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

Jose M.F. Babarro[1*], María José Abad[2]

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

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

*Corresponding author. Email: jbabarro@iim.csic.es

Tel.: +34 986 231930 Ext. 207; Fax: +34 986 292762

ABSTRACT

The co-existence patterns of two mytilid species were studied, in order to evaluate the performance of the alien mussel *Xenostrobus securis* and the indigenous one *Mytilus galloprovincialis* through independent and mixed co-habiting experiments in the Ría de Vigo (NW Spain). *Mytilus galloprovincialis* was found to be the best performer in all tests. Shell growth was approximately 4-fold greater for the indigenous mussel when deployed independently 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 influence layer. The alien *X. securis* however was found to inhabit underneath the *M. galloprovincialis* layer which resulted in higher mortality rates. Species-specific features like byssus filaments and lifestyle may account for such different behaviour. *Mytilus galloprovincialis* secreted thicker and stronger shells and byssus regardless of their density in both independent and mixed experiments. This might indicate that the indigenous mussel performs better when faced 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. *Xenostrobus* *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*; performance; competition; plasticity; byssus

INTRODUCTION

Biological invasions have emerged as a major topic in ecological studies and environmental policy issues (Pfeiffer and Voeks 2008). The presence of exotic species may bring significant changes in the recipient community structure as a consequence of inter-specific interactions which may give rise to the variability of species richness, community balance and diversity (Vermeij 1996; Crooks and Khim 1999; Grosholz 2002; Fridley et al. 2007). Such interactions between species may lead to competition and eventually the exclusion of the worst performer (Branch and 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 (Zardi et al. 2008; Rius and McQuaid 2006; Nicastro et al. 2010; Dutton and Hofmann 2008; Bownes and McQuaid 2010 among others) and even facilitation (Rius and McQuaid 2009) have been reported for the specific case of bivalves 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 displaced whenever the alien species show superior competitive abilities and physiological tolerance (Steffani and 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 latter cited surveys 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 invader species with respect to the indigenous species have been related to their abilities for escaping from natural enemies like predators and parasites (Shea and 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 and 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 and Steffani 2004; Bownes and McQuaid 2010), the Pacific Northwest front (Shinen and 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 is 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; Garci et al. 2007; Sabelli and Speranza 1994; 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. Such a species-specific feature is proposed as a trait that is potentially associated with rapid population growth and high fecundity (Ehrlich 1989). The life-span of *X. securis* is relatively short (about one year) and it usually inhabits high-density populations (Wilson 1969) that might occasionally smother the native infaunal communities (Zenetos et al. 2004). *Xenostrobus securis* is considered to be a serious threat as a bio-invader with negative impact on indigenous ecosystems (Darrigran 2002) and it has been listed among the “100 Worst Invasive Species” in the Mediterranean Sea (Streftaris and Zenetos 2006). The current distribution of *X. securis* in Galicia (NW Spain) is restricted to the mouth of the River Oitavén-Verdugo (Sampaio, SP; 8.700 ± 550 individuals m^{-2} according to Garci et al. 2007) where *M. galloprovincialis* is absent and the adjacent areas in the inner Ría de Vigo (San Simón, SS) (Figure 1) where it co-exists with the indigenous mussel at relatively balanced rates (Gestoso et al. 2012). The competition between both mytilids 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 and 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 and Lassudrie 2011). Although the alien mussel has shown an extraordinary ability for strong attachment in wide abiotic conditions, such 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 two competing species.

In Galicia (NW Spain), the cultivation of *M. galloprovincialis* represents a widely diversified industry with a great economic impact (Labarta et al. 2004). The potential expansion of the invader *X. 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 the 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 the mud component becomes significant on mussel beds; and (2) energetic constraints derived from 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. Independent and mixed co-habiting tests were carried out in two consecutive seasons and on different (soft and hard) substrates in order to cover both spatial and temporal components of inter-specific competition.

MATERIALS AND METHODS

Region and general approach

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

The competition ability of mytilids was assessed through a) mortality and growth estimates in the natural environment with mud transport influence, and b) the strength of both byssal attachment and shell which are indicative of energy investment into these protective tissues. A common mussel size of 23 mm (± 1.3) shell length was selected at the beginning of the experiments. The surface units were made up of 10 x 10 x 0.5 cm slate tiles with 9 and 3 different treatments at SS and SP sites, respectively, one treatment per tile (Table 1). Slate represents a high-energy surface and is a good substrate for mussel attachment (Young 1985; Babarro and Carrington 2011). Density of mussels per slate tile corresponded to 5, 10 and 20 individuals of each species within independent mussel beds (tiles 1-6 at SS and 1-3 at SP sites; Table 1). For mixed mussel beds at SS site (tiles 7-9; Table 1), a total of 20 mussels were used on each tile to establish a mixed balance (10 *M. galloprovincialis*, Mg / 10 *X. securis*, Xs) or unbalance (5 Mg / 15 Xs and 15 Mg / 5 Xs) rates (Table 1). Two hundred individuals of each species were collected in the field and transported to the laboratory. After cleaning the shell of any biofouling and removal of byssus from the ventral margin, individuals were allowed to establish primary attachment in the laboratory for 2 days prior to their transportation to experimental sites (see Babarro and 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 netting was progressively cut 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. Slate tiles were deployed haphazardly in the mesolittoral zone of both sites at approximately 20% of aerial exposure. Three replicates were deployed at each site which gave a sum total of 36 quadrants (27 in San Simón and 9 in Sampaio). The first experiment was carried out during autumn 2010 (September-December). This experimental set-up was repeated in winter-spring 2011 (February-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 animals were maintained in the field for 3 months in both cases.

Growth and mortality rates

Shell growth was reported by measuring shell length using Vernier callipers (precision ± 1 mm) at the beginning and end of the experiment. The initial mussel shell length (23 mm) allowed easy differentiation between experimental animals and new recruits. Animals were not marked and mussel growth was measured as the mean shell length value of all survivors on a single tile unit per replicate. As described above, mortality represented dead animals plus any individual that had disappeared from the tiles. Growth and mortality rates were obtained for both autumn and spring-winter experiments.

Byssal attachment and shell compressive forces

Before measuring the shell length 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 individuals on the substrate or to each other’s shells was measured by connecting the mussel to a spring scale (Digital Force Gauge DN431 with peak hold measurement, resolution of 0.01N). The spring scale was pulled perpendicular (normal) to the substrate until dislodgement occurred (Bell and Gosline

1997; Babarro and 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 five individuals 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 0-25 mm, ± 0.01mm, Made in Japan) 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 slate tiles, any mud accumulated was scraped and collected as a function of mussel density (independent test) and species dominance (mixed test). The sediment was dried separately to constant weight (60ºC, 48h).

