



Non-native barnacle accelerates the recovery from disturbance of intertidal mussel beds

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ABSTRACT: The barnacle *Balanus glandula* is a non-native species inhabiting Argentinian rocky shores. The native mussel *Brachidontes rodriguezii* forms extensive beds in the mid-intertidal zone of these shores, generating a physical structure that determines the diversity of the assemblage. Yet, this native foundation species is prone to mortality due to disturbances associated with extreme climatic events. The aim of this study was to experimentally investigate the role of early-colonizing, non-native *B. glandula* in the succession process and the recovery of mussel beds following disturbance. Experimental plots were demarcated in the mussel bed and initially cleared of mussels, to produce exposed rock surfaces similar to those that form after a disturbance event. Half of these plots were kept barnacle-free throughout the experiment by removing all recruiting *B. glandula*, whereas all recruits were allowed to develop in the remaining plots. Our results showed that mussel cover at the end of the experiment was higher in the plots with barnacles. The plots with and without barnacles followed different successional trajectories, with increasing limpet densities and reduced cover of crustose algae in the presence of barnacles during early successional stages. The results indicate that the presence of *B. glandula* at the early stages of succession can alter successional dynamics and facilitate the recovery of mussel bed cover after disturbance events. More broadly, this study also shows that non-native species, although frequently considered a 'nuisance', can accelerate the recovery of foundation species that characterize entire communities and sustain the greatest share of their diversity.

KEY WORDS: *Balanus glandula* · *Brachidontes rodriguezii* · Non-native species · Facilitation · Foundation species · Succession

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1. INTRODUCTION

The biodiversity and functioning of many ecosystems are often under the control of foundation species, i.e. a species or group of functionally similar taxa that dominates an assemblage numerically and in overall size, and controls community diversity pri-

marily via non-trophic interactions (e.g. trees in forests, seagrass in seagrass meadows, hermatypic corals in coral reefs; Ellison 2019, see also Dayton 1971). Anthropogenic disturbances to foundation species (e.g. exploitation, physical disruption, climate-related impacts) are major sources of biodiversity loss and ecosystem degradation under current global

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change (Ellison et al. 2005, Alongi 2008, Waycott et al. 2009, Smale et al. 2022, Wernberg et al. 2024), and the recovery of foundation species from such disturbances can be slow or even impossible (e.g. O'Brien & Scheibling 2018, Viehman et al. 2018, Hall et al. 2021). Foundation species recovery depends on the ecological interactions that take place during the secondary succession process – i.e. the sequential replacement of species following a disturbance (Prach & Walker 2011). These interactions can be trophic (e.g. grazing, predation) or structure-mediated (i.e. physical ecosystem engineering: sensu Jones et al. 1994) and can range from inhibitory effects that slow down or prevent foundation species recovery, to facilitative effects that enhance their establishment and recovery rates (e.g. Lubchenco 1983, Bertness 1991, Davidson 1993).

The deliberate or accidental introduction of non-native species can lead to novel ecological interactions during secondary succession processes, and concomitantly affect foundation species recovery rates (e.g. Bando 2006, Biswas et al. 2012). Many non-native species are, indeed, aggressive colonizers of disturbed areas, whose interactions with native species and the physical environment alter successional trajectories and typically slow down or even stall the successional process (see Meiners & Pickett 2011). For example, shade-tolerant invasive shrubs colonizing disturbed forests inhibit tree regeneration by harboring high densities of seed predators and by resource (primarily light) competition (Gorchov & Trisel 2003, Meiners 2007). Moreover, densely growing, invasive floating macrophytes in disturbed mangrove forests block the transport of floating mangrove propagules from channels to forest interiors, thus reducing forest regeneration rates (Biswas et al. 2012). On the other hand, examples of invasive species that accelerate secondary succession processes mediating the recovery of foundation species are rare at best, even when non-native species are well known to facilitate native ones (see Crooks 2002, Rodriguez 2006 for reviews).

Several mussel species are well known foundation species in the intertidal zone of temperate rocky shores across 5 continents (Suchanek 1985, Gutiérrez et al. 2003, 2022). The dense beds they form provide attachment surfaces, sediments, and protected interstitial spaces to a variety of other organisms (Gutiérrez et al. 2003, 2011), thereby supporting rich species assemblages (including many species that would not otherwise occur in the rocky intertidal zone; see Suchanek 1985, Tokeshi & Romero 1995, Borthagaray & Carranza 2007, Bagur et al. 2016).

