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ORIGINAL PAPER

Salt marsh colonization by a rocky shore invader: *Balanus glandula* Darwin (1854) spreads along the Patagonian coast

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Abstract *Balanus glandula*, an east Pacific acorn barnacle from rocky shores, was introduced to Mar del Plata, Argentina more than 40 years ago and has spread over 17 latitudinal degrees southward. Here we report the first record of this species living in a soft-bottom environment colonizing the salt marsh plant species *Limonium brasiliense*, *Spartina densiflora*, *S. alterniflora* and *Sarcocornia perennis*. In addition, we describe the size frequency distribution, density and spatial distribution of the barnacles colonizing the different plant species. The size frequency distribution of *Balanus* showed a bimodal pattern in all plants. Barnacles were mostly large in *S. densiflora*, but small in *S. alterniflora*, with more balanced distributions of small and large barnacles on *S. perennis* and *L. brasiliense*. The highest density of barnacles was observed on *S. perennis* ($x = 35.8$ ind/cm^2, SD $=$ 40.5) and *S. alterniflora* ($x = 33.8$ ind/cm^2, SD $= 23$), while the lowest on *L. brasiliense* ($x = 1.5$ ind/cm^2, SD $= 1.18$) and *S. densiflora* ($x = 0.17$ ind/cm^2, SD $= 0.09$). More than 90% of the barnacles on any given plant were found living. While barnacles colonized only the first few centimeters above the soil surface level in *S. alterniflora* and *L. brasiliense*, they reached their highest point on *S. perennis*. The finding of a rocky shore species successfully colonizing soft-bottom marshes within an invaded region brings new perspectives to discussions in biological invasion ecology, and raises additional considerations for coastal environmental management.

Keywords *Balanus glandula* · Salt marsh · Exotic species · Patagonia

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Introduction

Biological invasions are currently considered among the more serious threats to global biodiversity. Through competitive exclusion, habitat alteration, facilitation and predation (Race 1982; Crooks 1998; Grosholz et al. 2000; Ruiz et al. 1999), invasive species are able to modify the environment where they are introduced causing drastic changes in the native faunal and floral assemblages and leading to the homogenization of the global biodiversity (Carlton 1989). Although the Argentinean coastline was long considered pristine, it is now severely affected by biological invasions (Orensanz et al. 2002; Bortolus and Schwindt 2007). Among the most emblematic exotic species in this region is the acorn barnacle *Balanus glandula* Darwin (1854); which was introduced during the early 1970's and first reported from Mar del Plata Harbor (38° S; Spivak and L'Hoste 1976). Nowadays, almost 40 years later, *B. glandula* is well established on most rocky shores and in ports along the coast of Argentina from San Clemente del Tuyú (36°21′ S 56°43′ W) to Río Grande (53°50′ S 67°33′ W, Schwindt 2007). This barnacle is native to the Pacific coast of North America, ranging from the Bering Sea to Baja California (Newman and Ross 1976) and it has been introduced only to Japan and Argentina (Kado 2003).

Balanus glandula was described exclusively populating rocky shore environments in native and non-native regions (Spivak and L'Hoste 1976; Lohse 1993; Connolly and Roughgarden 1998; Schwindt 2007). However, this barnacle was recently reported living in two of the twenty seven largest salt marshes of the Argentinean Patagonia (Idaszkin and Bortolus 2006; Bortolus 2007). In this work we supply the first comparative description of the size frequency distribution, density and spatial distribution of the barnacles colonizing the different plant species of the invaded marshes. Our findings highlight the hypothesis that exotic species may show different behaviors between native and non-native areas, leading to a more advantageous but less predictable habitat use after introduction.

Materials and methods

Study sites

In the Argentinean Patagonia, *B. glandula* lives attached to a variety of substrata naturally available in most marshes like stones, cobbles, plants, trash (bottles, cans, etc.), mussels and other organisms (Schwindt 2007). Two marshes, Riacho (R) and Loros (L, Fig. 1), covering an area of ~17 ha were sampled during summer between December 2006 and March 2007. In Riacho marsh, *B. glandula* was observed colonizing the marsh shrub *Limonium brasiliense*, the perennial glasswort *Sarcocornia perennis* and the austral cordgrass *Spartina densiflora*, while in Loros marsh it was found attached to smooth cordgrass *Spartina alterniflora*, the only species present in this salt marsh (Bortolus unpubl. data; Fig. 2a–e).

