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The invasion of the acorn barnacle *Balanus glandula* in the south-western Atlantic 40 years later

Evangelina Schwindt

Centro Nacional Patagónico (CENPAT-CONICET), Blvd. Brown 2825, Puerto Madryn (9120), Argentina.
E-mail: schwindt@cenpat.edu.ar

The acorn barnacle *Balanus glandula* (Darwin 1854) is native to the Pacific coast of North America and was accidentally introduced in Argentina in the early 1970s. Here the invasion status of this species is reviewed in the south-western Atlantic focusing on geographical patterns of density, cover, biomass, size and recruitment, and also estimating its rate of spread. Field surveys along rocky shores and a literature review show that *B. glandula* invaded most of the rocky shores of Argentina at a high rate of spread. Density and cover of barnacles do not follow a latitudinal trend; instead both variables show a bimodal pattern with the highest values in two distant locations (Puerto Lobos and Bahía Bustamante). However, the size of the barnacles increases with latitude, and is positively related to biomass. Recruitment of this species varies between wave exposed and protected areas, and over time. At lower latitudes barnacles recruit in winter, while at higher latitudes they recruit in spring and summer. The differences observed in density and recruitment suggest that along the Argentinean coast, oceanographic processes have a stronger influence in the distribution and success of the barnacles than the gradient in wave exposure. *Balanus glandula* is a successful invader which has completely re-shaped the native intertidal landscape. Moreover, considering the wide temperature range that this barnacle tolerates in native and invaded regions, the entire coastline of South America could be colonized by this species in the future.

INTRODUCTION

The introduction of exotic species into new habitats has been recognized as one of the major threats to native biodiversity worldwide. New species in new habitats can alter ecological interactions, the regional economy (Darrigran & Ezcurra de Drago, 2000) and/or have a variety of social consequences (Mooney & Hobbs, 2000). In marine ecosystems, the main focus of attention is usually given to aggressive invasive species that rapidly capture the public attention, mainly due to the direct economic and social impacts that they cause (e.g. the water flea *Cercopagis pengoi*, Leppäkoski et al., 2003; the macroalga *Undaria pinnatifida*, Casas et al., 2004). However, some invasions can cause profound changes at different ecological and evolutionary scales without a direct economic and/or social impact (e.g. the polychaete *Ficopomatus enigmaticus*, Schwindt et al., 2001; 2004). Most barnacles are among these non-famous introduced organisms (e.g. *Eliminius modestus* in Ireland, Lawson et al., 2004) which were often overlooked, after being introduced in areas where native barnacles were already abundant (e.g. *Balanus glandula* in Japan, Kado, 2003). However, although cryptic and often overlooked, barnacles play important roles in marine community ecology, for example in the dynamics of succession by being the early colonizers and facilitating the recruitment of other organisms such as mussels and algae (Dayton, 1971), and also participating in fundamental ecological processes such as competition and predator–prey interactions (Connell, 1961; Harley, 2003).

Zonation is one of the most conspicuous patterns on rocky shores, which are typically divided into three levels based on the distribution of the dominant organisms. The higher level is often dominated by organisms that tolerate dehydration such as barnacles and limpets. Mussels are dominant at the mid level, and macroalgae and other invertebrates occupy the lower level of the shore. This spatial pattern can dramatically shift from wave-exposed to wave-protected areas; although there are biogeographical variations in the zonation patterns among cold, temperate and tropical regions, this general scheme is usually present in most intertidals worldwide. In Argentina, early descriptions of rocky shores showed that limpets, mussels and macroalgae were the dominant organisms at the high, mid and low intertidal levels respectively (Ringuelet et al., 1962; Olivier et al., 1966a,b). With the exception of the rocky shores of Ushuaia (Zaixso et al., 1978), the absence of barnacles was intriguing. However, during the early 1970s three exotic barnacles, *Balanus glandula*, *B. trigonus* and *B. amphitrite*, were introduced in Mar del Plata Harbour (38° SL; Spivak & L'Hoste, 1976). Nowadays, almost 40 years later, only *B. glandula* is well established in most rocky shores and ports along the coast of Argentina. This barnacle is native to the Pacific coast of North America, ranging from the Bering Sea to Baja California (Newman & Ross, 1976). It has been introduced only to Japan and Argentina (Kado, 2003). In spite of the fact that *B. glandula* currently spreads over more than 10 latitudinal degrees along the coast of Argentina (Orensanz et al., 2002), there are few studies