However, intertidal mussel beds are affected by various forms of anthropogenic disturbance, including harvesting, trampling, and anthropogenically enhanced increases in the frequency and intensity of storms and extreme temperature events (both heat waves and cold spells) (e.g. Tsuchiya 1983, Donker et al. 2015, Micheli et al. 2016, Mendez et al. 2018, Cameron & Scrosati 2023). These disturbances reduce mussel cover to varying degrees, sometimes leading to local mussel disappearance (e.g. Tsuchiya 1983, Cameron & Scrosati 2023). Yet, even when disturbance-induced mortality is patchy and remnants of the mussel bed persist, recolonization of the exposed rock surfaces is usually quite slow (e.g. 5 yr; see Micheli et al. 2016). Mussel recolonization rates can, however, be enhanced if exposed rock surfaces are previously colonized by other sessile organisms such as barnacles, which increase surface rugosity, thus providing potentially suitable microhabitats for mussel recruitment, attachment, and survival (Menge 1976, Lively & Raimondi 1987, Petraitis 1990, Hunt & Scheibling 1996).

The mussel *Brachidontes rodriguezii* is a foundation species that characterizes rocky shores on the northern Argentinean coast (37° to 41° S; Arribas et al. 2013, Trovant et al. 2013). This relatively small mytilid (up to 55 mm length, most individuals <30 mm length) forms dense and primarily single-layered beds (up to 2000 ind. dm⁻²; Penchaszadeh et al. 2007, Arribas et al. 2015, Gutiérrez et al. 2015) that support rich species assemblages (including many species that would not otherwise occur in the rocky intertidal zone; Penchaszadeh et al. 2007, Arribas et al. 2013, Gutiérrez et al. 2019, Soria et al. 2022). Whilst these beds can cover up to 90% of the rocky substrate in the mid-intertidal zone, they are commonly interspersed by a larger proportional cover of gaps (see Soria et al. 2022). These gaps portray different stages of the secondary succession process and typically form after patchy mussel dislodgment due to strong wave action as well as patchy mortality and concomitant dislodgment due to extreme temperatures and desiccation at low tide (Gutiérrez et al. 2015, 2023).

Non-native acorn barnacles *Balanus glandula* are important early colonists of gaps, together with the native pulmonate limpets *Siphonaria lessonii* and crustose algae (Soria et al. 2022, 2023). These barnacles, which are native to the west coast of North America, were first detected in Argentina in the 1970s (port of Mar del Plata: 38° 01' S, 57° 31' W; Bastida et al. 1980), and are now widespread all across the Argentinian coastline (36° to 54° S;

Schwindt 2007), including the northern rocky intertidal shores dominated by *B. rodriguezii* (37° to 41° S; see previous paragraph). Considering (1) the ability of these barnacles to colonize the relatively flat rock surfaces that become exposed after the formation of gaps in mussel beds (Vallarino & Elías 1997, Soria et al. 2023), (2) the lack of native barnacle species (or other species that contribute to surface rugosity in a similar fashion) in these mussel-dominated shores (Penchaszadeh et al. 2007), and (3) the known role of surface roughness elements — and barnacles in particular — in facilitating mussel colonization (e.g. Dayton 1971, Petraitis 1990, Köhler et al. 1999, Erlandsson & McQuaid 2004, Menge et al. 2011), here we predicted that non-native *B. glandula* facilitates gap recolonization by *B. rodriguezii* and that this novel interaction accelerates the recovery of mussel coverage. Additionally, as *B. glandula* is known to positively affect densities of the pulmonate limpet *S. lessonii* (Hesketh & Harley 2023), and these limpets are early gap colonists and dominant grazers in our study system (indeed, they are the only grazing gastropod species in these shores; Penchaszadeh et al. 2007, Soria et al. 2022, 2023), we predicted that non-native barnacles affect overall successional trajectories in gaps by exacerbating the grazing impacts of limpets.