Sampling

Balanus glandula was observed inhabiting the branches of *S. perennis* (Fig. 2b) and *L. brasiliense* (Fig. 2c) that live in the middle-low marsh level, the superficial rhizomes and roots of *S. densiflora* (Fig. 2e) in the high marsh, and the stems in *S. alterniflora* in the low marsh level (Fig. 2d). Since the different plant species vary in general architecture (*Spartina* species are tall grasses, and *Sarcocornia* and *Limonium* are fleshy dwarf bushes; Cabrera 1978), sampling was designed to accommodate differences in their morphology. The variables measured were: (a) barnacle size frequency distribution, (b) barnacle density and (c) the spatial distribution of the barnacles on the plant species.

(a) Size: size of the barnacles ($n = 400$ for each plant species) was obtained with digital caliper (precision $\pm$ 0.01) by measuring the orifice length along the carinal and rostral plates. The barnacles measured were randomly chosen from different plants for each plant species. In addition, the size of the barnacles habiting a rocky shore close to the marshes (Fig. 1) was measured with the same method in order to compare the size frequency of the barnacles in the marsh with those in the most common habitats where barnacles lives in the same region. The null hypothesis of no difference in barnacle size among the different plant species and the rocky shore was evaluated with a one-way ANOVA (Zar 1999). If the assumptions of homoscedasticity and normality were not met, data were log transformed. An a posteriori Tukey test was used to identify differences between means (Zar 1999).

(b) Density: branches and stems of individual plants were measured in length and diameter and their surface area calculated by using the formula for the surface of a cylinder ($2 * \pi *$ radius * (height + radius)). Then, the number of barnacles was counted and density estimated for each of the three plant species *S. perennis*, *L. brasiliense* and *S. alterniflora* (quadrat area = 4 cm^2, $n = 37$ for each species). Density was then referred as individuals per cm^2. In *S. densiflora* barnacles settle on unburied superficial rhizomes and roots. In this case, density was obtained from 25 quadrates (15 $\times$ 15 cm each) randomly placed and photographed with a high resolution digital Sony DSC-W55 camera. Photos were analyzed to determine barnacle density

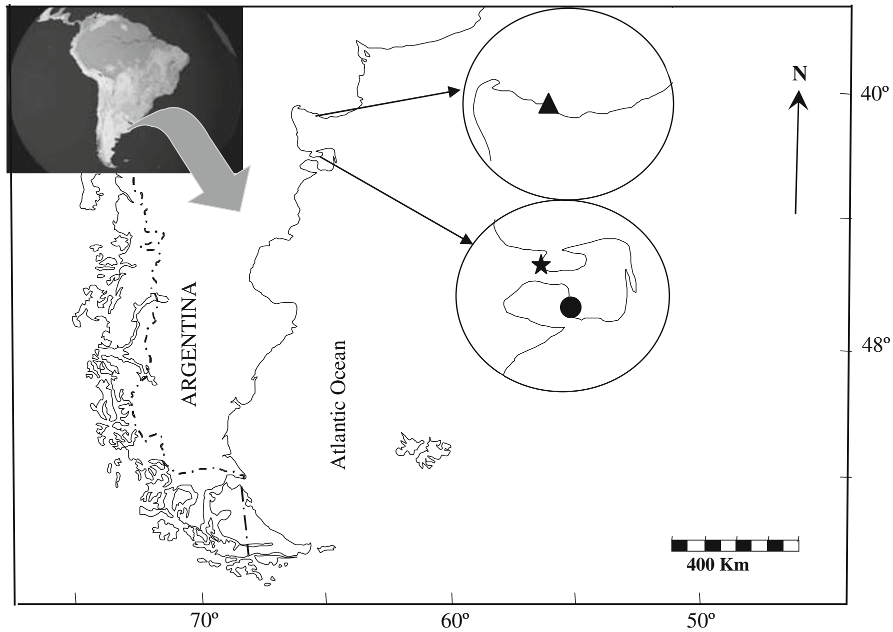

Fig. 1 Map showing the location of the two salt marshes (Loros: black triangle and Riacho: black star) and intertidal rocky shore (black circle) invaded by the exotic barnacle *Balanus glandula* in the Patagonian coast of Argentina

