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Influence of the physical structure of an invasive barnacle in structuring macroinvertebrate assemblages

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ABSTRACT. Many invertebrate species use the microhabitats generated by barnacles to settle and to avoid predation and desiccation. In Argentina, the acorn barnacle *Balanus glandula* not only colonizes rocky shores but has also successfully invaded soft bottom salt marshes, where it form large three-dimensional structures that facilitate the presence of other invertebrates, thus affecting the whole species assemblage. Artificial barnacles were deployed on a Patagonian salt marsh to reproduce the physical structure of natural aggregates. The experiment included natural and material controls and two levels of structural complexity that represent the variety of aggregates found in nature: (i) aggregates with internal empty spaces and galleries among barnacles and (ii) aggregates without spaces and galleries. After nine months, the macroinvertebrate assemblages were compared between treatments. The results showed that the composition of the assemblage differed significantly between artificial treatments and control plots. However, there was no effect of the mimic barnacles on macroinvertebrate richness and diversity. In this way, our results suggest that the physical structure of *B. glandula* could modify the composition of macroinvertebrate assemblages. Besides, *B. glandula* recruits were registered on the mimics highlighting the importance that the physical structure supplied by this species could have on its own persistence within invaded soft bottom salt marshes.

[Keywords: habitat-forming species, *Balanus glandula*, artificial structures, salt marshes, Patagonia]

RESUMEN. La estructura física de un cirripedio invasor influye los ensambles de macroinvertebrados. Para asentarse y evitar la depredación y la desecación, muchas especies de invertebrados usan los microhábitats que generan los cirripedios. En la Argentina, el cirripedio acorazado invasor *Balanus glandula* no sólo coloniza las costas rocosas; también ha invadido con éxito marismas de fondos blandos, donde forma grandes estructuras tridimensionales que facilitan la presencia de otros invertebrados. Esto afecta la estructura de la comunidad. Se colocaron cirripedios artificiales en una marisma de la Patagonia para imitar la estructura física de los agregados naturales. El experimento incluyó controles naturales y de materiales, y dos niveles de complejidad estructural que representaron la variedad de los agregados que se encuentran en la naturaleza: (i) agregados con espacios vacíos internos y galerías entre los cirripedios, y (ii) agregados sin espacios y galerías. Después de nueve meses, el ensamble de macroinvertebrados se comparó entre tratamientos. La composición del ensamble fue significativamente diferente entre los tratamientos artificiales y las parcelas control, pero no hubo efecto de los cirripedios artificiales sobre la riqueza y diversidad de macroinvertebrados. Esto sugiere que la estructura física de *B. glandula* podría explicar el efecto ejercido sobre la comunidad. Por otra parte, se registraron reclutamiento de *B. glandula* sobre los cirripedios artificiales, lo que resalta la importancia que la estructura física de esta especie tendría sobre su persistencia en las marismas de fondos blandos.

[Palabras clave: especies formadoras de hábitat, *Balanus glandula*, estructuras artificiales, marismas, Patagonia]

INTRODUCTION

Interactions between organisms have been recognized for decades as one of the main drivers of the distribution and abundance of species (Dayton 1971; Paine 1974; Menge 1976; Rohde 1984). Through the creation, modification and maintenance of habitats, ecosystem engineer species (sensu Jones et al. 1994) are able to ameliorate key physical stressors and facilitate the colonization and survival of a variety of other organisms (Crooks 2002; Gutiérrez et al. 2003; Bouma et al. 2009). Furthermore, it is important to establish which engineers would exert most significant effects in the communities where they inhabit (Jones et al. 1994; Wright and Jones 2006). There are several inherent factors that determine the effect of ecosystem engineers: the lifetime of the organisms, their population densities and the persistence over time of their structures. Concurrently, the number, type and manner in which resources are controlled also define effects of ecosystem engineers (Jones et al. 1997). Inherent factors are relatively simple to measure (Berkenbusch and Rowden 2003; Gutiérrez et al. 2003; Prado and Castilla 2006). In contrast, the number and type of resources, and how they are affected, impose higher methodological