Statistical analysis

The two-way ANOVA was used for the autumn experiment, in order to estimate the effects of species (fixed, two levels: *X. securis* and *M. galloprovincialis*) and density (fixed, three levels: n = 5, 10, 20 for independent tests) or co-habiting balance (fixed, three levels: Mg / Xs 5 / 10, 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 independent and mixed beds, respectively. The two-way ANOVA was also performed to estimate the effects of site (fixed, two levels: San Simón and Sampaio) and density (fixed, three levels: n = 5, 10, 20 for independent tests) between the previous response parameters for the alien *X. securis* and the autumn experiment. The latter results for the alien mussel at the two very distinct sites are presented in appendix 1.

The three-way ANOVA was selected to test the effect of species (fixed, two levels: *X. securis* and *M. galloprovincialis*), substrate (fixed, two levels: mud and hard rocks) and density (fixed, three levels: n = 5, 10, 20 for independent tests) or co-habiting balance (fixed, three levels: Mg / Xs 5 / 10, 10 / 10 and 15 / 5) on mortality, shell length growth and byssal attachment force of the mussels, respectively, and deployed either within independent or mixed mussel beds for the winter-spring experiment. Normality and homogeneity of variances were tested by Shapiro-Wilk´s W and Levene tests. Homogeneous groups were established *a posteriori* by using Tukey 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 independently at San Simón was clearly dependent on the interaction term (species x density) which is on the basis for the significant effect of both species and density factors (Figure 2A; Table 2A). Mortality was higher for the alien *X. securis* in the species comparison and the highest value (50.0%) was obtained with the lowest density (Figure 2A). By contrast, mortality of *M. galloprovincialis* remained much lower regardless of density (0-2.5%; Figure 2A). Habitat comparison for the alien *X. securis* in the independent experiments showed that mortality was consistently lower in Sampaio at the mouth of the River and similarly to San Simón, high density caused greater mortality rates (Figure 2A; Appendix 1).

Mortality was also higher for the alien mussel in the mixed beds deployed in San Simón but interestingly, its presence caused an increase in the mortality of the indigenous mussel with regard to independent tests

(Figure 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 unit dropped significantly whenever there was abundance of the indigenous mussel (Figure 2B).

Mud accumulation on slate tiles varied within a narrow range for the independent experiment in San Simón, regardless of the mytilid species present (Figure 2C). The only exception was reported for the lowest density of the alien mussel (Figure 2C). Habitat comparison for the alien *X. securis* showed that mud accumulated was much lower in the Sampaio samples regardless of density (Figure 2C). The mud content on the slate tiles within mixed beds represented also a narrow range for the different co-habiting balance rates between mytilids (Figure 2D).

The shell length growth of mussels deployed independently at San Simón was significantly affected by the factor species which accounted for a 4-fold higher growth for the indigenous *M. galloprovincialis* (Figure 2E; Table 2B). By contrast, no effect of density was reported (Table 2B) with mean values of 38.42 and 9.34 µm day^{-1} for *M. galloprovincialis* and *X. securis*, respectively (Figure 2E). Habitat comparison for the alien *X. securis* showed that the shell growth rate was significantly greater in the San Simón (4-fold factor) than in the Sampaio samples (Figure 2E). Just as at the San Simón site, density did not cause any significant change in shell growth in the Sampaio samples (Figure 2E; Appendix 1).

Surprisingly though, the shell growth of the indigenous *M. galloprovincialis* was also significantly higher within mixed beds and regardless of any population balance (Figure 2F; Table 2B). Despite any inter-specific competition on mixed beds, the magnitude of differences between the species was similar than that reported for the independent tests. This result can be linked to mussel behaviour illustrated in Figures 3A-B for mixed experiments in which two 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 (Figure 3A).

Mortality and shell growth rates: winter-spring 2011

Mussel mortality within independent tests varied slightly with species factor and more significantly within substrates comparison (Figure 4A; Table 3A). The alien *X. securis* presented higher mortality rates as compared to *M. galloprovincialis* when deployed on hard rocks (Figure 4A). However, mortality increased significantly for both species on soft bottoms (Figure 4A).

In like manner, mussel mortality on mixed beds varied significantly with species and substrate factors (Figure 4B; Table 3A). Significance of interaction terms for co-habiting experiments (Table 3A) indicated that survival of both mytilids benefited again from fixation on hard rocks although the alien mussel still showed higher mortality whenever its balance rate was observed to be favourable (5 / 15 Mg / Xs; Figure 4B). The winter-spring experiment confirmed the differentiation in two layers within mixed beds as presented in Figures 3A-B and regardless of substrate used which indicated the great ability of the indigenous mussel to climb upwards to the top layers not only to escape the mud influence but also to smother the alien mussel.

The mud accumulated on slate tiles deployed independently varied inversely with the density of individuals (Figure 4C). Moreover, mud content accumulated in the winter-spring experiment was much higher than in the autumn experiment, especially at low densities (Figures 2C, 4C). Mud content on the slate tiles used for the mixed co-habiting populations varied within a narrow range (Figure 4D).

The shell growth of mussels sampled within the independent series varied significantly with all fixed factors such as species, density and substrate (Figure 4E; Table 3B). Significance of the density interacting with species and substrate factors (Table 3B) was, at least partially, linked to mud content (Figures 4C, 4E). Growth of *M. galloprovincialis* on soft bottoms was highest when animals were deployed at the highest density and occupied most of the substrate area, which coincided with the lowest mud accumulation. Such benefit of a higher occupation area was not observed when animals were deployed on hard substrates away from the mud effect (Figure 4E). The growth rate of the alien *X. securis* did not respond to different mud accumulation patterns but also increased when deployed on hard rocks (Figure 4E). As general pattern, shell growth was much higher for the indigenous *M. galloprovincialis* in the species comparison and on hard rocks for substrate comparison (Figure 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) (Figure 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; Figure 4F).

Byssal attachment and shell compressive forces: autumn 2010

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

With regard to mixed mussel beds, the indigenous mussel showed greater attachment force regardless of the co-habiting balance (Figure 5B; Table 4A). Strength of attachment for the mixed population as a unit dropped with abundance of the indigenous mussel (Figure 5B; Table 4A).

The indigenous mussel *M. galloprovincialis* secreted 15% thicker and stronger shells than the alien *X. securis* deployed independently in San Simón and regardless of the density (Figures 5C, 5E; Tables 4B, 4C). Habitat comparison for the alien *X. securis* showed no significant differences for shell compressive force values despite the slightly thinner shells secreted by this species at the Sampaio site and regardless of density values (Figures 5C, 5E) (Appendix 1).

