

Co-existence of two mytilid species in a heterogeneous environment: mortality, growth and strength of shell and byssus attachment

Jose M. F. Babarro^{1,*}, María José Abad²

¹Instituto de Investigaciones Marinas CSIC, Eduardo Cabello 6, 36208 Vigo, Spain

²Grupo de Polímeros (CIT), Campus de Esteiro, C/Dr Vázquez Cabrera s/n, 15403 Ferrol, A Coruña, Spain

ABSTRACT: The co-existence patterns of 2 mytilid species were studied in order to evaluate the performance of the alien mussel *Xenostrobus securis* and the indigenous *Mytilus galloprovincialis* through monospecific and mixed co-habiting experiments in the Ría de Vigo (northwest Spain). *Mytilus galloprovincialis* was found to be the best performer in all tests. Shell growth was ~4-fold greater for the indigenous mussel when deployed without interspecific competition and regardless of density. Differences in shell growth were found to be similar within mixed populations wherein *M. galloprovincialis* showed greater ability for upward migratory movements on the mixed beds and distanced itself from the mud influenced layer. The alien *X. securis*, however, was found to inhabit underneath the *M. galloprovincialis* layer, which resulted in higher mortality rates. Species-specific features such as byssus filaments and lifestyle may account for such different behaviour. *M. galloprovincialis* secreted thicker and stronger shells and byssus regardless of their density in both monospecific and mixed experiments. This might indicate that the indigenous mussel performs better when confronted with abiotic stress or biotic pressure. The alien *X. securis* is currently found to establish high-density patches of individuals at the confluence of main rivers that flow into the estuary (highly heterogeneous scenario). Such behaviour favours its settlement far from the native mussel influence area. *X. securis* also colonises hard substrates that are not fully occupied by other invertebrates, but its range was found to be limited by the presence of the indigenous mussel.

KEY WORDS: *Mytilus galloprovincialis* · *Xenostrobus securis* · *Limnoperna* · Performance · Competition · Plasticity · Byssus

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INTRODUCTION

Biological invasions have emerged as a major topic in ecological studies and environmental policy issues (Pfeiffer & Voeks 2008). The presence of exotic species may induce significant changes in the recipient community structure as a consequence of interspecific interactions, which may give rise to the variability of species richness, community balance and diversity (Vermeij 1996, Crooks & Khim 1999, Groscholz 2002, Fridley et al. 2007). Such interactions between species may lead to competition and eventually the exclusion of the worst performer (Branch &

Steffani 2004, Castilla et al. 2004). Nevertheless, this negative consequence for the indigenous inhabitants does not occur in all cases because aspects like habitat heterogeneity may play a significant role, and examples of co-existence (Rius & McQuaid 2006, Zardi et al. 2008, Dutton & Hofmann 2008, Nicastro et al. 2010, Bownes & McQuaid 2010 among others) and even facilitation (Rius & McQuaid 2009) have been reported for the specific case of bivalve performance. Sará et al. (2008) found that the potential for invasion can be enhanced through a number of advantageous physiological mechanisms of the exotic species. Although indigenous species may be

*Email: jbabarro@iim.csic.es

displaced whenever the alien species shows superior competitive abilities and physiological tolerance (Steffani & Branch 2005), the interactions with the environment and native species would nevertheless make such invasion unpredictable. The potential for adhesion by using byssus filaments within a changing abiotic scenario is a key feature for sessile mytilids survival.

The surveys cited in the previous paragraph have reported co-existence mechanisms in native and exotic bivalves with similar niches based on ecological traits comparison. Examples of certain competitive advantages of the invasive species with respect to the indigenous species have been related to their ability to escape from natural enemies such as predators or parasites (Shea & Chesson 2002). In our case, the alien mussel *Xenostrobus securis* has been reported to house fewer parasites than the native mussel (Pascual et al. 2010) and to be less vulnerable to predation by *Carcinus maenas* (Veiga et al. 2011). Therefore, such ecological release from parasites and predators (enemy release hypothesis) would facilitate invasion by *X. securis*. The spatial-temporal resource competition theory furthermore predicts that environmental disturbances in both space and time may produce major and different effects on indigenous and exotic species, which would favour one or the other at different locations and times (Shea & Chesson 2002).

Interestingly, the indigenous mussel *Mytilus galloprovincialis* involved in the present study is a successful invader in other latitudes, e.g. along the South African coastline (Branch & Steffani 2004, Bownes & McQuaid 2010), the Pacific Northwest front (Shinen & Morgan 2009) and many other areas in America, Africa, Australia and Japan (Sanjuan et al. 1997). The presence of *Xenostrobus securis* (black pygmy mussel) in Galician waters was reported by Garci et al. (2007); however the species was endemic to the brackish waters of New Zealand and Australia. The introduced black pygmy mussel is nowadays found in very different areas of Europe (Spain and Italy; Sabelli & Speranza 1994, Garci et al. 2007, Barbieri et al. 2011) and Japan (Kimura et al. 1999), and represents a relatively small mytilid whose size may have played a role in its invasion ability. The small size is supposed to be associated with rapid population growth and high fecundity (Ehrlich 1989). The life-span of *X. securis* is relatively short (~1 yr) and it usually forms very dense populations (Wilson 1969) that might occasionally smother the native infaunal communities (Zenetos et al. 2004). *X. securis* is considered to be a serious threat as a bio-invaser with

negative impact on indigenous ecosystems (Darrigran 2002), and it has been listed among the '100 worst invasive species' in the Mediterranean Sea (Streftaris & Zenetos 2006). Currently, the distribution of *X. securis* in Galicia (NW Spain) is restricted to the mouth of the River Oitavén-Verdugo (Sampaio; mean \pm SD = 8.700 ± 550 ind. m^{-2} according to Garci et al. 2007), where the indigenous *M. galloprovincialis* is absent, and the adjacent areas in the inner Ría de Vigo (San Simón) (Fig. 1), where it co-exists with *M. galloprovincialis* at relatively balanced rates (Gestoso et al. 2012). The competition between both mytilid species was observed to take place on hard rocks along the intertidal coastline but the invader sometimes colonised muddy soft bottoms in the inner Ría (Garci et al. 2007, Pascual et al. 2010) by producing a great amount of byssal threads (Babarro & Lassudrie 2011). Such mud (and sand) accumulation in the inner areas of the estuary may eventually affect stability of mussel attachment (Zardi et al. 2008) and would therefore determine any co-existence pattern. Besides its potential to settle on very different substrates, *X. securis* also shows extremely high tolerance to salinity and flow speed variation (Wilson 1968, Babarro & Lassudrie 2011). Although the alien mussel has shown an extraordinary ability for strong attachment in wide abiotic conditions, its attachment strength never exceeded that reported for the native mussel. No studies with mixed populations have been carried out to certify survival and growth performance of the 2 competing species.

