Competition between a native mussel and a non-indigenous invader for primary space on intertidal rocky shores in Chile

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ABSTRACT: Non-indigenous marine species have significant effects on rocky intertidal native biota and ecological processes. The tunicate *Pyura praeputialis*, a recent invader in the Bay of Antofagasta, Chile, has monopolized the low and mid-low rocky intertidal fringe and apparently constrained the native mussel *Perumytilus purpuratus* to the mid-upper fringe. We performed field experiments to determine interspecific competitive strengths and quantify survival and growth rates between these species at 2 intertidal heights: mid-low and mid-upper intertidal fringes. Our results showed that at the mid-low fringe *P. praeputialis* had greater competitive strength than *P. purpuratus*. In fact, the survival and growth rates of *P. praeputialis* were not significantly affected by the presence of *P. purpuratus*. Further, while the survival of *P. purpuratus* was not significantly affected by the presence of *P. praeputialis*, its growth rate was affected by the degree of encroachment by the tunicate. Mussels encroached by *P. praeputialis* grew significantly less than non-encroached ones. At the mid-upper intertidal fringe, the survival of *P. praeputialis* was significantly decreased by the presence of *P. purpuratus*: the tunicate is unable to grow at this intertidal fringe. At the low-intertidal fringe mussel growth rates were significantly greater than at the mid-upper fringe, while survival rates were similar. Our results support the hypothesis that in the Bay of Antofagasta the invading tunicate *P. praeputialis* is responsible for a major rocky intertidal ecological impact, outcompeting the native mussel from the mid-low fringe and thereby substantially modifying the zonation pattern.

KEY WORDS: Invasion · *Pyura praeputialis* · *Perumytilus purpuratus* · Tunicate · Rocky intertidal · Antofagasta Bay

INTRODUCTION

Biological invasions, defined as the arrival, establishment and subsequent spread of species beyond their historical range, have emerged as a major topic in ecology. Non-indigenous species (NIS) have significant effects on native biota, natural patterns and ecological processes through a variety of direct and indirect mechanisms occurring at genetic, individual, population, community and ecosystem scales (Griffiths et al. 1992, Lambert et al. 1992, Ruiz et al. 1997, 2000, Crooks 2002, Grosholz 2002, Olyarnik et al. 2009, Rilov & Crooks 2009). NIS can produce significant effects on local communities including changes in the species richness and local diversity (Fridley et al. 2007), the strength and direction of interspecific interactions (Holway et al. 2002, Eastwood et al. 2007) and the use of resources (Bubb et al. 2006). In many ecosystems, the success of NIS is facilitated by the absence of natural predators in the locality invaded, making the

unchecked growth of the invasive population possible (Kolar & Lodge 2001, 2002, Keane & Crawley 2002). Alternatively, successful invasion might also be regulated by the competitive ability of NIS. In general, invasive success may be explained by 'the enemy release hypothesis' (Colautti et al. 2004) and by high competitive ability. NIS are characterised by their ability to adapt establish themselves in new environments and become successful competitors against native species. For example, between 1970 and 2000, the competitive dominant mussel, *Mytilus galloprovincialis*, aggressively invaded the rocky intertidal shore of South Africa. The species has spread rapidly, over thousands of kilometres, along sheltered and exposed rocky west and east shores of South Africa, displacing the mussels, *Aulacomya ater* and *Choromytilus meridionalis* (Griffiths et al. 1992, Collins et al. 1996, Robinson et al. 2007), and outcompeting the mid-intertidal limpet, *Scutellastra argenvillei* (Steffani & Branch 2003a,b, 2005, Branch & Steffani 2004).

Perumytilus purpuratus (Lamarck 1918) is a native mussel of South American rocky coasts and is distributed in coastal waters of the southeastern Pacific Ocean from Ecuador to the Strait of Magellan, and around Cape Horn into the South Atlantic as far north as La Lobería, Argentina (Bertness et al. 2006, Prado & Castilla 2006). This species forms extensive and dense tridimensional beds in the mid-intertidal zone and is an important bioengineer species (Prado & Castilla 2006). *P. purpuratus* is the dominant competitor for primary substrate in the mid-intertidal fringe of the rocky shores of north-central Chile, outcompeting other sessile species such as barnacles, algae and other mussel species (Castilla & Durán 1985, Paine et al. 1985, Durán & Castilla 1989, Guiñez & Castilla 1999, Navarrete et al. 2005, Prado & Castilla 2006).