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difficulty (Schwindt et al. 2001; Hastings et al. 2007; Sueiro et al. 2011). For example, in Mar Chiquita coastal lagoon (Argentina), the invasive reef-building polychaete *Ficopomatus enigmaticus* creates refuge for other species and changes the physical factors of the invaded environment (modifying deposit transport and water flow, among others). To determine density, size and distribution of the reefs requires simple methods (Schwindt and Iribarne 2000; Schwindt et al. 2004). However, field manipulations and more complex experiments were necessary to establish how the reefs alter the physical and biological conditions of the environment (Schwindt et al. 2001; Schwindt et al. 2004). In this sense, the addition or removal of species and their handling is extremely useful to elucidate these factors (Bertness 1984; Bortolus et al. 2004; Sueiro et al. 2012). Thus, manipulative field experiments are an appropriate tool to understand the role of engineer species on the ecosystem, as it has been demonstrated before in different invertebrate species (Kelaher 2002; Callaway 2003; Sueiro et al. 2012).

Ecosystem engineer's effects on the community may have a biotic or abiotic origin, or a combination of both (Jones et al. 1994; Crooks 2002; Bouma et al. 2009). In the rocky intertidal community, for example, the multi-layers of mussels increase the accretion of soil and promote its deposition and stabilization (reviewed in Gutiérrez et al. 2003; Sousa et al. 2009). At the same time, valves provide new surfaces for larval settlement and shelter for stressful conditions or predation for many invertebrates (Thiel and Ullrich 2002; Commito et al. 2005; Buschbaum et al. 2009). Thereby, these examples illustrate how structural properties (such as the spatial distribution of the shells) and ecological processes (for example the competition for food) are simultaneously responsible for the effect of a given engineer on the associated fauna (Crooks 2002; Bouma et al. 2009). In this sense, it is interesting to distinguish the relative importance of the biotic and abiotic component of the effect. This has been tested by comparing the assemblages associated to mimic structures with the natural habitats (Kelaher 2002; Palomo et al. 2007; Sueiro et al. 2012). Mimic structures have similar physical properties to the natural habitats without biological properties. Therefore, the use of mimic structures allows establishing whether the effects generated by ecosystem engineers are a result of their physical structure (Kelaher 2002).

Several invasive species increase physical complexity of environments by adding their own structures and affect natural assemblages (e.g., macroalgae [Irigoyen et al. 2011], polychaetes [Schwindt et al. 2001], bryozoans [Sellheim et al. 2010], ascidians [Castilla et al. 2004]). The physical structure provided by barnacles offer new microhabitats that different benthic species utilize to evade physical and biological constrains (reviewed in Barnes 2000). *Balanus glandula* is a barnacle native to the Pacific coast of North America that was introduced to Argentina in the 1970s (Spivak and L'Hoste 1976). Nowadays, the species has spread along the entire Argentinean coast, covering 17 latitudinal degrees, from San Clemente del Tuyú (36° S) to Río Grande (53° S) (Schwindt 2007). The species usually dominates the upper intertidal of rocky shores. However, in 2005, *B. glandula* was registered in soft bottom Patagonian salt marshes (Schwindt et al. 2009), mostly within areas dominated by the smooth cordgrass *Spartina alterniflora*, also exotic (Bortolus et al. 2015). In these coastal environments, the species is now well established, colonizing all the hard substrata available and forming large three-dimensional structures (or aggregates) (Mendez et al. 2013; Mendez et al. 2015). The increase in structural complexity of these aggregates enhances habitat quality by raising the availability of settling spaces, food, and/or refuge, facilitating the presence of other invertebrates; thus, affecting local communities (Mendez et al. 2015). It is presently unknown whether the effects generated by barnacles are the product of biotic factors, the physical structure, or a combination of both. Therefore, in the current study we evaluate the effects of the addition of barnacle mimics on the composition, diversity and richness of the associated macroinvertebrate assemblage. Our results will help to determine the relative importance of *B. glandula* physical structure on marsh benthic communities.

