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Effect of the substratum in the recruitment and survival of the introduced barnacle *Balanus glandula* (Darwin 1854) in Patagonia, Argentina

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ABSTRACT

The barnacle *Balanus glandula* was introduced in Argentina in the 1970s, and today it dominates the high intertidal level in most Argentinean rocky shores. The aim of this work was to evaluate the effect of the type of substrata and intertidal height on a population of *Balanus glandula* by conducting field surveys and one-year field experiments in which we combined different substrata (hardness: hard and soft, and texture: smooth and rough) at two intertidal heights (mid and high). In natural populations, the highest density of adults and recruits occurred on soft–rough substratum and in the high intertidal. The different textures were important only on the soft substrata and high intertidal, and the density of barnacles of the soft–rough substrata was higher than soft and smooth ones. The most suitable experimental substratum was the soft–rough of the high intertidal, which had the highest recruitment, survival and final density of barnacles at the end of the experiment. In contrast, the hard and smooth of the high and middle intertidal were the least suitable in all cases. Although the recruitment of *B. glandula* occurred throughout the year, it was higher in the high intertidal, and it showed a recruitment peak in the winter and a second in the summer. While most studies on this barnacle investigated the effects of granite or other volcanic hard substrata, our study also focused on soft substrata. The effects of soft substrata are particularly important because soft sedimentary rocks characterise the southern Atlantic coast of South America and the presence of soft rocks appears to optimize the success of *Balanus glandula*.

1. Introduction

Biological invasions are a major threat to biological communities and endangered species worldwide (Carlton, 1989). The spread of non-native species has led to a breakdown of traditional faunal boundaries and contributed to the homogenization of flora and fauna around the world in what has been called the largest biological crisis in history (Elton, 1958). In marine environments, the introduction of species commonly occurs through the release of ballast water from large ships. During the last century, the success of marine invasion increased (Ruiz et al., 1997) and altered diversity and community structure by mechanisms such as competitive exclusion (Race, 1982), predation (Ruiz et al., 1997), and habitat alteration (Crooks, 1998; Crooks and Khim, 1999; Talley et al., 2001).

The coastline of Argentina has been invaded by a variety of exotic species, and the rocky shores are no exception. During the 1960s, descriptive studies of local biodiversity did not report the presence of barnacles in the intertidal fauna (Ringuelet et al., 1962, Olivier et al., 1966a,b). However, less than a decade, later three species of barnacles were found populating the rocky shores of the Buenos Aires province: *Balanus glandula* (Darwin 1854), *B. trigonus* and *B. amphitrite* (Spivak and L'Hoste, 1976). Since then, only *B. glandula*, native to the west coast of North America, has successfully invaded most of the coast of Argentina from San Clemente del Tuyú (36°21′ S, 56°43′ W) to Río Grande (53°50′ S, 67°33′ W; Fig. 1, Schwindt, 2007), the west coast of Japan (Kado, 2003) and South Africa (Simon-Blecher et al., 2008). One of the most conspicuous changes resulting from the invasion of *B. glandula* in Argentina was the modification of the traditional zonation of rocky shores. According to studies conducted before the invasion (Ringuelet et al., 1962; Olivier et al., 1966a,b), coastal communities were dominated by macroalgae, mussels and limpets in the low, mid and high intertidal, respectively. Currently, *B. glandula* has successfully colonized and dominated the high intertidal in most Argentinean rocky shores by forming a compact zone of up to 40,000 individuals per square meter (Schwindt, 2007).