Pyura praeputialis (Heller 1878) is a solitary tunicate that inhabits intertidal and shallow subtidal habitats, showing a conspicuous, disjointed geographical distribution (Castilla & Guiñez 2000, Castilla et al. 2002). This tunicate inhabits wave-swept headlands on the southeastern shores of Australia, from where it appears to have originated (Fairweather 1991, Monteiro et al. 2002). This species is also found in northern Chile (Castilla et al. 2002), where it lives exclusively along approximately 70 km of rocky coast inside the Bay of Antofagasta (23° 38′ S, 70° 23′ W, Fig. 1) (Guiller 1959, Paine & Suchanek 1983, Underwood & Fairweather 1986, Castilla 2008). Molecular evidence has demonstrated that *P. praeputialis* is a recent NIS invader to this bay, probably having arrived a few hundred years ago from Australia (Astorga et al. 2002, Castilla et al. 2002). In the rocky shore of the Bay of Antofagasta, *P. praeputialis* generates dense collective
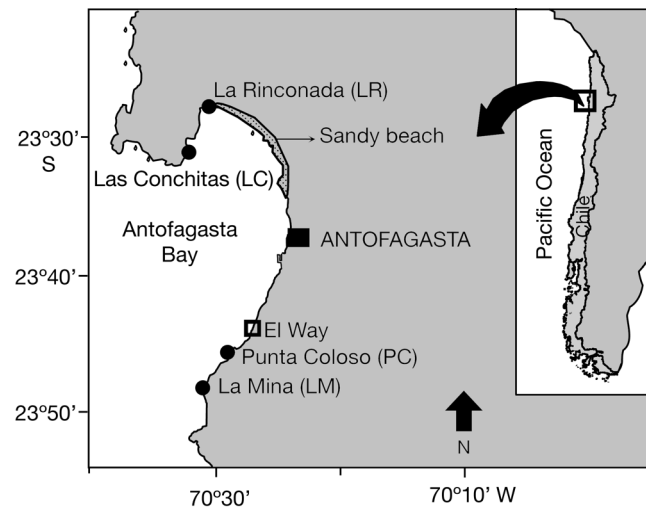

Fig. 1. Experimental sites (●) in the Bay of Antofagasta. Inset: study area in northern Chile

unities (pseudo-coloniality) forming extensive aggregations in the mid- and low-intertidal zones (Paine & Suchanek 1983, Castilla et al. 2004, 2007).

In a previous study Castilla et al. (2004) showed that *Pyura praeputialis* is an aggressive interspecific competitor for primary space at the mid-low rocky intertidal fringe inside the Bay of Antofagasta. At this intertidal fringe the species appears to have the ability to overgrow the native mussel *Perumytilus purpuratus*. However, to date there are no experimental studies evaluating the strength of mussel–tunicate competition, thereby assessing the competitive performance of mussels and tunicates in the presence and absence of their competitors in the mid-low and mid-upper intertidal fringes. In this study, we use field experimental approaches to assess the interspecific competitive strength and physiological restrictions of both species at the mid-intertidal fringe. Hence, we attempt to deepen the understanding of the ecological processes determining the unique intertidal zonation pattern observed in the rocky shore of the Bay of Antofagasta. The aim of this work is to quantify growth, survival rates and the strength of competition between the native mussel *P. purpuratus* and the non-indigenous tunicate *P. praeputialis*, based on cross-transplants (alone and mixed treatments), at 4 different sites inside the Bay of Antofagasta within 2 intertidal subfringes: the mid-low intertidal fringe (M-LIF) where *P. praeputialis* dominates, and the mid-upper intertidal fringe (M-UIF) where *P. purpuratus* dominates. We hypothesized that at the M-UIF the mussel *P. purpuratus* is a stronger competitor than the tunicate *P. praeputialis*, while at the M-LIF *P. praeputialis* is a stronger competitor than *P. purpuratus*.
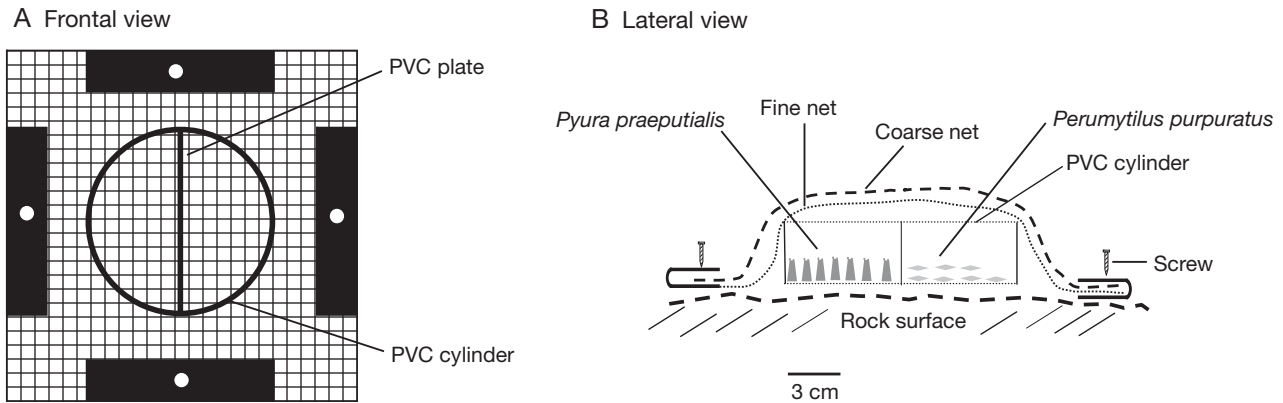
A Frontal view

