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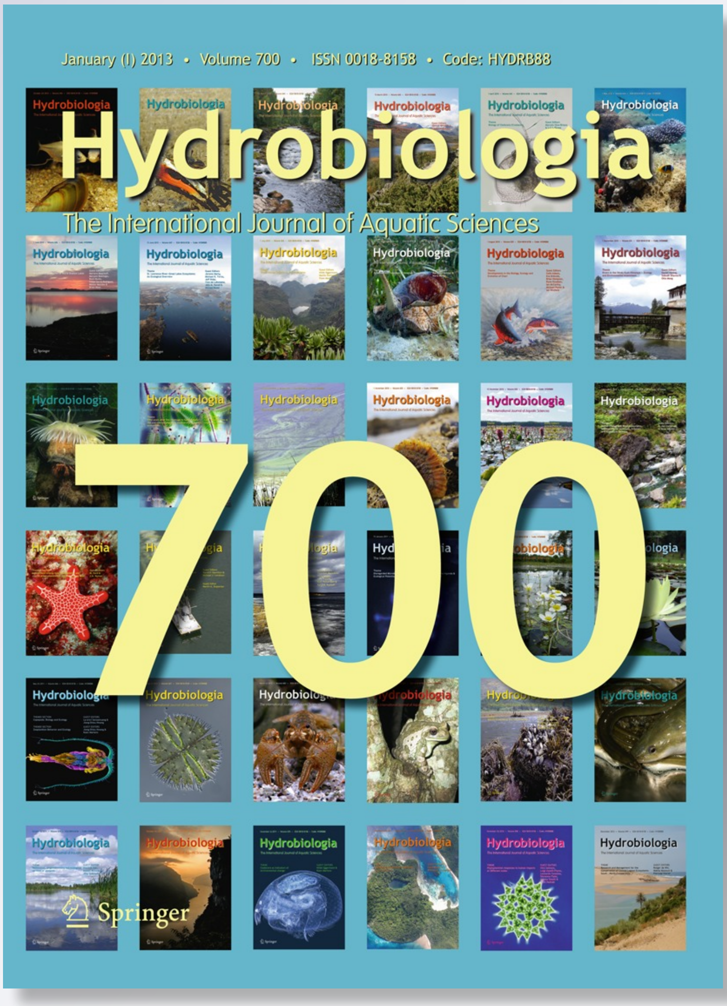

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PRIMARY RESEARCH PAPER

Patterns of substrata use by the invasive acorn barnacle *Balanus glandula* in Patagonian salt marshes

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Abstract *Balanus glandula* is a native barnacle of the rocky shores in the west coast of North America. Forty years after its introduction in Argentina, this species is the only barnacle dominating the high intertidal of local rocky shores and more interesting, it was also reported successfully colonizing soft-bottom salt marshes. In this study, we identified and characterized the substrata most successfully colonized by *B. glandula* in Patagonian salt marshes through descriptive and experimental means. We surveyed and compared two Patagonian salt marshes and the substrata colonized by *B. glandula*. Our results show that barnacles utilize more than 10 types of different substrata. Mussel valves were the most frequent type of substrata utilized in Riacho marsh, whereas the dominant halophyte *Sarcocornia perennis* was the substratum most utilized in Fracasso marsh where mussels were mostly absent. When the five most utilized substrata were experimentally offered, the halophyte shrub *Limonium brasiliense* was the most densely colonized of the experimental substrata, with the largest sizes and the lowest proportion of dead barnacles. Density and size of the barnacles recruited on plants were similar to that observed in nearby invaded rocky shores. Our study strongly suggests that soft-bottom environments, where hard substrata are available, have to be seriously considered when designing early detection plans targeting *B. glandula* and other similar rocky shore invasive species.