Materials and Methods

Study Site

The study was performed in Riacho marsh, Chubut, Argentina (hereafter Riacho, 42°24′ S, 64°37′ W). The low and high marsh levels were +4.4 m and +5.8 m, respectively (relative to the Argentinean hydrographic zero supplied by the Servicio de Hidrografía Naval 2012 (for further description see Bortolus et al. 2009)). The low marsh is dominated by *Spartina alterniflora* and *S. densiflora*, whilst *Sarcocornia* *perennis* dominates the high marsh (Isacch et al. 2006; Bortolus et al. 2009). The invasive barnacle *Balanus glandula* is well established within Riacho marsh (Schwindt et al. 2009) and its distribution in the marsh is patchy. *B. glandula* uses the hard substrata present in the marsh to settle and it is found in areas where the seawater flows with the tides (Mendez et al. 2013). In Riacho, *Mytilus* sp. mussel valves are the most frequent type of substrata used for settlement and where three-dimensional aggregates of barnacles are largest (Mendez et al. 2013; Mendez et al. 2015).

Effect of artificial structures on the benthic fauna

To test the effects of the addition of barnacle mimics on benthic fauna, a manipulative field experiment was conducted. The experiment included two treatments with inert models that resemble *Balanus glandula* (Figure 1). Inert epoxy putty (Parsecs®) was used to make barnacle mimics. The two treatments represented the most contrasting complexities observed in the field: high complexity mimics (aggregates with internal empty spaces and galleries among barnacles. Hereafter: HCM) and low complexity mimics (aggregates without free spaces and galleries among barnacles. Hereafter: LCM). Each experimental unit consisted of five mimics of the same treatment placed together (area= 175 cm^2 per unit) in order to reflect natural aggregates density (n=10 replicate units per treatment). The units were interspersed in the experimental site (~300 m^2) and distributed according to the natural pattern. Mimics were fixed to PVC tubes (2 cm in diameter) pinned to the substrate. To evaluate if the PVC tubes affect the fauna, a control treatment was also performed (hereafter CM). Each control unit consisted of five PVC tubes pinned to the substrate with the same spatial arrangement as the HCM and LCM treatment units (n=10 replicate units, area=175 cm^2 per unit). Each experimental unit was periodically monitored for maintenance, and after nine months (October 2011 to July 2012), all units were transported to the laboratory. Units were removed by using a PVC core (diameter=15 cm, depth=10 cm, volume=1766 cm^3). At the same time, ten additional units (diameter=15 cm, depth=10 cm, volume=1766 cm^3. Natural control, hereafter: NC) were randomly collected in the experimental site in order to compare the similarity between the experimental treatments and the natural assemblage (no barnacles).

In the laboratory, units were sieved through 0.5 mm mesh size and the organisms retained were fixed in 4% formalin, preserved in 70% ethanol and identified to the lowest taxonomic level possible under a dissecting stereo microscope. A voucher of the taxa collected was deposited in the CENPAT invertebrate collection. Taxonomic richness and Shannon diversity index (Shannon and Weaver 1949) were calculated for each experimental unit. Nonmetric multidimensional scaling (MDS) was used to explore similarities and differences among assemblages, and a similarity percentage analysis (SIMPER) was used to determine the taxa responsible for the differences between treatments. A permutational analysis of variance (PERMANOVA) was used to determine if there were differences in the invertebrate assemblage composition among treatments, with treatment as fixed factor (using Primer 6 PERMANOVA + extension software v.6.1.7 Primer-E, Plymouth) (Anderson et al. 2008). Pair-wise comparisons were then performed among all pairs of levels. PERMANOVA and MDS were made with a Bray-Curtis similarity matrix using a dummy variable and the abundance of all invertebrate

