and *Caprella dilatata*) were only found in the non-indigenous species. Epibenthic assemblages associated with the three ecosystem engineers were significantly different (PERMANOVA test, $F_{(2, 23)} = 5.42$ $p < 0.001$; $p < 0.01$ in all pair-wise comparisons; Fig. 4). For mussel beds, the species that

contributed the most to the similarities within the assemblage were the limpet *Siphonaria lessoni* (SIMPER test, Contribution = 46.26 %) and the polychaete *Syllis gracilis* (SIMPER test, Contr. = 35.24 %), while in *Ahnfeltiopsis* habitat, it was the mussel *Mytilus edulis* (SIMPER test, Contr. = 46.61 %). In *S. dubyi* habitats, the isopod *Idotea baltica* was the species that most contributed to the similarities within the assemblages (SIMPER test, Contr. = 38.89 %). These same species contribute the most to the dissimilarities among groups as well (Table 2). Mean species number per volume of habitat did not change among habitats (ANOVA test, $F_{(2, 21)} = 0.02$, $p > 0.05$), but abundance of macroinvertebrates significantly decreased on the NIMS habitats (ANOVA test, $F_{(2, 21)} = 15.9$, $p < 0.001$).

Sediment retention was different among the three habitats. *Schizymenia dubyi* did not trap any sediment. Comparisons between the other two habitats, i.e., the mussel beds and the *Ahnfeltiopsis* sp. patches, showed that sediment was significantly higher inside the mussel bed matrix (mean \pm SD $18,296 \pm 7508$ vs. 6424 ± 7720 gr.m²; t test, t (df = 18) = 3.5, $p < 0.005$, Fig. 5a). Organic matter content of the sediment was also higher inside mussel beds (t test, t (df = 6) = 3.89, $p < 0.05$). The size frequency distributions of sediment trapped in *B. rodriguezii* mussel beds

Fig. 3 Total algal biomass measured as wet weight (g m^{-2}) for each macroalgae species sampled at eight sampling dates in Mar del Plata shore: **a** high intertidal level, **b** mid-intertidal level and **c** low intertidal level. “Others” include 9 macroalgae species usually present but with low biomass: *Bryopsis* sp., *Chaetomorpha aerea*, *Cladophora* sp., *Enteromorpha* sp., *Hildenbrandia* sp., *Jania* sp., *Nemalion elminthoides*, *Porphyra* sp., *Ralfsia* sp