B Lateral view

Fig. 2. (A) Frontal and (B) lateral views of cages used for tunicate–mussel competition experiments

MATERIALS AND METHODS

To evaluate the competitive interaction between the NIS tunicate *Pyura praeputialis* and the native mussel *Perumytilus purpuratus* in the Bay of Antofagasta, we transplanted juveniles of both species, using PVC cages installed at 2 tidal heights: the mid-low intertidal fringe and the mid-upper intertidal fringe (Castilla 1981, Castilla et al. 2004), where *P. praeputialis* and *P. purpuratus*, respectively, have higher densities (Castilla & Camaño 2001). The experiments were carried out at 4 sites inside the Bay of Antofagasta: (1) La Mina (LM; 23° 48′ S, 70° 30′ W), (2) Punta Coloso (PC; 23° 45′ S, 70° 27′ W), (3) La Rinconada (LR; 23° 27′ S, 70° 30′ W) and (4) Las Conchitas (LC; 23° 31′ S, 70° 32′ W) (Fig. 1).

Juveniles of *Pyura praeputialis* between 13 to 17 mm in diameter and 19 to 24 mm maximum height were collected from El Way (23° 44′ S, 70° 26′ W) (Fig. 1). In the laboratory, total wet mass, maximum height and maximum dorsal diameter were recorded for each tunicate. *Perumytilus purpuratus* juveniles of maximum length between 5 to 10 mm were collected from mussel beds at El Way. Before experiments began, to quantify shell growth, the left shell of each mussel was marked at the posterior growth border by means of a dentist drill (Guiñez & Castilla 1999). Mussels and tunicates were maintained in running seawater 24 h before being transplanted to the field.

Cages were made from open PVC cylinders 10.7 cm in diameter and 4 cm high (surface area: ~90 cm^2; volume: ~360 cm^3). Cylinders were covered with 2 types of plastic nets: (1) a fine net (20 × 20 cm, mesh aperture: 2 mm) and (2) a coarse net (20 × 20 cm, mesh aperture: 6 mm) (Fig. 2). At the beginning of the experiment, animals were placed loosely in the cages covered with both nets. After ~1 mo individuals had attached to the substrate either through byssus threads (*Perumytilus purpuratus*) or tunic production (*Pyura praeputialis*). The fine net facilitated the adhering processes, reducing hydrodynamic forces within the cages and was removed in the second month. The coarse net prevented predators from entering the cages and was maintained throughout the experiment. Since *P. praeputialis* and *P. purpuratus* juveniles have different sizes and forms, to standardize the intra- and interspecific competition to the same biomass by unit surface area, we kept a constant biomass (20 ± 2 g) by cage area. Three competition treatments were carried out: (1) Treatment A: 10 *P. praeputialis* (10 g) were randomly mixed with 20 *P. purpuratus* individuals (10 g), (2) Treatment B: 10 *P. praeputialis* (10 g) were randomly placed alone, (3) Treatment C: 20 *P. purpuratus* (10 g) were randomly placed alone. In Treatment A, the full cage volume was used; while, in Treatments B and C, the experimental cage was divided in 2 halves (surface area: ~45 cm^2; volume: ~180 cm^3; Fig. 2) by means of a PVC plate. In the latter treatments, 1 of the halves, determined at random, was used for experimentation and the other remained empty. A set of 3 cages (1 per treatment) was arranged as a plot, and cages were attached to the intertidal rocks with stainless steel screws (Fig. 2). For each combination of site and tidal heights 5 replicate plots were randomly assigned. Experiments ran from 11–15 July to 19–21 December 1999. The nets covering the cages were cleaned of epibionts at least once a month and predator presence or absence on the experimental units was verified.

