



INVASIVE BARNACLE FOULING ON AN ENDEMIC BURROWING CRAB: MOBILE BASIBIONTS AS VECTORS TO INVADE A SUBOPTIMAL HABITAT

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ABSTRACT

Neohelice (Chasmagnathus) granulata is an ecosystem engineer endemic of salt marshes and mudflats of the southwestern Atlantic coast, where several Patagonian salt marshes were invaded by the acorn barnacle *Balanus glandula*, a typical rocky shore species. In this work, we supply the first report of the occurrence of epibiosis of *B. glandula* on *N. granulata* in these salt marshes and we describe the major ecological features of this invader/native association in order to generate sound baseline for further investigations and management decisions. Our results show that barnacles are found in the entire dorsal and lateral surface of the crabs, and specially in vital zones such as the basal insertion of the chelipeds, walking appendages, ocular peduncles, jaws, mouth with the carapace. Furthermore, the size reached by barnacles suggest that they are sexually mature and can reproduce while fouling on the crabs, being the maximum size of barnacles tightly associated and determined by the duration of the crab's inter-molt span. Our results highlight the mechanisms by which an invasive rocky shore invader can exploit an unfavorable environment (i.e. mobile substratum) to persist on soft bottom systems.

Key words: Invasive species, fouling, *Balanus glandula*, *Neohelice granulata*, salt marshes.

RESUMEN

Neohelice (Chasmagnathus) granulata es un ingeniero de ecosistemas endémico de las marismas y planicies barrosas de la costa atlántica sud-occidental, donde varias marismas patagónicas han sido invadidas por el cirripedio *Balanus glandula*, una especie típica de intermareales rocosos. En este trabajo, se proporciona el primer reporte de la ocurrencia de epibiosis de *B. glandula* sobre *N. granulata* en estas marismas y se describen las principales características ecológicas de esta asociación invasor/nativo con el objetivo de generar información de línea de base adecuada para investigaciones futuras y la toma de decisiones de manejo. Nuestros resultados muestran que los cirripedios se encuentran en la superficie dorsal y lateral de los cangrejos y, en especial, en zonas vitales como la inserción basal de los quelípedos, los apéndices caminadores, los pedúnculos oculares, las mandíbulas y la boca, con el caparazón. Además, el tamaño medio de los cirripedios sugiere que alcanzan la madurez sexual y son capaces de reproducirse mientras se encuentran adheridos a los cangrejos. Por otra parte, el tamaño máximo de los cirripedios se encuentra fuertemente asociado y determinado por la duración del intervalo entre-mudas de los cangrejos. Así, nuestros resultados ponen de manifiesto los mecanismos por los cuales un invasor de intermareales rocosos es capaz de explotar un entorno desfavorable (es decir, sustratos móviles) para persistir en intermareales de fondos blandos.

Palabras clave: Especies invasoras, epibiosis, *Balanus glandula*, *Neohelice granulata*, marismas.