Table 1. *Geographical positions of the locations mentioned in the text and the individual and population variables studied at each site.*

Location	Geographical position	Variable
San Clemente del Tuyú (SCT)	36°21'S 56°43'W	lr
Mar del Plata (MDP)	38°02'S 57°32'W	d, c, s, b, r, rp, lr
Quequén Harbor (QH)	38°34'S, 58°38'W	lr
Ingeniero White Harbor (IWH)	38°47'S, 62°16'W	rp, lr
Punta Mejillón (PM)	41°01'S; 64°08'W	d, c
Puerto Lobos (PL)	41°59'S, 65°03'W	d, c, s, b
San José Gulf (SJG)	42°15'S, 64°06'W	lr
Punta Pardelas (PP)	42°36'S, 64°15'W	d, c, s, b
Punta Ameghino (PA)	42°37'S, 65°37'W	d, c, s, b, r, rp, lr
Nuevo Gulf (NG)	42°46'S, 65°02'W	lr
Punta Ninfas (PN)	42°57'S, 64°25'W	d, c, s, b
Playa Escondida (PE)	43°40'S, 65°20'W	d, c, s, b
Punta Tombo Protected Area (PTPA)	44°02'S, 65°12'W	p/a
Cabo Dos Bahías (CDB)	44°53'S, 65°37'W	d, c, s, b, r, rp
Bahía Bustamante (BB)	45°05'S, 66°30'W	d, c, s, b
Comodoro Rivadavia (CR)	45°52'S, 57°28'W	r, rp, lr
Rada Tilly (RT)	45°55'S, 67°33'W	lr
Caleta Olivia (CO)	46°26'S, 67°31'W	d, c
Puerto Deseado (PDe)	47°44'S, 65°59'W	d, c, s, b
San Julián (SJ)	49°14'S, 67°40'W	d, c, s, b
Punta Quilla (PQ)	50°07'S, 68°22'W	p/a
Monte León National Park (MLNP)	50°20'S, 68°52'W	p/a
Punta Loyola (PLo)	51°36'S, 69°01'W	p/a
Río Grande (RG)	53°50'S, 67°33'W	p/a
Ushuaia (U)	54°49'S, 68°13'W	p/a

d, density; c, cover; s, size; b, biomass; r, recruitment; rp, recruitment peak; lr, literature report; and p/a, presence/absence of *Balanus glandula*. Abbreviations of the site locations are in parentheses.

focused on population dynamics at local scale (Vallarino & Elias, 1997; Rico et al., 2001). Little is known about how successful it is throughout the entire invaded area. Here I combine a literature review with regional-scale fieldwork in order to clarify the current invasion status of the acorn barnacle *B. glandula* in the south-western Atlantic, focusing on geographical patterns of density, cover, biomass, size and recruitment, and estimating its rate of spread.

MATERIALS AND METHODS

I conducted surveys between 2002 and 2005 in different rocky shores, at the high level of the intertidal in wave exposed and wave protected areas along the Argentinean coast. The acronyms of all study sites, their respective geographical positions, and the variables studied at each site are shown in Table 1.