by counting all barnacles from each quadrate. A one way ANOVA was performed to evaluate the null hypothesis of no difference in barnacle density among the plant species invaded, and a posteriori Tukey test was used to identify differences between means (Zar 1999). If the assumptions of homoscedasticity and normality were not met data were square root transformed. In addition, for each plant species, the proportion of dead (i.e. empty) and live barnacles was measured to evaluate their success in this new environment.

(c) Spatial distribution: the existence of a vertical stratification of barnacles on the plants where they settle was evaluated by combining the following measurements: the maximum height reached by the barnacles on the stems or branches, the height of the plant at which the 90% of the barnacles live, and the total height of each plant species ($n = 40$ for *L. brasiliense*, $n = 62$ for *S. perennis*, $n = 29$ for *S. alterniflora* and $n = 60$ for *S. densiflora* for each variable). The differences in maximum height reached by the barnacles among plant species was evaluated with a one way ANOVA and the same analysis was used to evaluate differences in the height of the plant at which the 90% of the barnacles live (Zar 1999). An a posteriori Tukey test was used to identify differences between means (Zar 1999).

Results and discussion

The size frequency distributions of *B. glandula* in all the plant species we studied were bimodal. With *S. densiflora*, the barnacles were mostly represented by large individuals while with *S. alterniflora* most barnacles were small (Fig. 3). *Limonium brasiliense* and *S. perennis* were more balanced with respect to large and small barnacles and showed patterns more similar to the rocky shore than to the *Spartina* species (Fig. 2). The mean size of barnacles was significantly different among habitats ($F = 133.53$, $df = 4$, $P < 0.05$, Fig. 4a). An a posteriori Tukey test showed that the barnacles living in *S. densiflora* were not only the largest among the plant species but also that they were larger than those in the rocky shore ($P < 0.05$, Fig. 4a). We found the smallest mean orifice sizes in *S. perennis* and *S. alterniflora* and intermediate values in *L. brasiliense* and the rocky shore ($P < 0.05$, Fig. 4a). Recent experimental work focused on the recruitment of *B. glandula* in locally invaded rocky shores, showed that barnacles reach a mean orifice size of up to 3.21 mm in 1 year (Savoya 2006). If growth rates are similar in salt marshes, the