At the end of the experiment we determined (1) the number of individual *Pyura praeputialis* and *Perumytilus purpuratus* alive, and (2) *P. praeputialis* and

P. purpuratus growth. For *P. praeputialis*, the initial dry viscera mass for each individual was estimated by means of a nonlinear equation: dry viscera mass = 6.7 × 10^{-5} × (diameter)$^{2.448}$, (see Eq. 2 in Castilla et al. 2004). The initial total dry mass was estimated with the linear equation: total dry mass = 0.160 + 0.286 × wet mass (see Eq. 1 in Castilla et al. 2004). The initial tunic dry mass was estimated as the difference of initial total dry mass minus initial visceral dry mass. Final dry masses were determined in grams with a digital balance (accuracy: ±0.001 g,) after drying the respective tissues in an oven at 70°C for 72 h. The growth rate of *P. purpuratus* was determined as the increment in shell size and was quantified as the distance between the initial drill mark and the new border of the shell. After the experimental units were removed from the field and brought to the laboratory, we used digital photography to determine the degree to which *P. praeputialis* had encroached (i.e. overgrown) *P. purpuratus* inside the cylinders. This procedure was applied only to those experimental units containing both species. The criteria to estimate *P. praeputialis* encroachment was the percentage of mussel shells covered by the tunicates (from a frontal view of the experimental unit) according to the following scale: (1) total encroachment: >80%; (2) partial encroachment: ≤80% and ≥20%; (3) no encroachment: <20% of shells covered.

For each species we performed a 3-way mixed analysis of covariance (ANCOVA) with 'Site' as a random factor and 'Treatment' and 'Tidal height' as fixed effects. For both species we used survival as the dependent variable and initial dry biomass as a covariate. For *Perumytilus purpuratus*, we used differential shell growth (final length minus initial shell maximum length) as the dependent variable. For *Pyura praeputialis*, we used differential mean tunic mass and visceral dry tissue growth as dependent variables, and survival number as a covariate. We also conducted a 3-way blocked ANOVA (factors were: Site, Tidal height, Degree of encroachment) for mussel growth, with Site as a random blocking factor. For statistical analyses we used PROC GLM (SAS 2002). When interaction terms in factorial designs were significant we compared cell means using the SLICE option in PROC GLM (SAS 2002). We estimated the intensity of interspecific competition (Lotka & Volterra competitive coefficients) separately at both intertidal heights, estimated as the per capita effect on ratio between the initial and final survival during the 5 mo of the experiment. To estimate this coefficient, we fitted linear regressions of the ratios between the initial and final survival of the focal species (in logarithmic scale) versus time. The slope of this regression is an estimator of the interspecific competition coefficient among transplanted individuals at each site.

RESULTS

Pyura praeputialis survival varied with competition treatment and tidal height (Treatment × Tidal height interaction, p = 0.050; Table 1A, Fig. 3A,B), but did not vary with Site and other Site interactions (Table 1). In the M-LIF *P. praeputialis* survival was not affected by the presence of *Perumytilus purpuratus* (p = 0.432;

Table 1. *Pyura praeputialis*. (A) Three-way (Site, Tidal height and Treatment) mixed ANCOVA for survival. The covariate was the initial biomass. (B) Treatment × Tidal height effect sliced by Tidal height (see 'Materials and methods'; SAS 2002). p-values in **bold** text are significant (p < 0.05)

A) 3-way ANCOVA

Source of variation	df	MS	*F*	p
Covariate	1	5.8378	1.38	0.244
Site	3	11.0009	0.58	0.655
Tidal height	1	386.8427	32.54	**0.010**
Treatment	1	8.0207	0.88	0.419
Site × Tidal height	3	11.9952	4.73	0.097
Site × Treatment	3	9.0791	3.72	0.158
Treatment × Tidal height	1	22.3499	8.86	**0.050**
Treat × Site × Tidal height	3	2.4535	0.58	0.629
Error	63	4.2184		

B) Treatment × Tidal height effect sliced by Tidal height

Tidal height	df	SS	MS	*F*	p
M-LIF	1	2.0119	2.0119	0.82	0.432
M-UIF	1	28.8933	28.8933	11.78	**0.042**

Table 2. *Pyura praeputialis*. (A) Three-way (Site, Tidal height and Treatment) mixed ANCOVA for growth: dry viscera mass (final minus initial). The Site × Tidal height × Treatment interaction was used as an error term. Survival as a covariate was not significant ($F_{1,36}$ = 0.62, p = 0.43). (B) Site × Treatment effect sliced by Site (see 'Materials and methods'; SAS 2002). p-values in **bold** text are significant (p < 0.05)

A) 3-way ANCOVA

Source of variation	df	MS	*F*	P
Site	3	0.0028	1.09	0.452
Tidal height	1	0.0111	17.16	**0.014**
Treatment	1	0.0048	2.26	0.219
Site × Tidal height	3	0.0007	1.38	0.265
Site × Treatment	3	0.0028	5.62	**0.003**
Treatment × Tidal height	1	0.0005	0.92	0.344
Error	37	0.0005		

B) Site × Treatment effect sliced by Site

Site	df	SS	MS	*F*	p
La Mina	1	0.0017	0.0017	3.34	0.076
Punta Coloso	1	0.0032	0.0032	6.43	**0.016**
La Rinconada	1	0.0012	0.0012	2.42	0.129
Las Conchitas	1	0.0055	0.0055	11.00	**0.002**

Table 1B, Fig. 3A), but in the M-UIF its survival was lower in the presence than in the absence of *P. purpuratus* (p = 0.042; Table 1B, Fig. 3B). At this tidal height, *P. praeputialis* survival in Treatment A (both species mixed) decreased by about 75% compared with Treatment B (*P. praeputialis* alone; Fig. 3B).