Keywords Invasive species · *Balanus glandula* · Recruitment · Salt marshes

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Introduction

The pelagic larvae of most benthic marine invertebrates need a suitable substratum to settle, complete their metamorphosis become adults and reproduce (Ruppert & Barnes, 1994). Settlement and recruitment are currently considered two of the major processes shaping communities and populations (Denley & Underwood, 1979; Connell, 1985; Rodriguez et al., 1993). Studying and understanding these processes is crucial to describe realistic patterns of distribution, abundance, and general dynamic of populations in time and space (Denley & Underwood, 1979; Satumanatpan & Keough, 2001; Barnes et al., 2010). Indeed, during the last decades many marine biologists and ecologists focused on the settler-recruit relationship (Raimondi, 1990; Gosselin & Qian, 1996; Delany et al., 2003) and on the importance of post-settlement mortality (Connell, 1985; Hunt & Scheibling, 1997; Delany et al., 2003). These studies have shown that finding of the proper substratum is critical, especially for sessile organisms, due to their impossibility to move away from predation and/or desiccation stress (Crisp & Meadows, 1963; Menge & Branch, 2001; Gedan et al., 2011).

The settlement of marine invertebrates can involve gregarious behavior (Knight-Jones, 1953; Crisp & Meadows, 1963), recognition of bacterial films (Cole & Knight-Jones, 1949; Maki et al., 1990; Berntsson et al., 2000), selection of surface (Crisp & Meadows, 1963; Raimondi, 1990; Savoya & Schwindt, 2010) and ecological interactions like competition (Grosberg, 1981) or facilitation (Bortolus et al., 2002). In addition, substratum characteristics like hardness, texture, mineralogical composition, color, and the presence of crevices may determine the recruitment pattern of marine invertebrates (Crisp & Meadows, 1963; Raimondi, 1990; Lohse, 1993). For instance, these substratum characteristics are likely to modulate and determine the surface temperature. During low tide phases, heat represents one of the major stressors for intertidal marine invertebrates (Bertness, 1989; Menge & Branch, 2001; Gedan et al., 2011) which may control the mortality of the new recruits (Huey, 1991; Berntsson et al., 2000; Somero, 2002).

Balanus glandula is an acorn barnacle native of the rocky shores in the west coast of North America. More than 40 years ago this species invaded the southwestern Atlantic coast (SWA) (Spivak & L'Hoste, 1976) and, currently, it has become the most abundant barnacle on rocky shores along an extension of 17 latitudinal degrees (Schwindt, 2007). This barnacle dominates the high intertidal by forming dense zones of up to 40,000 ind m^{-2} (Schwindt, 2007). Surprisingly, this hard-bottom barnacle seems to be optimizing the habitat use within the invaded region by colonizing also soft-bottom environments, such as the salt marshes (Schwindt et al., 2009). In these environments, *B. glandula* colonizes the branches, roots and rhizomes of the dominant salt marsh plants: *Sarcocornia perennis*, *Spartina alterniflora*, *Spartina densiflora*, and *Limonium brasiliense* (Schwindt et al., 2009). Barnacles are one of the best known groups of marine fauna recorded in the scientific literature. However, the great majority of the studies focusing on them were conducted in rocky shores which is the most characteristic habitat reported (e.g., Connell, 1961; Denley & Underwood, 1979; Bertness, 1989; Menge, 1991; Tapia & Navarrete, 2010). On the other hand, studies describing aspects of barnacles inhabiting soft-bottom environments are extremely rare and usually consider it an accidental, random, and even irrelevant event (but see Young, 1991; Bayliss, 1993; Ross & Underwood, 1997; Satumanatpan & Keough, 2001; Neira et al., 2006). The recent finding of *B. glandula* successfully invading several Patagonian salt marshes along the SWA coast has motivated the development of local research programs aimed to identify the ecological processes that determine the success of this invasion. In this study, we identified and characterized the substrata most successfully colonized by *B. glandula* in Patagonian salt marshes through descriptive and manipulative experiments.