In Galicia, the cultivation of *Mytilus galloprovincialis* represents a widely diversified industry of great economic importance (Labarta et al. 2004). The

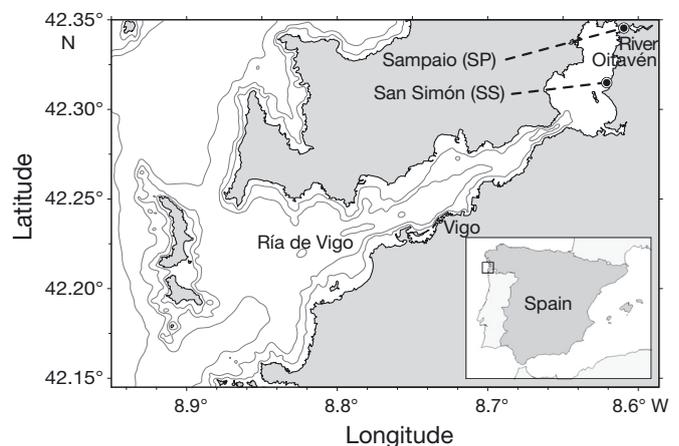


Fig. 1. Experimental sites at the inner Ría de Vigo (NW Spain). San Simón (SS): inner sheltered site. Sampaio (SP): mouth of River Oitavén-Verdugo flowing into the Ría

potential expansion of the invader *Xenostrobus securis* from the inner to the outer areas of the Ría de Vigo may threaten such successful activity and disturb ecological relationships in the Ría ecosystem. Biological interactions between species and their responses to environmental heterogeneity would provide a useful scheme to understand community structure (Nicastro et al. 2010) and any potential future changes. The crucial aspect to research here corresponds to the ability of the alien mussel to expand further from its main concentration site into other inner areas of the Ría de Vigo where *M. galloprovincialis* co-exists on mixed mussel beds. The aim of our study was to test the hypotheses that (1) *X. securis* excludes *M. galloprovincialis* because of the poor growth rates and high mortality of the indigenous mussel, especially when mud accumulation becomes significant on mussel beds; and (2) energetic constraints derived from the competition processes would distinctly limit energy allocation to protective structures (byssal and shell strength) of both species, in which the alien mussel would take advantage of its better adaptation to the heterogeneous environment. Monospecific and mixed co-habiting tests were carried out during 2 consecutive seasons and on different (soft and hard) substrates in order to study both spatial and temporal components of interspecific competition.

MATERIALS AND METHODS

Region and general approach

Field survey was conducted at 2 sites of the inner Ría de Vigo (NW Spain; Fig. 1) where (1) *Xenostrobus securis* is highly and exclusively present (Sampaio = SP) and (2) co-habiting with *Mytilus galloprovincialis* forming mixed mussel beds (San Simón = SS). SP represents a highly changing environment for salinity and water flow values that depend on the river influence and tidal regime (Babarro & Lassudrie 2011). By contrast, soft muddy bottoms characterise the intertidal coastline of the sheltered and shallow SS waters and may at times cover hard substrates where mytilids settle.

The competition ability of mytilids was assessed through (1) mortality and growth estimates in the natural environment with mud transport influence, and (2) the strength of both byssal attachment and shell, which indicate the energy investment into these protective tissues. Common sized mussels of 23 ± 1.3 mm shell length (mean \pm SD) were selected

Table 1. *Mytilus galloprovincialis* (*Mg*) and *Xenostrobus securis* (*Xs*). Experimental design: number of mussels per treatment in 2 sites in NW Spain, to study competition patterns between the 2 mytilid species. Slate tile surface: 100 cm²

San Simón (SS)									
	SS 1	SS 2	SS 3	SS 4	SS 5	SS 6	SS 7	SS 8	SS 9
<i>Mg</i>	5	10	20	–	–	–	5	10	15
<i>Xs</i>	–	–	–	5	10	20	15	10	5
Sampaio (SP)									
	SP 1	SP 2	SP 3						
<i>Mg</i>	–	–	–						
<i>Xs</i>	5	10	20						

at the beginning of the experiments. The experimental surface units for settlement tests were made from 10 × 10 × 0.5 cm slate tiles in 9 and 3 different treatments at SS and SP sites, respectively: 1 treatment per tile (Table 1). Slate represents a high-energy surface and is a good substrate for mussel attachment (Young 1985, Babarro & Carrington 2011). Density of mussels per tile corresponded to 5, 10 and 20 ind. of each species within monospecific mussel beds (Tiles 1 to 6 at SS and 1 to 3 at SP; Table 1). For mixed mussel beds at SS (Tiles 7 to 9; Table 1), 20 ind. were used on each tile to establish mixed balanced (10 *Mytilus galloprovincialis* [*Mg*], 10 *Xenostrobus securis* [*Xs*]) or unbalanced ratios (5 *Mg* and 15 *Xs*, or 15 *Mg* and 5 *Xs*) (Table 1). For each species, 200 ind. were collected in the field and transported to the laboratory. After stripping biofouling from the shells and removing byssus from the ventral margin, individuals were allowed to establish primary attachment in the laboratory for 2 d prior to their transportation to experimental sites (see Babarro & Fernández Reiriz 2010 for details on animal maintenance). Nylon netting (5 mm mesh size) was used to cover mussels in order to allow seawater to flow in but prevent any initial predation by macro-invertebrates, especially when attachment was relatively weak. The nylon net was progressively cut over the following days and individuals were allowed to freely attach to slate tiles and move. Mussel death and disappearance from the slate tiles was likewise taken into account for mortality values. In the mesolittoral zone of both sites, slate tiles were deployed haphazardly at a depth corresponding to ~20% of aerial exposure. Triplicates were deployed at each site, which gave a total of 36 square experimental tiles (27 in SS and 9 in SP). The first experiment was carried out during autumn 2010 (September to December). This experimental set-up

was repeated in winter–spring 2011 (February to April) by including a new factor, i.e. substrate, with the aim of eliminating any mud deposition effect on the mussel beds by placing slate tiles on hard rocks. The experimental bivalves were maintained in the field for 3 mo in both cases.

Growth and mortality rates

Shell growth was reported by measuring shell length (SL) using Vernier callipers (precision ± 1 mm) at the beginning and end of the experiment. The initial SL of 23 mm allowed easy differentiation between experimental mussels and new recruits. Mussels were not marked and growth was expressed as the mean SL of all survivors on a single tile unit per replicate. As described above, mortality represented dead or disappeared mussels. Growth and mortality rates were obtained for both autumn and spring–winter experiments.