The intertidal is a very stressful area where the survival of organisms depends on overcoming several factors including wave exposure, temperature stress, and desiccation (Menge and Branch, 2001). Desiccation and temperature stress are often strongly and positively correlated with intertidal elevation and characteristics of the substratum (Wethey, 1983; Harley, 2003). In addition, rock characteristics like hardness, texture, mineralogical composition, colour, and the presence of crevices may modulate the intensity of the desiccation and temperature stress, and

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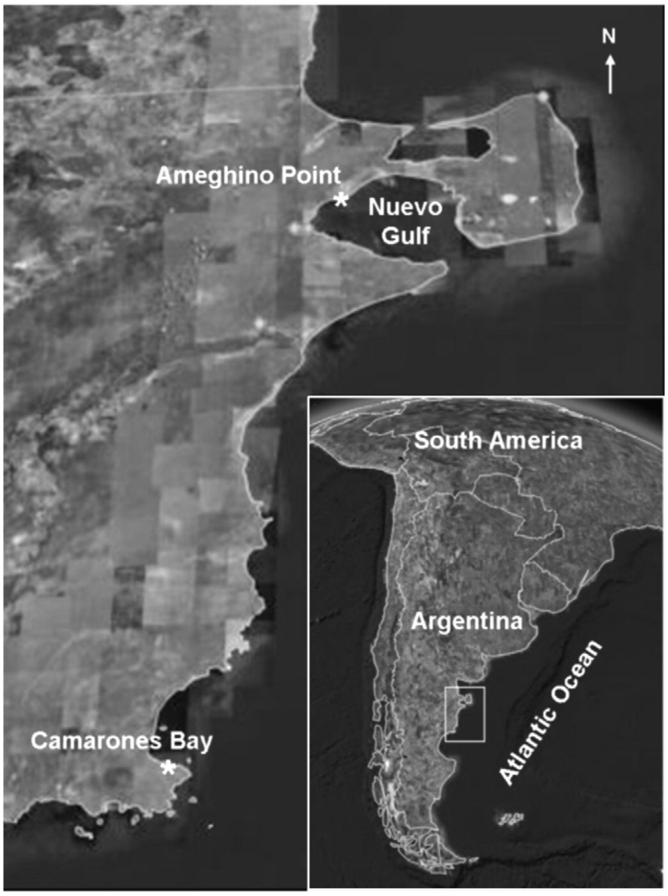

Fig. 1. Location of sites where the density pattern of *Balanus glandula* was studied (AP, CB) and where the experiment (AP) was performed (image source: Google Earth).

therefore the performance of the many marine organisms settling on them (Raimondi, 1988; Lohse, 1993; Herbert and Hawkins, 2006). The intertidal height in combination with the substratum plays a key role in the performance of sessile intertidal species like barnacles. Sessile species are not able to move to safer habitats (e.g., crevices, tide pools, or under macroalgae) to reduce desiccation and temperature during low tides (Menge and Branch, 2001). These variables may be particularly critical to marine biological invasions, which commonly start with the introduction of a relatively small number of individuals. In this sense, the characteristics of the recipient area, including the type of substratum, could determine the success or failure of the invasion just by reducing or increasing the stressful conditions in the intertidal environment.

In areas where *Balanus glandula* is native, the most suitable habitat for recruitment, survival and growth is characterised by hard substrata with crevices in the highest height of the intertidal (Lohse, 1993). However, the settlement preferences of *B. glandula* in invaded habitats are still unknown; consequently, we studied: a) the density of *B. glandula* at different intertidal heights and substrata on the rocky shores of the Nuevo Gulf and Camarones Bay (Argentina) and b) the influence of the type of substratum on the recruitment and survival of *B. glandula*.

2. Materials and methods

2.1. Study area

The study on density patterns was performed in two rocky shores of the Argentinean Patagonia: Ameghino Point (hereafter AP; 42°36′ S, 64°52′ W) and Camarones Bay (hereafter CB; 44°49′ S, 65°42′ W, Fig. 1) where the tidal mean amplitude is 4 m. AP is a wave-protected intertidal zone situated in the Nuevo Gulf coast, while CB is an irregular coast with a mix of wave exposure and protected areas. The experimental study was conducted in wave-protected areas in AP. During this study, the summer and winter mean temperatures were 21 °C and 9 °C, respectively, and the mean wind speed was 14.5 km per hour in both seasons. The substratum in AP is sedimentary rock (fine sandstone) while in CB it is volcanic rock. The latter represented the hardest rock in the first component of the study.