In this study, we investigated the effect of the non-native barnacle *B. glandula* on the recovery of mussel cover and secondary succession trajectories in experimentally disturbed plots where barnacles were allowed and not allowed to recruit. Specifically, we examined the effects of barnacles on the proportional recovery of mussels (i.e. relative to the pre-experimental 100% cover status) and the identity and abundance of benthic taxa over the succession process during 542 d.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted at Playa Grande (38° 01' 31.1" S, 57° 31' 45.6" W), an intertidal rocky shore in Mar del Plata, Buenos Aires province, Argentina. This site is about 1 km distant from the port of Mar del Plata (the site where *Balanus glandula* was first detected in Argentina; Bastida et al. 1980). Playa Grande is characterized by hard, orthoquartzite platforms, which form relatively continuous horizontal surfaces (Gutiérrez et al. 2018). The shore at this site

faces southeast, which is the direction of the strongest swells (Fiore et al. 2009), and can be classified as 'exposed' according to the MarLin wave exposure categories (i.e. an open coast facing away from prevailing winds but with a long fetch, and where strong winds are frequent; see <https://www.marlin.ac.uk/glossarydefinition/waveexposure>). Tides along this area are semidiurnal and microtidal (0.83 m mean amplitude; Servicio de Hidrografía Naval, www.hidro.gov.ar).

2.2. Field experiment

A succession experiment was conducted from October 2015 to May 2017 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m732p073_supp.pdf). Twelve 25 × 25 cm square plots spaced at least 3 m apart were randomly demarcated on horizontal surfaces in the mid-intertidal zone of a ~40 m long platform, and the mussel layer in these plots was removed with the aid of a putty knife to simulate the gaps formed due to natural disturbances (typically ranging between 4 and 3500 cm², most of them <1500 cm²; Soria et al. 2022). Mussels were deliberately removed in October, as we have previously observed barnacle recruitment in spring at this site (see also Vallarino & Elías 1997). Barnacles recruited in all of these plots after 28 d (i.e. 11 November 2015; mean = 96 ind. dm⁻², SD = 37; see also Fig. S1). In 6 of these experimental plots, all *B. glandula* recruits were removed with the aid of a putty knife leaving no barnacle residues adhered to the rock, and these plots were kept barnacle-free throughout the experiment (Fig. S1, hereafter 'No barnacles' treatment). In the other 6 plots, all *B. glandula* recruits were allowed to develop (Fig. S1, hereafter 'Barnacles' treatment). Of note, *B. glandula* recruitment was minimal during the rest of the experiment (see Broitman et al. 2008 for examples of annual recruitment failure in *B. glandula*).

The experimental plots were monitored on a nearly monthly basis (see Table S1). On each visit, barnacles were removed from the 'No barnacles' treatment plots (see Fig. S1), whereas the percent cover of sessile species (mussels, barnacles, algae) and the densities of limpets (5 × 5 cm subsample) were quantified in each plot. The percent cover of sessile species was quantified using the point-intersection counting method (5 × 5 cm grid and 36 total points including edge; see Soria et al. 2023), whereas limpet densities were calculated as the number of individuals per 25 cm².

2.3. Data analyses

Generalized linear models with generalized estimation equations (GEEs; Zuur et al. 2009) were used to analyze variation in mussel cover and the abundance of other dominant species or groups (crustose algae, macroalgae, and pulmonate limpets *Siphonaria lessonii*; see Section 3) between Treatments (fixed effect) over Time (within subjects, repeated measure). A binomial distribution was used for the analyses of the percent cover of mussels, crustose algae, and macroalgae and a Poisson distribution for the analysis of *S. lessonii* densities. Several models with different correlation matrices (i.e. autoregressive, exchangeable, and independent) were compared using the quasi-probability information criterion (QIC) to identify the appropriate correlation structure for the model that used each response variable. According to QIC, an unstructured correlation matrix was the appropriate correlation structure for the percent cover of mussels and macroalgae and the density of limpets, whereas an independent matrix was the appropriate correlation structure for the percent cover of crustose algae. All GEEs were performed with the 'geepack' package in R (Halekoh et al. 2006, R Core Team 2020). *p*-values < 0.05 were considered significant in these and subsequent statistical tests.