Byssal attachment and shell compressive forces

Before measuring SL of the survivors, a representative number of individuals were used for dislodgement and shell compressive force measurements (sub-samples). About a half (lowest density) to a fourth (highest density) of the mussel population on each slate tile was selected to that end. The attachment force of a mussel to the substrate or to another shell was measured by connecting the mussel to a spring scale (Digital Force Gauge DN431 with peak hold indication, resolution of 0.01 N). The spring scale was pulled perpendicular (normal) to the substrate until the individual dislodged (Bell & Gosline 1997, Babarro & Carrington 2011). Care was taken to avoid disturbing neighbours when sampling one individual. Therefore, mussels that were immediately adjacent to those selected for dislodgement were not considered when they had interconnected byssus threads. Byssal attachment of mussels was measured in both autumn and spring–winter experiments.

A group of 5 ind. from those selected for dislodgement measurements were also considered for shell compressive force analyses in the autumn 2010 experiment. The left valve was chosen for all compressive analyses. The compressive force required to crack the shell was measured using an universal testing machine, Instron 5566, with 1 kN load cell and at the rate of 2 mm s^{-1} . Each specimen was placed horizontally with the shell edge on the plane surface. The

compressive force was then applied with a 2 mm diameter steel tip placed on the curved surface at the highest point of an isolate dry single valve. Load-displacement curves up to shell break point were obtained. Shell strength was calculated from the maximum force measured in the curves and was then normalized by the shell thickness measured using a micro-calliper (Mitutoyo $0\text{--}25 \pm 0.01$ mm) at the point where the force was applied. Although such data do not provide an absolute value for compression strength of the shells, they can be used to compare the mechanical behaviour of the different shells.

After removing the mussels from the tiles, the accumulated mud was scraped off and collected as a function of mussel density (monospecific test) and species dominance (mixed test). The sediment was dried separately to constant weight (60°C , 48 h).

Statistical analysis

The 2-way ANOVA was used for the autumn experiment in order to estimate the effects of species (fixed, 2 levels: *Xenostrobus securis* and *Mytilus galloprovincialis*) and density (fixed, 3 levels: $n = 5, 10, 20$ for monospecific tests) or co-habiting balance (fixed, 3 levels: *Mg:Xs* 5:15, 10:10 and 15:5 for mixed tests) on mortality, shell length growth, byssal attachment, shell thickness and compressive force of the mussels deployed for both monospecific and mixed beds, respectively. The 2-way ANOVA was also performed to estimate the effects of site (fixed, 2 levels: SS and SP) and density (fixed, 3 levels: $n = 5, 10, 20$ for monospecific tests) between the previous response parameters for the alien *X. securis* and the autumn experiment. The results for *X. securis* at the 2 very distinct sites are presented in Appendix 1.

The 3-way ANOVA was selected to test the effect of species (fixed, 2 levels: *Xenostrobus securis* and *Mytilus galloprovincialis*), substrate (fixed, 2 levels: mud and hard rocks) and density (fixed, 3 levels: $n = 5, 10, 20$ for monospecific tests) or co-habiting balance (fixed, 3 levels: *Mg:Xs* 5:15, 10:10 and 15:5) on mortality, shell length growth and byssal attachment force of the mussels, respectively, and deployed either within monospecific or mixed mussel beds for the winter–spring experiment. Normality and homogeneity of variances were tested by Shapiro–Wilk's *W* and Levene's tests. Homogeneous groups were established *a posteriori* by using Tukey's test. Whenever the analysis of variance assumption was violated, rank transformation to create data with a perfect fit to a uniform distribution was followed.

All analyses were performed using the STATISTICA 7.0 software.

RESULTS

Mortality and shell growth rates: autumn 2010

Variability of the mortality of mytilids deployed monospecifically at SS was clearly dependent on the interaction term (species \times density), which is on the basis for the significant effect of both species and density factors (Fig. 2A, Table 2A). Mortality was higher for the alien *Xenostrobus securis* in the species comparison and the highest value (50.0%) was obtained with the lowest density (Fig. 2A). By contrast, mortality of *Mytilus galloprovincialis* remained much lower regardless of density (0–2.5%; Fig. 2A). Habitat comparison for the alien *X. securis* in the monospecific experiments showed that mortality was consistently lower in SP at the mouth of the River, and similarly to SS, high density caused greater mortality rates (Fig. 2A, Appendix 1).

Mortality was also higher for the alien species in the mixed beds deployed in SS but interestingly, its presence caused an increase in the mortality of the indigenous mussel with regard to monospecific tests (Fig. 2B). This is reflected in the significant incidence of species and co-habiting balance factors (Table 2A), and indicates that mortality in the mixed population as a whole per slate tile dropped significantly whenever *Mytilus galloprovincialis* was abundant (Fig. 2B).

Mud accumulation on slate tiles varied little for the monospecific experiment in SS, regardless of the mytilid species present (Fig. 2C). The only exception was for the lowest density of *Xenostrobus securis* (Fig. 2C). Habitat comparison for the alien species showed that mud accumulation was much lower in the SP samples regardless of density (Fig. 2C). The mud deposition on the slate tiles within mixed beds represented also a narrow range for the different co-habiting balance rates between mytilids (Fig. 2D).

The shell length growth of mussels deployed monospecifically at SS was significantly affected by the factor species, which accounted for a 4-fold higher growth of *Mytilus galloprovincialis* (Fig. 2E, Table 2B). By contrast, no effect of density was observed (Table 2B) with mean values of 38.42 and 9.34 $\mu\text{m d}^{-1}$ for *M. galloprovincialis* and *Xenostrobus securis*, respectively (Fig. 2E). Habitat comparison for the *X. securis* showed that the shell growth rate was significantly greater in SS (factor 4) than in SP samples (Fig. 2E). Just as at the SS site, density did not cause any significant change in shell growth in the SP samples (Fig. 2E, Appendix 1).

Surprisingly though, the shell growth of the indigenous *Mytilus galloprovincialis* was also significantly higher within mixed beds and regardless of any population balance (Fig. 2F, Table 2B). Despite any inter-specific competition on mixed beds, the magnitude of differences between the species was similar to that reported for the monospecific tests.