2.1.1. Density patterns of Balanus glandula at different heights and substratum on rocky shores

In summer 2004 (January and February), the density of *B. glandula* was estimated at the high and middle intertidal in protected areas of CB (hard substrata: high = 2.6 m above to mean low lower water, hereafter MLLW, middle = 1.6 m above MLLW) and AP (soft substrata: high level = 3.75 m above MLLW, middle level = 2.45 m above MLLW), on rough and smooth surfaces. Twenty samples were randomly obtained (20 × 20 cm) at each intertidal height (high and middle) and type of substratum (N_{total} = 160). A three-way ANOVA (considering the height above MLLW, location and surface texture) was used to evaluate the null hypothesis of no difference between densities on different substrata (Zar, 1999). The normality and homogeneity assumptions were evaluated using the Kolmogorov–Smirnov and Levene test, respectively, and when these assumptions were not met, data were transformed (square root transformation). We used Tukey post hoc tests when differences among mean values were significant.

2.1.2. Effect of the type of substrata on Balanus glandula recruitment and survival

To evaluate if the type of substratum affects the recruitment and survival of *B. glandula*, an experiment with four different substrata was conducted at AP (Fig. 2). Originally the experimental design was planned to include natural substrata, however, the sedimentary rock forming the natural coastal shore gets so fragile that it was impossible to cut clean portions (experimental units) without breaking it in small heterogeneous pieces. Commercial tiles were used to create the hard substratum and the sedimentary rock that naturally forms a wave-cut platform at AP provided the soft substratum. Then, two categories of hardness and texture were combined to generate the following four experimental treatments: soft–smooth (SS), soft–rough (SR), hard–smooth (HS), and hard–rough (HR). *SS*: This treatment was created by cleaning and smoothing ten 20 × 20 cm quadrants on top of the wave-cut platform with a scraper (Fig. 2A). *SR*: The same procedure used in SS was repeated; then, 12 parallel lines (20 cm long, 0.5 cm wide and 0.5 cm deep) 1 cm apart were engraved by hand on each of the ten quadrants (Fig. 2B). Both substrata, soft–smooth and soft–rough, were marked with nails on their corners (Fig. 2A and B). *HS*: To create the hard substratum, 10 tiles with a smooth surface (i.e., with no visible crevices) were affixed to the rock surface. To avoid small scale hydrodynamic differences caused by the tiles, an area of the same size of the tiles was excavated to a depth of approximately 2 cm. The tiles were glued to the rock to form a continuous surface with constant relief (Fig. 2C). Tiles were affixed to the rock with marine epoxy and a nail (10 cm long). *HR*: Tiles with parallel lines engraved along the surface were affixed in the same manner as the HS treatment (Fig. 2D). Barnacles recruited on the borders of the quadrants and around the nails were not considered in the analyses.

In order to evaluate the influence of the substrata on recruitment and density, only barnacles that settled on the substratum were included and those on other barnacles were excluded. The percentage of available substratum was calculated in each sampling. Then, total recruitment values at time $t + 1$ were calculated relative to the substratum available at time t. Finally, the survival rate was calculated from the first cohort, which allowed us to obtain the most survival data.

The treatments were repeated on the high (3.75 m above MLLW) and mid (2.45 m above MLLW) intertidal of AP (N_{total} = 80). Every quadrant was initially photographed every 15 days and then once a

