

Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy

G. I. Zardi · K. R. Nicastro · C. D. McQuaid ·
M. Rius · F. Porri

Received: 23 February 2006 / Accepted: 25 March 2006 / Published online: 29 April 2006
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Abstract The ability of a mussel to withstand wave-generated hydrodynamic stress depends mainly on its byssal attachment strength. This study investigated causes and consequences of different attachment strengths of the two dominant mussels species on the South African south coast, the invasive *Mytilus galloprovincialis* and the indigenous *Perna perna*, which dominate the upper and the lower areas of the lower balanoid zone, respectively and co-exist in the middle area. Attachment strength of *P. perna* was significantly higher than that of *M. galloprovincialis*. Likewise solitary mussels were more strongly attached than mussels living within mussel beds (bed mussels), and in both cases this can be explained by more and thicker byssal threads. Having a wider shell, *M. galloprovincialis* is also subjected to higher hydrodynamic loads than *P. perna*. Attachment strength of both species increased from higher to lower shore, in response to a gradient of stronger wave action. The morphological features of the invasive species and its higher mortality rates during winter storms help to explain the exclusion of *M. galloprovincialis* from the low shore. The results are discussed in the context of the evolutionary strategy of the alien mussel, which directs most of its energy to fast growth and high reproductive output, apparently at the cost of reduced attachment strength. This

raises the prediction that its invasive impact will be more pronounced at sites subject to strong but not extreme wave action.

Introduction

Intertidal organisms are often exposed to large hydrodynamic forces associated with wave action (Denny 1985, 1995; Denny and Gaines 1990; Gaylord et al. 1994). Because they can regulate the supply of food or propagules and break or dislodge organisms, wave forces play an important role in determining the structure and dynamics of many intertidal communities (Menge 1976; Lubchenco and Menge 1978; Paine and Levin 1981; Sousa 1985; Bustamante and Branch 1996).

Wave action affects entire intertidal communities, influencing both the vertical distribution of biomass and the trophic composition of that biomass (McQuaid and Branch 1985), and can have strong species-specific effects (McQuaid and Branch 1984). Mussels are often the major occupiers of primary space on rocky intertidal shores (Seed and Suchanek 1992) and, growth rates of mussels are faster at exposed sites than sheltered ones (McQuaid and Lindsay 2000), while mussels experiencing high hydrodynamic stress also tend to increase shell thickness (Steffani and Branch 2003a).

The Mediterranean mussel *Mytilus galloprovincialis* has become invasive in many parts of the world (i.e. Wilkins et al. 1983; Lee and Morton 1985; McDonald et al. 1991; Apte et al. 2000; Steffani and Branch 2003a, b; Branch and Steffani 2004) and now has an anti-tropical distribution, occurring in the temperate zones of the northern and southern hemispheres while absent

Communicated by R. Cattaneo-Vietti, Genova

G. I. Zardi (✉) · K. R. Nicastro · C. D. McQuaid ·
M. Rius · F. Porri
Department of Zoology and Entomology,
Rhodes University, Grahamstown 6140, South Africa
e-mail: zardi73@yahoo.it

from the tropics (Hilbish et al. 2000). In South Africa, it is the most abundant alien marine species (De Moor and Bruton 1988) and, together with the indigenous *Perna perna*, it dominates the south coast. Both species live on the lower shore (referred to here as the mussel zone), but the upper and the lower areas of the mussel zone are dominated by *M. galloprovincialis* and *P. perna*, respectively, while the two co-exist in the mid-mussel zone (Hockey and van Erkom Shurink 1992; Robinson et al. 2005). The responses of an introduced species to variations in time and space of resource availability, natural enemies and physical factors determine its ability to invade and the dynamics of co-existence with indigenous species. *M. galloprovincialis* shows several characteristics of an aggressive invasive species. These include features that should make it an effective interference and exploitation competitor. Rapid growth rate over a range of water temperatures (Griffiths et al. 1992; Hockey and van Erkom Shurink 1992), high fecundity (van Erkom Shurink and Griffiths 1991), high recruitment rate (Harris et al. 1998) and resistance to desiccation (Hockey and van Erkom Shurink 1992), parasites (Calvo-Ugarteburu and McQuaid 1998) and sand stress (Zardi et al. 2006) are all hallmarks of a strong competitor. However, waves can be the major cause of mussel mortality in the intertidal zone (Paine and Levin 1981) and the ability to resist dislodgment will be an important attribute for a potentially invasive species.

Several studies have reported differences in the strength of byssal attachment for mussel species that compete for space (Willis and Skibinski 1992; Bell and Gosline 1997; Hunt and Scheibling 2001; Schneider et al. 2005). Greater attachment strength could contribute to competitive dominance seasonally during winter storms, geographically along gradients of wave exposure among shores, and vertically within shores, leading to habitat partitioning.