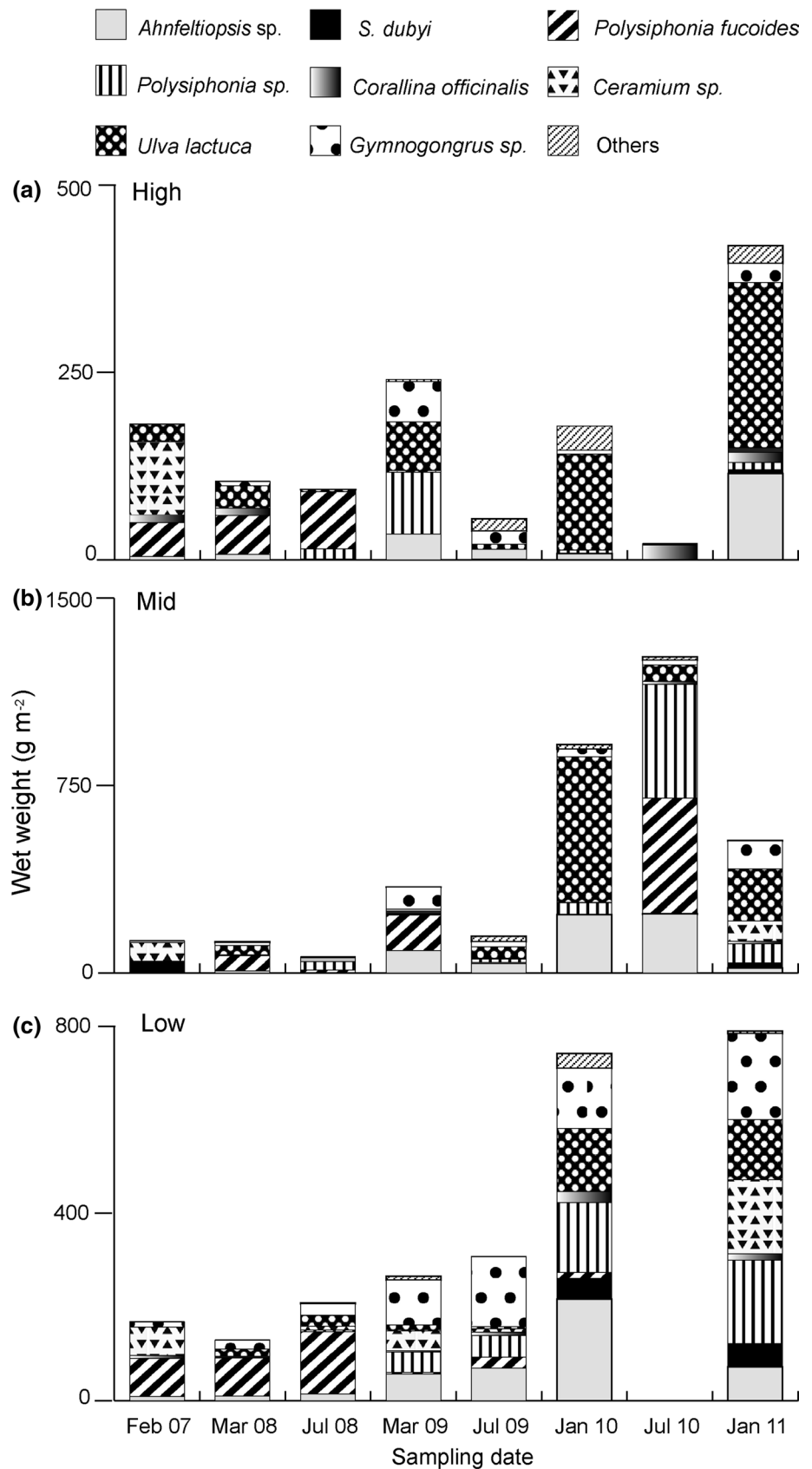


Table 2 Results of SIMPER abundance data in three ecosystem engineers (*Brachidontes rodriguezii*, *Schyzimonia dubyi* and *Ahnfeliopsis* sp.)

	Av. Abund		Av. Diss.	Contrib. %	Cum. %
1) Groups	<i>Schyzimonia</i>	<i>Ahnfeliopsis</i>			
Average dissimilarity = 81.50					
<i>Mytilus edulis</i>	0	3.5	14.25	17.48	17.48
<i>Idotea baltica</i>	3	0.88	11.74	14.4	31.88
<i>Syllis prolixa</i>	2.5	1	9.37	11.5	43.38
<i>Siphonaria lessoni</i>	3.75	0.75	9.06	11.11	54.49
<i>Syllis gracilis</i>	2	3.88	8.62	10.57	65.06
2) Groups	<i>Schyzimonia</i>	<i>Brachidontes</i>			
Average dissimilarity = 83.28					
<i>Siphonaria lessoni</i>	3.75	17.88	26.22	31.48	31.48
<i>Syllis gracilis</i>	2	13	17.71	21.26	52.75
Nemertean	0.38	6.63	8.54	10.25	63
3) Groups	<i>Ahnfeliopsis</i>	<i>Brachidontes</i>			
Average dissimilarity = 82.23					
<i>Siphonaria lessoni</i>	0.75	17.88	25.62	31.15	31.15
<i>Syllis gracilis</i>	3.88	13	17.64	21.45	52.6
Nemertean	2.38	6.63	9.86	11.99	64.6

Test shows species contributing most to dissimilarity in paired comparisons between engineers ranked by decreasing discriminating power (%). Only species with >10 % contribution were listed

showed that the average diameter of the sediment particles corresponds to fine sand and very fine sand, while sediment trapped in *Ahnfeliopsis* sp. patches contained bigger particles, i.e., medium and fine sand (Fig. 5b).