(a) Patterns of density, cover, biomass and size

In order to study cover and density of barnacles, between 10 and 20 random and independent samples were obtained for each variable and measured in the field (Table 1). The sample unit consisted of 10×10 cm quadrats placed in areas with high density, and quadrats of 50×50 cm in areas with low density of barnacles. Density was determined by counting all individuals living inside each quadrat. Cover was determined as percentage of area covered by barnacles alive and the sample size of the plots was the same as for density. Samples were obtained on rocks considered as primary substrate (i.e. data from barnacles living on other organisms were not considered, Table 1). To estimate biomass approximately 50 solitary barnacles were carefully removed from each site and placed in separate bags. Samples were kept frozen and once at the laboratory each barnacle was oven-dried at 70°C until reaching constant weight and weighed using a digital balance (precision ±0.001 g). To estimate the average size of the barnacles from each location (Table 1), 50 solitary individuals were removed and the basal diameter was measured along the carinal and rostral plates using digital callipers (precision ±0.01). To evaluate if there is a relationship between the variables studied and latitude, non-parametric correlation analysis (Spearman's rank) was performed independently for each variable. Parametric correlations were used to evaluate relationships among the pairwise variables (Conover, 1980; Zar, 1999).

(b) Recruitment patterns

'Recruitment' was measured as the density of recruits recorded along the year and 'recruitment peak' was defined measured as the period of the year where the highest density of recruits was recorded. Both variables were studied through an extensive review of the available literature included in peer-reviewed papers, reports and proceedings published since 1970. Mean monthly recruitment was calculated for rocky shores and artificial structures such as ports

Table 2. *Results of the parametric (R) and non-parametric (Spearman's rank=R_s) correlation analyses between the individual and population variables and latitude and between the pairwise of variables.*

Variables	R_s	R	*t*	*P*
Latitude vs density	−0.55	−	−2.09	>0.05
Latitude vs cover	−0.51	−	−1.91	>0.05
Latitude vs size	0.69	−	2.74	<0.05
Latitude vs biomass	0.47	−	1.54	>0.05
Density vs cover	−	0.87	5.71	<0.01
Density vs biomass	−	−0.43	−1.37	>0.05
Density vs size	−	−0.48	−1.57	>0.05
Cover vs size	−	−0.55	−1.88	>0.05
Cover vs biomass	−	−0.52	−1.73	>0.05
Size vs biomass	−	0.96	10.01	<0.01

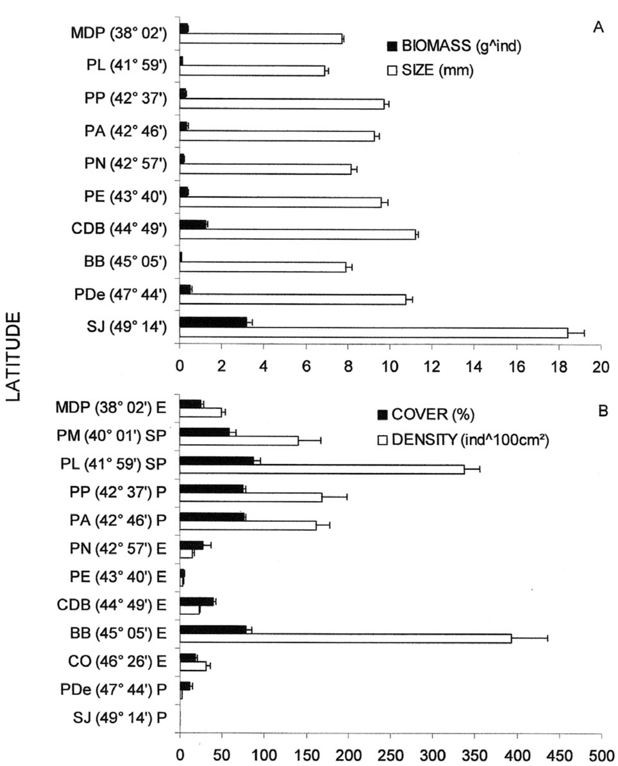

Figure 1. (A) Mean (±SE) biomass and size and (B) cover and density of *Balanus glandula* on the rocky shores surveyed at different latitudes. Abbreviations of locations are as in Table 1.