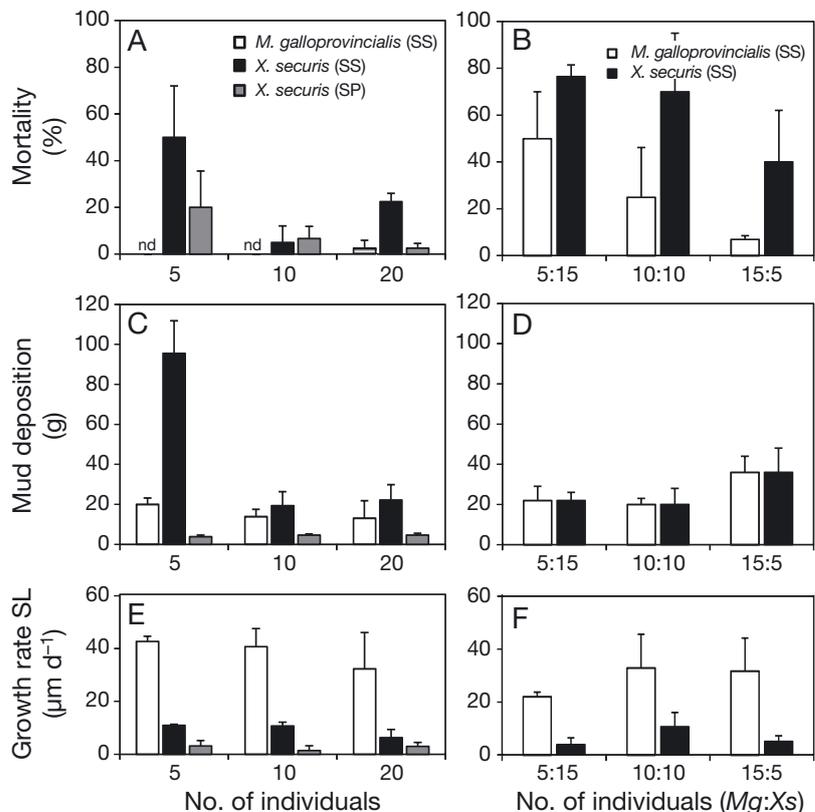


Fig. 2. *Mytilus galloprovincialis* (Mg) and *Xenostrobus securis* (Xs). Autumn. Mortality rates (%), mud deposition and shell length (SL) growth rate of mussels deployed in monospecific (A,C,E) and mixed co-habiting (B,D,F) beds as function of density and population balance at San Simón (SS). All means \pm SD. (A,C,E) Values obtained in monospecific tests with alien *X. securis* deployed at Sampaio (SP) are shown for site comparison. Ratios 5:15, 10:10 and 15:5 are balance rates of Mg:Xs in mixed mussel beds at SS. nd: not detected

This result can be linked to mussel behaviour illustrated in Fig. 3 for mixed experiments in which 2 differentiated layers were obtained at the end of the experiment, each corresponding to a different mytilid. The indigenous mussel climbed to the upper layers of the bed while the alien mussel was

clearly smothered and obliged to attach underneath within the mud influence zone (Fig. 3A).

Mortality and shell growth rates: winter–spring 2011

Mussel mortality within monospecific tests varied slightly with species factor and more significantly within substrates comparison (Fig. 4A, Table 3A). *Xenostrobus securis* showed higher mortality rates than *Mytilus galloprovincialis* when deployed on hard rocks (Fig. 4A). However, mortality increased significantly for both species on soft bottoms (Fig. 4A).

In like manner, mussel mortality on mixed beds varied significantly with species and substrate factors (Fig. 4B, Table 3A). Significance of interaction terms for co-habiting experiments (Table 3A) indicated that survival of both mytilids benefited again from hard rock substrate although *Xenostrobus securis* still showed higher mortality whenever its balance rate was observed to be favourable (5:15 *Mg:Xs*; Fig. 4B). The winter–spring experiment confirmed that the mussels differentiated into 2 layers within mixed beds (Fig. 3). Layer formation was regardless of substrate used, which indicated the great ability of *Mytilus galloprovincialis* to climb to the top layer to escape the mud and to smother the alien mussel.

The amount of mud that accumulated on the slate tiles deployed monospecifically varied inversely with the density of individuals (Fig. 4C). Moreover, mud deposition in the winter–spring experiment was much higher than in the autumn experiment, especially at low densities (Figs. 2C & 4C). Mud deposi-

Table 2. *Mytilus galloprovincialis* (*Mg*) and *Xenostrobus securis* (*Xs*). Two-way ANOVA of (A) mean mortality and (B) shell length growth rates of mussels as a function of species (*sp*) (fixed: *Mg* and *Xs*) and density (fixed: $n = 5, 10, 20$ for monospecific experiments, or 5:15, 10:10 and 15:5 *Mg:Xs* for mixed co-habiting experiments). Autumn 2010. **Bold**: significant values

Factor	df	MS	F	p
(A) Mortality (%)				
Monospecific expt				
sp	1	27.2321	118.4752	<0.001
n	2	3.1866	13.8635	<0.001
sp × n	2	2.0377	8.8652	<0.01
Error	12	0.2299		
Co-habiting expt				
co-habiting (n)	2	2.6106	10.9013	<0.01
sp	1	5.0469	21.0747	<0.001
co-habiting (n) × sp	2	0.4480	1.8708	0.196
Error	12	0.2395		
(B) Shell growth ($\mu\text{m d}^{-1}$)				
Monospecific expt				
sp	1	9.1784	89.5570	<0.001
n	2	0.3581	3.4950	0.064
sp × n	2	0.0166	0.1620	0.853
Error	11	0.1025		
Co-habiting expt				
co-habiting (n)	2	0.7550	3.0352	0.089
sp	1	10.7308	43.1368	<0.001
co-habiting (n) × sp	2	0.2344	0.9422	0.419
Error	11	0.2488		



Fig. 3. *Mytilus galloprovincialis* and *Xenostrobus securis*. Autumn. Mussel bed disposition observed at the end of experimental time illustrating the differentiation of the 2 interacting species into 2 layers. In mixed beds, indigenous *M. galloprovincialis* (A) colonise on top of alien *X. securis* smothering them underneath and restricting them to the mud influence layer or (B) simply colonise top layers on hard rocks

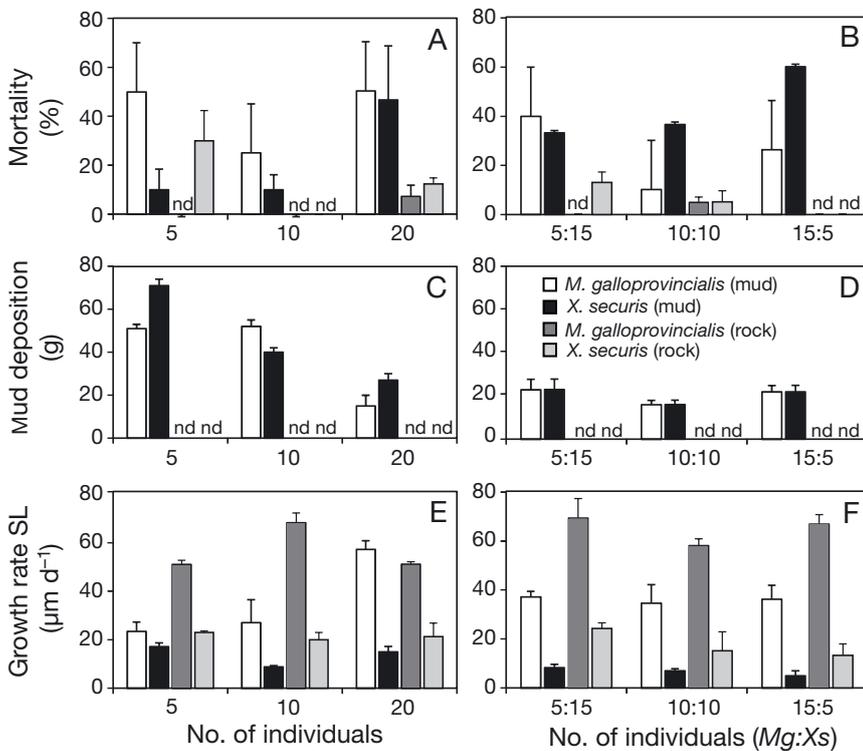


Fig. 4. *Mytilus galloprovincialis* (Mg) and *Xenostrobus securis* (Xs). Winter-spring. Mortality rates, mud deposition and shell length (SL) growth rate values of the mussels deployed in monospecific (A,C,E) and mixed co-habiting (B,D,F) beds as function of density, population balance and type of substrate. All means + SD. For further details, see legend of Fig. 2

tion on the slate tiles used for the mixed co-habiting populations varied little (Fig. 4D).