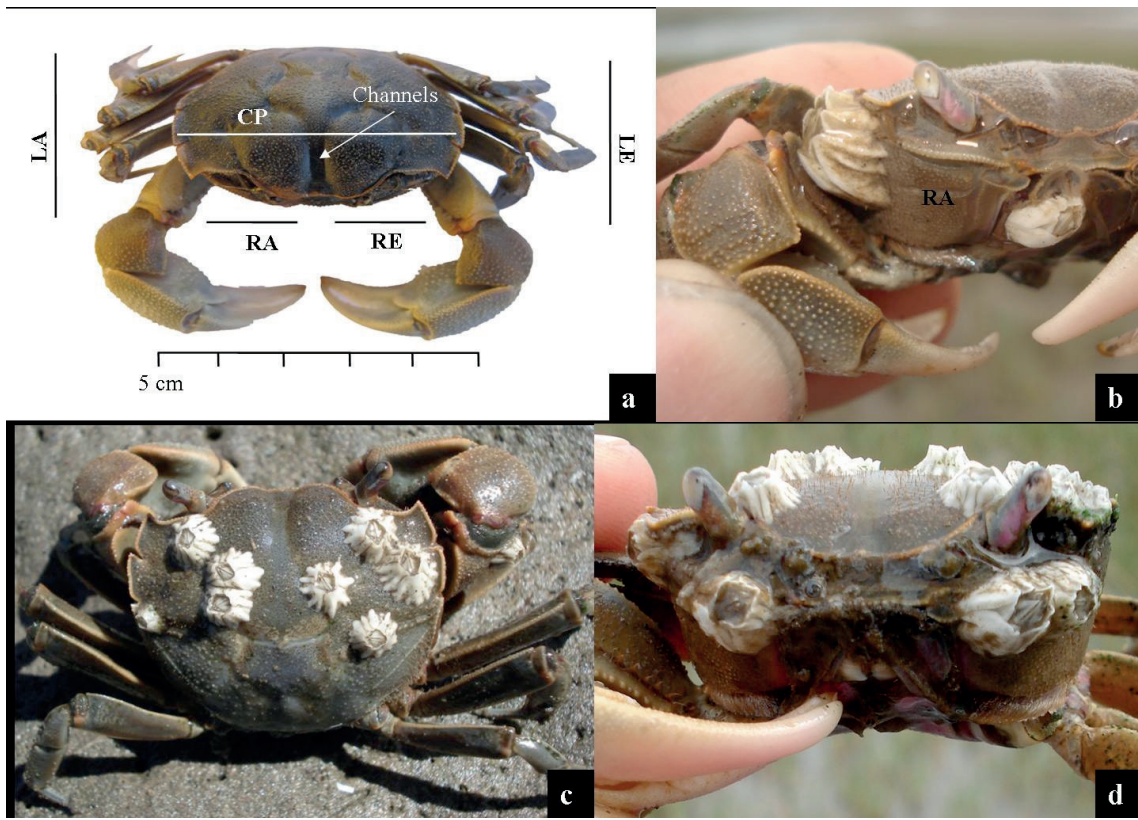


Figure 1:

a: Photograph of *Neohelice granulata* showing the attachment sites examined for epibionts (photo: M. C. Sueiro). b-d: Photographs of *Neohelice granulata* fouled by *Balanus glandula* showing barnacles attached to vital sites (photos: A. Bortolus). LA: left appendices zone, RA: right appendices zone, LE: left eye zone, RE: right eye zone and CP: carapace.

INTRODUCTION

In temperate regions around the world, estuarine and protected coastal areas are often characterized by the presence of salt marshes and mudflats. *Neohelice (Chasmagnathus) granulata* (Dana 1851) is a semi terrestrial burrowing crab endemic of the southwestern Atlantic coast, distributed from Río de Janeiro, Brazil to Central Patagonia in Argentina (Boschi, 1964; Sakai *et al.*, 2006; Spivak, 2010). Marine burrowing macrofauna are excellent examples of ecosystem engineer species, causing physical state changes in abiotic materials deriving in a marked influence on the associated communities (Jones *et al.*, 1994). Furthermore, the role of *N. granulata* as a key ecosystem engineer in salt marshes includes the alteration of most edaphic conditions through its burrowing activities, and the associated deposit-feeder behavior (Iribarne *et al.*, 1997; Bortolus & Iribarne, 1999; Escapa *et al.*, 2008). Several studies have shown that bioturbation by *N. granulata* leads to profound changes in the structure, quality and dynamic of sediments with concomitant impacts on the native flora and fauna (Iribarne *et al.*, 1997; Botto & Iribarne, 1999; Bortolus *et al.*, 2002). For