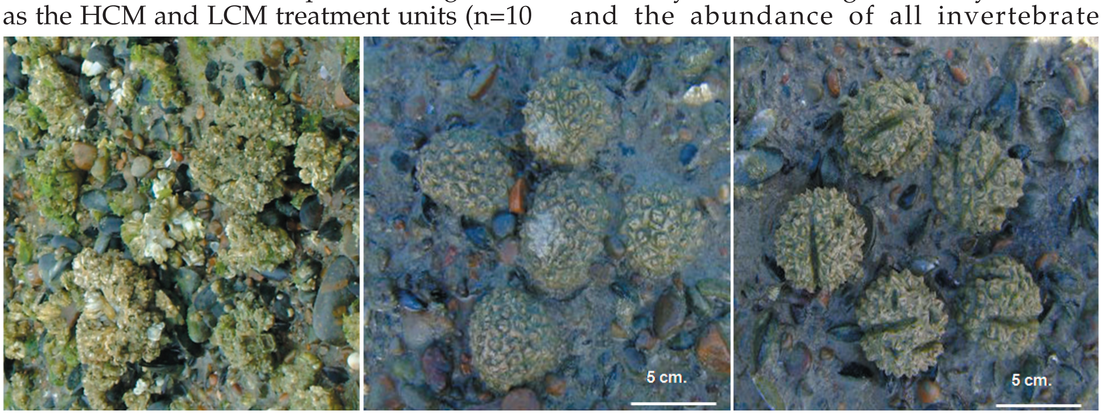

Figure 1. Photographs of living barnacles (left), low complexity mimics (center) and high complexity mimics (right).

Figura 1. Fotografías de cirripedios vivos (izquierda), mímicas de baja complejidad (centro) y mímicas de alta complejidad (derecha).

species was fourth-root transformed. Since PERMANOVA routine creates a non-parametric, permutational analogue of ANOVA when applied to univariate data; the same PERMANOVA model was employed to determine if there were differences in richness and diversity of macroinvertebrates among treatments (9999 permutations (Anderson 2001; Anderson et al. 2008) and pair-wise comparisons were also performed. Prior to PERMANOVA analyses, homogeneity of multivariate dispersion was tested using PERMDISP tests.

Effect of artificial structures on the recruitment of Balanus glandula

The abundance and size of *Balanus glandula* recruits found on barnacle mimics (HCM and LCM) were recorded to assess the effect of the physical structure of barnacles on recruitment of conspecifics. All barnacles larger than 0.15 mm in rostral-carinal length settled directly on the mimics were considered recruits and counted. The sizes of the recruits were obtained by measuring the orifice length along the carinal and rostral plates with a digital caliper (precision±0.01; n=100 for each treatment). The measured barnacles were randomly chosen from mimics of different experimental units. Differences in the abundance of barnacle recruits between treatments were evaluated using a t test (Zar 1999). A square root-transformation of data was done to meet homoscedasticity assumption. Sizes were compared with a Mann-Whitney U-test, because data were not normally distributed (Zar 1999).

Results

Effect of artificial structures on the benthic fauna

A total of 11 macroinvertebrate taxa were recorded in the experiment. The MDS plot was unable to clearly separate treatments (Figure 2). Composition of the assemblage differed among treatments, whilst richness and Shannon diversity index did not (Table 1, Figure 3). Pair-wise comparisons of assemblage composition showed that HCM and LCM were no different (Table 2). Also, HCM was different to controls while LCM was different to CM (Table 2). Nevertheless, CM was found different from NC (Table 2). SIMPER identified *Tanais dulongii*, Syllidae and Maldanidae as characteristic of NC while Capitellidae, crabs and Chironomidae were typical of the experimental treatments (Table 3). For the analysis, *Neohelice granulata*, *Cyrtograpsus altimanus* and *Cyrtograpsus angulatus* were grouped together since most of the individuals were juveniles in which the correct species identification was not possible (named as crabs).

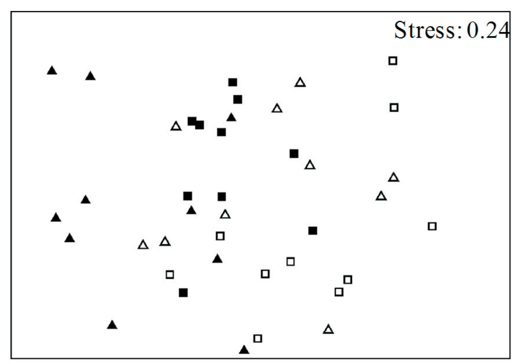

Figure 2. Two-dimensional MDS ordination comparing macroinvertebrate assemblages associated with the experimental treatments (high complexity mimics: white squares, low complexity mimics: white triangles, control of materials: black triangles and natural control: black squares).

Figura 2. Análisis de ordenamiento bidimensional MDS comparando los ensambles de macroinvertebrados asociados a los tratamientos experimentales (mímicas de alta complejidad: cuadrados blancos, mímicas de baja complejidad: triángulos blancos, control de materiales: triángulos negros y control natural: cuadrados negros.