The effects of barnacles on the identity and relative abundance of benthic groups or taxa (i.e. the abundance of groups or taxa as a proportion of a total assemblage) along the successional process were evaluated with multivariate methods. Differences in assemblage structure were evaluated using permutational multivariate analysis of variance (PERMANOVA) with Treatments (No barnacles, Barnacles) and Time (i.e. sampling dates) as fixed factors and Replicates (nested within Treatment) as a random factor to account for the temporal non-independence of the data. Successional trajectories of assemblage structure were visually represented with non-metric multidimensional scaling (nMDS) using Bray-Curtis distance as the dissimilarity index with PRIMER 6.0 (Clarke 1993). Percent cover and density data were standardized to unify units using a standardization based on the range within a variable (Quinn & Keough 2002). To achieve this, each observation was divided by the maximum value of its variable, so that each observation was expressed as a proportion of the largest value for its variable (see Quinn & Keough 2002, Soria et al. 2023). Pairwise PERMANOVA tests were performed *a posteriori* to analyze significant differences among factor levels, and an analysis of similarity percentages (SIMPER) was then conducted to

identify the taxa that contributed the most to the differences in the relative abundance between treatments with PRIMER 6.0 (Clarke 1993).

3. RESULTS

Mussel cover was higher in the 'Barnacles' plots than in the 'No-barnacles' plots and did not follow the same pattern over time (i.e. the interaction between Treatment and Time was significant, Table 1, Fig. 1). Maximum percent cover of mussels was observed 440 d after the beginning of the experiment (summer), with $79.17 \pm 8\%$ (mean \pm SD) in the 'Barnacles' plots and $59.26 \pm 13.57\%$ in the 'No barnacles' plots (Fig. 1).

The identity of species in the plots did not diverge between treatments over time (Table 2, Fig. 2). On the other hand, the relative abundance of species establishing into the plots during the successional process was affected by the presence of *Balanus glandula* (Table 2, Fig. 2). During early successional stages, the data points occupied a similar location in the multivariate space regardless of the presence of *B. glandula*, but after the third month, successional trajectories progressively diverged for plots with and without *B. glandula*. Differences in the relative abundance of species in the assemblage between both treatments were observed from Days 97 to 383 (i.e.

Table 1. Analysis of the Wald statistic for generalized linear models with generalized estimation equations relating mussel cover, *Siphonaria lessonii* density, crustose algae cover, and macroalgae cover between Treatments ('Barnacles' and 'No barnacles') and Time. Asterisks indicate significant effects ($p < 0.05$)

Variable	χ^2	df	p
Mussel cover			
Treatments	8.2	1	<0.001*
Time	55.3	1	<0.001*
Treatments \times Time	22.3	1	<0.001*
<i>Siphonaria lessonii</i> density			
Treatments	27.4	1	<0.001*
Time	35.8	1	<0.001*
Treatments \times Time	1.2	1	0.28
Crustose algae cover			
Treatments	77.2	1	<0.001*
Time	48.1	1	<0.001*
Treatments \times Time	0	1	0.86
Macroalgae cover			
Treatments	0.032	1	0.86
Time	2.229	1	0.14
Treatments \times Time	0.029	1	0.86

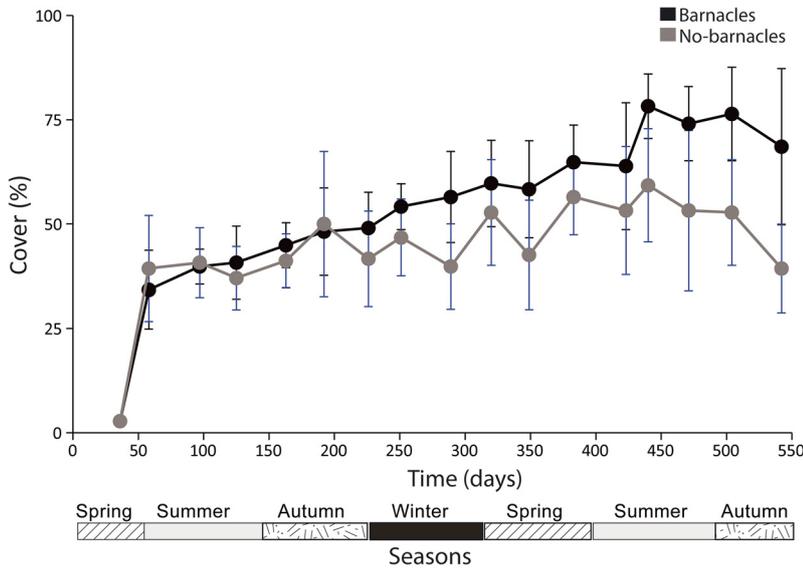


Fig. 1. Percent cover of the mussel *Brachidontes rodriguezii* through time in the 'Barnacles' (black) and 'No barnacles' (grey) experimental plots ($n = 6$). Error bars indicate standard deviation