Discussion

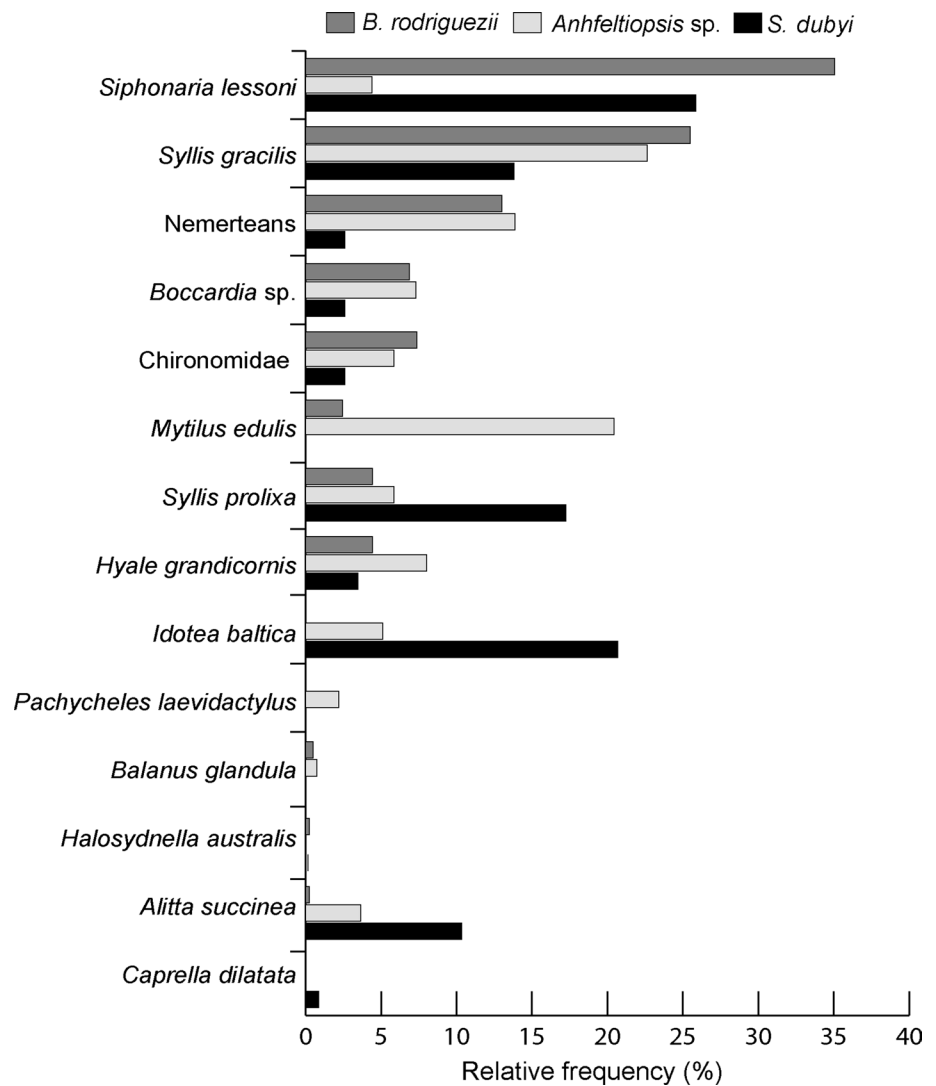
The two non-indigenous algal species, *Ahnfeliopsis* sp. and *Schyzimonia dubyi*, increased in abundance and biomass and expanded along the intertidal on the urban rocky shore in Playa Chica from February 2007 to November 2011, and results suggest a trend to continuous increase beyond 2011. These two non-indigenous algae were also found to cover great amounts of the intertidal and provide quite extensive new habitat types in the area. Consistent with our predictions, the benthic assemblage in areas with NIMS differed from that of the native mussel habitat. Hence, these NIMS have the potential to modify the structure and composition of the benthic biota in the area, although the species were similar to that of the native habitat. The steady increase in algal biomass and presence along the intertidal suggest that these species have probably expanded further in the years since our last sampling campaign, and therefore, the effects on native assemblages might be greater than the ones reported here.