The success of mussels in withstanding strong wave forces is largely due to the byssus, an extracellular bunch of collagenous threads that is secreted in the ventral groove of the foot, which allows mussels to attach firmly to the substratum and to each other (Waite 1992). Each byssal thread is proximally attached to a common stem which connects via the root to the byssus retractor muscle (Brown 1952), and is composed of three distinct parts that differ in their ultra structure, protein composition and physical properties (Bairati and Vitellaro-Zuccarello 1976; Benedict and Waite 1986). Each thread terminates in an adhesive plaque containing water-insoluble adhesive proteins that enable mussels to anchor to solid surfaces (Waite 1992).

Mussels adjust their attachment strength in response to their flow environment. In the laboratory, attachment strength increases with water agitation (Young 1985; Lee et al. 1990) and in the field it increases with increasing wave exposure seasonally (Price 1982; Hunt and Scheibling 2001; Carrington 2002), between sites (Witman and Suchanek 1984) and between habitats within a site; mussels living in tide pools are less strongly attached than those on emergent rocks (Hunt and Scheibling 2001). Moreover, attachment strength is lower in mussels sheltered within a bed than in those living outside the bed or at its fringe (Witman and Suchanek 1984; Bell and Gosline 1997). Attachment strength increases with increasing mussel size (Harger 1970; Witman and Suchanek 1984; Hunt and Scheibling 2001), but differences between species can be explained mainly by differences in thread thickness, while thread number is the primary mechanism affecting attachment strength within a species (Bell and Gosline 1997).

The ability of a mussel to survive wave action depends not only on its attachment strength but also on the magnitude of the hydrodynamic forces experienced. These forces are mainly determined by the size and shape of the mussel itself and the flow regime to which it is subjected (Denny et al. 1985; Denny 1988, 1995). Breaking waves can expose mussels to forces due to the water's velocity, drag and lift, and to its acceleration (Denny 1995), though acceleration forces are relatively insignificant on such small scales (Gaylord 2000). Lift is the main hydrodynamic force exerted on mussels living tightly packed in mussel beds (Denny 1987). Lift is generated by water flowing over the bed and creating a difference in pressure between the top and the bottom of each mussel. This force can be strong enough to pull a mussel up and dislodge it. Bed mussels are usually arranged with the anterior–posterior axis perpendicular to the substratum, reducing the area exposed to lift forces. Mussels living outside beds (solitary mussels) are mainly subject to drag forces acting in the direction of flow and are usually arranged with their anterior–posterior axis parallel to the substratum (Bell and Gosline 1997).

This study reports differences in byssal attachment strength of two co-existing and competing mussel species, *M. galloprovincialis* and *P. perna*, and investigates the mechanical causes contributing to these differences. We hypothesised that hydrodynamic stress is higher on the low shore and consequently contributes to the vertical zonation of the two species. This hypothesis was tested in the field by measuring mortality rates of *M. galloprovincialis* and *P. perna* when they were subjected to severe hydrodynamic stress during a winter storm.

Materials and methods

All mussels used in this study were collected from a granite shore in Plettenberg Bay (34°05'S, 23°19'E), on the south coast of South Africa, during summer low tides on 22 and 23 January 2003. The sampling area was small (~20 m²) and topographically uniform, so all mussels were assumed to be exposed to similar abiotic conditions. Mussels living within a monolayered mussel bed (referred to hereafter as 'bed mussels') and those living outside the bed (solitary mussels) were considered separately. Multilayered mussel beds were not investigated.

Shapiro's and Levene's test were used to assess normality and homogeneity of variances, respectively. When data failed the requirements for parametric analysis, they were transformed as indicated; when transformation was successful, parametric analysis was performed, otherwise non-parametric analysis was used.

Attachment strength and failure location

Mytilus galloprovincialis and *P. perna* individuals (2.3–6.9 cm shell length; $n = 75$ for each species and for each position, i.e. bed or solitary mussels), were tested for attachment strength in the mid mussel zone. To measure mussel attachment strength, a 2-mm diameter hole was drilled through the shell valves close to the posterior margin using a hand-held battery-operated drill (Denny 1987). A fish hook, connected to a recording spring scale, was inserted through the hole. The scale was steadily and uniformly lifted normal to the rock surface until dislodgment occurred (after 1–3 s) and the force required to detach each mussel was recorded in Newtons. The minimum separation of bed mussels was 20 cm, so that measurements did not influence one another by disturbing the mussel bed. Two-way ANCOVA with shell length as a co-variate was used to evaluate the effects of species and position (fixed factors) on attachment strength. The location of byssus failure for each mussel dislodged from the mid zone was recorded in one of five categories: root, stem, byssal thread, plaque and substratum. In addition, attachment strengths of *M. galloprovincialis* in beds in the high and mid zones, and of *P. perna* in beds from the mid and low zones were measured using similarly sized individuals (3.5–4.5 cm shell length; $n = 50$ for species in each zone). The *P. perna* and *M. galloprovincialis* are absent or rare in the high and low mussel zone, respectively. Kruskal–Wallis-tests were performed to evaluate the effect of zone on attachment strength for each species separately.