Table 2. Two-way PERMANOVA testing the fixed effect of Treatment ('Barnacles' and 'No barnacles') and the random effect of Time (replica nested in treatment) on the relative abundance and identity of benthic groups or taxa. MS: mean squares; Pseudo- F : PERMANOVA statistic; perms: number of permutations. Asterisks indicate significant effects ($p < 0.05$)

Source	df	MS	Pseudo- F	perms	p(perm)
Abundance					
Treatments	1	22000	9.41	410	0.003*
Time	16	5775	14.05	996	0.001*
Replicate (Treatments)	10	2337	5.68	997	0.001*
Treatments:Time	16	831	2.02	998	0.001*
Residual	160	411			
Total	203				
Presence/absence					
Treatments	1	2985	2.9	462	0.057
Time	16	2226	13.3	992	0.001*
Replicate (Treatments)	10	998	5.9	994	0.001*
Treatments:Time	16	255	1.5	922	0.090
Residual	160	167			
Total	203				

late summer to late spring) and from Days 471 to 542 (i.e. late summer to autumn; pairwise PERMANOVA: $t > 1.48$, $p < 0.05$ in all of these cases; Fig. 2b). Limpets (*Siphonaria lessonii*) contributed most to differences between treatments from Days 97 to 192 (mid-summer to late autumn; SIMPER: 32–52% contribution to assemblage dissimilarity in all cases; Table S2). Crustose algae (*Ralfsia* sp.) contributed the most to differences between treatments in 2 periods (from Days 226 to 349 and 471 to 542, i.e. winter to spring and late summer to autumn, respectively;

SIMPER: 14–40% contribution to assemblage dissimilarity; Table S2). In addition, mussels also contributed to differences from Days 471 to 542 (late summer to autumn; SIMPER: 20–30% contribution to assemblage dissimilarity; Table S2).

The species that characterized the early- to mid-successional stages in this experiment were *S. lessonii* limpets and crustose algae (*Hildenbrandia* sp. and *Ralfsia* sp.). 'No barnacles' plots showed lower limpet densities and higher cover of crustose algae than 'Barnacles' plots, and both variables followed a similar pattern over time (non-significant interaction between time and treatment was observed, see Table 1, Fig. 3). The percent cover of macroalgae (see species in Table S3) in the 'Barnacles' and 'No barnacles' plots did not differ throughout the experiment (Table 1, Fig. 3).

4. DISCUSSION

Our findings indicate that the presence of *Balanus glandula* in experimentally exposed rock surfaces comparable to gaps affects the successional process and accelerates recovery of mussel cover. As many studies illustrate, sessile organisms such as barnacles can facilitate subsequent mussel establishment by increasing surface rugosity and providing potentially suitable microhabitats for recruitment, attachment, and survival (Menge 1976, Lively & Raimondi 1987, Petraitis 1990, Hunt & Scheibling 1996). A peculiarity of our study is that it illustrates that

similar facilitative effects on mussels can be mediated by non-native barnacles, even though they lack a shared evolutionary history. Due the lack of native barnacle species (or other species that contribute to surface rugosity in a similar fashion) in the northern Argentinean rocky shores dominated by the mussel *Brachidontes rodriguezii*, we posit that this novel facilitative interaction may have increased the capacity of this mussel foundation species to recover from disturbances and, ultimately, its overall resilience against various anthropogenic or anthropogenically en-