Table 1. PERMANOVA results for the field experiment (d.f.=3).

Tabla 1. Resultados del PERMANOVA para el experimento a campo (g.l.=3).

Source	Composition			Richness			Diversity		
	Pseudo-F	*P*	Perms	Pseudo-F	*P*	Perms	Pseudo-F	*P*	Perms
Treatment	4.22	0.0001	9921	1.94	0.1249	9702	1.58	0.2099	9944
PERMDISP	1.79; P>0.05			1.04; P>0.05			1.61; P>0.05		

Table 2. Pairwise comparison results for assemblage composition for the PERMANOVA analysis.

Tabla 2. Resultados de las comparaciones de a pares para la composición del ensamble en el análisis de PERMANOVA.

Comparison	NC vs. CM	NC vs. LCM	CM vs. LCM	NC vs. HCM	CM vs. HCM	LCM vs. HCM
T	2.19	1.42	2.00	2.19	2.77	1.32
P	0.002	0.111	0.005	0.002	0.000	0.155
Perms	9428	9421	9447	9419	9413	9419

Table 3. SIMPER routine results showing the taxa which made the greatest contributions to dissimilarity between treatments (HCM: high complexity mimics, LCM: low complexity mimics, CM: control of materials and NC: natural control). Lists were truncated when cumulative percentage reached 50%.

Tabla 3. Resultados del análisis SIMPER que muestran los taxa con las mayores contribuciones a la disimilitud entre tratamientos (HCM: mímicas de alta complejidad, LCM: mímicas de baja complejidad, CM: control de materiales y NC: control natural). Las listas fueron truncadas cuando el porcentaje acumulado alcanzó el 50%.

Comparison	Average dissimilarity	Taxa	Contribution (%)	Cumulative (%)
NC and CM	43.04	*T. dulongii*	25.92	25.92
		Capitellidae	17.59	43.52
		Syllidae	17.12	60.64
NC and LCM	38.88	Maldanidae	17.51	17.51
		Capitellidae	14.98	32.49
		Eunicidae	11.11	43.61
		Syllidae	9.99	53.6
CM and LCM	48.14	*T. dulongii*	22.99	22.99
		Capitellidae	16.79	39.78
		Maldanidae	13.32	53.11
NC and HCM	43.15	Maldanidae	18.23	18.23
		Capitellidae	15.58	33.82
		Chironomidae	13.57	47.39
		Crabs	12.76	60.15
CM and HCM	53.08	*T. dulongii*	20.4	20.4
		Maldanidae	15.19	35.59
		Capitellidae	13.06	48.65
		Chironomidae	12.87	61.52
LCM and HCM	43.96	Capitellidae	16.15	16.15
		Chironomidae	13.64	29.79
		Crabs	13.07	42.86
		Maldanidae	12.52	55.38

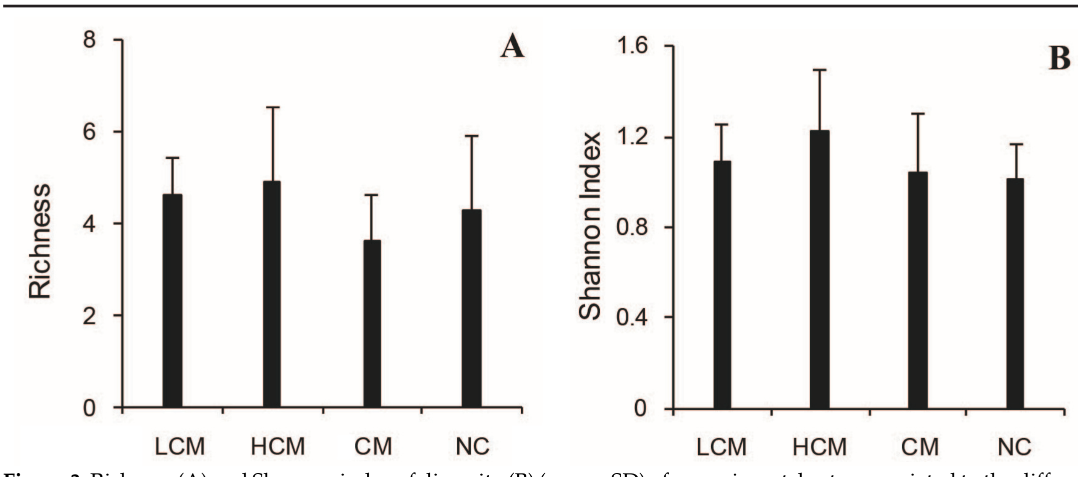

Figure 3. Richness (A) and Shannon index of diversity (B) (mean+SD) of macroinvertebrates associated to the different treatments (HCM: high complexity mimics, LCM: low complexity mimics, CM: control of materials and NC: natural control).