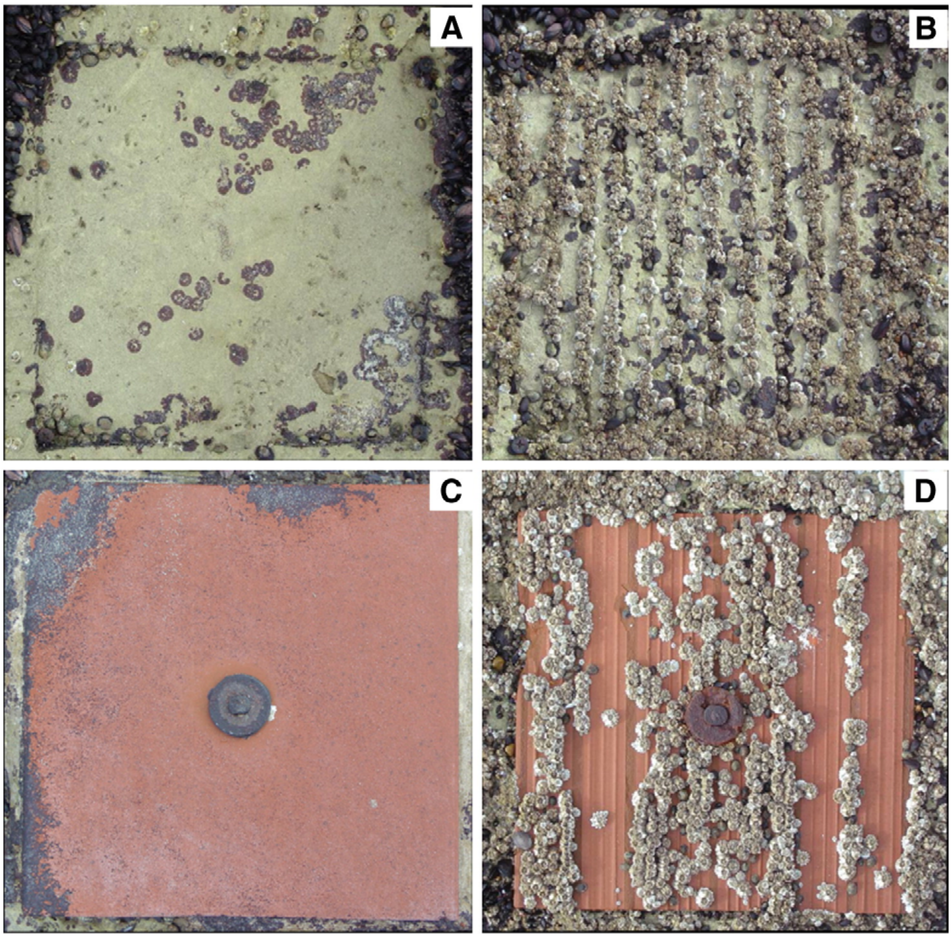

Fig. 2. Experimental substrata considered in the study: A) soft–smooth, B) soft–rough, C) hard–smooth and D) hard–rough.

month with a digital camera for 1 year (October 2003–October 2004). Each picture was processed in upward chronological order using Arc View 3.1. This methodology allowed the detection and identification of each recruited barnacle and allowed to follow survival for the duration of the study in each experimental unit. Additionally, this methodology allowed us to monitor the survival of the first cohort without the removal of subsequent cohorts. At the end of the experiment, the final density of barnacles was recorded for each quadrant. To determine whether the density of barnacles differed among the experimental substrata combinations, a three-way ANOVA was performed (intertidal height × hardness × texture, Zar, 1999). Normality and homogeneity of variances were evaluated with Kolmogorov–Smirnov and Levene tests, respectively, and data were transformed (quarter root transformation) when these assumptions were not met. Significant differences among mean values were evaluated with a Tukey post hoc test.

3. Results

3.1. Density patterns of *Balanus glandula* at different heights and substratum on rocky shores

There was a significant second order interaction among height, hardness and texture (square root transformation, $F = 20.37$, df = 152, $n = 160$, $p < 0.0000$, Table 1, Fig. 3A), where density did not vary between hardness and textures at the mid intertidal but did at the high intertidal. The mean barnacle density on the high intertidal in AP (soft substratum) was greater on the rough than on the smooth texture, but it did not differ between textures on the mid intertidal (density on HSR > HSS, $p = 0.000$; MSR = MSS, $p = 1$, Table 2, Fig. 3A). At the same time, intertidal height was an important variable in AP (density on HSS > MSS, $p = 0.000$; HSR > MSR, $p = 0.000$; Fig. 3A, Table 2). In contrast, the barnacle density in CB was not affected by intertidal elevation or texture (density on HHS = HHR = MHS = MHR, $p > 0.05$; Table 2; Fig. 3A). The highest density was registered on rough substrata in the high intertidal of AP, and this was significantly different from the density observed in all other substrata ($p = 0.000$, Table 2; Fig. 3A).