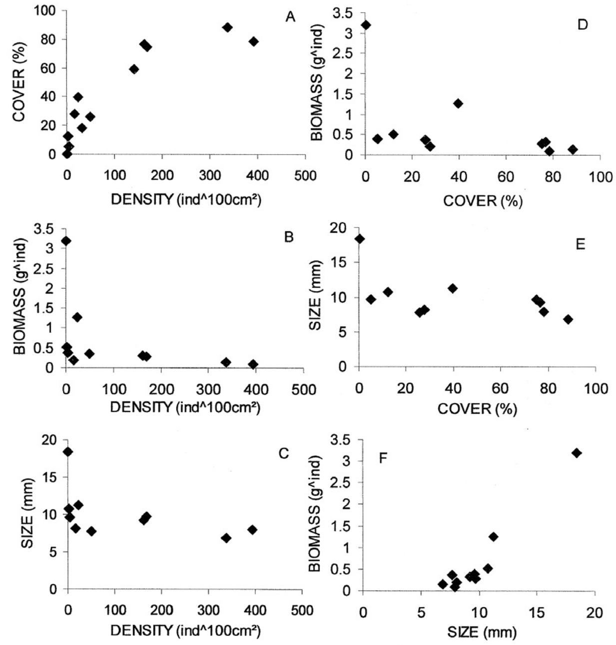

Figure 2. Pairwise comparisons of mean density, cover, biomass and size of *Balanus glandula* at the different rocky shores studied. (A) cover vs density; (B) biomass vs density; (C), size vs density; (D) biomass vs cover; (E) size vs cover; and (F) biomass vs size.

and harbours. Since reproduction in marine ecosystems, and consequently recruitment, is highly affected by water temperature (Stachowicz et al., 2002), mean annual surface seawater temperature (SST) data were compiled using the database of the Navy Hydrographic Service of Argentina (www.hidro.gov.ar) in order to associate SST with the recruitment data for the different sites.

(c) Rate of spread

To estimate the spread rate of *Balanus glandula* I considered the dates when the species was first observed or recorded in different locations along the Argentinean coast and the real distances in kilometres among those places. Also, in order to update the information about the present geographical distribution of the barnacles between the years 2004 and 2006, surveys were conducted to document new invaded locations from Mar del Plata to Ushuaia.

RESULTS

(a) Patterns of density, cover, biomass and size

Correlation analyses showed significant and positive relationships between latitude and average size of *Balanus glandula* (Table 2). Smaller barnacles were found at lower latitudes and the larger ones at higher latitudes (Figure 1A). Cover and density showed a bimodal pattern (Figure 1B), being highest at Puerto Lobos (42° SL) with 4 ind•cm^{-2} covering 88.5 % of the surface, and in Bahía Bustamante (45° SL) with 7 ind cm^{-2} covering 78.3% of the substrate. Cover and density were positively correlated (Table 2; Figure 2A), as well as the size and biomass of the barnacles (Table 2; Figure 2F). However, pairwise comparisons among the rest of the variables did not show significant relationships (Figure 2B–E).

(b) Recruitment patterns

Strongest recruitment was observed in the Mar del Plata and Comodoro Rivadavia harbours (Figure 3). Along rocky shores interannual variability was high and differences between protected and exposed areas were pronounced (Figure 3). Within each site, recruitment was highest in exposed areas (see Figure 3 for Mar del Plata and Cabo Dos Bahías), however, at a larger spatial scale, Punta Ameghino, which is a wave-protected area, showed the highest recruitment (Figure 3). Recruitment peaks were seasonally variable among latitudes. In the