Pyura praeputialis tunic dry mass (ANCOVA: $F_{1,3}$ = 19.82, p = 0.001; Fig. 3C,D) and viscera dry mass tissues (p = 0.014; Table 2A, Fig. 3E,F), grew more slowly at the M-UIF than at the M-LIF. At both tidal heights, tunic growth was faster in the *P. praeputialis* alone treatment than in the competition treatment (Treatment A), but this effect was not significant (ANCOVA: $F_{1,3}$ = 1.98, p = 0.214; Fig. 3C,D). Visceral tissue growth varied with site and competition (p = 0.003; Table 2A, Fig. 3E,F). This interaction reflects the negative effect of *Perumytilus purpuratus* on *P. praeputialis* visceral tissue growth at Punta Coloso and Las Conchitas (p = 0.016 and p = 0.002, respectively; Table 2B, Fig. 3E,F). Only marginal effects were observed at La Mina (p = 0.076; Table 2B, Fig. 3E,F) and no effect was observed at La Rinconada (p = 0.129; Table 2B, Fig. 3E,F).

Survival of the mussel *Perumytilus purpuratus* was not affected by the presence of *Pyura praeputialis* individuals (ANOVA: $F_{1,3}$ = 0.52, p = 0.522; Fig. 4A,B). Mussel growth, however, varied with both tidal height and the presence of the tunicate. *P. purpuratus* grew faster at the M-LIF (i.e. in the centre of the *P. praeputialis* belt, p = 0.006; Table 3, Fig. 4C,D) than at the M-UIF (i.e. in the centre of *P. purpuratus* belt), and even faster in the mixed treatment with *P. praeputialis*, than alone (p = 0.025; Table 3, Fig. 4C,D). Nevertheless, when the competition treatment was analyzed according to the degree of encroachment of *P. praeputialis* on *P. purpuratus*, as encroachment increased the growth of *P. purpuratus* decreased (p < 0.001; Table 4A, Fig. 5). The encroaching effect of *P. praeputialis* on *P. purpuratus* was more important at the M-LIF than at the M-UIF ($F_{2,95}$ = 239.80 and $F_{2,95}$ = 50.15, respectively; Table 4B, Fig. 5).
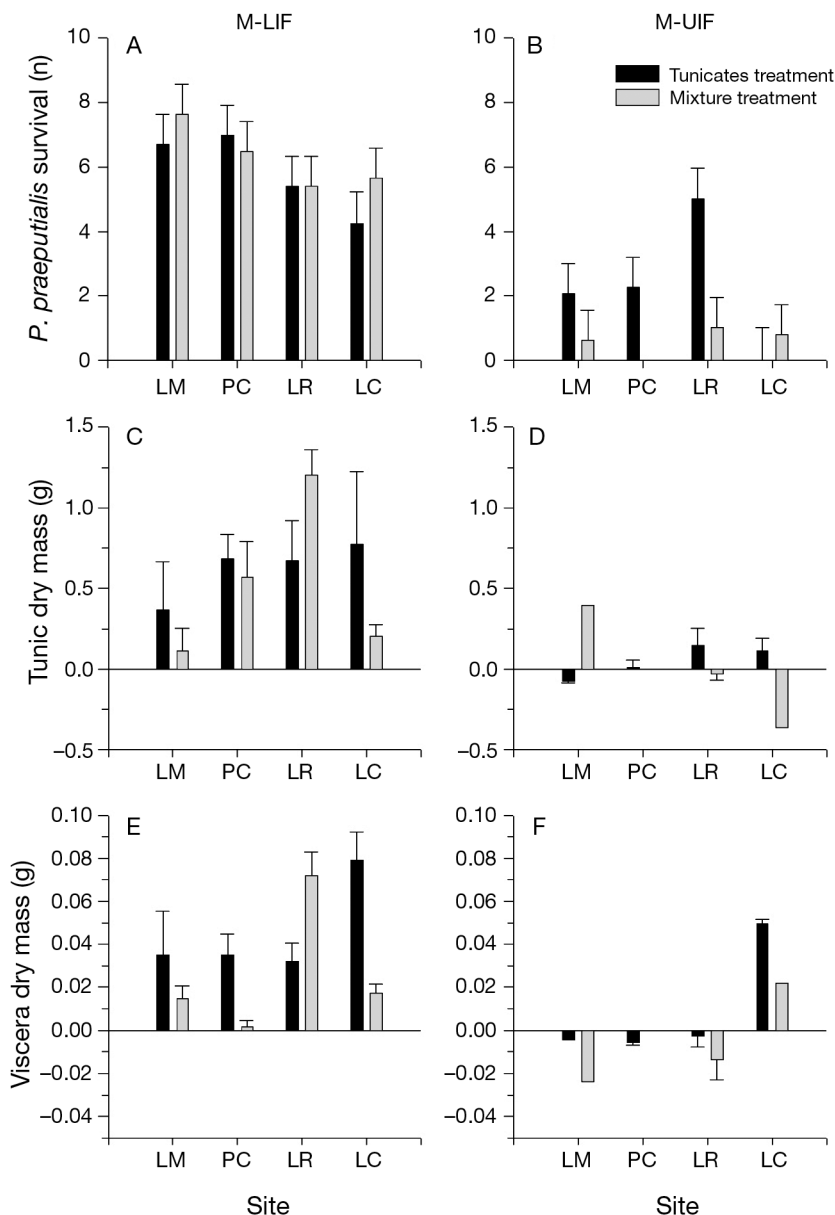