3.2. Effect of the type of substrata on *Balanus glandula* recruitment and survival

There were two significant first order interactions; one of these interactions was between hardness and intertidal height ($F = 4.59$, df = 72, $n = 80$, $p = 0.035$, Table 3, Fig. 3B), and the other was between hardness and texture ($F = 13.86$, df = 72, $n = 80$, $p = 0.0003$, Table 3,

Table 1
Results of the three-way ANOVA testing the *Balanus glandula* density on natural substrata considering the intertidal height, the hardness and the texture of the substrata.

	df	MS	F	p
Height	1	2048.11	107.01	**0.0000**
Hardness	1	723.94	37.82	**0.0000**
Texture	1	723.63	37.81	**0.0000**
Height × hardness	1	1413.56	73.86	**0.0000**
Height × texture	1	516.98	27.01	**0.0000**
Hardness × texture	1	286.34	14.96	**0.0001**
Height × hardness × texture	1	389.93	20.37	**0.0000**
Error	152	19.14		

Statistically significant differences are shown in bold.

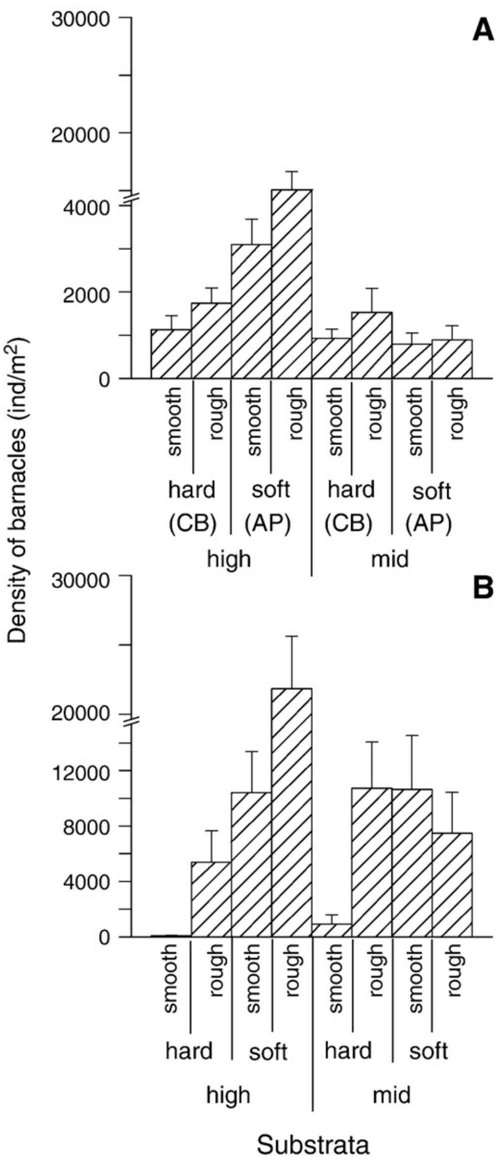

Fig. 3. A) Mean (±SE) density of *Balanus glandula* on different natural substrata with different surface textures (smooth, rough) in Camarones Bay (hard substrata) and Ameghino Point (soft substrata), on the high and mid intertidal. B) Mean (±SE) density of *B. glandula* on the different experimental substrata on the high and mid intertidal. The experimental substrata represent the hardness and texture of the rocky shores surveyed on the study of density pattern, Camarones Bay (CB) and Ameghino Point (AP). Parentheses below each type of hardness indicate the location considered for hard and soft substrata. The barnacle density was zero on HHS substrata. Note the change of the scale in the "*y*" axis.

Table 2
Results of the Tukey post hoc test of *Balanus glandula* density on natural substrata.