Materials and methods

Study site

The study was performed in Riacho marsh (hereafter Riacho, 42°25′S, 64°37′W) and Fracasso marsh (hereafter Fracasso, 42°25′S, 64°07′W), both located in the Península Valdés Natural Reserve (Chubut, Argentina; for further description see Bortolus et al., 2009), where *B. glandula* was first recorded successfully established (Schwindt et al., 2009). The height of the low and high marsh levels are +4.42 and +5.77 m, respectively, for Riacho and +5.67 and +6.32 m for Fracasso (relative to the Argentinean hydrographic zero; Idaszkin et al., 2011). Along the Atlantic coast of southern South America, *B. glandula* is the only barnacle forming dense patches within a marsh with up to 35 ind cm^2 (Schwindt et al., 2009). The distribution of the barnacles in both marshes is patchy and they are found exclusively on substrata located on tidal channels, where the seawater flows constantly with the tides. Riacho is dominated by *S. alterniflora* and *S. densiflora* while Fracasso is dominated by *S. perennis* with the less presence of *Spartina* species (Bortolus et al., 2009). Taxonomic identifications of the salt marsh plant species were made following the Flora Patagónica identification guide (Correa, 1998), updating the taxonomic status of the glasswort *Salicornia ambigua* Michx. to *S. perennis* (Mill.) A. J. Scott. (following Zuloaga & Morrone, 1999; but see Alonso & Crespo, 2008). The field experimental trials described below were conducted in Punta Ameghino (42°36′S, 64°52′W), a protected wave-cut platform located a few kilometers southward from Riacho and Fracasso marshes. Previous studies performed in Punta Ameghino showed that both recruits and adults of *B. glandula* are found in high density throughout the year (Schwindt, 2007; Savoya & Schwindt, 2010), which suggests that this site was appropriated to guarantee the achievement of our objectives.

Substrata utilized by *B. glandula*

We carefully surveyed Riacho and Fracasso marshes to identify the substrata utilized by *B. glandula* and to delimit the areas colonized by this barnacle with permanent color marks from November 2008 to February 2009 (hereafter "Survey 1"). Parallel lines, separated 2 m from each other, were installed in each area and a metal stake was introduced perpendicularly to the ground level every one meter. Then, the barnacle closest to the metal stick was identified and the type of substratum was recorded (hereafter "utilized substratum") for each point. In order to estimate the proportion of the different substrata available in the marshes, a second survey (December 2010–March 2011, hereafter as "Survey 2") was carried out by following the same method, only that in this case the nearest available substratum was also recorded (hereafter "available substratum"). For Survey 1, the frequency of use of the substratum type in each marsh was evaluated using a χ^2 test (Zar, 1999). For Survey 2, the frequency of utilized versus expected substratum type, based on the availability of substratum, was evaluated using a single χ^2 test for each marsh (Zar, 1999).

Manipulative field experiment

A manipulative experiment was conducted to compare the relative success of *B. glandula* in colonizing the different substrata naturally used by this species in salt marshes. The halophytes *Spartina* sp., *S. perennis*, and *L. brasiliense* represent the most common salt marsh plants in Patagonia, while gravel and mussel valves are among the most utilized natural substrata. The experiment consisted in plots of 100 cm^2, ($n = 11$–12) on top of which the five different substrata were deployed (one substrate per plot). Plant segments were used to cover the experimental plots by tying them up together with fine plastic cable tires and pinning them down to the ground with small stainless steel nails. All plant segments used in the experiment were consistent in shape and size. All attempts to drill gravel and valves to pin them down with nails, inevitably ended damaging the experimental substrata. Consequently, we decided to fix gravel and valves with marine epoxy on top of the glass fiber plates (area: 100 cm^2, $n = 10$ per substratum) which were in turn pinned down with stainless steel nails. A control treatment (hereafter "control") consisted of 12 plots of 100 cm^2, where the fauna was carefully scraped off. Parallel lines (approximately 5 mm wide and 5 mm depth) were engraved by hand across the control plots to recreate the best texture possible for *B. glandula* (following Savoya & Schwindt, 2010). Since the control plots are a local optimum substratum for this barnacle, we predicted this treatment will act as indicator of larvae presence during the study. In addition, considering that garbage is abundant in local salt marshes, a garbage substratum was added to the experiment ($n = 12$ plots, area: 100 cm^2). This garbage substratum (hereafter garbage) consisted on pieces of dark hard PVC (the most common kind of coastal garbage; author pers. obs.), bended and pinned down with nails. All the experimental plots were interspersed (sensu Hurlbert, 1984) within the tidal height were barnacles are most abundantly found, and where they remained exposed during low tide and submerged during high tide. The experiment lasted from February 2010 to February 2011. Once a month all the plots were photographed to record the density of living barnacles and also the dead ones. The later were quantified by counting the empty shells and the basal disc marks left by dead barnacles on the substratum (Spivak & Schwindt, in press). At the end of the experiment, all the plots were transported to the laboratory and the variables measured for every plot of each treatment were: (a) density of barnacles and (b) barnacle size frequency distribution.