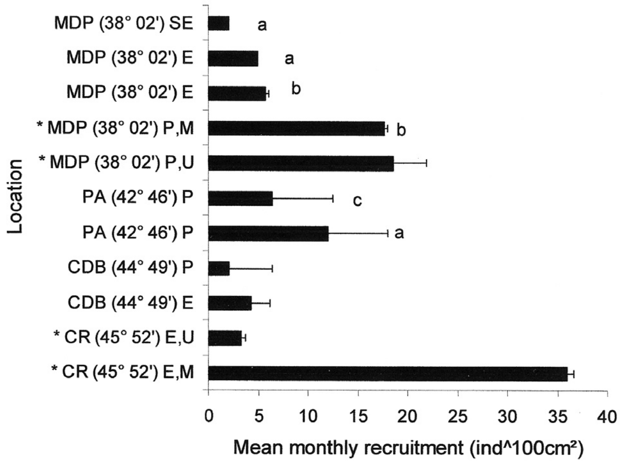

Figure 3. Mean monthly recruitment obtained from the literature records for the different ports (marked with asterisks) and rocky shores in wave protected (P), exposed (E) and semi exposed (SE) areas and at different intertidal levels (mid (M) and upper (U)). Literature records are marked with smaller letters: (a) Schwindt et al. (2003); (b) Vallarino & Elias (1997); (c) Savoya (2006); and (d) Rico et al. (1997). Abbreviations of the locations are as in Table 1.

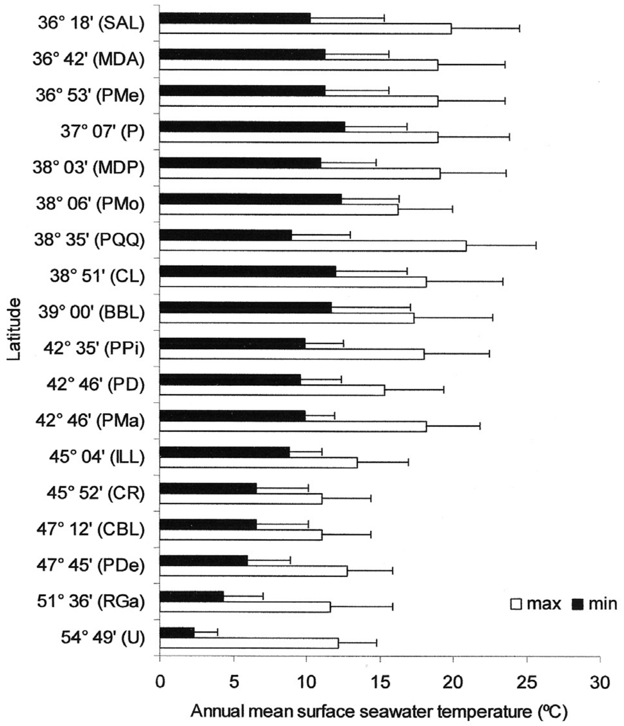

Figure 4. Maximum and minimum mean seawater surface temperature (±SE) for recording stations at different latitudes obtained from the database of the Hydrographic Navy Service (www.hidro.gov.ar): SAL, San Antonio Lighthouse; MDA, Mar de Ajó; PMe, Punta Médanos; P, Pinamar; MDP, Mar del Plata; PMo, Punta Mogotes; PQ, Puerto Quequén; CL, Claromecó Lighthouse; BBL, Bahía Blanca Lighthouse; PP, Puerto Pirámides; PD, Punta Delgada; PMa, Puerto Madryn; ILL, Isla Leones Lighthouse; CR, Comodoro Rivadavia; CBL, Cabo Blanco Lighthouse; PD, Puerto Deseado; RG, Río Gallegos; U, Ushuaia.