instance, the presence of crabs affect *Spartina* production and biomass by decreasing leaf survival through herbivory (Bortolus & Iribarne, 1999; Costa *et al.*, 2003), increase the abundance and richness of faunal communities through changes on grain size and water content (Iribarne *et al.*, 1997; Botto & Iribarne, 1999), facilitate fish predation on benthic fauna through changes on prey quality and sediment softness (Martinetto *et al.*, 2005) and modify the habitat use of birds through changes on prey availability (Iribarne *et al.*, 2005; Suárez *et al.*, 2012). Indeed, the combination of its ecosystem engineer activity, its effect on the associated benthic communities, and the large abundance of its populations, makes *N. granulata* a critical species for the conservation of intertidal environments in southern South America. Additionally, several Patagonian salt marshes were recently invaded by the acorn barnacle *Balanus glandula* Darwin, 1854 a typical rocky shore species native from the west coast of North America (Schwindt *et al.*, 2009; Mendez *et al.*, 2013). Surprisingly, this invasive barnacle not only colonizes the branches, roots and rhizomes of the salt marsh plants (Schwindt *et al.*, 2009; Mendez *et al.*, 2013) but also it has been observed fouling the endemic *N. granulata* (Alda *et al.*, 2011).

In marine environments, any exposed solid surface is likely to be colonized by benthic organisms or fouled (Wahl, 1989). Fouling may affect numerous species which are able to tolerate a certain degree of epibiosis (Wahl, 1989). Basibiont (substrata organism) and epibiont species (organisms growing attached) live in close spatial association often for the entire lifespan of at least one of the organisms (Wahl, 1989; Wahl, 2008). In densely populated marine environments, competition for space is critical (Connell, 1961; Jackson, 1977), thus the advantage of colonizing new surfaces is probably the major benefit of fouling. Specifically, the hard calcified body surfaces of crustaceans are suitable settling sites for sessile organisms (Connell & Keough, 1985) and barnacles are among the most common fouling organisms (Christie & Dalley, 1987). Such association occurs, for instance, between the blue crab *Callinectes sapidus* fouled by several species of *Balanus* and *Chelonibia patula* (Key *et al.*, 1997), between *Amphibalanus amphitrite* and the horseshoe crab *Tachypleus gigas* (Patil & Anil, 2000) and also between *A. amphitrite* and the shrimps *Penaeus setiferus* (Dawson, 1957) and *Sicyonia dorsalis* (Eldred, 1962).

In southern South America, the barnacle *Notobalanus flosculus* is a frequent epibiont on the carapaces of the false king crab *Paralomis granulosa* and the king crab *Lithodes santolla* and it is occasionally found on the brachyurans *Eurypodius latreillei* and *Peltarion spinosulum* (Calcagno & Lovrich, 2000). Epibiosis of invasive/cryptogenic species on native crabs occurs for instance in *Amphibalanus amphitrite* and *A. improvisus* fouling on *Cyrtograpsus angulatus*, *Platyxanthus crenulatus* and *Libinia spinosa* (Spivak, 2005; Alda *et al.*, 2011). However, these cases of epibiosis of invasive species on native ones are only personal observations or casual mentions devoid of a detailed description (Spivak, 2005; Alda *et al.*, 2011). Given the ecological and preponderant role of *Neohelice granulata* on southwestern Atlantic (Iribarne *et al.*, 1997; Botto & Iribarne, 1999; Bortolus *et al.*, 2002; Spivak, 2010), the potential negative effects that epibiosis might have on this specie deserves thorough attention. For instance, depending on the location of barnacles on crabs, feeding activities could be negatively affected as well as their defence mechanisms. If the epibiosis advances, these interactions could alter the patterns of distribution and abundance of burrowing crabs, triggering profound changes in the ecosystem. The objective of this work is supply the first detailed report of the occurrence of epibiosis of *B. glandula* on *N. granulata* in Patagonian salt marshes, as well as to describe the major ecological features of this invader/native association.