(a) *Density*: the area of each plot at the end of the experiment was accurately calculated using the software ImageJ (http://imagej.nih.gov/ij) to make all treatments comparables. All barnacles larger than 0.15 mm in rostral-carinal length colonizing the experimental substrata were counted for each plot and their density was then referred as individuals per 100 cm^2. The null hypothesis of no difference in barnacle density among the different substrata was evaluated using a one way ANOVA (Zar, 1999), and a posteriori Tukey test was used to identify differences among means (Zar, 1999). Data were square root transformed when the assumptions of homoscedasticity and normality were not met. In addition, the percentage of dead barnacles was calculated to estimate the mortality for each substratum to evaluate their success on the different substrata.

(b) *Size*: size of the barnacles ($n = 200$ for each substratum, excepting *S. densiflora* where only a total of 93 barnacles were found) was obtained with digital caliper (precision ± 0.01) by measuring the orifice length along the carinal and rostral plates. The barnacles measured were randomly chosen from different plots for each substratum. The null hypothesis of no difference in barnacle size among the different substrata was evaluated with a one way ANOVA (Zar, 1999), and a posteriori Tukey test was used to identify differences among means (Zar, 1999). Data were log transformed when the assumptions of homoscedasticity and normality were not met. Finally, parametric correlation was used to evaluate if there is a relationships between the mean density and the mean size of the barnacles on each substratum (Zar, 1999).

Results

Substrata utilized by *B. glandula*

The diversity of substrata where we found barnacles included halophyte plants, biogenic materials (i.e., valves and wood), living mussels, epifaunal organisms (i.e., clams), gravel, and trash (i.e., bottles, plastic materials, fishing nets and rest of fishing equipment). No individuals were found directly on mud. In Survey 1, we recorded the utilized substrata in 1959 points and we found that the mussel valves were the most frequent type of substratum utilized in Riacho, whereas in Fracasso was the salt marsh pickle weed *S. perennis* ($\chi^2 = 785$, df = 9, $P < 0.05$; Fig. 1a). In Survey 2, utilized substrata were recorded in 1,043 points and the available substrata in 1,869 points. We found significant differences between the frequency of utilized versus available substratum type for both marshes (Riacho: $\chi^2 = 3510$, df = 9, $P < 0.05$, Fracasso: $\chi^2 = 123$, df = 5, $P < 0.05$; Fig. 1b). In Riacho, gravels were under-utilized and mussel valves over-utilized; in Fracasso, instead, *Spartina* was under-utilized and gravel over-utilized. In Riacho, the most and least frequent substrata utilized were the mussel valves and the gravel respectively, while in Fracasso gravel and *Spartina* were the most and least used substrata, respectively.

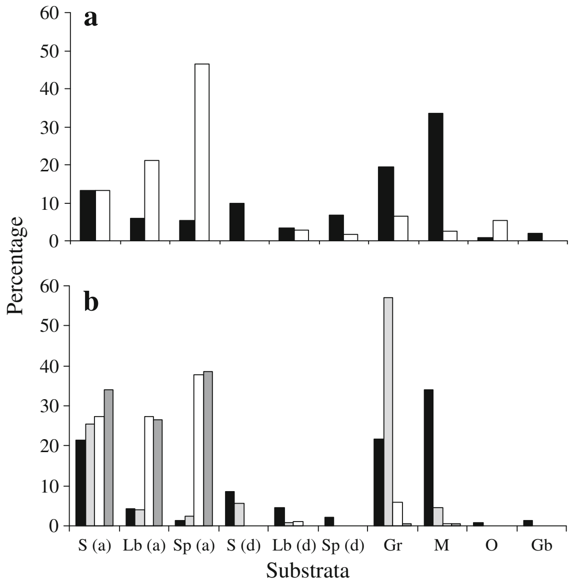


Fig. 1 Percentage of utilized substrata for Survey 1 (**a**) and Survey 2 (**b**) in Riacho (*black bars*) and Fracasso (*white bars*) marshes, and the percentage of available substrata in Riacho (*light gray bars*) and Fracasso (*dark gray bars*) marshes. S: *Spartina*, Lb: *Limonium brasiliense*, Sp: *Sarcocornia perennis*, Gr: Gravel, M: mussel valves, O: organic material and Gb: garbage. For plants in parenthesis the "a" indicates alive and the "d" indicates death