	HHS	HHR	HSS	HSR	MHS	MHR	MSS	MSR
HHS	–	0.817	**0.031**	**0.000**	0.999	0.999	0.842	0.906
HHR		–	0.687	**0.000**	0.470	0.927	0.069	0.104
HSS			–	**0.000**	**0.005**	0.069	**0.000**	**0.000**
HSR				–	**0.000**	**0.000**	**0.000**	**0.000**
MHS					–	0.993	0.986	0.995
MHR						–	0.688	0.782
MSS							–	1
MSR								–

The letters naming each substratum are based on the intertidal height (high = H, mid = M), then the hardness (hard = H, soft = S) and finally the texture (smooth = S, rough = R). Statistically significant differences are shown in bold.

Table 3
Results of the three-way ANOVA testing the *Balanus glandula* density on experimental substrata of Ameghino Point considering the intertidal height, the hardness and the texture of the substrata.

	df	MS	*F*	*p*
Height	1	2.94	1.60	0.209
Hardness	1	75.91	41.25	**0.0000**
Texture	1	43.56	23.67	**0.0000**
Height × hardness	1	8.45	4.59	**0.035**
Height × texture	1	2.66	1.44	0.232
Hardness × texture	1	25.51	13.86	**0.0003**
Height × hardness × texture	1	1.72	0.93	0.336
Error	72	1.84		

Statistically significant differences are shown in bold.

Fig. 3B). The height–hardness interaction indicates that the density of barnacles at the end of the experiment was higher in the soft substrata than in the hard substrata at both intertidal levels. The density of barnacles was significantly higher in HS and MS than in MH and HH substrata, while the density was not different between HS and MS and between MH and HH (Tukey post hoc test, pair-wise comparisons, minimum significant difference = 1.134, Fig. 3B). In contrast, the hardness–texture interaction was highly significant, where texture only had effect on the hard smooth substrata. The density of barnacles was lower in HS than in HR, SS and SR substrata, while the density was not significantly different among HR, SS and SR substrata (Tukey post hoc test, pair-wise comparison, minimum significant difference = 1.134, Fig. 3B).

Barnacle recruitment occurred throughout the year and was greater in the high intertidal than in the mid intertidal. Two recruitment peaks were observed; one was observed during the summer 2003–2004 (December–January) and the second during the winter 2004 (June–July, Fig. 4). The first peak was recorded on the soft substrata but not on the hard, while the second peak was observed on both soft and hard substrata.

Survival rate was highest in the high intertidal with soft and rough substrata, while survival was lowest in the middle intertidal with hard and rough substrata (S = 0.76, S = 0.39 respectively; Fig. 5).

4. Discussion

Our results suggest that substrata characteristics strongly affect the ability of the introduced barnacle *Balanus glandula* to colonize and spread along the coast of Patagonia. The barnacle density, recruitment and survival were highest on the soft–rough substratum in the high intertidal. In this study, the rough texture played a key role in maximizing the recruitment and survival of *B. glandula* on both hard and soft substrata.

The density of *Balanus glandula* was highest on the soft–rough substrata of the high intertidal on both the natural rocks and in the experimental study, although in the experimental study, the density on soft–rough substrata was not significantly different from the soft–smooth and hard–rough. These results suggest that the soft substratum is suitable for *B. glandula* regardless of the texture. In addition, the rough texture made the hard substratum more suitable, where hard–rough substratum was as suitable as soft substrata. Heat stress is one of the major challenges that intertidal invertebrates face during the low tide (Menge and Branch, 2001). Rock attributes such as colour, thermal capacity and roughness directly affect the surface temperature, and they may indirectly regulate the density of organisms by affecting recruitment and survival (Raimondi, 1988; Herbert and Hawkins, 2006). On natural rocks, the mean daily maximum temperature of sedimentary rock is 4 °C lower than volcanic (Harley and Schwindt, unpublished data); thus, the highest density of *B. glandula* obtained in AP and in soft experimental substrata could be due to less thermal stress during low tide. In this study, the temperature of the experimental hard substrata was not measured.