Figura 3. Riqueza (A) e Índice de Diversidad de Shannon (B) (media±DE) de los macroinvertebrados asociados a los diferentes tratamientos (HCM: mímicas de alta complejidad, LCM: mímicas de baja complejidad, CM: control de materiales y NC: control natural).

Effect of artificial structures on the recruitment of Balanus glandula

The mean abundance of barnacles recruited on the mimics were 32 individuals/experimental unit (SD=22) in HCM and 16 individuals/experimental unit (SD=9) in LCM. The mean size of recruited barnacles was 3.58 mm (SD=0.78) in HMC and 3.54 mm (SD=0.66) in LCM. Abundance and size of barnacles did not differ between treatments ($t_{abundance}$=-1.87, d.f.=18, *P*>0.05; U_{size}=4706, *P*>0.05). The size frequency distribution of *B. glandula* recruits in treatments was unimodal; sizes varied between 1.08 and 5.08 mm. Individuals between 3.51 and 4.5 mm were the most abundant.

Discussion

In the present work, the addition of barnacle mimics affects the composition of the macroinvertebrate assemblage in a Patagonian salt marsh. After nine months, the composition of the assemblage differed among artificial treatments of higher complexity and control plots with no barnacles. However, richness and diversity did not change with the presence of the artificial barnacles. Thereby, our findings suggest that the physical structure provided by the invasive barnacle *Balanus glandula* would be an important structural factor in salt marshes communities and that the chemical and biological properties of the barnacles would not be indispensable to affect the associated fauna. Moreover, barnacle mimics were used as settlement substratum for conspecifics, highlighting the importance that their own physical structure could have on the persistence of the species in this kind of environments.

The physical alteration of ecosystems by engineer species is a common phenomenon in all types of environments (Jones et al. 1994; Jones et al. 1997). Cases of habitat modification has been studied both for animals and plants in extremely varied environments, including terrestrial (Machiote et al. 2004; Badano et al. 2006), freshwater (Lougheed et al. 1998; Zhu et al. 2006) and marine systems (Castilla et al. 2004; Irigoyen et al. 2011). An emblematic example, commonly used to illustrate the concept of ecosystem engineering, is that of the beaver (*Castor canadensis*) (Naiman et al. 1988; Wright et al. 2002; 2003). These semi-aquatic rodents construct dikes and burrows in rivers and streams by using branches and tree trunks, drastically transforming the environments where they live (Naiman et al. 1988). Ecosystem engineers on intertidal coastlines buffer physical stress by providing freshly, moistly and hydro-dynamically benign microhabitats (Jones et al. 1994). The microenvironments generated by barnacles exemplify this, resulting in an increase in the abundance of many taxa in response to the presence of these new structures (Barnes 2000; Harley 2006; Mendez et al. 2015). Even though the majority of taxa were present in the different treatments of the experiment, the abundance of some of them was different between artificial treatments and control plots. For example, capitellid polychaetes, chironomid insects and juveniles of crabs showed higher densities in the mimic treatments. For these species, barnacle mimics would be providing a favourable habitat as they generate shelter from predators and environmental stressful conditions (Barnes 2000). These increments in the abundances suggest that, at least for the mentioned taxa, the effect of the barnacles' architecture was considerable. In the same marsh, a previous work also reported an increment in the abundance of several species (chironomid insects, juveniles of crabs and the isopod *Pseudosphaeroma* sp.) due to the presence of living barnacles (Mendez et al. 2015). Thus, our results were consistent with the pattern registered for living barnacles and could be suggesting that the physical structure of *B. glandula* is responsible for the effect exerted on the macroinvertebrate taxa in Riacho marsh. However, since we were not able to compare our mimics with living barnacles at the end of the experiment, we cannot conclude that the changes mediated by the mimics were at the same rate or with the same magnitude as the ones generated by living aggregates. However, the engineering effects of barnacles on the assemblage could be enhanced through indirect processes, promoting changes in biological interactions mediated by the taxa for which abundance was increased, raising, for example, the relative importance of herbivory (Harley 2006; Hoey and Bellwood 2011) and/or modifying micro-environmental conditions. Within this context, the new structure generated by the presence of the engineer species could alter the biogeochemical characteristics of the invaded ecosystems (reviewed in Gutiérrez and Jones 2006).