Fig. 3. *Pyura praeputialis.* Survival and growth under 2 competition treatments. Tunicates treatment (black bars) and Mixture treatment (grey bars) at 4 sites and 2 intertidal fringes: mid-low intertidal fringe (M-LIF: A,C,E) and mid-upper intertidal fringe (M-UIF: B,D,F). (A,B) Survival, (C,D) dry tunic mass, (E,F) dry visceral mass. Means +1 SE for 4 independent experimental units. LM: La Mina; PC: Punta Coloso; LR: La Rinconada; LC: Las Conchitas (for locations see Fig. 1)

The interspecific competition coefficients of *Pyura praeputialis* on *Perumytilus purpuratus* differed between tidal heights (p = 0.03; Fig. 6). *P. praeputialis* had a higher competitive performance in the mid-low intertidal fringe (Fig. 6), while in the mid-upper intertidal fringe its competitive performance decreased. *P. purpuratus* had a low competitive intensity at both intertidal heights (Fig. 6).
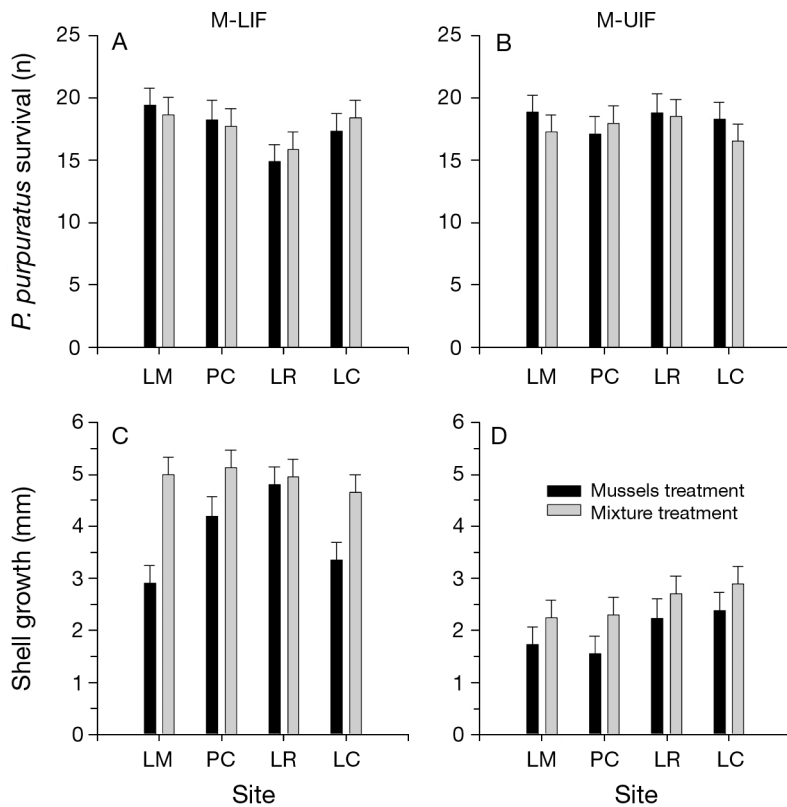
Fig. 4. *Perumytilus purpuratus.* Survival and shell growth under 2 competition treatments. Mussels treatment (black bars) and Mixture treatment (grey bars), at 4 sites and 2 intertidal fringes (M-LIF: A,C; M-UIF: B,D): (A,B) survival, (C,D) shell growth. Means +1 SE for 4 independent experimental units. Abbreviations as in Fig. 3