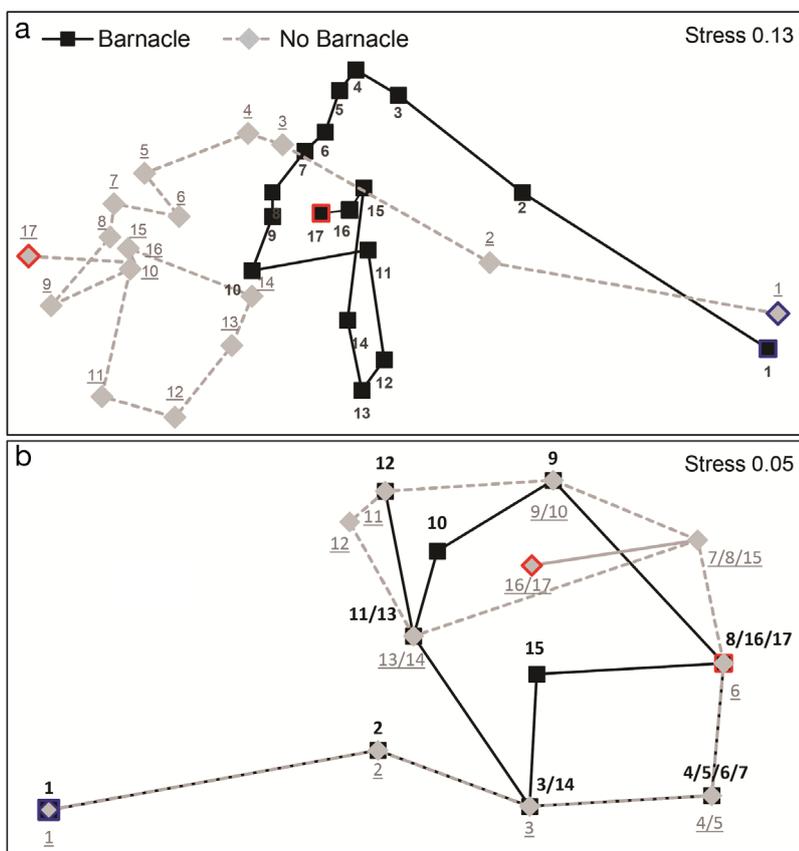


Fig. 2. Non-metric multidimensional scaling (nMDS) comparing temporal trajectories in (a) the relative abundance of species (after standardizing cover and count data) and (b) the identity of species between the 'Barnacles' and 'No barnacles' treatments. The numbers near data points indicate the order of the sampling dates (see Table S1 in the Supplement for detailed information on the precise number of days elapsed since the beginning of the experiment). Each point represents standardized abundances averaged across replicates ($n = 6$). The points with a blue and red edge indicate the first and last sampling date, respectively. The Bray-Curtis distance was used as a measure of dissimilarity in standardized abundances

hanced stressors that cause patchy mussel mortality (e.g. extreme climatic events such as heat waves or storms).

As for the mechanisms leading to the recovery of mussel cover in the experimental plots (not quantitatively addressed in this study), we observed that, even when mussels recruited into these plots, the recovery of mussel cover was primarily driven by the lateral expansion of the surrounding mussel bed (see also Penchaszadeh 1973, Soria et al. 2022 for further evidence of this in this study system). Mussel adults are known to move (e.g. in response to predators or crowding by neighbors; Nicastro et al. 2008, Garner & Litvaitis 2013, Brante et al. 2019). Mussel movement involves severing existing byssal threads and producing new ones with concomitant temporal reductions in

attachment strength (Garner & Litvaitis 2013, Brante et al. 2019). It seems plausible that barnacles aided the migration of adult mussels into the experimental plots by providing protected microhabitats and safer adhesion surfaces during the movement and reattachment phase, when they may be more vulnerable to hydrodynamic drag and dislodgment (see Nicastro et al. 2008, McQuaid et al. 2015).

Aside from its positive effects on recovery rates of mussel cover, the presence of non-native barnacles in early successional stages also alters the successional trajectories that follow the disturbance of mussel beds. Whilst the species recruiting in exposed rock areas with and without barnacles were virtually the same throughout the secondary succession process, their relative abundance varied depending on the presence of barnacles. In particular, the densities of the limpet *Siphonaria lessonii* were higher in the presence of non-native barnacles. At low tide, these limpets aggregate in pits and crevices, or around other organisms (e.g. mussels, conspecific limpets), possibly as a way to reduce their exposure to detrimental heat and desiccation levels (Bazterrica et al. 2007, Bagur et al. 2016, Soria et al. 2022). Facilitation of limpets by *B. glandula* (possibly via moisture retention) has recently been documented in an Argentinian rocky shore (Hesketh et al. 2021) and the ag-

gregation of these limpets around this non-native barnacle was observed during the course of this study and elsewhere along the Argentinian coast (J. Gutiérrez pers. obs.). Here, the positive effect of barnacles on limpets was accompanied by a reduced cover of crustose algae in the presence of barnacles, which suggests that barnacles inhibit the development of crustose algae indirectly via the increase in the density of grazing limpets (Adami 2008, see Hesketh et al. 2021 for additional evidence of this indirect facilitation interaction). Yet, the observed increases in limpet densities in the presence of barnacles had no effect on overall macroalgal cover as evidenced by similar temporal variations in both treatments. This suggests that limpets primarily graze on crustose algae, at least in this system.