Morphometrics

For each dislodged mussel, the shell length (anterior–posterior axis), height (dorso–ventral axis) and width (lateral axis) were measured to the nearest mm with vernier callipers. The minor shell planform area ($A_{p,min}$, minimum exposed shell area) was approximated as an ellipse and calculated using shell height and width as major and minor axes, respectively. The major shell planform area ($A_{p,max}$, maximum exposed shell area) was approximated as an ellipse using shell length and height. Data were log transformed and one-way ANCOVA was used to evaluate the effects of species (fixed factor) and shell length (co-variate) on $A_{p,min}$ and $A_{p,max}$, and on shell width and height. The number of byssal threads was counted from samples ($n = 50$) of solitary and bed mussels of both species collected in the mid mussel zone. To avoid breaking the byssal threads, each individual was carefully removed from the substratum using a scalpel. For each mussel, diameters of the root and of the proximal region of one newly formed, randomly selected byssal thread were measured. Data on thread numbers were square root transformed and two-way ANCOVA was performed to evaluate the effects of species, position (fixed factors) and shell length (co-variate) on number of byssal threads. Regression analysis was used to test the dependence of thread number and root diameter on shell length for each species and for each position. A Students' *t*-test was used to test equality of the coefficients for the shell length–species and shell length–position regressions.

Wave exposure

Exposure was quantified in October 2005 by measuring maximum wave force using dynamometers modelled on those used by Palumbi (1984). Fifteen dynamometers were placed, five in each of the three mussel zones, and removed the following day during very rough sea with over 5 m swells (South African Weather Service). Each dynamometer gave a single measurement of maximum wave force during the two tidal cycles, which was expressed as N m⁻². One-way ANOVA was performed to determine whether maximum wave force differed among zones.

Hydrodynamic forces

Bed mussels are oriented with their long axis perpendicular to the plane of the substratum. Lift was assumed to be the only hydrodynamic force imposed on such mussels (Denny 1987) and was calculated as

$$F_{\text{lift}} = 1/2\rho U^2 A_{p,\text{min}} C_l, \quad (1)$$

where ρ is the sea water density ($1,024 \text{ kg m}^{-3}$), U is the water velocity (m s^{-1}), C_l is the dimensionless coefficient of lift (0.88 for bed mussels, Denny 1987), and $A_{p,\text{min}}$ is the minor shell planform area, calculated as described. The posterior–anterior axis of solitary mussels is parallel to the plane of the substratum. For solitary animals, drag was assumed to be the only hydrodynamic force imposed on them (Denny 1987) and was calculated as

$$F_{\text{drag}} = 1/2\rho U^2 A_{p,\text{max}} C_d, \quad (2)$$

where C_d is the coefficient of drag. For *Mytilus californianus* this coefficient is 0.8 when drag acts perpendicular (worst case scenario) and 0.2 when it acts parallel (best case scenario) to the posterior–anterior axis, respectively (Denny et al. 1985). $A_{p,\text{max}}$ is the major shell planform area, calculated as described. Acceleration force was not considered because of the small spatial scales of surf-zone acceleration (Denny et al. 1985; Gaylord et al. 1994; Gaylord 2000). Formulas (1) and (2) were used to calculate hydrodynamic forces acting on both bed and solitary mussels. Two scenarios were investigated for solitary mussels: the direction of water flow perpendicular (worst case scenario) and parallel (best case scenario) to the posterior–anterior axis. Because differences in shell morphology between the two species were relatively subtle, we assumed that coefficients of drag and lift (C_d and C_l) were the same for the two species.

Field experiment

The experiment was run on a sandstone platform at Old Woman's River ($33^\circ 30'S$, $27^\circ 10'E$) from March 2003 to September 2003. Two similar areas of the platform about 20 m apart were selected, and the three mussel zones were identified in each area. Quadrats of $0.1 \times 0.1 \text{ m}^2$ were placed haphazardly in the study area and attached to the rock with screws. *M. galloprovincialis* and *P. perna* (20–30 mm shell length) were collected from Plettenberg Bay. The mussels were transported to the laboratory and placed in filtered oxygenated seawater ($\sim 20^\circ\text{C}$) for 24 h. The mussels were then placed in the quadrats at the study site and covered tightly with a shade cloth (2 mm mesh) to enable them to re-attach to the rocks. Thirty-six quadrats were placed in each of the low, mid and high mussel zones. After 4 weeks, when mussels were firmly attached, the mesh was removed. Mortality rates (dislodgment) of both species were monitored every

month. The experiment was designed to test for interspecific competition and quadrats contained treatments with various combinations and densities of species (Rius and McQuaid 2006). Storm damage disrupted the experiment and the data are used here to examine the effect of species and zone on dislodgment. Two factor RM-ANOVA was used to evaluate the effects of species and zone (fixed factors) on mussel mortality.