MATERIALS AND METHODS

Study Site

The study was conducted in Loros marsh at the natural reserve “Caleta de los Loros” (hereafter as Loros, 40° 46' S, 64° 50' W; Río Negro, Argentina; Bortolus *et al.*, 2009) which was one of the first salt marshes being invaded by *Balanus glandula* in this region (Schwindt *et al.*, 2009). Loros have an extension of approximately 1548 ha and the landscape is characterized by mudflats in the lower intertidal, salt marsh vegetation dominated by *Spartina alterniflora* (Bortolus *et al.*, 2009), and extensive sand dune fields forming the transition with terrestrial systems. The crab *Neohelice granulata* is the more abundant and characteristic macroinvertebrate in the system and its burrow fields areas, commonly called “cangrejales” (from the Spanish for crab: “cangrejo”), are found throughout the intertidal. Density of *N. granulata* in southern South America salt marshes varies between 20 to 120 ind/m², being the mean density of 60 ind/m² (Iribarne *et al.*, 1997; Bortolus & Iribarne, 1999; Bortolus *et al.*, 2002; Bas *et al.*, 2005; Escapa *et al.*, 2008). The proportion of sexes of the species is balanced (Spivak *et al.*, 1996). The invasive acorn barnacle *B. glandula* is found attached to a variety of substrata like branches and superficial rhizomes and roots of salt marshes plants, rest of organic materials, living mussels, gravels and trash (Schwindt *et al.*, 2009; Mendez *et al.*, 2013).

Sampling design and statistical analysis

In order to describe the epibiosis of the invasive barnacle *Balanus glandula* on the endemic crab *Neohelice granulata*, fouled crabs were collected by hand at random, during the summer season (January) of 2010 and 2011. Since the performance of an exhaustive sampling of the entire marsh was logistically impossible due to its dimensions, we focused on sampling only fouled crabs in order to make a sound first approach of this invader/endemic association and supply reliable baseline information for further investigations and management decisions. To do this, two people walked in a random direction during periods of 4-5 hours, picking up all fouled crabs in their way (approximately 1 m wide path). The total area covered by the people walking was 2 hectares each year. With this sampling effort, we achieve an appropriate sample size according to the aims of this work and following the standards used by Davis & White (1994), Buschbaum & Saier (2001), Bers & Wahl (2004) and Alda *et al.* (2011). Crabs were carefully transported in plastic bags with ice to the laboratory, where they were stored in 70% ethanol. Taxonomic identifications were made following Newman & Ross (1976) for *B. glandula* and

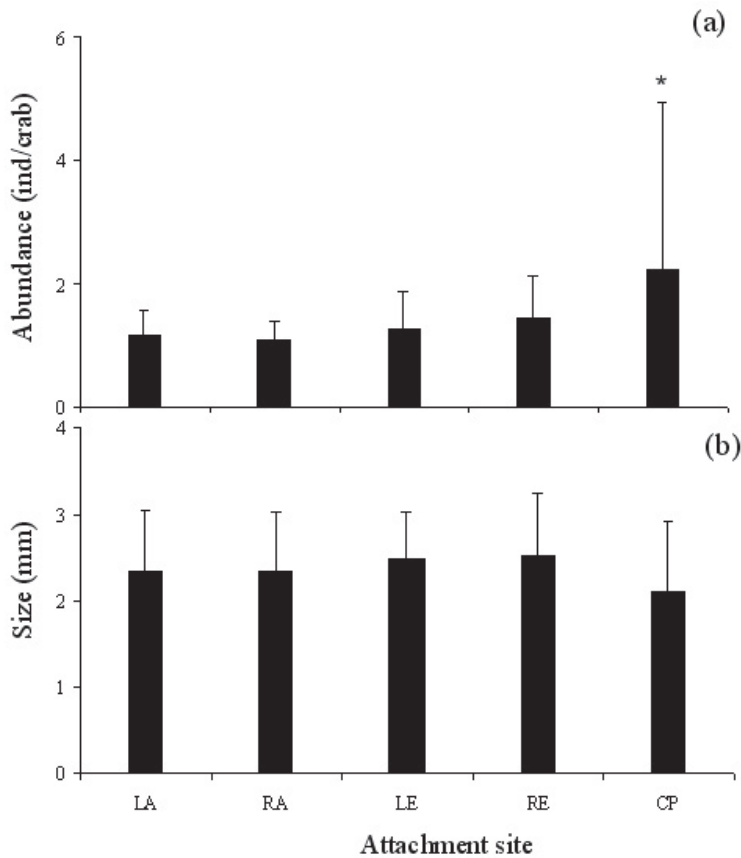


Figure 2:

(a) Mean abundance and (b) mean size (in mm, + SD) of *Balanus glandula* fouling on the different attachment sites provided by crabs. LA: left appendices zone, RA: right appendices zone, LE: left eye zone, RE: right eye zone and CP: carapace. * above bars indicate significant differences among attachment sites.