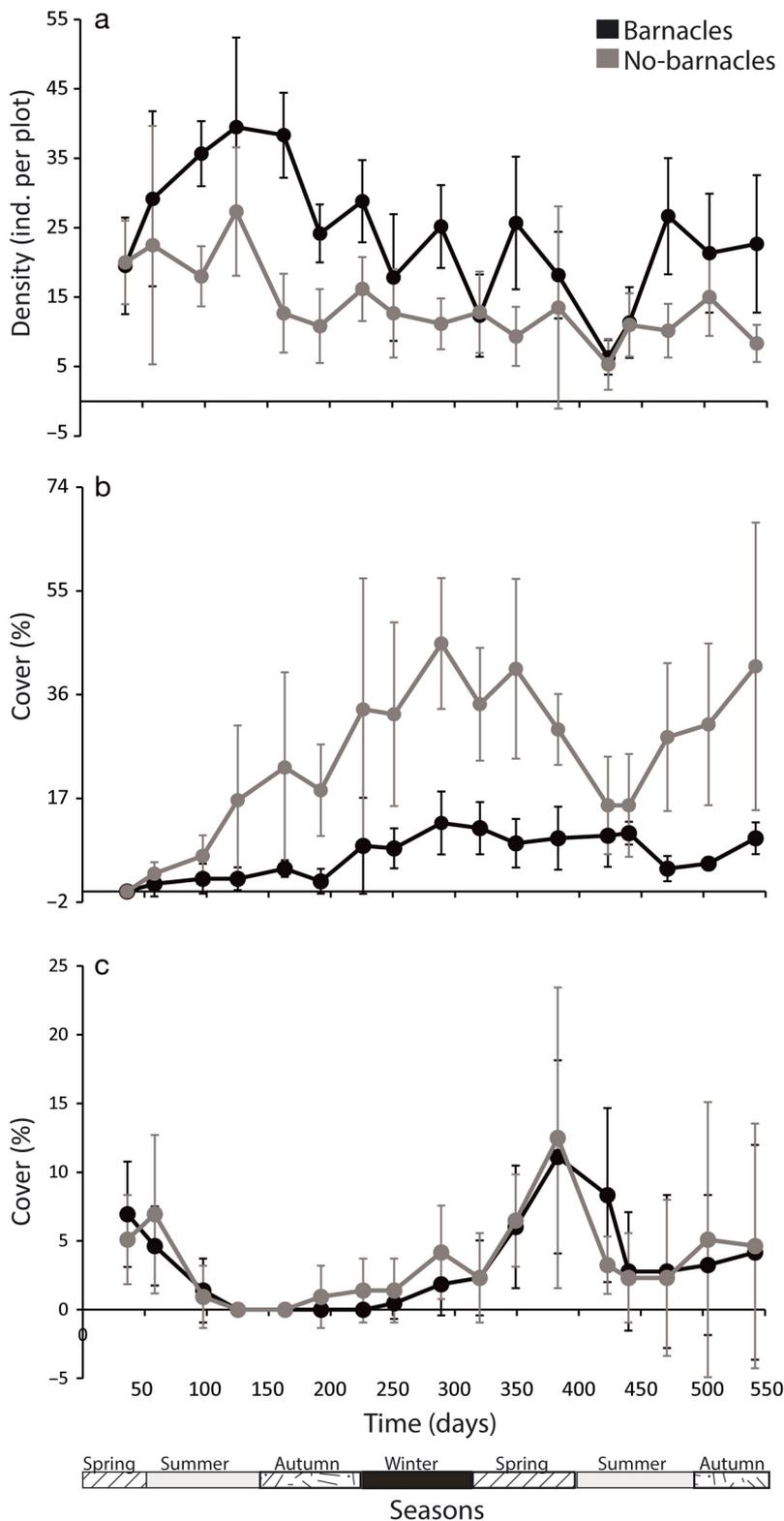


Fig. 3. (a) Limpet (*Siphonaria lessonii*) density, (b) percent cover of crustose algae, and (c) percent cover of macroalgae through time in the 'Barnacles' (black) and 'No barnacles' (grey) experimental plots ($n = 6$). Error bars indicate standard deviation