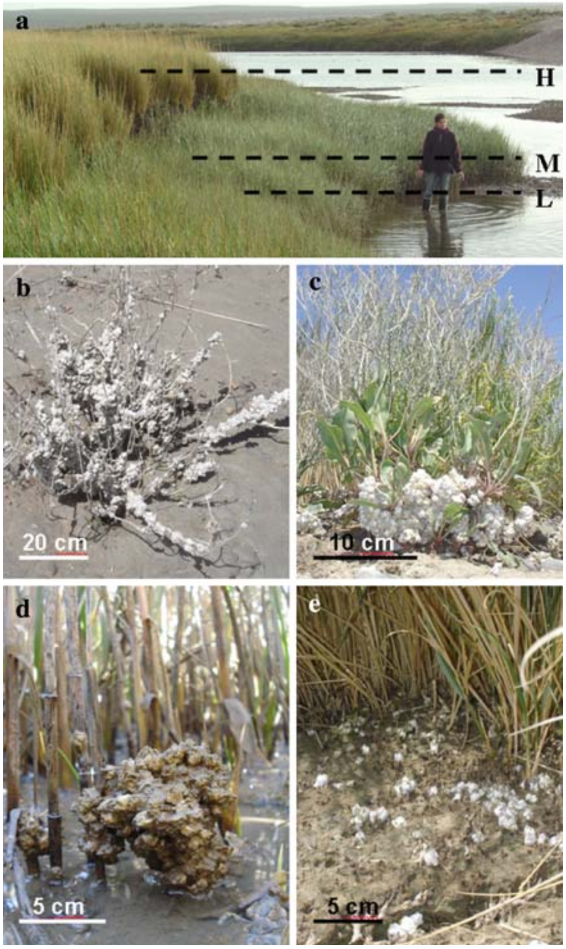

Fig. 2 Photographs showing (**a**) a typical Northern Patagonia salt marsh (H: high, M: medium and L: low marsh levels) and the different salt marsh plant species invaded by the exotic *Balanus glandula* and studied in this work: (**b**) *Sarcocornia perennis*, (**c**) *Limonium brasiliense*, (**d**) *Spartina alterniflora* and (**e**) *S. densiflora*. Photographs by A. Bortolus

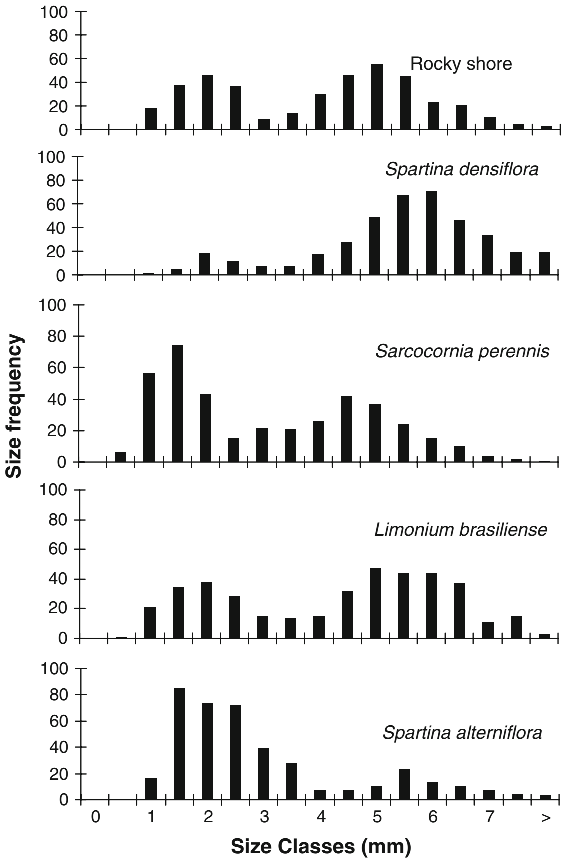

Fig. 3 Size frequency distributions of barnacles per class size (in mm) living in a rocky shore or in salt marsh in association with *Spartina densiflora*, *Sarcocornia perennis*, *Limonium brasiliense* and *S. alterniflora*

wide spectrum of size frequency distributions we found (min: 0.35 mm, max: 9.41 mm) suggests that recruitment of this population is likely to have occurred across the last 3 years. Since its introduction in this region 20 years ago, this is the first time it has been found in a salt marsh (Schwindt 2007). However, considering that *B. glandula* recruits throughout the year in rocky habitats along the entire Argentine coast (Schwindt 2007), the bimodal patterns of size frequency distributions and the mean sizes we reported here, strongly suggest that the invasion of *B. glandula* in these salt marshes is not a one time event and may have seasonal components.

The density of *B. glandula* was significantly different among the plant species colonized (square-root transformed, $F = 75.19$, df = 3, $P < 0.05$, Fig. 4b). An a posteriori Tukey test showed that the density of barnacles was significantly higher in *S. perennis* and *S. alterniflora* than in *L. brasiliense* and *S. densiflora* ($P < 0.05$, Fig. 4b). However, there were no significant differences either of the higher and lower density pairs of plant species ($P > 0.05$, Fig. 4b). This is remarkable given that in our study site, *S. perennis* and *L. brasiliense* occur at the same intertidal level and their architectures are similar. Moreover, the cordgrass *S. alterniflora* showed the same barnacle density as the shrubby *S. perennis* (Fig. 4b). In addition, in all plant species, the percentage of dead barnacles was always less than 6% (*L. brasiliense* = 4.5%, *S. alterniflora* = 5.5%, *S. perennis* = 1.43% and *S. densiflora* = 1.71%),