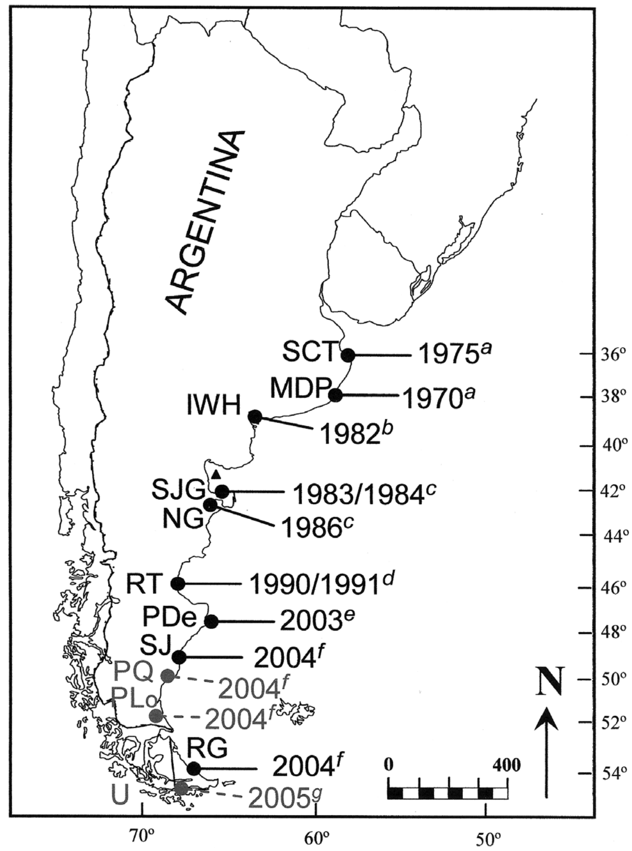

Figure 5. Locations and dates of first records of *Balanus glandula* along the Argentinean coast. Locations and dates marked in grey and dashed lines were surveyed but no *B. glandula* individuals were found. Information sources are marked with smaller and italics letters: (a) Spivak & L'Hoste (1975); (b) Wagner et al. (1993); (c) Gómez Simes (1993); (d) E. Gómez Simes, personal communication (2006); (e) J.P. Martín personal communication (2004); (f) E. Schwindt, C.D.G. Harley, A. Bortolus and V. Savoya, personal observations; (g) E. Schwindt, personal observation. Abbreviations of the locations are as in Table 1. Black triangle indicates the location of the San Matías Gulf.

northern populations (i.e. Mar del Plata and Ingeniero White harbour) recruitment occurs in winter while in the southern populations (i.e. Punta Ameghino, Cabo Dos Bahías and Comodoro Rivadavia) barnacles recruited in spring and/or summer. Most of the available literature focusing on this region reported that *B. glandula* recruits throughout the year with one recruitment peak per year, but Savoya (2006) found two peaks, winter and summer, in Punta Ameghino. Differences between the maximum and minimum temperatures were highly variable along the coast (Figure 4).

(c) Rate of spread

The estimated dispersion rate of *Balanus glandula* was 244 km y^{-1} (Figure 5 map). Of all the locations sampled, only Punta Quilla, Punta Loyola and Ushuaia (Figure 5, in grey) were not populated by *B. glandula*. It was recorded at very low densities (1 individual in approximately 2 m^2) in Quequén harbour, Punta Tombo Protected Area, Monte León National Park and Río Grande.

DISCUSSION

Almost 40 years after the initial introduction of the acorn barnacle *Balanus glandula* in Mar del Plata harbour (Argentina), this species is presently distributed over 2900 km, from San Clemente del Tuyú to Río Grande, showing a high biological plasticity by living in intertidals where the mean temperature ranges between 4.3°C and 21°C. This exotic barnacle has completely changed the native landscape of the Argentinean intertidal communities, originally dominated mainly by mussels, limpets and macroalgae, which suggests that also the ecological interactions have been altered.