Boschi (1992) for *N. granulata*. Vouchers of the identified species were stored at the Invertebrate collection of the CENPAT. In the laboratory, each crab was sexed based on the shape of the abdomen (Boschi, 1992) and the number of barnacles attached was registered. Size was obtained with a digital caliper (precision ± 0.01) by measuring carapace length and width for crabs and the orifice length along the carinal and rostral plates for barnacles. Crabs were visually inspected and the attachments sites (Figure 1a) of the epibionts were registered. The attachment sites considered were the carapace (hereafter CP), the left and right appendices zone (hereafter LA and RA, respectively) and the left and right eye zone (hereafter LE and RE, respectively), these last ones were delimited by the proximity to two critical zones: appendices insertion and ocular peduncle, respectively. In addition, the abundance, as the number of barnacles per crab, and barnacle size frequency distribution were calculated. Abundance and size of barnacles were compared between sexes with a t-test and among attachments sites using ANOVA tests or the nonparametric Kruskal–Wallis test when variances were heterogeneous and could not be stabilized after

proper transformations (Zar, 1999). Significant results were analyzed a posteriori with the Scheffé test after the ANOVA or with multiple comparisons of mean ranks after Kruskal–Wallis test (Zar, 1999).

RESULTS AND DISCUSSION

Of the total *Neohelice granulata* (n total = 69) fouled by *Balanus glandula*, 80% were males and 20% females. Considering local crab density and sampling effort, a conservative estimation shows that one fouled crab is found every 5.8 m². This means that the entire marsh contains more than 2.5 millions of fouled crabs. Additionally, the proportion of sexes observed suggests that barnacle settlement on male crabs occurs more frequently, possibly due to the fact that the species often exhibit sexual dimorphism in size and male reach bigger sizes than females (Spivak *et al.*, 1996). All the crabs collected were adults (minimum carapace width 23.12 mm; López Greco & Rodríguez, 1999), and no significant difference was found between sexes neither for abundance nor for mean size of epifaunal barnacles

($t_{abundance} = -0.65$, $df = 67$, $p > 0.05$, $t_{size} = -0.32$, $df = 192$, $p > 0.05$). The totality of the epibionts was observed on the dorsal and lateral surfaces of the crab, suggesting that the ventral surface is not suitable for barnacle recruitment and/or survival. The dorsal surface is relatively more available to larvae than the ventral surface, which experience constant abrasion when crabs walk along the substrate, or while digging to maintain their burrows clean. Recruits (i.e. individuals larger than 0.15 mm in rostral carinal length) of *B. glandula* were observed in all five attachment sites studied. The average number of barnacles per crab was 2.8 (SD = 3.37). This number was similar to the one reported for other epibiotic association, for instance between the blue crab *Callinectes sapidus* and the barnacle *Chelonibia patula* (Key *et al.*, 1997). The abundance of barnacles was higher in the carapace than in the rest of the attachment sites (Kruskal–Wallis test: $H = 44.79$, $p < 0.001$, post hoc test: $LA = RA = LE = RE > CP$. Figure 2a). This difference is likely to be a consequence of the different relative availability of surface among sites rather than an active selection of them. Moreover, since the invasion of barnacles in the marshes is a recent phenomenon (Schwindt *et al.*, 2009), colonization of crabs could increase in the near future together with the expansion of barnacles; thus the potential effects on the crab population could become more important.