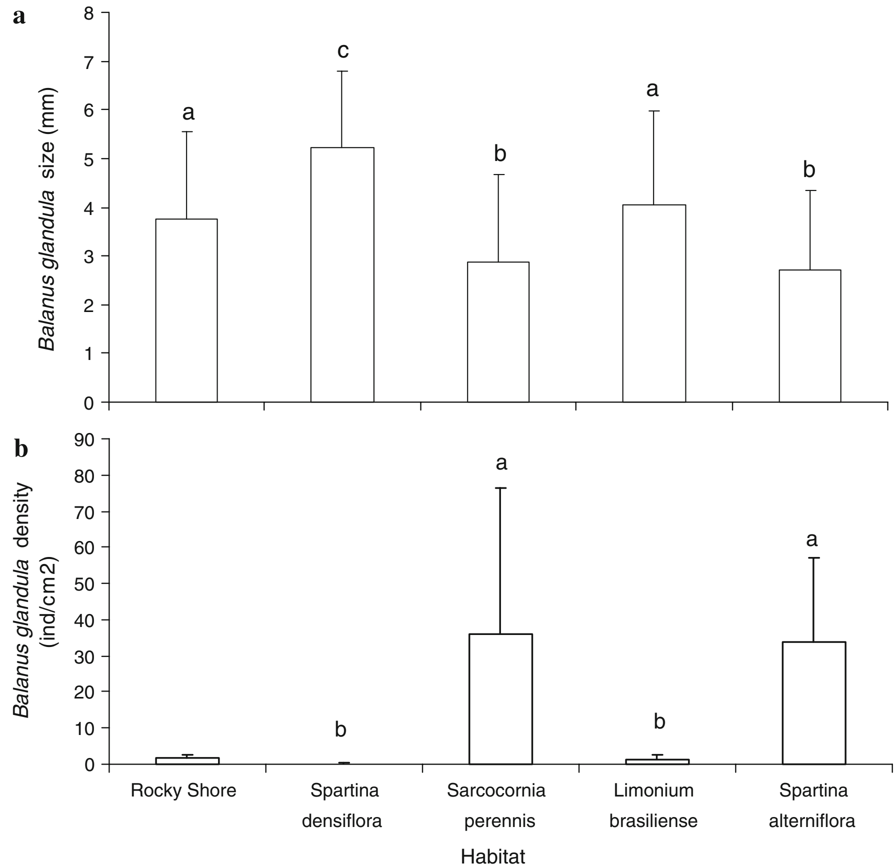

Fig. 4 (**a**) Size (in mm, bars with the mean plus SD); and (**b**) density (ind cm^{-2}, bars with mean plus SD) of *Balanus glandula* living on different marsh plant species and the rocky shore. Identical letters above the bars indicate non-significant differences (Tukey $P > 0.05$)

indicating that *B. glandula* is successful in this habitat. These results also indicate that the success of *B. glandula* may not relate to tidal height or plant architecture, but experimental work must be performed to appropriately evaluate these hypotheses and to determine if barnacles select preferentially among plant species. Our results show that salt marsh plants are able to offer suitable substrata for *B. glandula* larval settlement in soft bottom environments. Moreover, the variety of sizes and high densities we found suggest that the barnacle populations colonizing these marshes are capable of reproducing (Wu 1981) and may serve as important sources of local larval supply.