DISCUSSION

Our experiment demonstrated that at the M-LIF the non-indigenous tunicate *Pyura praeputialis* was a stronger competitor than the native mussel *Perumytilus purpuratus.* However, at the M-UIF the competitive ability of the tunicate was reduced. The survival of *P. praeputialis* at the M-LIF was not reduced by the presence of *P. purpuratus* (Fig. 3A). Nevertheless, tunicate survival was reduced in the mixed treatment at the M-UIF (where *P. purpuratus* dominates; Fig. 3B), while *P. purpuratus* survival was not affected by competition with *P. praeputialis* (Fig. 4A,B). Overall, the mussels grew faster when mixed with *P. praeputialis* than when grown alone (Table 3, Fig. 4C,D). This may be due to greater moisture retention in mixed than in non-mixed units, thereby reducing physiological stress for *P. purpuratus.* Nevertheless, at both tidal heights, *P. purpuratus* individuals that were totally or partially encroached by *P. praeputialis* inside the cages, grew less than the non-encroached ones (Table 4, Fig. 5). These results differ from those reported by Dalby &

Young (1992) on the suspected competition between the ascidian *Eudistoma capsulatum* and the oyster *Ostrea equestris* where ascidians overgrowing oysters had no effect on the final oyster size, but in 2 ascidia–oyster matrix experiments the final oyster size was enhanced. A previous study (Castilla et al. 2004) performed on the *P. praeputialis–P. purpuratus* interaction showed that *P. purpuratus* matrices transplanted to the M-LIF and in contact with natural beds of *P. praeputialis*, were systematically overgrown (encroached) by the tunicates. Those previous findings and our present results, based on experimental transplants of *P. praeputialis* juveniles, reinforce the hypothesis that since its arrival to the Bay of Antofagasta *P. praeputialis* have outcompeted *P. purpuratus* at the M-LIF.

Further, the present results show that *Pyura praeputialis* grew faster (tunic and viscera) at the M-LIF than at the M-UIF (Fig. 3C–F), suggesting that environmental conditions are more favorable for the tunicate at the M-LIF, but worse at the M-IUF. Therefore, our results are consistent with the suggestions made by Paine & Suchanek (1983) that the abrupt upper intertidal limit of this tunicate would be related to physiological stress and would not be the result of biological interactions. On the other hand, the mussel *Perumytilus purpuratus* grew faster at the M-LIF than at the M-UIF. Increased growth rates for the mussel in low intertidal and even shallow subtidal habitats, compared with those in mid-intertidal habi-

Table 3. *Perumytilus purpuratus.* Three-way (Site, Tidal height and Treatment) mixed ANCOVA for differential shell growth (final minus initial). The covariate was survival number. p-values in **bold** text are significant ($p < 0.05$)

Source of variation	df	MS	F	p
Covariate	1	3.2984	5.77	0.019
Site	3	1.5454	0.92	0.558
Tidal height	1	87.2487	50.51	**0.006**
Treatment	1	13.6821	17.49	**0.025**
Site × Tidal height	3	1.6895	2.10	0.274
Site × Treatment	3	0.7819	0.96	0.512
Treatment × Tidal height	1	1.4728	1.82	0.270
Treat × Site × Tide height	3	0.8110	1.42	0.246
Error	61	0.5719		

Table 4. *Perumytilus purpuratus*. (A) Three-way (Site, Tidal height and Scale of encroaching) mixed ANOVA for differential shell growth (final minus initial). (B) Tidal height × Scale of encroaching effect sliced by Tidal height. p-values in **bold** text are significant (p < 0.05)

A) 3-way ANOVA

Source of variation	df	MS	F	p
Site	3	0.4644	1.64	0.185
Tidal height	1	260.9348	921.24	**<0.001**
Scale of encroaching	2	71.0068	250.69	**<0.001**
Site × Tidal Height	3	1.4237	5.03	0.003
Site × Scale of encroaching	6	0.2872	1.01	0.421
Tidal height × Scale of encroaching	2	11.8192	41.73	**<0.001**
Site × Tidal height × Scale of encroaching	6	0.1497	0.53	0.785
Error			95	0.2832

B) Tidal height × Scale of encroaching effect sliced by Tidal height

Tidal height	df	SS	MS	F	p
M-LIF	2	135.8612	67.9306	239.80	**<0.001**
M-UIF	2	28.4094	14.2047	50.15	**<0.001**