Manipulative field experiment

Although present in all treatment plots, the total density of *B. glandula* was highest on *L. brasiliense* where it reached an average of 51,500 ind m^{-2} (SD = 21,100 ind m^{-2}). The first individuals were observed in *L. brasiliense* in autumn (March). The total abundance of barnacles increased over the next months in all plots but a peak was detected in spring (November), when the 90% of the plots were occupied by new individuals in all the treatments. No masive mortality events were registered during the experiment. The density of *B. glandula* was significantly different among substrata (square root transformed, $F = 35.5$, df = 6, $P < 0.05$; Fig. 2a). A posteriori Tukey test showed that the density of barnacles was significantly higher in *L. brasiliense*, mussel valves, control, *S. perennis,* and gravel than in *Spartina* and garbage ($P < 0.05$; Fig. 2a). Barnacle density on

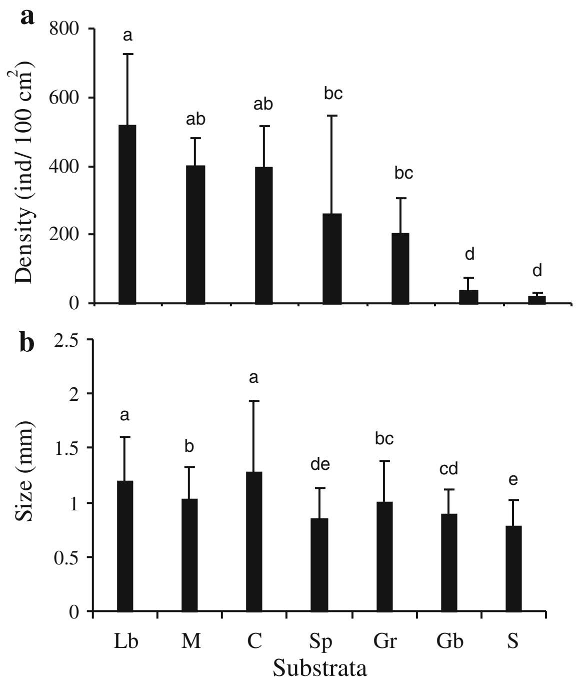


Fig. 2 **a** Mean density (+SD) and **b** mean size (+SD) of *Balanus glandula* recruited on different substrata: Lb: *Limonium brasiliense*, M: mussel valves, C: control, Sp: *Sarcocornia perennis*, Gr: Gravel, Gb: garbage and S: *Spartina*. *Different letters* on bars indicate significant differences among substrata

control plots (39,500 ind m^{-2}) was similar to that reported for rocky shores within this invaded area (40,000 ind m^{-2}; Schwindt, 2007), which confirmed the appropriate design of this treatment. In addition, the percentage of dead barnacles was higher in gravel and mussel valves (75 and 39%, respectively) and almost negligible in the rest (garbage = 3%, control = 2%, *L. brasiliense* = 0.27%, *S. perennis* = 0.21%). No dead barnacles were found on *Spartina*.

The size frequency distribution of *B. glandula* in all treatments was unimodal. In the *L. brasiliense* and control plots, barnacles tended to be represented by large individuals while in the plots with *Spartina* they were relatively smaller. The rest of the treatments showed a tendency for intermediate distributions, with large and small individuals represented (Fig. 3). The mean size of barnacles was significantly different among treatments (log transformed, $F = 40.68$, df = 6, $P < 0.05$; Fig. 2b). A posteriori Tukey test showed that the barnacles living on *L. brasiliense* and control plots were larger than those on the other treatments ($P < 0.05$; Fig. 2b). Finally, there was a significant positive correlation between mean size and mean density of barnacles in the substrata across the experiment ($r = 0.81$, $t = 3.14$, $P < 0.05$; Fig. 4).