The shell growth of mussels sampled within the monospecific series varied significantly with all fixed factors such as species, density and substrate (Fig. 4E, Table 3B). Significance of the density interacting with species and substrate factors (Table 3B) was, at least partially, linked to mud deposition (Fig. 4C,E). Growth of *Mytilus galloprovincialis* on soft bottoms was highest when the mussels were deployed at the highest density and occupied most of the substrate area, which coincided with the lowest mud accumulation. Such benefit of a densely occupied area was not observed when mussels were deployed on hard substrates where mud effect was low (Fig. 4E). The growth rate of *Xenostrobus securis* did not respond to different mud accumulation patterns, but increased when deployed on hard rocks (Fig. 4E). As a general pattern, shell growth was much higher for *M. galloprovincialis* in the species comparison and on hard rocks for substrate comparison (Fig. 4E). With regard to the mixed co-habiting experiment, the highest growth rates were also reported for *M. galloprovincialis* (species comparison) and hard rocks (substrate

comparison) (Fig. 4F, Table 3B). Differences encountered by the co-habiting balance (Table 3B) corresponded to a drop in growth rate of the alien *X. securis* when its abundance on the mixed bed was lower (15:5; Fig. 4F).

Byssal attachment and shell compressive forces: autumn 2010

Both mytilids exhibited similar byssal attachment force in the monospecific experiments with the only exception of the lowest density deployed for the *Mytilus galloprovincialis* whose force value increased significantly (Fig. 5A). The high value meant that the significance of the species factor would depend on density as illustrated by the interaction term (Table 4). Habitat comparison for *Xenostrobus securis* showed no differences for byssal attachment force between sites, regardless of mussel density (Fig. 5A, Appendix 1).

With regard to mixed mussel beds, *Mytilus galloprovincialis* showed greater attachment force regardless of the co-habiting balance (Fig. 5B, Table 4). Strength of attachment for the mixed population as a whole per slate tile dropped with abundance of *M. galloprovincialis* (Fig. 5B, Table 4).

Mytilus galloprovincialis secreted 15% thicker and stronger shells than *Xenostrobus securis* deployed monospecifically in SS and regardless of the density (Fig. 5C,E, Table 4). Habitat comparison for *X. securis* showed no significant differences in shell compressive force despite the slightly thinner shells secreted by this species at SP and regardless of density values (Fig. 5C,E) (Appendix 1).

Differences in shell thickness and strength between mytilids were even higher for the mixed beds (Fig. 5D,F) although the incidence of a high species factor for *Mytilus galloprovincialis* depended on the co-habiting density, i.e. equally balanced and more abundant rates for *M. galloprovincialis* (see interaction terms; Table 4).

The shell compressive forces standardized by shell thickness showed differences between species and densities for the monospecific experiment (Fig. 6A). Habitat comparison for the alien *Xenostrobus securis* likewise did not report any differ-

Table 3. *Mytilus galloprovincialis* (*Mg*) and *Xenostrobus securis* (*Xs*). Three-way ANOVA of (A) mean mortality and (B) shell length growth rate of mussels as a function of species (sp) (fixed: *Mg* and *Xs*), density (fixed: n = 5, 10, 20 for monospecific experiments, or 5:15, 10:10 and 15:5 *Mg*:*Xs* for mixed co-habiting experiments) and substrate (su) (fixed: mud and hard rock). Winter–spring 2011. **Bold**: significant values

Factor	df	(A) Mortality (%)			(B) Shell growth ($\mu\text{m d}^{-1}$)			
		MS	F	p	MS	F	p	
Monospecific expt	sp	1	12.1961	5.9192	<0.05	7.9929	256.2024	<0.001
	n	2	5.1036	2.4769	0.105	0.2302	7.3808	<0.01
	su	1	21.7075	10.5353	<0.01	2.4127	77.3321	<0.001
	sp × n	2	0.9617	0.4667	0.633	0.3427	10.9800	<0.001
	sp × su	1	0.0003	0.0001	0.991	0.0125	0.4014	0.533
	n × su	2	2.4615	1.1947	0.320	0.4722	15.1342	<0.001
	sp × n × su	2	1.4833	0.7199	0.497	0.1701	5.4510	<0.05
	Error	24	2.0605			0.0312		
Co-habiting expt	sp	1	3.153	12.2095	<0.01	21.6943	308.5390	<0.001
	co-habiting (n)	2	0.9796	3.3082	0.054	0.3415	4.8570	<0.05
	su	1	51.9631	175.4904	<0.001	5.1268	72.9140	<0.001
	sp × n	2	0.4256	1.4374	0.257	0.2537	3.6080	<0.05
	sp × su	1	0.1299	0.4387	0.514	0.2373	3.3750	0.079
	n × su	2	4.1539	14.0286	<0.001	0.0503	0.7150	0.499
	sp × n × su	2	4.7260	15.9608	<0.001	0.0196	0.2790	0.759
	Error	24	0.2961			0.0703		

Table 4. *Mytilus galloprovincialis* (*Mg*) and *Xenostrobus securis* (*Xs*). Two-way ANOVA of byssal attachment force, shell thickness and shell compressive force as a function of species (sp) (fixed: *Mg* and *Xs*) and density (fixed: n = 5, 10, 20 for monospecific experiments or 5:15, 10:10 and 15:5 *Mg*:*Xs* for mixed co-habiting experiments). Autumn 2010. **Bold**: significant values

Factor	df	MS	F	p	
Byssal attachment (N)					
Monospecific expt	sp	1	0.8752	6.3040	<0.05
	n	2	0.1023	0.7370	0.483
	sp × n	2	0.7389	5.3220	<0.01
	Error	59	0.1388		
Co-habiting expt	co-habiting (n)	2	0.6177	3.5150	<0.05
	sp	1	7.1651	40.6760	<0.001
	co-habiting (n) × sp	2	0.4521	2.5720	0.084
	Error	67	0.1758		
Shell thickness (mm)					
Monospecific expt	sp	1	0.1888	5.7386	<0.05
	n	2	0.0009	0.0267	0.974
	sp × n	2	0.0068	0.2062	0.815
	Error	22	0.0329		
Co-habiting expt	co-habiting (n)	2	0.0068	0.2746	0.763
	sp	1	0.1097	4.4039	<0.05
	co-habiting (n) × sp	2	0.1515	6.0813	<0.01
	Error	21	0.0249		
Shell compressive force (N)					
Monospecific expt	sp	1	0.3998	4.4004	<0.05
	n	2	0.0125	0.1378	0.872
	sp × n	2	0.0217	0.2391	0.789
	Error	21	0.0909		
Co-habiting expt	co-habiting (n)	2	0.0349	0.3150	0.733
	sp	1	0.9888	8.9307	<0.01
	co-habiting (n) × sp	2	0.7095	6.4083	<0.01
	Error	21	0.1107		

ence between sites and densities (Fig. 6A).