Results

Attachment strength and failure location

Mussel size, species and position (bed or solitary animals) were highly significant factors influencing attachment strength (two-way ANCOVA, $P < 0.0001$; with no significant interaction among factors; Fig. 1). On average, attachment strength of *P. perna* was 26 and 24% higher than for *M. galloprovincialis*, for solitary and bed mussels, respectively. Solitary mussels were 19 and 21% more strongly attached to the substratum than those sheltered within a mussel bed for *M. galloprovincialis* and *P. perna*, respectively. The effects of species and position increased with increasing shell length. Comparison of attachment strengths for mussels dislodged from the high, mid and low mussel zones showed a clear vertical gradient, with mussels living lower on the shore having stronger attachment in both species (Kruskal–Wallis-test, $P < 0.0001$ in both cases). On average, *M. galloprovincialis* in the mid zone were 46% more strongly attached

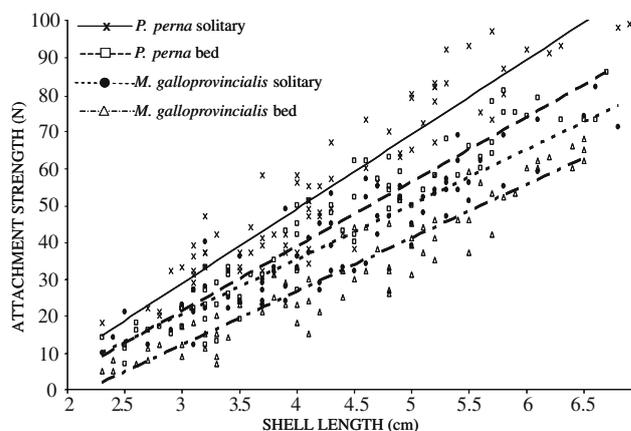


Fig. 1 *Mytilus galloprovincialis* and *Perna perna*. Relationship between shell length and attachment strength in *P. perna* solitary mussels ($y = 20.188x - 31.807$, $r^2 = 0.873$), *P. perna* bed mussels ($y = 17.492x - 31.32$, $r^2 = 0.9173$), *M. galloprovincialis* solitary mussels ($y = 14.868x - 24.337$, $r^2 = 0.8421$), and *M. galloprovincialis* bed mussels ($y = 14.49x - 31.52$, $r^2 = 0.8922$). $n = 75$ for each species and each position

Table 1 *Mytilus galloprovincialis* and *Perna perna*

Failure location	<i>Mytilus galloprovincialis</i>		<i>Perna perna</i>	
	Solitary	Bed	Solitary	Bed
Root	11.1	2.1	8	1.5
Thread	34.9	18.9	27	11.2
Plaque	42	30.9	48.9	36.3
Substratum	12	48.1	16.2	51

tached than those in the high zone, while *P. perna* attachment strength was 35% higher in the low zone than in the mid zone.

Stem failure was never observed (Table 1). Root failure was more frequent in solitary mussels (8–11%) than in bed mussels (1.5–2%). The frequency of substratum failure was higher in bed mussels (about 50%) than in solitary mussels (12–16%). Plaque was the weakest attachment location for solitary mussels, accounting for 42 and 49% for *M. galloprovincialis* and *P. perna*, respectively, while in bed mussels the values were 31 and 36%. Byssal threads failed more often in solitary mussels (35–27%) than in bed mussels (11–19%).

Morphometrics

Shell height did not differ significantly (ANCOVA, $P = 0.9$) between the two species, while *M. galloprovincialis* shells were 22% wider than *P. perna* shells for a given shell length (ANCOVA, $P < 0.0001$; Fig. 2). Consequently, *M. galloprovincialis* had a significantly bigger $A_{p,min}$ than *P. perna* (ANCOVA, $P < 0.0001$), but the morphometric relationship between shell length and $A_{p,max}$ did not differ significantly between species (ANCOVA, $P = 0.65$; data not shown). Byssal thread number increased with shell length and both species and position significantly affected byssal thread number (two-way ANCOVA, $P < 0.0001$ with no significant interaction; Fig. 3). On average, the number of byssal threads for *P. perna* was 23.6 and 18.5% higher than for *M. galloprovincialis*, for solitary and bed mussels, respectively. Solitary mussels had 22.6 and 27.5% more byssal threads than bed mussels for *M. galloprovincialis* and *P. perna*, respectively. Thread diameter increased with animal size for both species and for both positions (Regression, $P < 0.001$). The *p. perna* had significantly thicker threads than *M. galloprovincialis* (~14% for both solitary and bed; Students' *t*-test, $P < 0.0001$) and solitary mussels had significantly thicker threads than bed mussels (~12% for both species; Students' *t*-test, $P < 0.0001$; Fig. 4). Root