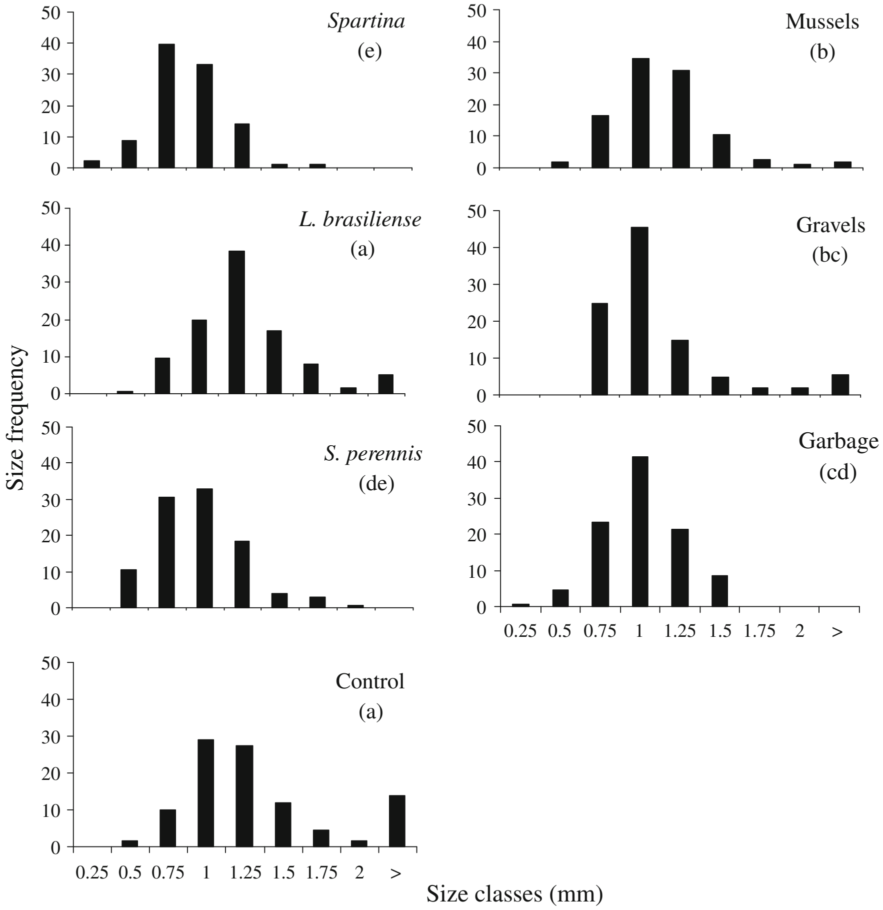
Discussion

Substrata utilized by *B. glandula*

Our surveys and experiments showed that the invasive barnacle *B. glandula* uses a variety of at least ten substrata, and this versatility is likely to favor its success and persistence within the Patagonian salt marshes it invades. Although the shrub *L. brasiliense* was the substratum more densely utilized, and where the barnacles showed the largest size values, our results strongly suggest that the *B. glandula* invasion on these salt marshes does not depend on the presence/availability of one substratum in particular. The fact that we found a higher density of barnacles on *L. brasiliense* (51,500 ind m^{-2}) than the reported for the local rocky shores (40,000 ind m^{-2}; Schwindt, 2007), suggests that this halophyte supplies a more suitable micro-environment compared to the typical rocky bottom. In addition, the barnacles living on *L. brasiliense* also showed the lowest percentage of dead individuals on this substratum too, including empty shells and basal disc marks. Therefore, salt marshes with this kind of vegetation might be an optimal habitat for *B. glandula* within the new host region. Indeed, it is unclear why this invasive species of barnacle is absent in most marshes along Argentinean coast (Bortolus et al., 2009) where *L. brasiliense* is present and abundant (Isacch et al., 2006). Nevertheless, it is probable that the pattern of geographic distribution is still developing. Considering that the invasion of barnacles in the marshes is a relatively recent phenomenon (Schwindt et al., 2009), our study suggest that more marshes along this coast are likely to be invaded in the near future. Unfortunately, the management and/or control of this species is not currently a high priority for local or regional environmental legislators.