By contrast, standardized compressive forces of the shell were significantly higher for *Mytilus galloprovincialis* when deployed on mixed beds, especially for the equal (10:10 *Mg*:*Xs*) and favourable (15:5 *Mg*:*Xs*) balance rates with values ranging from 156.4 to 157.1 and from 89.9 to 117.1 N mm⁻¹ for the indigenous and alien mussels, respectively (Fig. 6B, Appendix 1 for statistical analysis).

Byssal attachment force: winter–spring 2011

The byssal attachment force of mytilids varied significantly with the factors species, density and substrate (Fig. 7A, Table 5). Attachment strength was highest in *Mytilus galloprovincialis* for species comparison and on hard rocks for comparison between substrates (Fig. 7A). The significant effect of density (as monospecific and interaction terms; Table 5) in the statistical model was a consequence of the highest attachment strength recorded

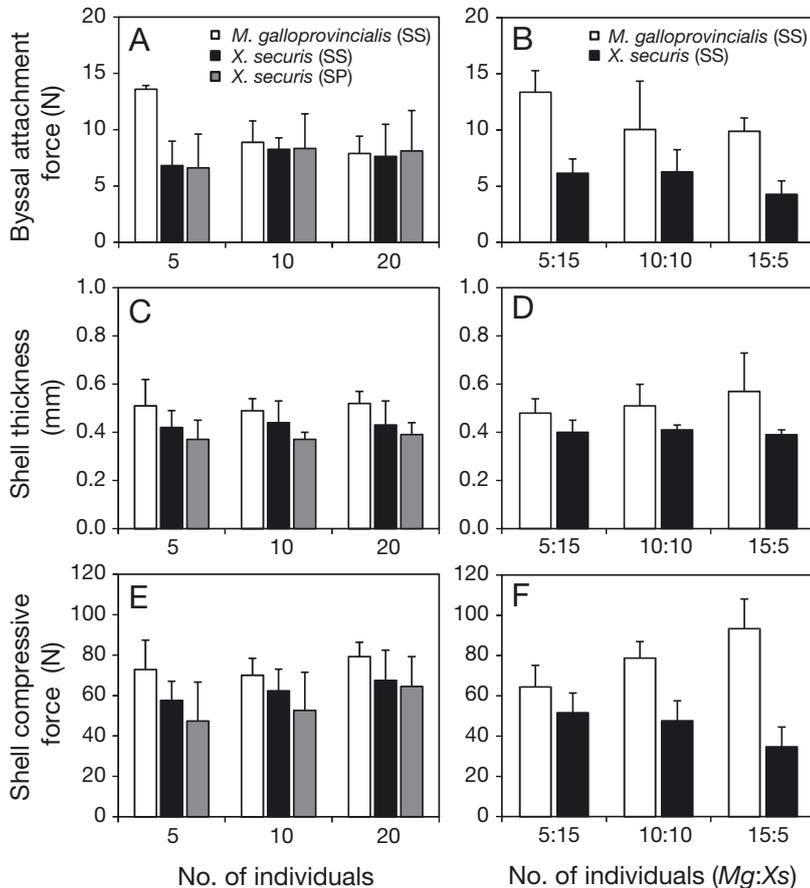


Fig. 5. *Mytilus galloprovincialis* and *Xenostrobus securis*. Autumn. Byssal attachment force, shell thickness and shell compressive force values of the mussels deployed in monospecific (A,C,E) and mixed co-habiting (B,D,F) mussel beds as function of density and population balance at San Simón (SS). (A,C,E) Values obtained in monospecific tests with alien *X. securis* deployed at Sampaio (SP) are shown for site comparison. For further details, see legend of Fig. 2

for *M. galloprovincialis* on soft bottoms with highest density (Fig. 7A), whereas values for the alien mussel remained unchanged for different densities. The attachment force of both mussel species deployed on hard rocks remained unchanged over densities although values were higher for the indigenous mussel (17.7 to 17.9 N) as compared to the alien mussel (9.5 to 12.1 N) (Fig. 7A).

The attachment force variability of mussels inhabiting mixed beds was significantly affected by species and substrate but not by the co-habiting ratio (Fig. 7B, Table 5). The attachment strength of the indigenous mussel increased from 10.6 to 16.6 N, when deployed on muddy bottoms, to 17.4 to 20.5 N on hard rocks (Fig. 7B). By contrast, the alien mussel attached with similar strength regardless of substrate but constantly weaker when compared to the indigenous mussel (Fig. 7B).

DISCUSSION

Successful invasions of bivalve species may be regulated by the competitive potential of the introduced species (Shinen & Morgan 2009, Caro et al. 2011). Nevertheless, co-existence of *Mytilus galloprovincialis* and *Xenostrobus securis* investigated here as well as prevention of competitive exclusion may occur as consequence of the relatively calm environment, i.e. moderate disturbance levels by hydrodynamics (Erlandsson et al. 2006). Deployment of both the mytilid species on space-limiting mussel beds revealed that the indigenous mussel *Mytilus galloprovincialis* was an extraordinary competitor and dominant species over the alien *Xenostrobus securis*. (1) The alien mussel showed much higher mortality rates within monospecific and mixed populations (Fig. 2A,B). (2) The indigenous survivors exhibited a 4-fold greater growth when deployed monospecifically regardless of density (Fig. 2E) and more surprisingly, similar growth differences were reported in the mixed experiments, also regardless of population balance rates (Fig. 2F).

Reduced growth and high mortality rates represent 2 basic consequences of competition (Fréchette et al. 2005). Interspecific competition within mixed beds of *Mytilus galloprovincialis* and *Xenostrobus securis* significantly increased

mortality in both species although in a higher magnitude for the alien *X. securis* (autumn experiment). High mortality of the independently deployed *X. securis* coincided with the highest mud accumulation (and lowest density). However, mortality within mixed beds cannot be accounted for by mud only but was rather due to the physical competition for space. Possibly due to this competition growth of the indigenous survivors was consistently higher for monospecific and mixed beds.