Magnitudes of differences in shell thickness and strength between mytilids were even higher for the mixed beds (Figures 5D, 5F) although incidence of the species factor with higher values for the indigenous mussel depended on the co-habiting density, i.e. equally balanced and more abundant rates for the latter mytilid (see interaction terms; Tables 4B, 4C).

The shell compressive forces standardized by shell thickness showed no differences between species and densities for the independent experiment (Figure 6A). Habitat comparison for the alien *X. securis* likewise did not report any difference between sites and densities (Figure 6A).

By contrast, standardized compressive forces of the shell were significantly higher for the indigenous mussel when deployed on mixed beds, especially for the equal (10 / 10 Mg / Xs) and favourable (15 / 5 Mg / Xs) balance rates with values ranging between 156.4-157.1 and 89.9-117.1 N mm^{-1} for the indigenous and alien mussels, respectively (Figure 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 (Figure 7A; Table 5). Strength of attachment was the highest in *M. galloprovincialis* for species comparison and on hard rocks for comparison between substrates (Figure 7A). The significant effect of density (as independent and interaction terms; Table 5) in the statistical model was a consequence of the highest attachment strength recorded for *M. galloprovincialis* on soft bottoms with highest density (Figure 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 (17.7-17.9 N) as compared to the alien mussel (9.5-12.1 N) (Figure 7A).

The attachment force variability of mussels inhabiting mixed beds was significantly affected by species and substrate but not by the co-habiting balance (Figure 7B; Table 5). The attachment values of the indigenous mussel increased from a range of 10.6-16.6 N when deployed on muddy bottoms up to values of 17.4-20.5

N on hard rocks (Figure 7B). By contrast, the alien mussel attached with similar strength values regardless of substrate but constantly weaker when compared to the indigenous mussel (Figure 7B).

DISCUSSION

Successful invasions of bivalve species may be regulated by the competitive ability of the introduced species into the new habitat (Shinen and Morgan 2009; Caro et al. 2011). Nevertheless, co-existence of the two mytilids investigated here as well as prevention of competitive exclusion may occur as consequence of the relatively calm environment i.e. moderate disturbance levels for water hydrodynamics (Erlandsson et al. 2006). Deployment of both mytilids on space-limiting mussel beds revealed that the indigenous mussel *Mytilus galloprovincialis* was an extraordinary competitor and dominant species over the alien *Xenostrobus securis*. Firstly, the alien mussel showed much higher mortality rates within independent and mixed populations (Figures 2A, 2B). Secondly, the indigenous survivors exhibited greater growth (4-fold higher) when deployed independently regardless of density (Figure 2E) and more surprisingly, similar growth differences were reported in the mixed experiments, also regardless of population balance rates (Figure 2F). Reduced growth and high mortality rates represent two basic consequences of competition (Fréchette et al. 2005). Inter-specific competition within mixed beds significantly increased mortality of both mytilids although in a higher magnitude for the alien *X. securis* (autumn experiment). Despite high mortality of the independently deployed *X. securis* coincided with the highest mud accumulation (and lowest density), mortality within mixed beds cannot be accounted for by mud only but rather due to the physical competition for space. Such competition made possible that growth of the indigenous survivors was consistently higher for independent and mixed beds.

These responses of both mytilids highly depended on behavioural patterns. Most mussels deployed within independent experiments maintained their positions (primarily attached to the substrate) while few others (mainly of the indigenous species) were found to attach on shells of other individuals (pers. obs. JMFB). Interestingly, a clear gradient between distinct layers occupied by both mytilids was observed within mixed beds (Figure 3). The alien *X. securis* was clearly smothered and restricted to the mud influence area whereas *M. galloprovincialis* migrated and colonised the upper sites with better access to cleaner seawater. Therefore, the native *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 outside any mud influence. Other surveys in which *M. galloprovincialis* was an invader also illustrated such potential for aggregation and restriction the mobility of other species e.g. *Mytilus californianus* (Shinen and Morgan 2009). In earlier studies, Paine and Levin (1981) showed how adult mussels can move short distances to establish a dynamic mussel bed structure with constant rearrangement of individuals, which led to significant changes in mortality (Schneider et al. 2005). Consequently, *M. galloprovincialis* as epibenthic mytilid was more vulnerable to the action of mud and escaped from the bottom layer aided by its extensible (and larger) byssus (Brazee and Carrington 2006; Babarro and Carrington 2011) and mobility patterns (Shinen and Morgan 2009; present study). In one hand, mud accumulation may exert a great influence on the competitive dynamics between mytilids (Zardi et al. 2008; Rius and McQuaid 2006) and 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 (Figures 4C, 2C). On the other hand, such ability of the indigenous mussel to migrate helped by its byssus features would represent a great advantage especially in calmer waters of the present survey in which the hydrodynamic load suffered on top of the mussel patches would not be excessive (Babarro and Carrington 2011).

With regard to byssus secretion, the native mussel possesses larger and much thicker (and stronger) filaments than the alien mussel (Babarro and Lassudrie 2011) and this would permit such performance on mixed mussel beds. Shorter byssus would oblige the alien mussel to be attached near the bottom where the mud influence is greater and could occasionally block its valve gaping and thus interfere with particle acquisition (Cheung and 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* (pers. obs. JMFB; see also Brazee and Carrington 2006) and its larger foot organ (Babarro and Lassudrie 2011) may be crucial to partially remove any accumulated mud for survival purposes (see Figure 2A and 2C 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 secreted huge amount of extremely thin byssus filaments (up to thousand; Babarro and 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 (Figures 5A-F). Better access to natural resources by being at the top of mussel beds and other species-specific features like greater filtration capacity (unpublished results) would permit to allocate more energy to these protective structures, providing better arguments for the indigenous mussel 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 independent 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 *C. maenas* because of its shorter handling and breaking time values as compared to *X. securis* which in turn might facilitate the invasion of the alien. Our results do not support such 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 and co-workers 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 other related eco-physiological responses such as attachment strength of both mytilids were recently highlighted (Babarro and Lassudrie 2011) based on the relatively short and long-term exposure of the mussels, respectively.