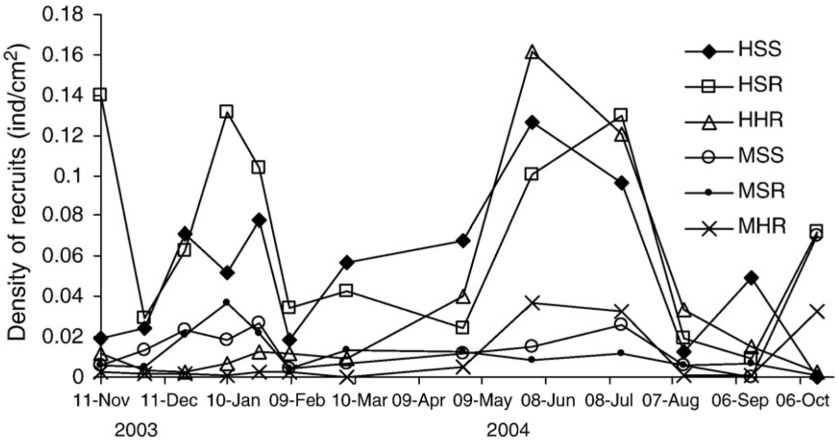

Fig. 4. *Balanus glandula* recruitment (recruits per cm^2) on the different experimental substrata in Ameghino Point. Recruitment was measured from November 2003 to October 2004. The letters naming each substratum are based on the intertidal height (high = H, mid = M), then the hardness (hard = H, soft = S) and finally the texture (smooth = S, rough = R).

However, because the density of barnacles on the hard–rough substrata was 300 and 57 times higher than on the hard–smooth substrata in the high and middle intertidal, respectively, the high differences in density between the hard–rough, soft–smooth and soft–rough substrata suggest that beyond the temperature of the substrata, texture is an important factor for recruitment and survival of the barnacles.

The density of barnacles on the mid intertidal was lower than the high intertidal in AP and CB, and this may have been due to the presence of the small mussels *Brachidontes rodriguezii* and *Perumytilus purpuratus*. Both species are competitively dominant over *Balanus glandula* (Vallarino and Elias, 1997). This interaction occurs regardless of the type of substratum and drives the zonation typical to Argentina rocky shores, with mussel beds and barnacles on the middle and high intertidal, respectively. In the experimental substrata, the mid intertidal also had a lower density of barnacles than the high intertidal at the end of the experiment. This may have been due to differences in the density of recruits or in the post-settlement survival of the barnacles. Two recognized factors may negatively affect post-settlement survival: the grazing effect exerted by limpets (Geller, 1991; Kwok Kan Chan and Williams, 2003) and sediment disturbance (Airoldi et al., 1996). In the mid intertidal of our study site, sediment and limpets were present throughout the experiment, suggesting they may be negatively affecting the post-settlement survival in this level.

Recruitment was not constant over time, and it showed two peaks: one in spring–summer and the other in fall–winter. These results

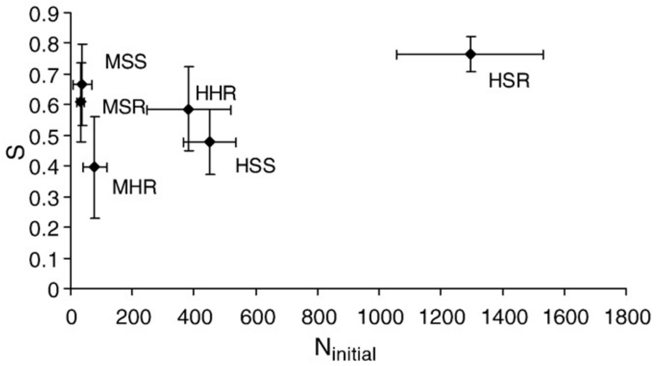

Fig. 5. Final survival (*S*) of the first cohort of *Balanus glandula* depending on the initial number ($N_{initial}$) of barnacles on the different experimental substrata. The bars point out the SE along both axes. The letters naming each substratum are based on the intertidal height (high = H, mid = M), then the hardness (hard = H, soft = S) and finally the texture (smooth = S, rough = R).