The majority of the 22 locations studied have been invaded by *Balanus glandula*. In the few locations where it is scarce or absent, other exotic barnacles such as *B. amphitrite* at Quequén harbour, colonized the intertidal but always in low density (Calcagno et al., 1997). In most intertidals of Argentina *B. glandula* forms monospecific dense belts devoid of other barnacle species as competitors. A conspicuous example of dominance by this species was observed in Mar del Plata rocky shores, where *B. trigonus* and *B. amphitrite* were introduced a few years earlier than *B. glandula* (Spivak, 2005). These two exotic species, however, were displaced to the lower shore level soon after the arrival of the exotic *B. glandula*. Although this process was not studied in detail, Spivak (2005) suggested that the differences in recruitment time may have caused the displacement of *B. trigonus* and *B. amphitrite* to the lower areas of the intertidal zone, because while these two barnacle species recruit in summer (Calcagno et al., 1997), *B. glandula* recruits earlier in winter, rapidly dominating the available free space (Spivak, 2005). The same process may be occurring in the invaded sheltered waters of Ofunato Bay (Japan), where *B. glandula* apparently can breed earlier and at smaller size than *B. albicostatus*, occupying the available space and dominating the intertidal (Kado, 2003). Therefore, *B. glandula* is a successful invasive species in terms of capability of colonization in both Argentina and Japan.

Considering the direction of spreading of the invasion, it could be expected that the density of *Balanus glandula* in Argentina would diminish toward higher latitudes. However, neither the cover nor the density of the barnacles followed a clear latitudinal pattern. The highest density found is similar to the highest density reported in other invaded areas (Japan: 4 ind cm^{-2}, Kado, 2003) but much higher than the reported densities in native areas (Glynn 1965, in California; Spight, 1981 in Washington). The highest mean cover found in this work is comparable only to that reported for Oregon (USA) but much higher than what was reported for California and Washington (Connolly & Roughgarden, 1998; Harley, 2003) These results support the hypothesis that *B. glandula* may be a successful invader not only in terms of capability of colonization, but also due to the massive density and cover that this species reaches at the invaded places.

Maximum density and cover were found in semi-protected and exposed areas (Puerto Lobos and Bahía Bustamante, respectively), suggesting that in the Argentinean coast the successful recruitment and survival of barnacles are not primarily driven by wave exposure. Since ports are built in sheltered waters on the open coast (Leppäkoski et al. 2003) and barnacles are fouling organisms very abundant in those areas, the expectation is to find the highest density of *B. glandula* in areas close to ports and harbours. Instead, Puerto Lobos and Bahía Bustamante are far away from all important port centres of the region (approximately 400 km to Puerto Madryn and 130 km to Comodoro Rivadavia). There is indirect evidence suggesting that the success of this species in these locations is related to oceanographic processes that may facilitate local recruitment. Puerto Lobos, for instance, is located on the south-west of San Matías Gulf (Figure 5). Although the length of the gulf's mouth is approximately 100 km, water exchange with the open sea is constrained by a depth difference between the mouth (70 m) and the inner part of the gulf (200 m) (Gagliardini & Rivas, 2004). Several physical, chemical and biological studies (Rivas, 1990; Esteves et al., 1995) suggest the existence of an upwelling system close to Puerto Lobos, resulting from strong and dominant westerly-south-westerly winds (Gagliardini & Rivas, 2004). Puerto Lobos is highly rated for mussel aquaculture due to strong spat fall, suggesting that it is an area with a high potential for larval retention. On the other hand, Bahía Bustamante is also highly productive. This region is exposed to the influence of cold waters from November through February and upwelling events at that time of the year are coincident with the distribution of seabird breeding colonies (Gagliardini et al., 2004). Moreover, Commendatore and colleagues (2000) working in the same region found high densities of solid waste derived from shipping activities and high hydrocarbon concentrations, suggesting the existence of a circulation pattern that would favour the concentration of planktonic larvae. Marine oceanographic processes may have an influence in the regional distribution and abundance patterns of this exotic species stronger than the wave exposure condition.