The maximum height reached by *B. glandula* on plants was significantly different among various plant species ($F = 181.14$, df = 2, $P < 0.05$, Fig. 5), and it was not clearly related to the intertidal level. It was highest in *S. perennis*. *Spartina alterniflora* and *L. brasiliense* had barnacles attached at similar heights ($P < 0.05$, Fig. 5), and in *S. densiflora* barnacles settled only at the soil surface level. Patterns were similar among plant species for barnacle colonization at the 90% cover level ($F = 119.2$, df = 2, $P < 0.05$, Fig. 5). We found that 20% (SD = 7.5) of the stems of *S. alterniflora* in Loros marsh were inhabited by barnacles, and 90% of these

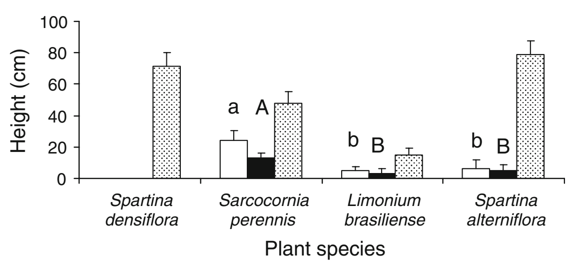

Fig. 5 Height (in cm) reached by barnacles on each plant species (white bars: maximum height; black bars: height reach by barnacles at a density ≥90% cover) and heights of the different marsh plant species invaded by barnacles (bars with stippling). All bars indicate mean plus SD. Identical letters above bars indicate non-significant differences (Tukey $P > 0.05$)

were dead standing stems. This result contrasts with the record of the barnacle *Chthamalus fragilis* that colonizes only the living stems of *S. alterniflora* in the southeastern coast of the USA where both species are native (Young 1991). *Balanus glandula* reached a higher height on *S. perennis* than on *L. brasiliense* within the same intertidal level ($P < 0.05$), probably because *Sarcocornia* branches tend to be longer and more erect than *Limonium* branches (Cabrera 1978). However, while 85% of the branches studied in *L. brasiliense* were live, 99% of the branches in *S. perennis* were standing dead. Although the association of barnacles with dead branches was common to all plants species in our surveys, detailed experimental work is needed to clarify whether *B. glandula* causes the death of the plants or if it recruits actively selecting dead stems. These contrasting hypotheses relate differently to concerns about the impact this invasive species may have in Patagonia marshes.

Salt marshes occur throughout the coast of Argentina intermingled with sandy and rocky shores. Although the introduction of *B. glandula* occurred in the northern part of Argentina, the presence of this species has never been reported in northern salt marshes (Bortolus and Iribarne 1999; Iribarne 2001; Escapa et al. 2004). Over twenty seven of the largest salt marshes along the Patagonian coast of Argentina have been recently surveyed, but barnacles were not detected except among the two marshes reported here. In fact, this is the first record of *B. glandula* colonizing salt marsh habitats in either native or invaded areas. Unfortunately, most marshes of South America from Southern Brazil to Argentina have vast areas dominated by *S. alterniflora* and *S. perennis* (Costa and Davy 1992). However, the greatest risk for potential invasion by *B. glandula* may be along the austral Patagonian salt marshes which are dominated by *S. perennis* (Bortolus 2007), where this barnacle seems to do better. This is a real risk considering that this barnacle has been recorded successfully invading most marine rocky shores within the region (Schwindt 2007). If *B. glandula* invades other Patagonian marshes with the same success we report in this study and negatively impacts the plants it colonizes, it may cause serious environmental damage. The magnitude of the potential effect of such an invasion may only compare to the dramatic effects of the golden mussel *Limnoperna fortunei*, introduced in the La Plata River in 1991 (Orensanz et al. 2002). The finding of dead standing branches and stems associated with barnacles in the invaded marshes raises an additional major warning to ecologists and environmental managers. Experimental work is urgently needed to evaluate if *B. glandula* affects the survival of *Sarcocornia* and *Spartina*, and what positive and/or negative effects this introduced species may have on the associated native invertebrate assemblages through habitat modification.

Balanus glandula is currently spreading its distributional range worldwide (Kado 2003; Schwindt 2007). The finding of this species colonizing a habitat extremely different from its native rocky shores may be an indication of evolutionary changes originated by introduction to a new habitat. Besides its theoretical relevance, this case also deserves urgent attention from ecologists, conservation biologists, environmental managers and decision makers in order to re-evaluate the status of exotic species that are commonly based on environmental scanning protocols for exotic species focused on habitat similarity with donor areas.

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