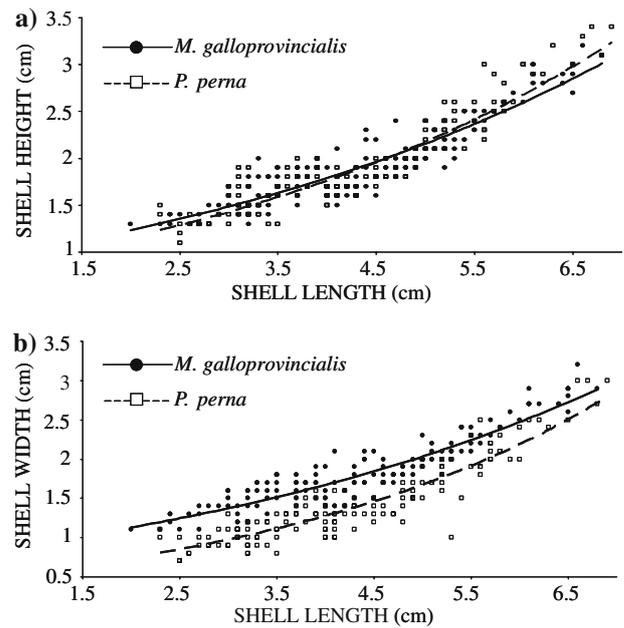


Fig. 2 *Mytilus galloprovincialis* and *Perna perna*. Relationships between shell length and (a) shell height (*P. perna* $y = 0.7587e^{0.2104x}$, $r^2 = 0.8618$; *M. galloprovincialis* $y = 0.8519e^{0.1858x}$, $r^2 = 0.8466$), and (b) shell width (*P. perna* $y = 0.4321e^{0.2701x}$, $r^2 = 0.8236$; *M. galloprovincialis* $y = 0.7645e^{0.1956x}$, $r^2 = 0.8422$). $n = 150$ for each species

diameter increased with animal size for both species and for both positions (Regression, $P < 0.001$). On average, the byssal root of *M. galloprovincialis* was 26.1% (Students' *t*-test, $P < 0.05$) thinner than that of *P. perna*. Position (solitary versus bed) had no significant effect (Students' *t*-test, $P > 0.5$; Fig. 5).

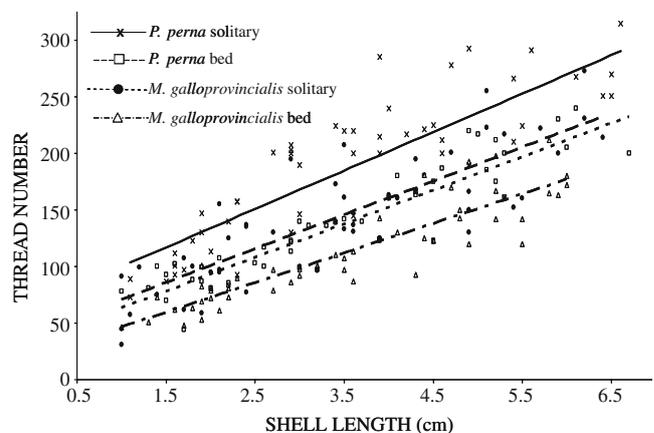


Fig. 3 *Mytilus galloprovincialis* and *Perna perna*. Relationship between shell length and thread number in *P. perna* solitary mussels ($y = 33.977x + 65.964$, $r^2 = 0.7107$), *P. perna* bed mussels ($y = 29.917x + 40.629$, $r^2 = 0.7133$), *M. galloprovincialis* solitary mussels ($y = 29.672x + 33.543$, $r^2 = 0.825$), and *M. galloprovincialis* bed mussels ($y = 26.144x + 20.125$, $r^2 = 0.806$). $n = 50$ for each species and each position

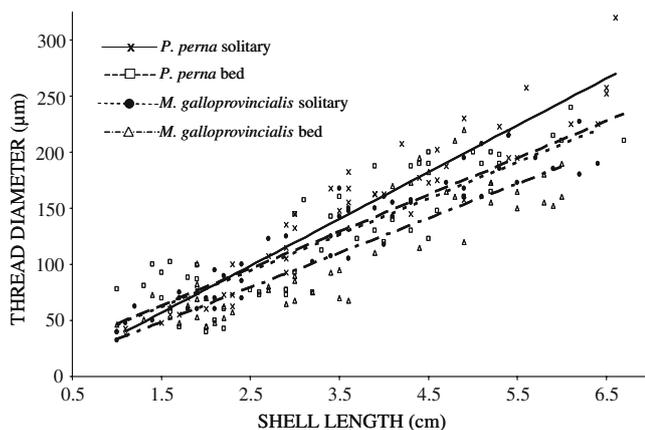


Fig. 4 *Mytilus galloprovincialis* and *Perna perna*. Relationship between shell length and thread diameter in *P. perna* solitary mussels ($y = 41.759x - 5.7193$, $r^2 = 0.9156$), *P. perna* bed mussels ($y = 32.858x + 13.73$, $r^2 = 0.7588$), *M. galloprovincialis* solitary mussels ($y = 32.191x + 13.426$, $r^2 = 0.9018$), and *M. galloprovincialis* bed mussels ($y = 30.837x + 1.9683$, $r^2 = 0.7566$). $n = 50$ for each species and each position

Wave exposure

One-way ANOVA showed that there was a significant ($P < 0.0001$) difference in the maximum wave forces recorded at different levels of the mussel zone. On average, maximum wave forces increased from the high zone ($9,682 \text{ N m}^{-2}$), through the mid zone ($19,206 \text{ N m}^{-2}$) to the low zone ($30,476 \text{ N m}^{-2}$).