Performance of the alien mussel at two 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 San Simón (Figure 2A, 2E). By contrast, no differences were obtained for the byssal attachment and shell compressive forces despite slightly thinner shells obtained in the mouth of the river 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 benefitted by the lower presence of predators in this highly variable habitat (Babarro and Lassudrie 2011) and by the lower mud content. On the other hand, the alien mytilid would have allocated more energy to shell growth when deployed in the inner Ría site (SS) because of the higher availability of resources in terms of total seston and specially other particulate material fraction of marine origin (Babarro and 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 and McQuaid 2006). When mussel responses were extended to another season and new substrate, the differences between species were even larger which ensured *M. galloprovincialis* as the dominant species regardless of any population balance rate and substrate. Surprisingly, despite its infaunal lifestyle, the alien *X. securis* was also able to extract a clear benefit (in terms of survival and growth), from the absence of mud on slate tiles which highlights the negative impact 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 and Chesson 2002), the alien mussel *X. securis* did not perform better than the native *M. 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 and 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 create optimal conditions for the great prevalence of the alien, outside the native mussel influence area. The larval dispersal of the alien mytilid might potentially reach other areas of the Ría according to the currents regime persistent 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 8-17.5 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.

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Table 1. Experimental design (number of mussels per treatment) followed to study competition patterns between both mytilids *Mytilus galloprovincialis* and *Xenostrobus securis*.
Slate tile unit: 100 cm^2

A. San Simón (SS)	SS 1	SS 2	SS 3	SS 4	SS 5	SS 6	SS 7	SS 8	SS 9
Mytilus galloprovincialis (number)	5	10	20	---	---	---	5	10	15
Xenostrobus securis (number)	---	---	---	5	10	20	15	10	5

B. Sampaio (SP)	SP 1	SP 2	SP 3
Mytilus galloprovincialis (number)	---	---	---
Xenostrobus securis (number)	5	10	20

Table 2. Two-way ANOVA of the mean mortality and shell length growth rates of the mussels as a function of species (fixed: sp *M. galloprovincialis* and *X. securis*) and density (fixed: n 5, 10, 20 for independent experiment or 5 / 15, 10 / 10 and 15 / 5 Mg / Xs for mixed co-habiting experiments). Autumn 2010.

A. Mortality (%)

	Factor	df	MS	F	p
Independent experiment	sp	1	27.2321	118.4752	**<0.001**
	n	2	3.1866	13.8635	**<0.001**
	sp x n	2	2.0377	8.8652	**<0.01**
	Error	12	0.2299		

	Factor	df	MS	F	p
Co-habiting experiment	co-habiting (n)	2	2.6106	10.9013	**<0.01**
	sp	1	5.0469	21.0747	**<0.001**
	co-habiting (n) x sp	2	0.4480	1.8708	0.196
	Error	12	0.2395		

B. Shell growth (µm day^{-1})

	Factor	df	MS	F	p
Independent experiment	sp	1	9.1784	89.5570	**<0.001**
	n	2	0.3581	3.4950	0.064
	sp x n	2	0.0166	0.1620	0.853
	Error	11	0.1025		

	Factor	df	MS	F	p
Co-habiting experiment	co-habiting (n)	2	0.7550	3.0352	0.089
	sp	1	10.7308	43.1368	**<0.001**
	co-habiting (n) x sp	2	0.2344	0.9422	0.419
	Error	11	0.2488		

Table 3. Three-way ANOVA of the mean mortality and shell length growth rate of the mussels as a function of species (fixed: sp *M. galloprovincialis* and *X. securis*), density (fixed: n 5, 10, 20 for independent experiment or 5 / 15, 10 / 10 and 15 / 5 Mg / Xs for mixed co-habiting experiments) and substrate (fixed: su mud and hard rock). Winter-spring 2011

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

Table 4. Two-way ANOVA of the byssal attachment force, shell thickness and shell compressive force of the mussels as a function of species (fixed: sp *M. galloprovincialis* and *X. securis*) and density (fixed: n 5, 10, 20 for independent experiment or 5 / 15, 10 / 10 and 15 / 5 Mg / Xs for mixed co-habiting experiments). Autumn 2010

A. Byssal attachment (N)

Independent experiment

Factor	df	MS	F	p
sp	1	0.8752	6.3040	**<0.05**
n	2	0.1023	0.7370	0.483
sp x n	2	0.7389	5.3220	**<0.01**
Error	59	0.1388		

Co-habiting experiment

Factor	df	MS	F	p
co-habiting (n)	2	0.6177	3.5150	**<0.05**
sp	1	7.1651	40.6760	**<0.001**
co-habiting (n) x sp	2	0.4521	2.5720	0.084
Error	67	0.1758		

B. Shell thickness (mm)

Independent experiment

Factor	df	MS	F	p
sp	1	0.1888	5.7386	**<0.05**
n	2	0.0009	0.0267	0.974
sp x n	2	0.0068	0.2062	0.815
Error	22	0.0329		

Co-habiting experiment

Factor	df	MS	F	p
co-habiting (n)	2	0.0068	0.2746	0.763
sp	1	0.1097	4.4039	**<0.05**
co-habiting (n) x sp	2	0.1515	6.0813	**<0.01**
Error	21	0.0249		

C. Shell compressive force (N)

Independent experiment

Factor	df	MS	F	p
sp	1	0.3998	4.4004	**<0.05**
n	2	0.0125	0.1378	0.872
sp x n	2	0.0217	0.2391	0.789
Error	21	0.0909		

Co-habiting experiment

Factor	df	MS	F	p
co-habiting (n)	2	0.0349	0.3150	0.733
sp	1	0.9888	8.9307	**<0.01**
co-habiting (n) x sp	2	0.7095	6.4083	**<0.01**
Error	21	0.1107		

Table 5. Three-way ANOVA of the byssal attachment force established by the mussels as a function of species (fixed: sp *M. galloprovincialis* and *X. securis*), density (fixed: n 5, 10, 20 for independent experiment or 5 / 15, 10 / 10 and 15 / 5 Mg / Xs for mixed co-habiting experiments) and substrate (fixed: su mud and hard rock). Winter-spring 2011

Byssal attachment (N)

Independent experiment

Factor	df	MS	F	p
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 x n	2	0.6993	4.5282	**<0.05**
sp x su	1	0.5245	3.3961	0.068
n x su	2	0.1882	1.2194	0.300
sp x n x su	2	1.2558	8.1312	**<0.001**
Error	103	0.1545		

Co-habiting experiment

Factor	df	MS	F	p
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 x n	2	0.4160	2.1372	0.123
sp x su	1	0.5774	2.9670	0.088
n x su	2	0.5154	2.6482	0.076
sp x n x su	2	0.2833	1.4564	0.238
Error	103	0.1946		

Legend of Figures

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

Figure 2. Autumn. Mean mortality rates (%), mud content (g) and shell length growth rate (µm day^{-1}) values of the mussels deployed in independent (A,C,E) and mixed co-habiting (B,D,F) beds as function of density and population balance at San Simón. Values obtained in the independent tests with the alien *Xenostrobus securis* deployed at Sampaio are also shown for site comparison (A,C,E). Numbers 5 / 15, 10 / 10 and 15 / 5 refer to the balance rates between both mytilids *Mytilus galloprovincialis* / *Xenostrobus securis* in the mixed mussel beds at San Simón. nd: not detected.