The potential effects generated by epibionts can be symmetric, asymmetric, beneficial, detrimental or a combination (reviewed in Wahl, 1989; Hay *et al.*, 2004) and they usually depends on the couple of the species associated (Wahl, 1989; Wahl, 2008). For the species involved in this work, it is expected that the additional weight supplied by fouling barnacles negatively affects the movement of fouled appendages. This would make the crab less suitable for mating and more vulnerable to physiological stress (including starvation and dehydration) and predation (including cannibalism which is common among individuals of this species). *Neohelice granulata* face an intense predation pressure from fishes and several birds, both with high developed sense of sight (Delhey *et al.*, 2001; Molina & López Cazorla, 2011; Suárez *et al.*, 2012). In this sense, the elevated contrast of colors derived from the presence of white barnacles growing over brown crabs that walk on dark substrate, might alert potential predators. This crab species is the main prey of the Olrog's gull (*Larus atlanticus*, in Spanish "gaviota cangrejera") which feeds during the breeding season almost exclusively on crabs (Delhey *et al.*, 2001; Suárez *et al.*, 2012) being *Balanus glandula* the main prey during winter (Delhey *et al.*, 2001). Thus, epibiosis not only make the crab more vulnerable to predation due to the colour contrast but also increase preys offer to crab's predators.

Additional negative effects that barnacles could have on crabs are illustrated with the finding of epibionts near the insertion of chelipeds and all walking appendages, ocular peduncles, jaws and mouth (Figure 1 b-d). We observed in the field that crabs with barnacles growing at the base of the chelipeds were unable to reach their own mouth while trying to deposit-feed. Indeed, the settlement and growing of barnacles in the place where the appendages articulate with the main carapace is likely to cause that (a) chelipeds and legs will not perform adequately during walking, swimming, feeding, mating, antipredatory escaping or defensive activities, (b) pedunculate eyes will be unable to close enough to stay wet and clean, (c) the performance of most feeding activities is also likely to decrease when half of the mouth pieces are cemented together by barnacles, (d) digging behavior (a major ecological feature for this crab species) is likely to fail too when chelipeds and legs are not working properly and (e) survival to semi-terrestrial conditions during low tides will be reduced when barnacles modify the shape of the web of channels distributed along and across the carapace (Figure 1a) and used to oxygenate the respiratory water circulating from and to the branchial chamber (Santos *et al.*, 1987). Only by performing carefully designed lab and field experiments with exclusion-inclusion caging, tethering and/or other manipulative methods will reveal the total and partial impacts that barnacles have on crab populations.

The mean size of barnacles was slightly statistically different among attachment sites ($F = 2.46$, $df = 4$, $p = 0.047$, Figure 2b), nevertheless, the *a posteriori* Scheffé test did not show statistical differences ($p > 0.05$). Barnacles settled on the carapace showed a large variation in sizes with a mean size lower than the other settlement sites, where barnacles were mostly represented by large individuals (Figure 2b). Furthermore, unlike previous reports showed for natural populations established in rocky shores or marshes, the size frequency distribution of *Balanus glandula* was unimodal (Figure 3). The range of sizes was from 0.4 to 4.83 mm and no dead (i.e. empty) barnacles were found. Barnacles between 2 and 2.5 mm were the most abundant and only 10% of epibionts were larger than 3.2 mm. Given the capacity of *B. glandula* to recruit throughout the year along the entire Argentine coast (Schwindt, 2007; Savoya & Schwindt, 2010) and the characteristics and searching behavior of the larvae of this species, the colonization of crabs is expected to occur throughout the year. The fact that the majority of barnacles recruited on crabs are nearly half the size of most barnacles living in nearby rocky shores and salt marshes (Schwindt *et al.*, 2009; Savoya & Schwindt, 2010) suggests the existence of a limiting factor that decrease their survival before they reach maximum size.