These responses of both mytilid species highly depended on behavioural patterns. Most mussels deployed within monospecific experiments maintained their positions (primarily attached to the substrate). Only few specimens (mainly of the indigenous species) were found to attach on shells of other individuals (J. M. F. Babarro, pers. obs.). Interestingly, a clear distribution between 2 distinct layers

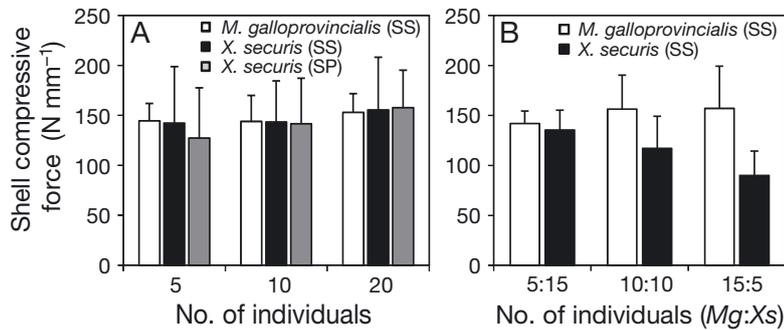


Fig. 6. *Mytilus galloprovincialis* (Mg) and *Xenostrobus securis* (Xs). Autumn. Standardized shell compressive force values of mussels deployed in (A) monospecific and (B) mixed co-habiting mussel beds as function of density and population balance at San Simón (SS). (A) Values obtained in monospecific tests with alien *X. securis* deployed at Sampaio (SP) are shown for site comparison. Further details, see legend of Fig. 2

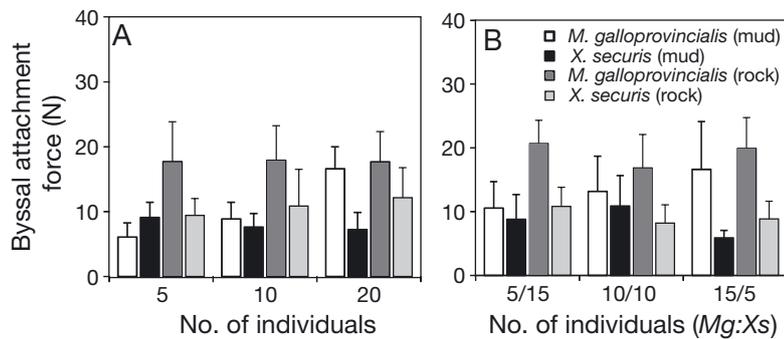


Fig. 7. *Mytilus galloprovincialis* (Mg) and *Xenostrobus securis* (Xs). Winter-spring. Byssal attachment force of mussels deployed in (A) monospecific and (B) mixed co-habiting mussel beds as a function of density, population balance and type of substrate

was observed within mixed beds (Fig. 3). *Xenostrobus securis* was clearly smothered and restricted to the lower mud influenced layer, whereas *Mytilus galloprovincialis* migrated and colonised the upper sites with better access to clean seawater. Therefore, the indigenous *M. galloprovincialis* interacted with the alien *X. securis* primarily through physical interference competition (see also Fréchette et al. 1992, Alunno-Bruscia et al. 2001) because of its higher ability to move and occupy more advantageous positions above the mud. Other surveys in which *M. galloprovincialis* was an invader also illustrated such potential for aggregation on top and restricting the mobility of other species, e.g. *M. californianus* (Shinen & Morgan 2009). Paine & Levin (1981) showed how adult mussels can move short distances to establish a dynamic mussel bed structure with constant rearrangement of individuals that led to significant changes in mortality (Schneider et al. 2005). Consequently, *M. galloprovincialis* as an epibenthic mytilid was more sensitive to mud and escaped from the bot-

tom layer aided by its extensible (and larger) byssus (Brazee & Carrington 2006, Babarro & Carrington 2011) and its high mobility (Shinen & Morgan 2009, present study). On one hand, mud accumulation may exert a great influence on the competitive dynamics between mytilids (Rius & McQuaid 2006, Zardi et al. 2008). This is clearly reflected in the higher mortality rates of *M. galloprovincialis* after the winter-spring experiment with regard to autumn most likely linked to higher mud accumulation on experimental substrates (Figs. 2C & 4C). On the other hand, the migration ability of the indigenous mussel represented a great advantage especially in calm waters in which the hydrodynamic load affecting the mussel patches would not be excessive (Babarro & Carrington 2011).

Mytilus galloprovincialis possesses larger, much thicker and stronger byssus filaments than *Xenostrobus securis* (Babarro & Lassudrie 2011); this would permit such performance on mixed mussel beds. Shorter byssus would oblige the alien *X. securis* to be attached near the bottom where the mud influence is greater and could occasionally interfere with valve gaping, filtering (Cheung & Shin (2005) and gas exchange. The latter

scenario may include anoxic events with negative consequences for survival. In case the amount of mud becomes significant, the radial byssus disposition adopted by *M. galloprovincialis* (J. F. M. Babarro, pers. obs., see also Brazee & Carrington 2006) and its larger foot (Babarro & Lassudrie 2011) may be crucial to remove accumulated mud for survival purposes (see Fig. 2A,C for zero mortality of the indigenous mussel at lower density linked to much lower mud accumulation). By contrast, the alien mussel has shown great ability to secrete a huge amount of extremely thin byssus filaments (up to 1000; Babarro & Lassudrie 2011) which may favour better attachment on soft bottoms through many anchorage points.

As a general pattern, *Mytilus galloprovincialis* secreted thicker and stronger shells as well as byssus filaments especially within mixed experiments (Fig. 5). Better access to natural resources by attaching on top of the beds and other species-specific features such as greater filtration capacity (unpubl. data) would permit to allocate more energy to these protective

Table 5. *Mytilus galloprovincialis* (Mg) and *Xenostrobus securis* (Xs). Three-way ANOVA of byssal attachment force (N) established by mussels as a function of species (sp) (fixed: Mg and Xs), density (fixed: n = 5, 10, 20 for monospecific experiment or 5:15, 10:10 and 15:5 Mg:Xs for mixed co-habiting experiments) and substrate (su) (fixed: mud and hard rock). Winter–spring 2011. **Bold**: significant values