Figure 3. Autumn. Mussel bed disposition observed at the end of the experimental time illustrating the two layers differentiation after interaction of mytilids. The indigenous *Mytilus galloprovincialis* colonised top layers of the mixed beds smothering the alien *Xenostrobus securis* underneath and restricting the latter species in the mud influence layer (A) or simply colonising top layers on hard rocks (B).

Figure 4. Winter-spring**.** Mean mortality rates (%), mud content (g) and shell length growth rate (µm day^{-1}) values of the mussels deployed in independent (A,C,E) and mixed co-habiting (B,D,F) beds as function of density, population balance and type of substrate. For other specificities, see legend of Figure 2.

Figure 5. Autumn. Byssal attachment force (N), shell thickness (mm) and shell compressive force (N) values of the mussels deployed in independent (A,C,E) and mixed co-habiting (B,D,F) mussel beds as function of density and population balance at San Simón. Values obtained in the independent tests with the alien *Xenostrobus securis* deployed at Sampaio are also shown for site comparison (A,C,E). For other specificities, see legend of Figure 2.

Figure 6. Autumn. Standardized shell compressive force (N mm^{-1}) values of the mussels deployed in independent (A) and mixed co-habiting (B) mussel beds as function of density and population balance at San Simón. Values obtained in the independent tests with the alien *Xenostrobus securis* deployed at Sampaio are also shown for site comparison (A). For other specificities, see legend of Figure 2.

Figure 7. Winter-spring**.** Byssal attachment force (N) of the mussels deployed in independent (A) and mixed co-habiting (B) mussel beds as a function of density, population balance and type of substrate.

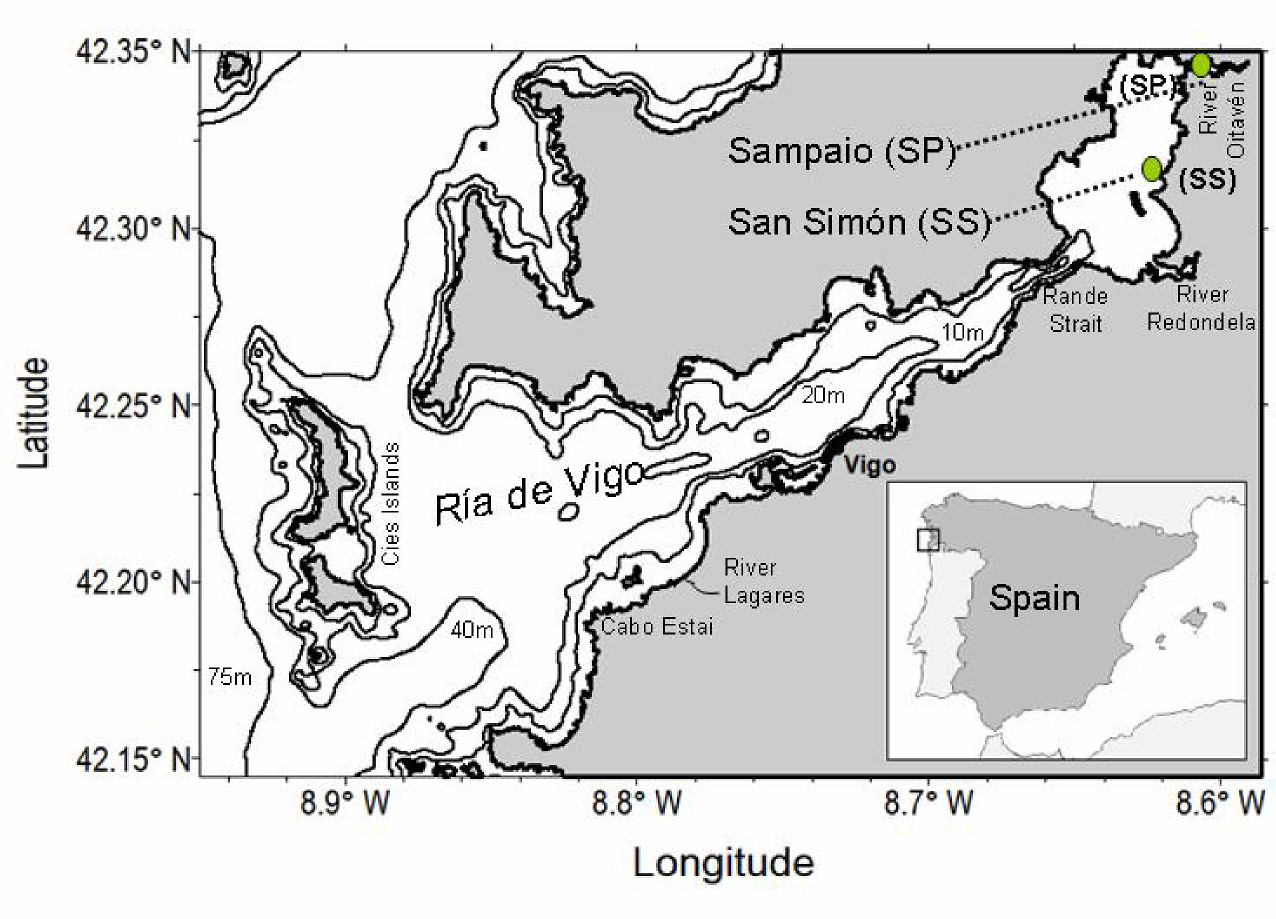
42.35° N
42.30° N
42.25° N
42.20° N
42.15° N
Latitude
8.9° W
8.8° W
8.7° W
8.6° W
Longitude
Sampaio (SP)
San Simón (SS)
(SP)
(SS)
River Oitavén
Rande Strait
River Redondela
10m
20m
40m
75m
Vigo
Ría de Vigo
Cies Islands
River Lagares
Cabo Estai
Spain