Hydrodynamic forces

Estimated drag forces acting on $A_{p,max}$ of solitary mussels did not differ between species, because there

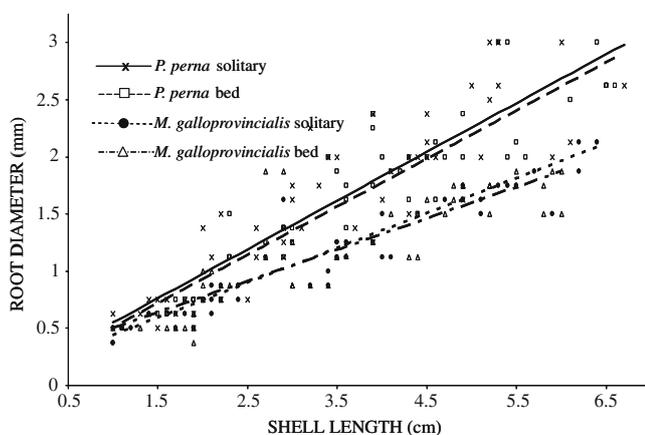


Fig. 5 *Mytilus galloprovincialis* and *Perna perna*. Relationship between shell length and root diameter in *P. perna* solitary mussels ($y = 0.4267x + 0.124$, $r^2 = 0.7653$), *P. perna* bed mussels ($y = 0.4213x + 0.085$, $r^2 = 0.8551$), *M. galloprovincialis* solitary mussels ($y = 0.3048x + 0.1337$, $r^2 = 0.8461$), and *M. galloprovincialis* bed mussels ($y = 0.274x + 0.2254$, $r^2 = 0.7368$). $n = 50$ for each species and each position

was no significant difference in morphometric scaling of $A_{p,max}$ on shell length. On average, the predicted scaled hydrodynamic drag force for a solitary mussel exposing $A_{p,max}$ to water flow (worst case scenario) was 60.5% higher than for mussels exposing $A_{p,min}$ (solitary in best case scenario and bed mussels). On average, under both best case solitary and bed conditions, forces acting on $A_{p,min}$ for *M. galloprovincialis* were approximately 22% higher than for *P. perna* for a 4.5 cm shell length (Fig. 6). Scaled hydrodynamic force was size-dependent: it increased by approximately 66% between shell lengths of 4.5 and 7 cm (data not shown). At velocities lower than 6 m s^{-1} the predicted hydrodynamic force was approximately $2.13 \times 10^4 \text{ N m}^{-2}$, while at higher water velocities ($14\text{--}20 \text{ m s}^{-1}$) it was 31.86×10^4 and $80.57 \times 10^4 \text{ N m}^{-2}$ for mussels exposing $A_{p,min}$ and $A_{p,max}$, respectively.

Field experiment

Mortality was first recorded in April 2003. In early June 2003 a storm destroyed most plots. In the months before and after the storm, total mortality remained relatively low (on average 4.8–6.9% per month), with no obvious effects of species in any zone. However, in June, 68% of *M. galloprovincialis* and 38% of *P. perna* individuals were lost, most of them from the low and mid shore (Fig. 7). Mussel mortality was significantly affected by both species and zone (RM-ANOVA, $P < 0.01$). There were within-subjects effects of time and its interaction with the factors ($P < 0.001$). Mortality due to wave action decreased up shore, but in all zones mortality of *M. galloprovincialis* was roughly twice that of *P. perna*.

Discussion

Mytilus galloprovincialis has many characteristics of an invasive species, especially a much higher recruitment rate than *P. perna* (Harris et al. 1998), giving it the ability to outcompete the indigenous mussel for free space through exploitation competition (Erlandsson et al. 2006). However, this advantage appears to be balanced against lower energetic investment in attachment strength.