(1) Many of such cases may not exist. It is possible, for example, that ecologically drastic alterations, such as modifications in intertidal zonation, may be rare owing to negative biotic interactions with native species and/or to abiotic factors preventing rocky shore invasive species from becoming established (Reusch & Williams 1999). (2) Major inshore ecological modifications exist but have not been properly documented (but see Crooks & Khim 1999, Steffani & Branch 2005). (3) There is a lack of experimental approaches (but see Troost 2010) since most reported studies are descriptive (for example see Griffiths et al. 1992, Vermeij 1996, Orensanz et al. 2002). Undoubtedly, more field experimental approaches and manipulations, such as that presented here, are needed to fully understand the consequences of interactions between native and invasive species in coastal marine environments.

tats (where they normally live), have been also reported in central Chile (Cancino & Rojas 1986). Hence, our results suggest that environmental conditions are generally better for both species at the M-LIF than the M-UIF, but also that the tunicate is the competitive dominant species lower on the shore and, via competitive effects, restricts the mussel beds to the upper shore where the tunicate can not tolerate the environmental conditions. This supports the hypothesis that in the Bay of Antofagasta the invasive tunicate *P. praeputialis* has had a major ecological impact, outcompeting the native mussel *P. purpuratus* from the M-LIF. The estimated competition coefficients show that *P. praeputialis* gains in competition to *P. purpuratus* at the M-LIF and dominates this intertidal fringe (Fig. 6). The experimental and analytical procedures used in this study allow us to compare the intensity of interspecific competition with other competitive interactions in nature.

So far, the experimental ecology of marine, non-indigenous, competitively dominant invertebrate species, which can potentially cause major ecological modifications to inshore systems, has received little attention in the literature (but see Crooks 2002, Rilov & Crooks 2009). This may be due to a number of reasons.
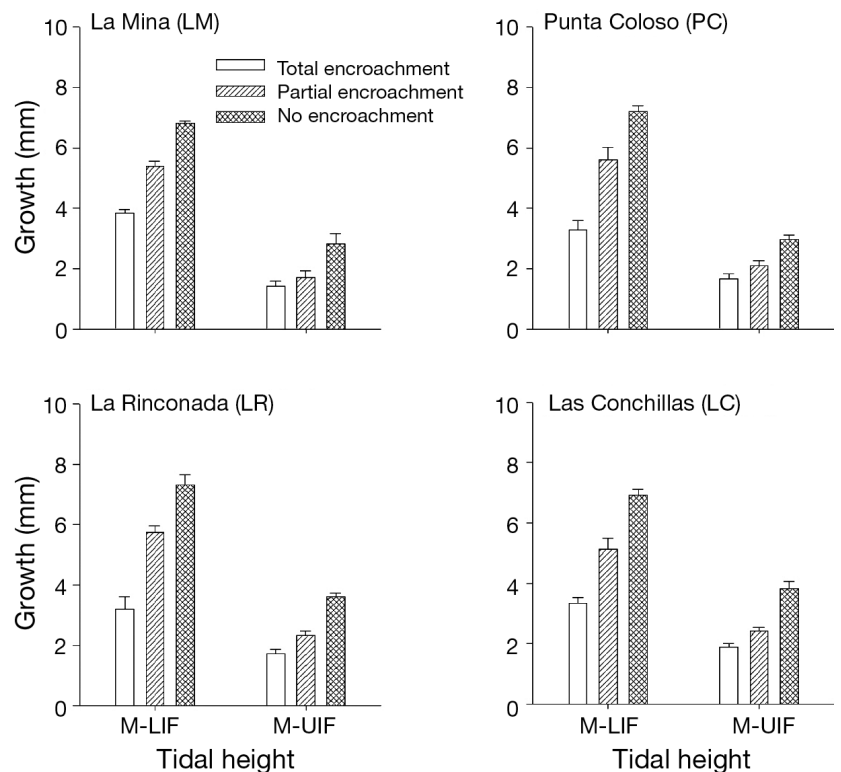

Fig. 5. *Perumytilus purpuratus*. Shell growth under 3 degrees of *Pyura praeputialis* encroachment at 4 sites and 2 intertidal fringes: M-LIF and M-UIF. The following degree of encroachment was used, according to the percentage of individual mussel shells covered by *P. praeputialis*: >80% = total encroachment (□); ≤80% to ≥20% = partial encroachment (▨); <20% = no encroachment (▨). For abbreviations see Fig. 3
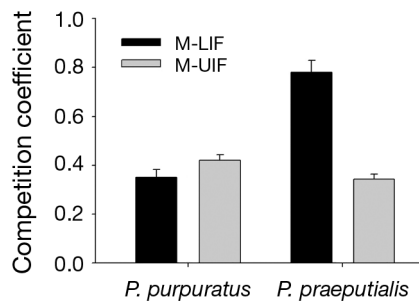
Fig. 6. Interspecific competition coefficients for the native mussel *Perumytilus purpuratus* and the invader tunicate *Pyura praeputialis* at 2 intertidal heights: mid-low intertidal fringe (M-LIF) and mid-upper intertidal fringe (M-UIF)

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