Figure 1

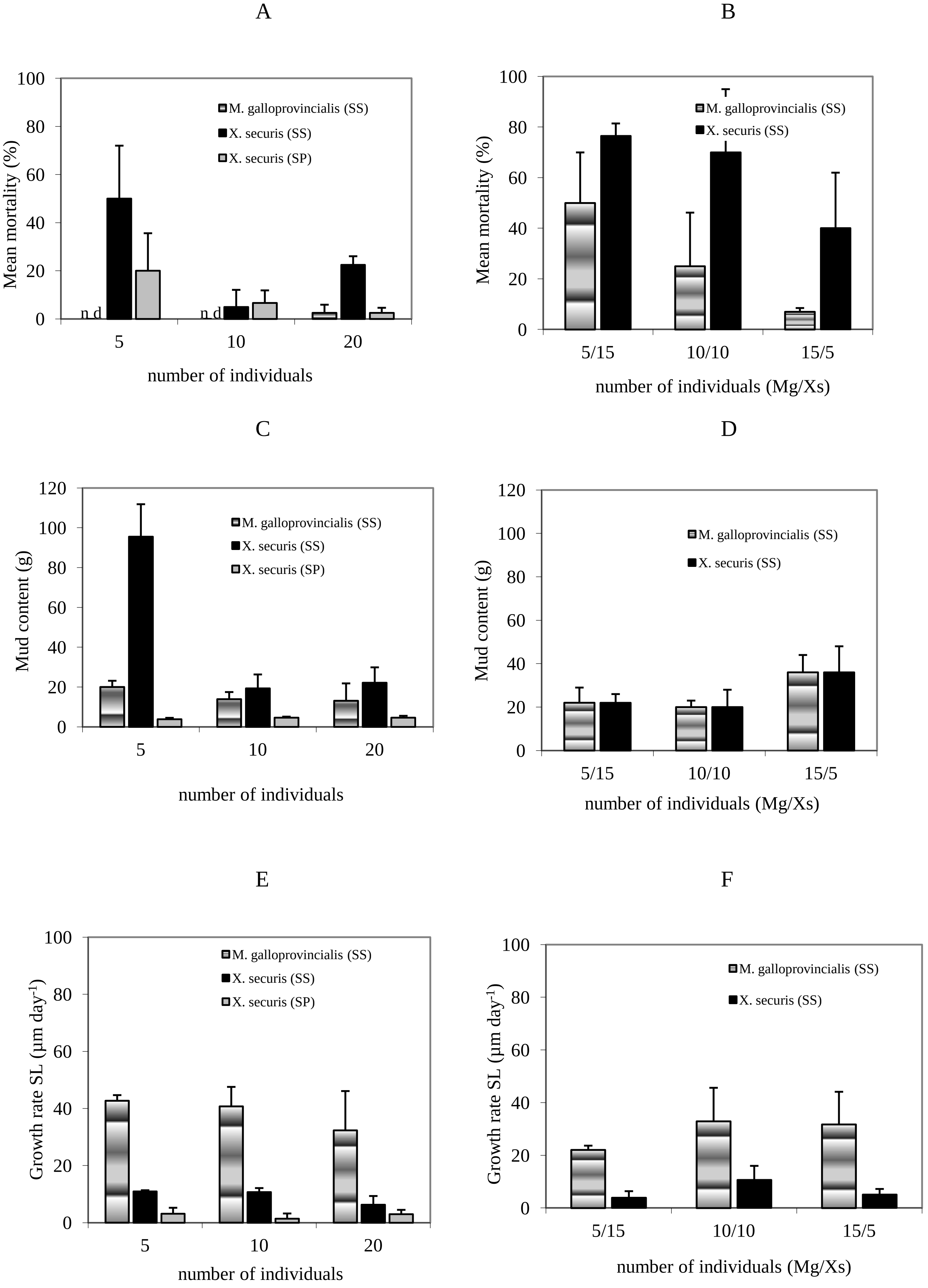A
B
100
80
60
40
20
0
Mean mortality (%)
M. galloprovincialis (SS)
X. securis (SS)
X. securis (SP)
n d
n d
5
10
20
number of individuals
5/15
10/10
15/5
number of individuals (Mg/Xs)
C
D
120
Mud content (g)
E
F
Growth rate SL (µm day-1)

Figure 2

Figure 3

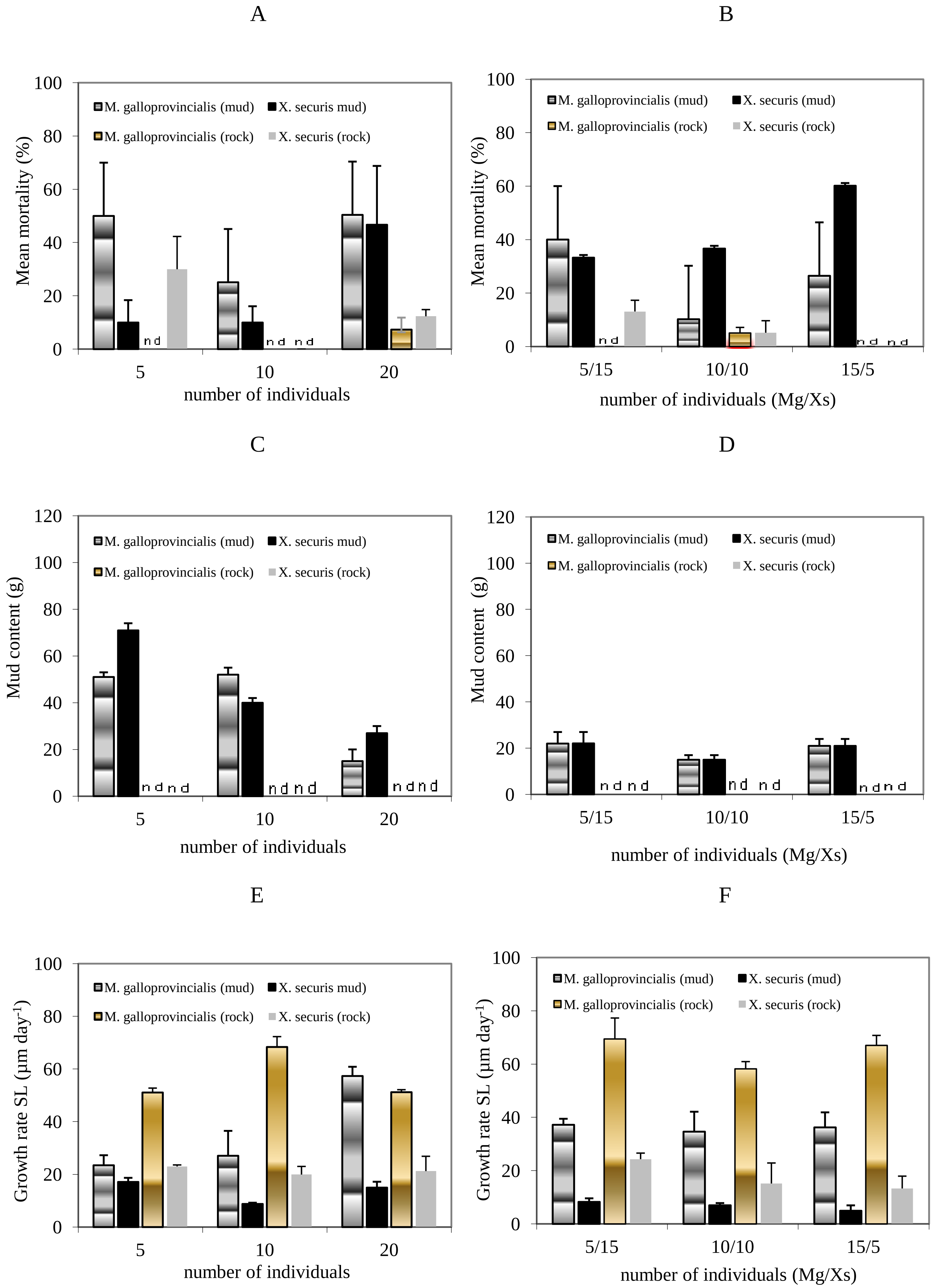
A
B
Mean mortality (%)
0
20
40
60
80
100
M. galloprovincialis (mud)
X. securis mud)
M. galloprovincialis (rock)
X. securis (rock)
nd
nd nd
5
10
20
number of individuals
X. securis (mud)
nd
nd nd
5/15
10/10
15/5
number of individuals (Mg/Xs)
C
D
Mud content (g)
120
nd nd
number of individuals
Mud content (g)
number of individuals (Mg/Xs)
E
F
Growth rate SL (μm day-1)
number of individuals
number of individuals (Mg/Xs)