The potential impacts of introduced macroalgal species have been studied only for the 10 % of the total number of globally introduced species (Davidson et al. 2015). The main ecological effects reported were changes in

competitive relationships among primary producers; i.e., introduced species increased in abundance resulting in a monopolization of space (Davidson et al. 2015). In most cases, the NIMS had a strong negative impact on resident primary producer assemblages, but their effects on density/cover of higher trophic groups were mostly neutral (Maggi et al. 2015) or even positive, increasing the diversity of consumers (Thomsen et al. 2014). These results showed that herbivores, such as the isopod *Idotea baltica*, were often found among seaweeds but rarely seen in mussel beds. The NIMS also provided habitat for two native species of deposit feeders not found in mussel beds. Therefore, food/refuge preferences of invertebrate species might explain differences among habitats.

In addition, algal morphology could also explain the differences in assemblages between the algal NIMS. First, our results indicate that *Ahnfeliopsis* sp. trapped a considerable amount of sediment, whereas *Schyzimonia dubyi* only trapped a few grains of sand. Therefore, the differences found in epifaunal assemblages might be due to the differences in sediment retention and composition between the NIMS and the native mussel, as sediment quantity, grain size and type has shown to be an important factor in determining the distribution of epifaunal organisms (Giménez et al. 2014). This would explain the higher densities of polychaetes and nemertean found in *Ahnfeliopsis* patches compared to *Schyzimonia* patches. Second, the fact that *Ahnfeliopsis* sp. is an erect algae and retains its structure even at low tide makes it a stable habitat that could facilitate the settlement of sessile species such as the mussel

Fig. 4 Relative frequency (%) of invertebrates associated with the three ecosystem engineers (*B. rodriguezii*, *Ahnfeltiopsis* sp. and *S. dubyi*) in the study area



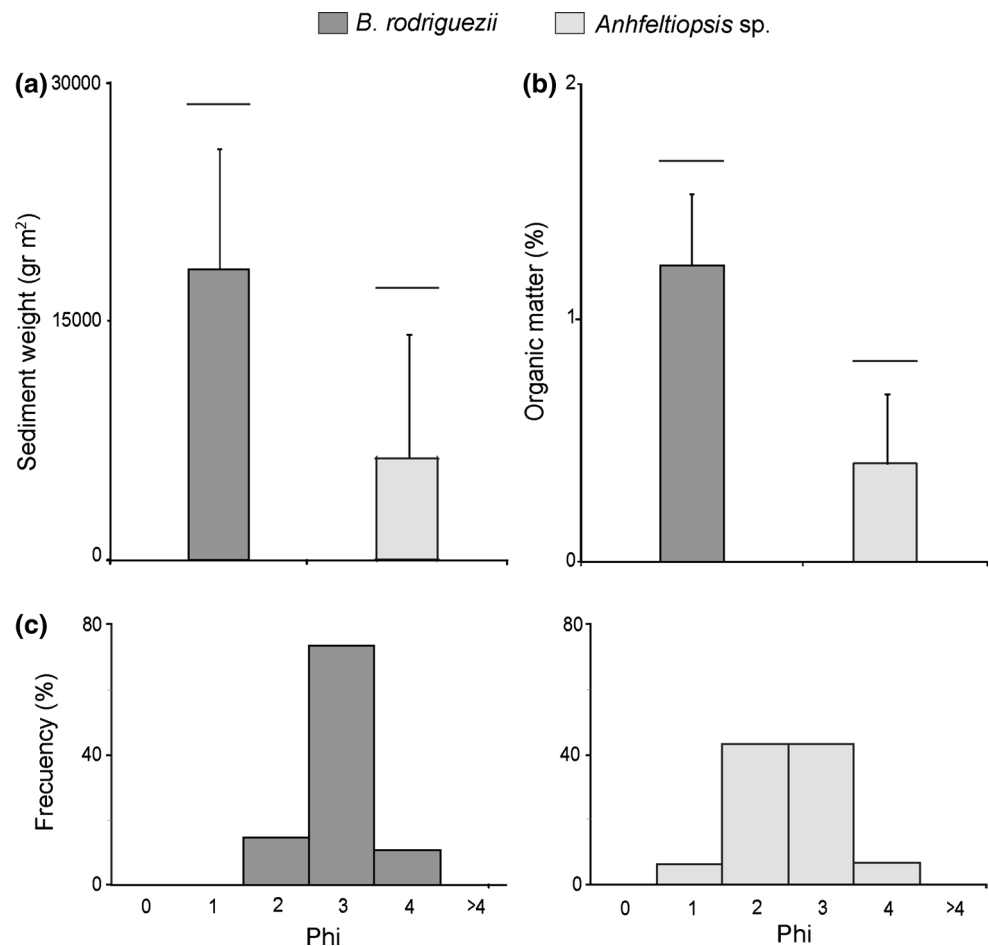
Mytilus edulis or the barnacle *Balanus glandula*, which were found inhabiting the patches of this species but not found in *S. dubyi* patches.