More complex habitats are usually associated with increments in density and/or species richness. Since greater structural complexity could provide more resources, habitats and niches for a greater number of species to exploit (Schwindt et al. 2001; Thiel and Ullrich 2002; Bouma et al. 2009). In the last years, several studies showed that in some cases when structural complexity is increased the effects on communities are neutral (Almany 2004; Prado and Castilla 2006; Sellheim et al. 2010) or even negative (Callaway 2003; Neira et al. 2006). In a previous work, we found that the richness and diversity of macroinvertebrates in Riacho marsh did not vary between areas with barnacles settled on mussel and areas of mussels without barnacles; thus, barnacles add no significant effect on richness and diversity to that already generated by mussels (Mendez et al. 2015). In the same way, in the current experiment we did not observed significant effect on invertebrate richness and diversity when barnacle mimics were added. Furthermore, despite of the differences in architectures between the two mimic treatments; richness and diversity did not differ significantly among them. Moreover, the difference found between control treatments (NC and CM) (Table 2) suggests that part of the detected effect was an artefact caused by the pvc pipes in addition to the mimics. These cases illustrate that when a particular level of complexity is reached, later increments will not alter the effects previously generated on the assemblage (Prado and Castilla 2006; Sellheim et al. 2010; Sueiro et al. 2011). It appears that the two levels of complexity used in the experiment (i.e., HCM and LCM) were not different enough to differentially affect the associated fauna, and both architectures would be redundant (sensu Kelaher et al. 2007) in providing habitats within the marsh.

Our experiment showed that barnacle mimics offered an appropriate substratum for the recruitment of *Balanus glandula* as recruits of the species were recorded on the artificial barnacle's treatments. This suggests that barnacles could favour the recruitment of conspecifics via provision of proper substrata for larval settlement, as it has been previously observed for this species (Qian and Liu 1990; Schubart et al. 1995). Substratum roughness and the presence of crevices are essential for the recruitment of *B. glandula* (Lohse 1993; Savoya and Schwindt 2010; Mendez et al. 2013). Even though HCM treatment was characterized by a more complex structure (with crevices) than LCM treatment, the structural differences between treatments were not enough to produce an effect on the abundance and size of barnacles. The largest size registered was 5.08 mm and barnacles between 3.51 and 4.5 mm were the most abundant. In previous experimental studies focused on *B. glandula* recruitment (Savoya and Schwindt 2010; Mendez et al. 2013; Mendez et al. 2014), barnacles reached an average size of 3.5 mm after one year. Our experiment lasted nine months, suggesting that growth of barnacles could be higher on artificial than in natural substrates. Thereby, the effect of the physical structure provided by the barnacles is important not only for the benthic fauna but also ensures the persistence of *B. glandula* in the invaded salt marshes.

The acorn barnacle *Balanus glandula* is presently a successful invader of, at least, three continents; distributed along the coast of Asia (Kado 2003), Africa (Simon-Blecher et al. 2008) and South America (Schwindt 2007). In Argentina, this barnacle has shown a great plasticity in their ecological requirements and it has successfully colonized unexpected environments by settling on hard (and even mobile) substrata and persisting on soft bottom systems like salt marshes (Mendez et al. 2013; Mendez et al. 2014). The current work establishes that the physical structure of the barnacle aggregates is important to the associated macroinvertebrate assemblages and the main determinant for the changes in the distribution and abundance of some species of the benthic assemblage (including its own recruitment). Given the persistence of the physical structure of barnacles over large period of time and the expansion of this species observed along the Argentinean coast, effects on native communities as those reported herein is likely to be a common phenomenon.

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