At higher latitudes *Balanus glandula* individuals are larger than at lower latitudes. The largest size was 23.8 mm recorded in San Julián, where this species is found at very low density. Although biomass did not follow the same pattern, both variables were linear and positively related. As expected, since the size and the biomass were studied from solitary barnacles, these variables were not correlated with density and cover. However, all the barnacles with smallest sizes and with the lowest biomass values were found in the locations with the highest densities (i.e. Puerto Lobos and Bahía Bustamante). Considering that individuals of *B. glandula* must be very close to each other to allow cross-fertilization and reproduce effectively (<6 cm, Wu, 1981), these results suggest that the population at San Julián is not self-maintained with local production of larvae, but with constant immigration of larvae coming from other intertidal zones. The geographical differences in biomass suggest that while in San Julián barnacles seem to be investing more effort into growth, the barnacles of Puerto Lobos and Bahía Bustamante seem to be putting their effort into reproduction.

Recruitment of *Balanus glandula* shows high among-places variation. The highest density of recruits was observed in ports, Comodoro Rivadavia and Mar del Plata, which are respectively exposed and protected from wave action. On rocky shores recruitment is highest in Punta Ameghino, a protected area of the Nuevo Gulf, than in Cabo Dos Bahías and Mar del Plata that are exposed areas. These results are consistent with the patterns of density and cover, supporting the idea that success of recruits at the regional scale is not primarily linked to local wave exposure conditions. Moreover, the same areas showed different density of recruits and recruitment peak over time (Punta Ameghino: Schwindt et al., 2003; Savoya, 2006; Mar del Plata: Vallarino & Elias, 1997; Schwindt et al., 2003). While the barnacles are able to breed all year round, recruitment peaks occur in winter at northern locations and in spring/summer at southern locations. At these sites, the maximum mean seawater temperatures recorded during the recruitment season ranged between 10°C and 22°C (Ingeniero White harbour and Punta Ameghino respectively). Instead, the minimum mean seawater temperature for the same periods ranged between 4°C and 11°C (Ingeniero White harbour and Cabo Dos Bahías respectively). Also reflected by the wide latitudinal range in the native region of *B. glandula*, the wide temperature range in which this species can reproduce points to high plasticity (Barnes & Barnes, 1958; Menge, 2000), which suggests that the colder and southern areas of the South American Continent, such as Ushuaia, are likely to be receptive in the near future.

The rate of spread for *Balanus glandula* in Argentina is much higher than any other reported elsewhere in marine ecosystems (Grosholz, 1996). Assuming that this barnacle follows the 'stepping stone model' of invasion, its arrival to Puerto Deseado was reported 13 years after being detected in Rada Tilly (from the early 1990s to 2003), which results in a very low rate of spread in comparison with the invasion observed in other places (Figure 5). Considering the estimated rate of spread in this work, it is likely that the arrival of *B. glandula* to Puerto Deseado occurred much earlier than 2003. Besides, the density found at this location is similar to other northern invaded areas (e.g. Playa Escondida), and much higher than other southern and more recent invaded areas (e.g. San Julián), suggesting that the invasion of *B. glandula* occurred before 2003 and went overlooked. The existence of isolated individuals in Monte León National Park and Río Grande suggests that the invasion of *B. glandula* is in an early stage.

The acorn barnacle *Balanus glandula* has successfully invaded, at high rate of spread, virtually the entire coast of Argentina in less than 40 years. At some of the invaded locations, the barnacles reach higher cover and size than in its native area. This exotic species seems to have encountered habitats without competitors in Argentina, in contrast with Japan, where at least six endemic barnacle species were already present in the shores before the arrival of *B. glandula* (Kado, 2003). Many important questions still need further attention and research. Why this abundant species in its native area has only invaded Argentina and Japan? What is its effect on native intertidal communities? Will *B. glandula* be able to reach the Pacific coast of South America and to invade the Chilean rocky shores? Answering these questions would be relevant to better understand the ecology of the invasive species and to set management conservation priorities at a large geographical scale.

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