The percentage cover of the mussel *B. rodriguezii* has remained the same over the years, even when there has been an increase in the cover of NIMS. This seems to indicate that these seaweeds are either colonizing bare space or patches colonized by other algae. A recent study has shown that, due to wave action, patches of bare rock are often opened in *B. rodriguezii* beds (Gutiérrez et al. 2015). These disturbances are expected to be more frequent in the future, since the intensity and frequency of storms are increasing at the study zone (Fiore et al. 2009). Preliminary observations have shown that when a patch is opened, recolonization begins with incrusting algae, and then, the succession can be followed with native algae such as *Polysiphonia* sp., the mussel *B. rodriguezii* or the NIMS seaweeds, without a clear pattern (Cuevillas 2014). Near the sewage discharge outfall in Mar del Plata, the reef-forming

non-indigenous polychaete *Boccardia proboscidea* has displaced *B. rodriguezii* from the intertidal zone (Jaubet et al. 2013). If these algal NIMS colonize bare rock faster than the native mussel, they could potentially displace it. Further experiments must be done to determine the colonization capacity of *Ahnfeltiopsis* sp. and *S. dubyi* over bare rock patches.

The introduction of these non-indigenous sessile species has the potential to affect the spatial distribution of native dominant species by occupying primary space, thus decreasing the dominance of native species. In addition, these NIMS can have a positive impact on some native species, by providing a greater availability of suitable habitat (Fowler-Walker and Connell 2007, Simberloff and Von Holle 1999, Ricciardi 2001, Simberloff 2006). This study constitutes the first step in understanding the ecological consequences of the invasion by *Ahnfeltiopsis* sp and *S. dubyi* in Argentina and the first record of *S. dubyi* outside its natural range (Ramirez et al. 2012). Further manipulative experiments are

Fig. 5 **a** Sediment weight (g m^{-2}) and **b** organic matter content (%) retained in the mussel matrix and in *Ahnfeltiopsis* sp. patches. Horizontal lines over the bars mean significant differences after *t* test ($p > 0.05$). **c** Size frequency distributions of sediment grains trapped in *B. rodriguezii* and *Ahnfeltiopsis* sp



needed to understand the invasion dynamics under present conditions and predict the potential impacts under future environmental conditions. These combinations studies will provide the knowledge of the dynamics of these invasions critical for managers to make decisions on the control strategies to follow.

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Compliance with Ethical Standards

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Ethical approval This article does not contain any studies with animals performed by any of the authors.

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