Figure 4

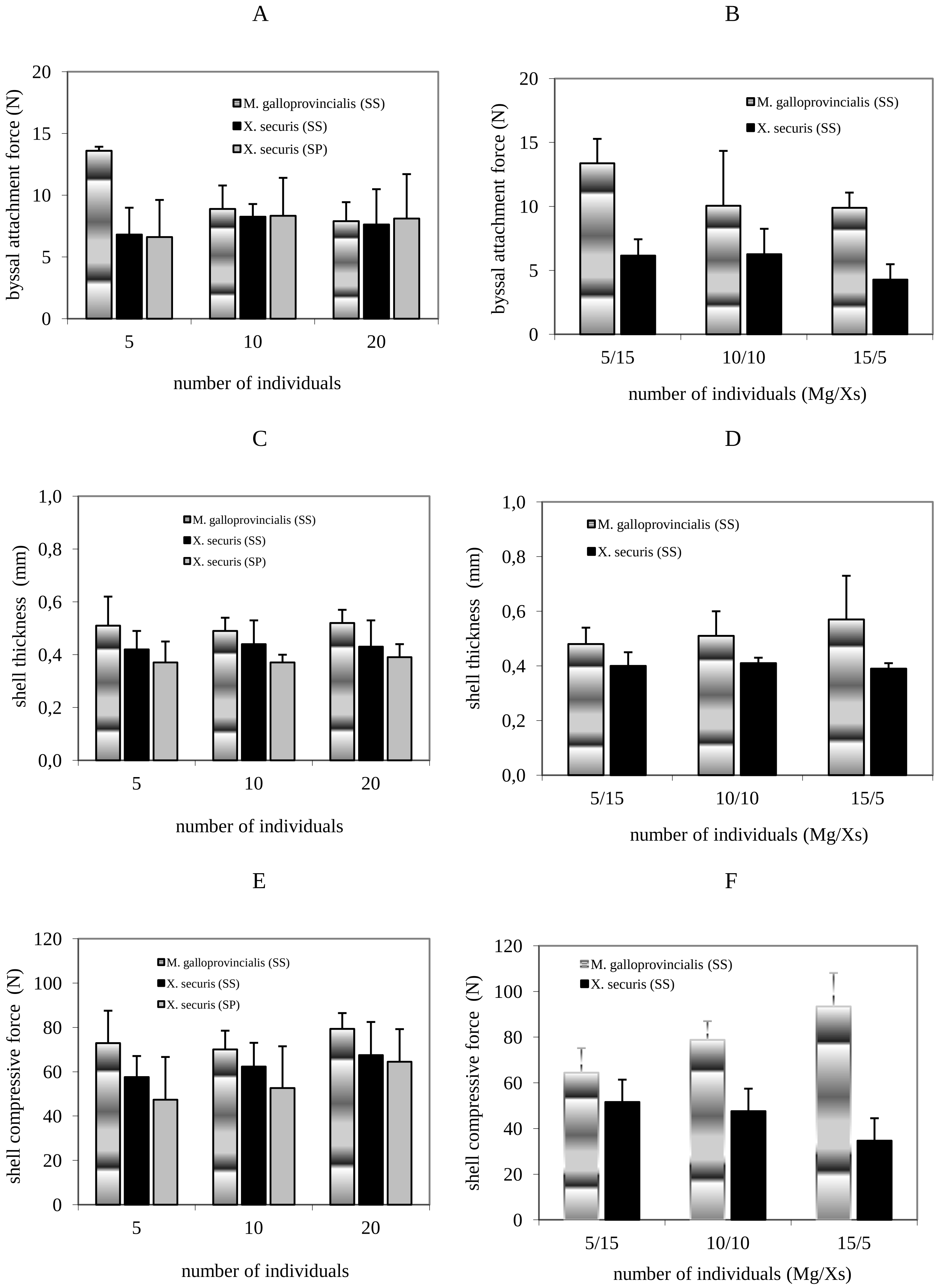
A
B
C
D
E
F
byssal attachment force (N)
shell thickness (mm)
shell compressive force (N)
number of individuals
number of individuals (Mg/Xs)
M. galloprovincialis (SS)
X. securis (SS)
X. securis (SP)
0
5
10
15
20
0,0
0,2
0,4
0,6
0,8
1,0
0
20
40
60
80
100
120
5
10
20
5/15
10/10
15/5