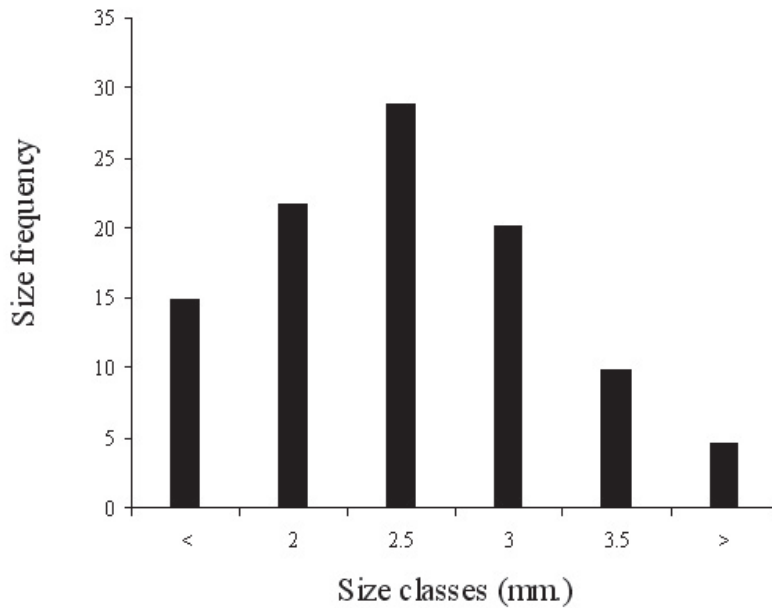


Figure 3:
Size frequency distributions of barnacles per class size (in mm) fouling on crabs.

It is known that in Crustacean, growth and physiological development are achieved by molting repeatedly. In adult individuals of *N. granulata*, both males and females commonly molt at the beginning of the non reproductive season (i.e., April and May; López Greco & Rodríguez, 1999). The inter-molt period might provide the best time window for a successful colonization of crabs and barnacles settled after crabs molting could reach the biggest sizes. In this sense, recent experimental work focused on the recruitment of *B. glandula* on a Patagonian invaded rocky shores, showed that barnacles reach a mean orifice size of up to 3.21 mm in 1 year (Savoya & Schwindt, 2010). Assuming a similar growth rate in salt marshes, our results suggest that the maximum size reached by fouling barnacles is tightly associated and determined by the duration of the inter-molt span during the non-reproductive season. However, given that *B. glandula* sexually matures at age of six months (Hines, 1978), most barnacles fouling on crabs are likely to reproduce during this period unless they are isolated from potential mates.

Although epibionts may compete with their host for food resources (Wahl, 1989), this does not seem likely to be happening between *Neohelice granulata* and *Balanus glandula*, since the former is a generalist species that shifts from deposit feeder habits in mud flats to active herbivore in the *Spartina*-dominated areas (Iribarne *et al.*, 1997; Bortolus & Iribarne, 1999) whereas the barnacles

are strict planktivore filter feeders (Marchinko, 2007). In a similar vein, the semi-terrestrial habit of *N. granulata* does not seem to affect *B. glandula*, typically abundant in the highest part of the intertidal as a result of its high tolerance to dehydration and heat stress (Schwindt, 2007). Due to the intense competition for space in intertidal environments (Connell, 1961; Jackson, 1977), recruitment on living substrata may be beneficial to epibionts. Since barnacles are exposed to intense substrate competition (Connell, 1961), the epibiosis on crabs has been suggested to evolved in response to this force (Foster, 1987). Besides, the epibiotic relationship may have potential benefits for barnacles, since their reproductive success relied on the proximity of the mating individuals (Wahl, 1989). Thereby, crabs not only provide a suitable substratum for mating to happen in a suboptimal environment; they literally might turn themselves into walking larvae pumps across the marsh. Indeed, every fouled crab can be seen as a motile vector speeding *B. glandula* regional invasion by assisting the dispersion of their larvae.

Balanus glandula is currently expanding its distributional range worldwide, colonizing at least three continents. Firstly was reported colonizing the Argentinean coast (Spivak and L’Hoste, 1976) and nowadays it is also registered successfully established on rocky shores of the west coast of Japan (Kado, 2003) and south of South Africa (Simon-Blecher *et al.*, 2008). The results found in the present work highlight the elevated

plasticity shown by this invasive species to persist in this new habitat, and the broad potential effects that its introduction could have on the native fauna. Despite the fact that the number of barnacles per crab is relatively low and taking into account that the invasion of barnacles in the marshes is a recent phenomenon, the results have to be considered as an initial state of the epibiotic relationship. Temporal and spatial monitoring becomes critical, making the system an excellent case to study the advancement of an invader/endemic association and the potential derived effects. From the ecological and evolutionary perspectives, it is striking how this invasive rocky shore invader can exploit a non optimal environment (i.e. mobile substrata on soft bottom systems). This kind of evidence should be seriously considered in environmental managing strategies where designing early detection plans to prevent biological invasions is a priority.

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