differ from other studies in areas where *Balanus glandula* is native (e.g. Spight, 1981; Menge, 2000; Connolly et al., 2001) and invasive (Schwindt, 2007). Although in its native area, one peak of recruitment is typically observed, there are also records of two recruitment peaks occurring in spring and summer seasons (Navarrete et al., 2008). In this study, the first recruitment peak was observed in summer and the second in fall–winter. The occurrence of two recruitment peaks might be due to adequate water temperature, food availability and favourable currents inside the protected gulf (Rivas, 1983; Gil, 2001). However, because recruitment in marine species depends on many biological and oceanographic factors, it is variable among years (Gaines and Bertness, 1992; Carroll, 1996; Watson et al., 2005). This work was performed over a time period of 1 year. Future studies should investigate which other variables affect the recruitment and survival of the introduced *Balanus glandula* and how population dynamics vary across years.

Factors other than the oceanographic characteristics of the study site, such as texture and the biofilm, could potentially explain the pattern of recruitment observed in this study. Texture is a physical factor, which may highlight the influence of the substratum characteristics on recruitment regulation (Skinner and Coutinho, 2005). In this study, the contrasting recruitment between hard and soft rough and hard–smooth substrata could be explained by the different textures. In particular, the fact that there were almost no recruits on hard–smooth substrata suggests that texture is important to recruitment on hard substrata. In addition, biofilm is a biological factor that can have a positive or negative influence on the recruitment of barnacles. The presence of biofilm may inhibit barnacle recruitment (Maki et al., 1990), but also it has been shown stimulating the settlement of their larvae (Wieczorek et al., 1995). However, these differences were probably due to different substrata, season, biofilm age and the barnacle species studied. For example, Faimali et al. (2004) showed that different types of substrata with different degrees of biofilm directly affected larval settlement in *Balanus amphitrite* Darwin, 1854. In the present study, the delayed recruitment of barnacles on the hard–rough substratum relative to the soft substratum may be related to a slower development of the biofilm necessary to the settlement and survival of the larvae.

In this study, the survival of *Balanus glandula* was highest in the soft rough substrata of the high intertidal and lowest in the hard rough substrata of the mid intertidal. Some authors found that survival in areas with a higher density of recruits was lower than those with a lower density, and this was probably due to higher intraspecific competition in high-density areas (Connolly and Roughgarden, 1998; Menge, 2000). However, the opposite pattern was reported by Bertness and Leonard (1997), who proposed that high densities of barnacles located on stressful sites might buffer the desiccation stress, which in turn would increase barnacle survival. On the other hand, a complex surface topography may increase the survival of intertidal barnacles by providing refuge from competitors, predators and desiccation (Raimondi, 1988; Herbert and Hawkins, 2006). Within this context, the high survival in the soft–rough substrata of the high intertidal may be the result of a lower desiccation stress from the high density of barnacles in the rough substratum. Thus, although the recruitment of *B. glandula* was similar in soft–rough and soft–smooth substrata, the high post-recruitment mortality appears to be an important factor limiting the success of this barnacle on soft–smooth substrata.

Balanus glandula is a successful invader of the Argentinean (Schwindt, 2007), Japanese (Kado, 2003) and South Africa coasts (Simon-Blecher et al., 2008). This species has reshaped the zonation of the native community in rocky shores and salt marshes (Schwindt et al., 2009). Considering the wide temperature range that this barnacle tolerates in native and invaded regions, *B. glandula* has great potential for colonizing the entire South America coast in the near future (Schwindt, 2007; Schwindt et al., 2009). Our results suggest that the characteristics of the substratum are an important factor affecting the success of *B. glandula* invasion. Therefore, further effort should be directed towards conducting regional surveys with special emphasis on selecting areas with soft and rough rocky bottoms in order to predict new invasions and to preserve native biodiversity.

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