Moreover, the positive effect of barnacles on limpet densities further reinforces our above arguments on the prominence of adult immigration over recruitment in driving mussel cover recovery on the experimental plots. Indeed, limpets and other grazing gastropods are known to reduce mussel recruitment by mechanically dislodging—or 'bulldozing'—their recently settled larvae (e.g. Steffani & Branch 2005). While bulldozing of mussel larvae by *S. lessonii* might have occurred in our experiment, the results suggests that any reduction in mussel recruitment due to limpet bulldozing was overcompensated by positive effects of barnacles on adult immigration.

The net positive impact of barnacles on mussel bed recovery rates is expected to vary depending on the timing of disturbance relative to the barnacle recruitment season. In our experiment, barnacles quickly recruited into the experimental plots (i.e. within the first month from initial disturbance; see Section 2), which means that they began facilitating mussel recovery quickly after disturbance. Clearly, slower mussel recovery rates should be expected with an increasing time interval from disturbance to barnacle settlement. Yet, previous studies suggest that the recruitment of barnacles quickly after mussel bed disturbance should be frequent in our region. Indeed, *B. glandula* recruitment in this region was observed to occur from July to December (Vallarino & Elías 1997), whereas storm disturbances occur all year round in a nonseasonal fashion (Fiore et al. 2009, Gonzalez et al. 2021). This implies that there are 6 months per year where quick barnacle recruitment after wave disturbance is plausible to occur. Additionally, since mussels recruit all year round in this region (Arribas et al. 2015) and also immigrate into disturbed plots from adjacent beds (see previous paragraph), their positive responses to barnacle presence are expected to be rapid irrespective of the time of the year.

The facilitative impact of barnacles on mussel bed recovery and the concomitant potential for increases in the resilience of mussel beds to disturbance could help counteract some of the detrimental impacts of anthropogenic climate change on mussel bed habitats (e.g. increasing gap formation rates and persistence due to increased frequency of storms and heat waves; Soria et al. 2023). As with other foundation species (Ellison et al. 2005, Alongi 2008, Waycott et al. 2009, Smale et al. 2022), anthropogenic losses of mussel bed habitats are raising concern from the conservation standpoint given their importance in supporting biodiversity and functions in coastal ecosystems (e.g. Mendez et al. 2021, Fields & Silbiger 2022). In this context, non-native species are typically viewed as threats to mussel bed habitats that can out-compete, or otherwise detrimentally affect, mussels (e.g. Nehls et al. 2009, Mainwaring et al. 2014). Our findings, however, illustrate that a non-native species such as *B. glandula* can aid the persistence of mussel foundation species against increasing disturbances associated with anthropogenic global change.

Although invasion biologists initially emphasized detrimental impacts of non-native species, the positive effects of non-native species on native ones have received increasing attention over the last 2 decades (e.g. Rodriguez 2006, Davis et al. 2011, Doody et al. 2013, Pintor & Byers 2015, Ramus et al. 2017). Our study adds to this growing body of literature by illustrating that non-native barnacles facilitate the recovery of a native mussel foundation species following a disturbance. This novel, facilitative interaction can be construed as a habitat cascade (Thomsen et al. 2010), where non-native barnacles, as primary habitat-modifying species, facilitate the establishment of native mussels that act as foundation species and support much of the rocky shore biodiversity. Yet, we prefer to be cautious about whether non-native *B. glandula* can be considered as a 'beneficial' non-native species in the recipient rocky shore communities. Even when mussel beds support a substantial fraction of the overall biodiversity in these communities (Bagur et al. 2016, Soria et al. 2022), gap specialists might be negatively affected by the presence of barnacles as they positively affect limpet densities and grazing rates (Hesketh et al. 2021) while narrowing the timeframe available for gap colonization by accelerating the recovery of mussel cover. As is usually the case with non-native species impacts (e.g. Ruesink et al. 2005, Ward & Ricciardi 2007, Byers et al. 2012), there should be both winners and losers from the establishment of non-native *B. glandula* in the recipient rocky shore communities.

Knowledge on the species that lose from accelerated mussel recovery rates and studies in other rocky shores in our region are still needed for a more definitive and general assessment of the impact of *B. glandula* in these communities.

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