	Factor	df	MS	F	p
Monospecific expt	sp	1	3.2038	20.7431	<0.001
	n	2	0.6123	3.9643	<0.05
	su	1	5.1931	33.6220	<0.001
	sp × n	2	0.6993	4.5282	<0.05
	sp × su	1	0.5245	3.3961	0.068
	n × su	2	0.1882	1.2194	0.300
	sp × n × su	2	1.2558	8.1312	<0.001
	Error	103	0.1545		
Co-habiting expt	sp	1	8.4211	43.2712	<0.001
	Co-habiting (n)	2	0.0181	0.0931	0.911
	su	1	2.0512	10.5407	<0.01
	sp × n	2	0.4160	2.1372	0.123
	sp × su	1	0.5774	2.9670	0.088
	n × su	2	0.5154	2.6482	0.076
	sp × n × su	2	0.2833	1.4564	0.238
	Error	103	0.1946		

structures, providing better capacity for *M. galloprovincialis* to withstand biotic and abiotic stress and show competitive dominance. Surprisingly, standardized shell compressive force (by shell thickness) showed no differences between species for the monospecific tests but were significantly higher for the indigenous mussels on mixed mussel beds, which indicated that shell thickness alone does not explain strength differences (i.e. energy allocation patterns from available resources). Veiga et al. (2011) observed that *M. galloprovincialis* is greatly consumed by *Carcinus maenas* because of its shorter handling and breaking time values as compared to *Xenostrobus securis*, which in turn might facilitate the invasion of the alien. Our results do not support such a hypothesis although other factors like shell morphology especially on the ventral side and umbones curves for predator's access (Veiga et al. 2011) could have played a role. Veiga et al. (2011) carried out their survey in controlled laboratory conditions and results may vary significantly in the field where mussels form dense conglomerates firmly attached to the substratum and other congeners with less space available for predator attack. Differences between laboratory and field results on related eco-physiological responses such as attachment strength of both mytilids were recently highlighted (Babarro & Lassudrie 2011) based on the relatively short and long-term exposure of the mussels, respectively.

Performance of *Xenostrobus securis* at 2 very different sites showed that mortality was consistently lower at the mouth of the river although growth rate of survivors was observed to decrease here as compared to SS (Fig. 2A,E). By contrast, no differences were obtained for the byssal attachment and shell compressive forces despite slightly thinner shells in the river mouth samples, which represent a rather constant energy investment in protective tissues regardless of environment. The alien *X. securis* established densely aggregated assemblages at the river site and most likely benefited from the low presence of predators in this highly variable habitat (Babarro & Lassudrie 2011) and by the low mud deposition. On the other hand, *X. securis* would have allocated more energy to shell growth when deployed in the inner Ría site (SS) because of the higher availability of total seston and other particulate material of marine origin (Babarro & Carrington 2011).

Competition patterns between species can vary over space and time and consequently, dominance features of one species over the other cannot be fixed (Rius & McQuaid 2006). When mussel responses were extended to another season and new substrate, differences between species were even larger, which evidenced *Mytilus galloprovincialis* as the dominant species regardless of any population balance rate and substrate. Surprisingly, despite its infaunal lifestyle, the alien *Xenostrobus securis* clearly benefited (in terms of survival and growth) from the absence of mud on slate tiles, which highlights the negative effect of mud accumulation on population dynamics.

Although theory predicts that a successful invader must have some advantageous features over indigenous species, at least over particular time or space scales (Shea & Chesson 2002), the alien *Xenostrobus securis* did not perform better than the indigenous *Mytilus galloprovincialis* in any parameter tested for different seasons and substrates. Nevertheless, aspects like fecundity, re-colonisation rates, early recruitment, good dispersal ability and large genetic variations (Erlandsson et al. 2006) may help to complete the actual invasive potential towards other areas. Given the fact that the distribution of mytilids along the sheltered waters of the inner Ría coastline does not follow any clear vertical segregation, factors like tidal movements, salinity or predation pressure would play a significant role for the expansion of the alien species in the near future. The much lower biotic pressure and extreme salinity variation at the mouth of the river would be the basis for the greater prevalence of the alien here, far from competition interference of the native mussel. The larval disper-

sal of the alien mytilid might potentially reach other areas of the Ría according to the persistent currents regime that exchange surface waters between the inner and outer areas (Álvarez Salgado et al. 2000), even though eggs of the alien might be successfully fertilised in salinities within the range of 8 to 17.5 ppt (Santaclara et al. 2007). If larval dispersal patterns of the alien mytilid expand far from the highly variable inner Ría, *X. securis* would suffer physical interference by the indigenous mussel even at higher magnitudes than shown here. The displacement of the native species will not take place just by aggression of the alien *X. securis* but rather as a consequence of its worse performance on a large-scale mud influence and extreme salinity exposure that would limit the performance of the indigenous mussel.

NOTE ADDED IN PROOF

During the acceptance and proof procedure of the article, a new reference on the alien mussel *Xenostrobus securis* appeared (Guerra et al. 2013). The genus name *Limnoperna* was established after analysing a number of shell parameters as well as molecular identification against available sequences from GenBank and web servers of the National Center for Biotechnology Information (USA). To date, all studies on the black pygmy mussel used the genus *Xenostrobus* as a synonym for *Limnoperna*. However, from now onwards and according to recent knowledge the correct name *Limnoperna securis* instead of *Xenostrobus securis* should be used for this alien mytilid.

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Appendix

Table A1. *Mytilus galloprovincialis* (*Mg*) and *Xenostrobus securis* (*Xs*). Two-way ANOVA of the mean mortality, shell length growth, byssal attachment, shell thickness and shell compressive force of the mussel *X. securis* as a function of site (fixed: San Simón and Sampaio) and density (fixed: $n = 5, 10, 20$) for the monospecific experiments. Standardized shell compressive force variability was analysed as a function of species (*sp*) (fixed: *Mg* and *Xs*) and co-habiting number (fixed: 5:15, 10:10 and 15:5 for *Mg*:*Xs*) for the mixed experiments. Autumn 2010. **Bold**: significant values

Factor	df	MS	F	p
Mortality (%)				
site	1	0.2395	9.2261	<0.05
n	2	0.1567	6.0366	<0.05
site × n	2	0.0680	2.6211	0.1136
Error	12	0.0259		
Shell growth ($\mu\text{m d}^{-1}$)				
site	1	3.0396	50.7355	<0.001
n	2	0.0983	1.6408	0.2345
site × n	2	0.1886	3.1490	0.0795
Error	12	0.0599		
Byssal attachment (N)				
Monospecific expt				
site	1	0.0006	0.0189	0.8910
n	2	0.0864	2.8095	0.0673
site × n	2	0.0069	0.2257	0.7892
Error	67	0.0308		
Shell thickness (mm)				
site	1	0.1552	5.1994	<0.05
n	2	0.0008	0.0268	0.9736
site × n	2	0.0140	0.4695	0.6317
Error	21	0.0299		
Shell compressive force (N)				
sp	1	0.0380	1.1628	0.2931
n	2	0.0250	0.7649	0.4779
sp × n	2	0.0152	0.4657	0.6340
Error	21	0.0327		
Standardized shell compressive force (N mm^{-1})				
Co-habiting expt				
co-habiting (n)	2	0.0229	1.5332	0.2399
sp	1	0.0905	6.0702	<0.05
co-habiting (n) × sp	2	0.0352	2.3592	0.1191
Error	21	0.0149		