Within the native range of *B. glandula*, the causes of mortality of its early juveniles include salinity, delay of metamorphosis, biological and physical disturbance, hydrodynamic conditions, physiological stress, predation and competition (Newman, 1967; Gosselin & Qian 1996; Hunt & Scheibling, 1997;

Fig. 3 Size frequency distributions of barnacles per class size living in the most frequent utilized substrata of salt marshes. *Different letters* below the names of substrata indicates significant statistical differences on mean size



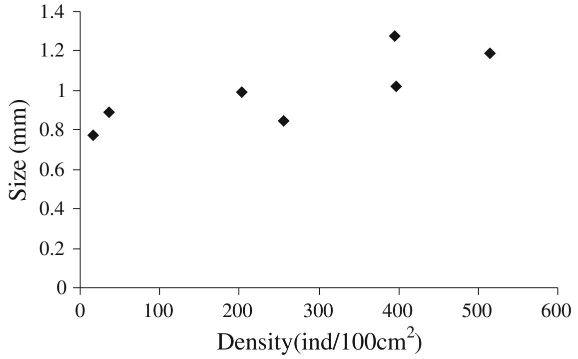


Fig. 4 Parametric correlation between density and size of *Balanus glandula* in selection experiment ($r = 0.81$)

Berger et al., 2006). Of all these causes, the thermal stress mediated by the physical constitution of the substratum stands out as a crucial factor setting the patterns of survival and distribution of marine organisms (Huey, 1991; Somero, 2002; Gedan et al., 2011) considering that desiccation is a major challenge to overcome, especially during the low tide (Bertness, 1989; Adam, 1993; Menge & Branch, 2001; Gedan et al., 2011). Our results agree with this hypothesis, as the only dead barnacles we found by the time the experiment ended were located on the gravel and mussel valves substrata. This pattern may be partially explained by the capacity of most intertidal plants to retain water and humidity during low tides, buffering heat stress (Salisbury & Ross, 2000), and creating a favorable microenvironment for marine invertebrates (Bortolus et al., 2002; Sueiro et al. 2012). In contrast, the compact and relatively impermeable substrata supplied by gravels (Spaletti et al., 1986) and mussel valves (Ruppert & Barnes, 1994) tends to heat up relatively quickly and indirectly raising the temperature of the fouling fauna to lethal values (Harley, 2008).

Potential expansion on soft-bottom environments

The invasive acorn barnacle *B. glandula* is currently expanding its distributional range worldwide. First reported in the Argentinean coast (Spivak & L'Hoste, 1976; Schwindt, 2007) and few years later on rocky shores along the west coast of Japan (Kado, 2003) and south coast of South Africa (Simon-Blecher et al., 2008) were it occurs over 400 km of coastline (Laird & Griffiths, 2008). Our results show the ability of this rocky shore invader to exploit a variety of hard substrata to colonize soft-bottom environments. Therefore, rocky shores should not be the only kind of environment considered for potential barnacle invasions, and soft-bottom environments must be included in early detection plans focusing on this barnacle. Furthermore, our results also highlight the idea that salt marshes with similar vegetal composition than the study sites may present a high risk for potential invasion by *B. glandula*. For instance, the salt marshes of Japan and South Africa are dominated by the lawngrass *Zoysia sinica* (Adam, 2002) and by *Sarcocornia pillansii* (Adam, 2002; Bornman et al., 2004), respectively. Both species create micro habitats potentially vulnerable to barnacle invasion (Schwindt et al., 2009; this work). Although the marshes of South Africa are mostly estuarine environments (Adam, 2002; Bornman et al., 2004), an invasion by marine barnacles may occur in specific sites where substrate, salinity and other vital parameters are suitable for them to recruit. Locally, Northern Argentinean salt marshes are dominated by *Spartina* grasses and austral salt marshes by *S. perennis* with a significant presence of *L. brasiliense* (Bortolus et al., 2009; Idaszkin & Bortolus, 2011). Considering this plant species distribution pattern and the results of our study, we predict a high risk for *B. glandula* to invade austral salt marshes of Southern South America.

Conclusion

Together, field surveys and manipulative experiments lead us to identified colonization patterns of *B. glandula* in salt marshes substrata. Our study has shown that acorn barnacles utilize more than 10 types of substrata in different frequency, and that the shrub *L. brasiliense* is the most optimal one. Density and size of the barnacles on this plant species were similar to that observed in the rocky shores. Understanding the ecological plasticity exhibited by this rocky shore invader to successfully colonize soft-bottom habitats and its persistence in this environment is critical to predict future invasions on similar areas and assess the impact of both current and future invasions.

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