The risk of dislodgment of a mussel is proportional to the square of maximum water velocity. Dynamometers showed a vertical gradient of maximum wave forces in the mussel zone, with more intense hydrodynamic forces lower on the shore. This mirrored a vertical gradient in mussel attachment strength for both species. Moreover, *P. perna* living lower on the

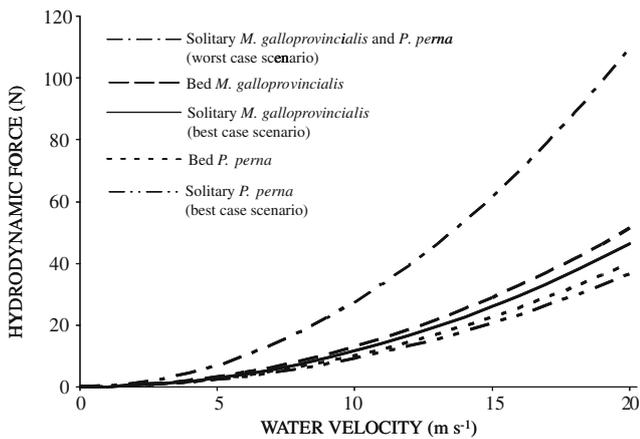


Fig. 6 *Mytilus galloprovincialis* and *Perna perna*. Predicted scaled hydrodynamic forces as a function of water velocity for solitary (worst and best case scenario) and bed mussels (4.5 cm shell length). The *P. perna* solitary worst case ($y = 0.274x^2 + 6 \times 10^{-14}x$) and best case scenario ($y = 0.091x^2 - 7 \times 10^{-15}x + 3 \times 10^{-14}$), *P. perna* mussel bed ($y = 0.1x^2 + 10^{-14}x - 3 \times 10^{-14}$), *M. galloprovincialis* solitary worst case ($y = 0.274x^2 + 6 \times 10^{-14}x$) and best case scenario ($y = 0.116x^2 + 10^{-14}x$), *M. galloprovincialis* mussel bed ($y = 0.128x^2 + 3 \times 10^{-14}x - 6 \times 10^{-14}x$)

shore will experience not only higher maximum water velocity but, during a single tidal cycle, it will be subjected to hydrodynamic stress for a longer period than *M. galloprovincialis* living in higher intertidal areas.

Hydrodynamic stress depends not only on water velocity but also on shell shape and the area over which the force acts. Scaled to mussel shell length, *M. galloprovincialis* has a wider shell than *P. perna*, increasing its hydrodynamic load. *M. galloprovincialis* has an $A_{p,\min}$ 21.7% larger than *P. perna*. Consequently, when exposing $A_{p,\min}$ to wave forces, it will experience about 22% greater hydrodynamic stress. The morphometric relationship for shell length versus $A_{p,\max}$ did not differ significantly for the two species; thus they will experience similar hydrodynamic drag forces when exposing $A_{p,\max}$ to water flow. Possible morphometric differences between bed and solitary mussels of the same species were not obvious and were not investigated.

The risk of dislodgement, of course, depends on a mussel's attachment strength. Hydrodynamic forces can affect the integrity of the byssus by damaging or breaking some of the byssal threads, or by dislodging the whole animal when the forces exceed total byssal strength. On average, *P. perna* was 25% more strongly attached than *M. galloprovincialis*, and the attachment strength of solitary mussels was 20% higher than that of bed mussels; these differences are due to an increased thread number and thread diameter. Differences in thread strength were not investigated.

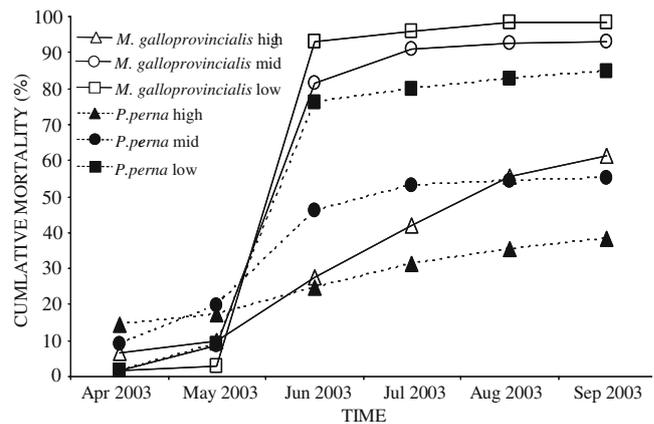


Fig. 7 *Mytilus galloprovincialis* and *Perna perna*. Total cumulative percentage mortality of *P. perna* and *M. galloprovincialis* in the field (treatments pooled) from the high, mid and low mussel zones. $n = 600$ each species each zone

A wider shell and weaker byssal attachment in *M. galloprovincialis* could explain the vertical zonation of the two species, and the restriction of *M. galloprovincialis* to the higher mussel zones, where water velocity is less intense and exposure to wave action is briefer. Moreover, *M. galloprovincialis* has a greater tolerance to desiccation than *P. perna* and that allows the invasive species to penetrate further up the shore (van Erkom Schurink and Griffiths 1993). However, field experiments indicate that the exclusion of *M. galloprovincialis* from the low zone on the south coast is due not only to the effects of wave action, but also to competitive interaction with *P. perna* (Rius and McQuaid 2006).