Figure 5

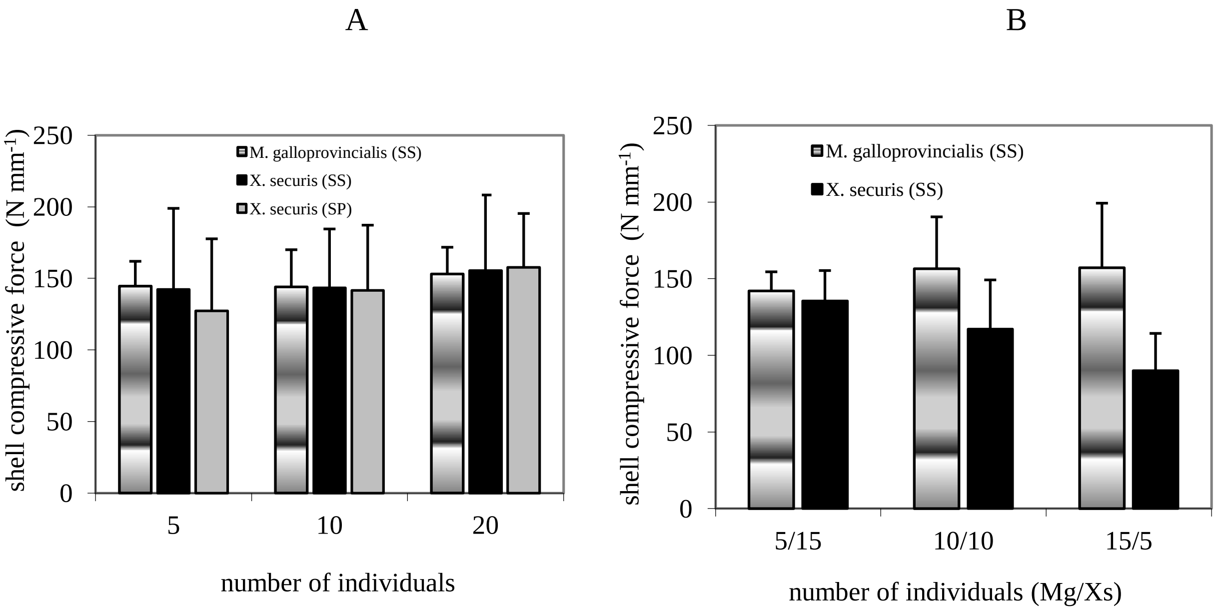
A
B
shell compressive force (N mm-1)
250
200
150
100
50
0
■ M. galloprovincialis (SS)
■ X. securis (SS)
■ X. securis (SP)
5
10
20
number of individuals
5/15
10/10
15/5
number of individuals (Mg/Xs)

Figure 6

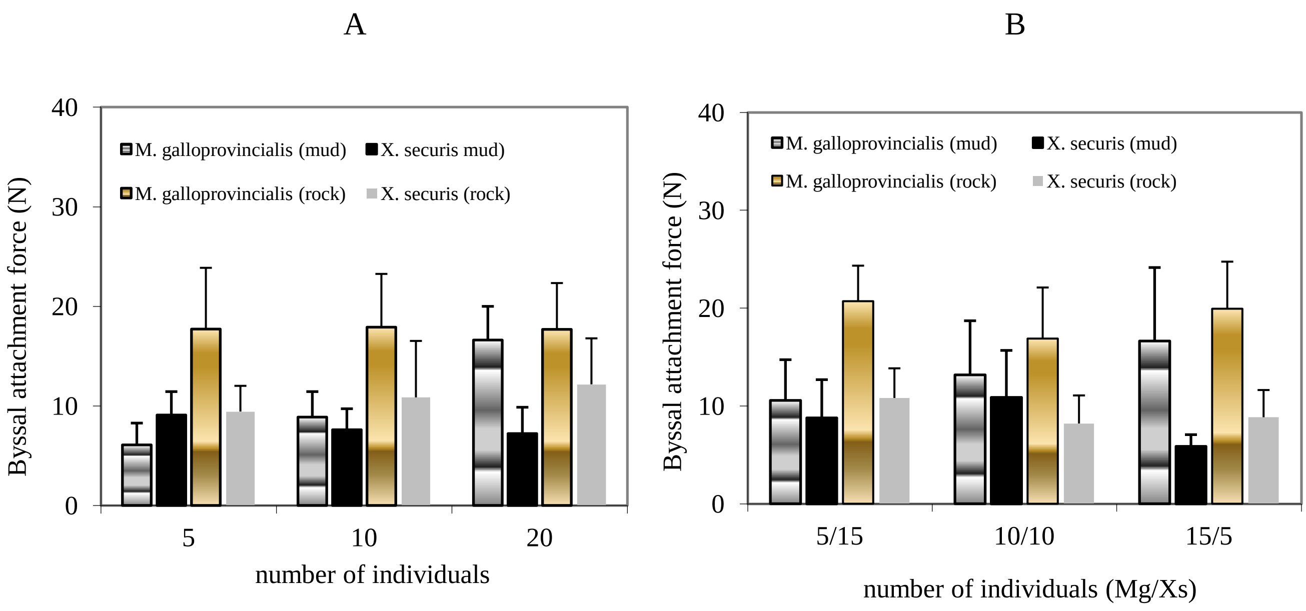
A
B
Byssal attachment force (N)
0
10
20
30
40
M. galloprovincialis (mud)
X. securis mud)
M. galloprovincialis (rock)
X. securis (rock)
5
10
20
number of individuals
M. galloprovincialis (mud)
X. securis (mud)
M. galloprovincialis (rock)
X. securis (rock)
5/15
10/10
15/5
number of individuals (Mg/Xs)

Figure 7

Appendix 1.

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

Mortality (%)

Independent experiment

Factor	df	MS	F	p
site	1	0.2395	9.2261	**<0.05**
n	2	0.1567	6.0366	**<0.05**
site x n	2	0.0680	2.6211	0.1136
Error	12	0.0259		

Shell growth (μm day^{-1})

Independent experiment

Factor	df	MS	F	p
site	1	3.0396	50.7355	**<0.001**
n	2	0.0983	1.6408	0.2345
site x n	2	0.1886	3.1490	0.0795
Error	12	0.0599		

Byssal attachment (N)

Independent experiment

Factor	df	MS	F	p
site	1	0.0006	0.0189	0.8910
n	2	0.0864	2.8095	0.0673
site x n	2	0.0069	0.2257	0.7892
Error	67	0.0308		

Shell thickness (mm)

Independent experiment

Factor	df	MS	F	p
site	1	0.1552	5.1994	**<0.05**
n	2	0.0008	0.0268	0.9736
site x n	2	0.0140	0.4695	0.6317
Error	21	0.0299		

Shell compressive force (N)

Independent experiment

Factor	df	MS	F	p
sp	1	0.0380	1.1628	0.2931
n	2	0.0250	0.7649	0.4779
sp x n	2	0.0152	0.4657	0.6340
Error	21	0.0327		

Standardized shell compressive force (N mm^{-1})

Co-habiting experiment

Factor	df	MS	F	p
co-habiting (n)	2	0.0229	1.5332	0.2399
sp	1	0.0905	6.0702	**<0.05**
co-habiting (n) x sp	2	0.0352	2.3592	0.1191
Error	21	0.0149		