Due to their orientation and position on the rocks, bed and solitary mussels are primarily subjected to lift and drag force, respectively. Laboratory studies showed that solitary mussels tend to arrange the posterior–anterior axis perpendicular to water flow and parallel to the substratum, thus exposing a smaller area and reducing hydrodynamic stress (Dolmer and Svane 1994). In the field, this ideal orientation is difficult to maintain due to the variable and unpredictable flow of breaking waves. On average, a 4.5 cm solitary mussel in the worst position (broadside to the flow) exposes 60% more surface area than a solitary mussel of the same size positioned end on, and will experience proportionally larger hydrodynamic stress. In contrast, bed mussels lie vertical to the substratum, exposing the smallest shell area to lift, which is independent of the direction of water flow. Consequently bed mussels are subject to a more predictable hydrodynamic environment (Denny 1987). On average, a solitary mussel is about 20% more strongly attached than a bed mussel; however, its increased attachment strength is not enough to compen-

sate for the higher hydrodynamic load (between 53.4 and 63.5%, for 4.5 cm shell length) when exposing the large shell area, making this position less secure.

Attachment strength was quantified by pulling the mussel normal to the substratum until dislodgement occurred, which simulates lift forces, but not drag; thus it is an adequate method for bed but not solitary mussels. Bell and Gosline (1996) predicted that the tenacity measured parallel to the substratum for a solitary mussel with uniformly distributed byssal threads is 53–57% of that measured perpendicular to the substratum. According to this prediction, solitary mussels would be even more prone to dislodgement. A mussel living in a densely packed bed is protected from hydrodynamic stress and predation by nearby mussels and can decrease the metabolic cost of byssus production, allowing more energy to be invested in growth and reproduction. However, in a mussel bed, reduced food availability leads to slower growth and lower reproductive output (Okamura 1986; Frechette et al. 1989; O’Riordan et al. 1993; Butman et al. 1994). Moreover, mussel beds can form a very dense and intricate matrix of byssal threads attaching to the substratum and linking mussels to each other. When mussel density is very high, the byssal matrix can lose contact with the substratum, resulting in a slight elevation of the mussel bed, a hummock, that is relatively easily dislodged by wave action (e.g. R. Seed and T.H. Suchanek 1992, personal observation). Removed individuals deprive neighbouring mussels of shelter and of area to which byssal threads can attach, so that their attachment strength is lowered. In addition, being connected to each other, the hydrodynamic stress suffered by one mussel can be partially transferred to nearby individuals.

Generally, the plaque was the most common failure location for both species. Plaque fallibility could have been overestimated due to difficulties in distinguishing between plaque failure and failure of a thin layer of substratum to which the plaque adheres. This miscalculation would have been more pronounced in bed mussels than solitary mussels because of the higher amount of sediment (sand, shell fragments etc.), which tends to accumulate within a bed. The large amount of sediment could also explain the higher substratum fallibility of bed mussels compared to those not living in patches. Stem failure never occurred and our results show that the root was the second least common failure location. Threads failed more in solitary mussels than in bed mussels, probably because the former are attached to the primary substratum, while at least some of the threads of bed mussels are attached to less secure secondary substratum. Root failure occurs only when the root is weaker than the total byssal thread

strength and may be more common in solitary mussels because they have more and thicker threads attached to primary substratum.

Mussel dislodgements are sporadic events, which can occur unpredictably throughout the year, but strong storms during winter render mussels particularly prone to hydrodynamic disturbances (Brundrit and Shannon 1989). A storm in June 2003 dislodged a high proportion of the mussels in the field experiment. Mortality showed a marked decrease from the low zone, through the mid zone to the high zone, indicating that mussels on the low shore were significantly more susceptible to storms. In all mussel zones the mortality of *M. galloprovincialis* was higher than that of *P. perna*, highlighting the ability of the indigenous *P. perna* mussel to withstand hydrodynamic stress better.

Overall this study shows that, while *P. perna* has a narrower shell, its ability to withstand waves more than *M. galloprovincialis* is mainly due to the higher attachment strength it gains from more and thicker byssal threads. During gonad development, mussels are subjected to very high energetic demands and invest up to 90% of their energy in gamete production (Seed and Suchanek 1992), while the replacement of decayed byssal threads can take up 8–15% of total energy expenditure (Griffiths and King 1979; Hawkins and Bayne 1985). Differences in attachment strength between the two species can be seen as a consequence of the evolutionary strategy of the invasive mussel, which directs most of its energy into fast growth and high reproductive output (20–200% greater than that of indigenous mussel species; van Erkom Schurink and Griffiths 1991). Although the reproductive strategy of *M. galloprovincialis* has played a crucial role in its ability to invade rocky shores worldwide, and its ability to re-colonise free space more quickly than *P. perna* (Erlandsson et al. 2006), it can also set the limits of its invasive ability. Our results and the decreased growth rates and condition values of *M. galloprovincialis* on extremely exposed shores (Steffani and Branch 2003a), support the prediction that the ability of *M. galloprovincialis* to displace *P. perna* will be more pronounced at moderately exposed sites.

Acknowledgment This research was funded by Rhodes University and the National Research Foundation of South Africa.

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