

Wave action and competitive interaction between the invasive mussel *Mytilus galloprovincialis* and the indigenous *Perna perna* in South Africa

Marc Rius · Christopher D. McQuaid

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Abstract On the south coast of South Africa, the invasive alien mussel *Mytilus galloprovincialis* shows partial habitat segregation with the indigenous mussel *Perna perna*. *P. perna* predominates in the lower mussel zone and *M. galloprovincialis* in the upper zone, with mixed beds where the two overlap. We examined competitive interactions between these species by translocating mussels into small plots at high densities. Treatments involved different combinations of species and densities placed in each zone. Mortality was monitored regularly and at the end of each experiment, growth and condition index were measured. The experiment was attempted three times. The first two attempts were disrupted by wave action, especially winter storms, but provided information on species-specific effects of wave action. In experiment one, wave induced mortality decreased from a mean for both species of approximately 90% on the low shore to ca. 50% on the high shore, and was 15–30% lower for *P. perna* than *M. galloprovincialis* in each zone. In experiment two, *M. galloprovincialis* mortality was not affected by zone (Kruskal–Wallis test, $P > 0.05$), but was higher than *P. perna* mortality in the low zone ($P < 0.05$). *P. perna* survival was significantly ($P < 0.05$) lower on the high than mid and low zones, apparently due to the effects of greater emersion. Condition index showed a similar pattern, being lowest in the low zone for *M. galloprovincialis* and in the high

zone for *P. perna* (3-way ANOVA, $P < 0.05$). Growth rates were fastest for both species in the low zone (Kruskal–Wallis, $P < 0.05$ in both cases). The third experiment was run for 12 months in the low zone only and provided evidence of intraspecific competition for *P. perna* and of interspecific competition. Condition was significantly greater for *P. perna* in all treatments (2-way ANOVA), as was growth (Kruskal–Wallis $P < 0.05$). Significant treatment effects indicated that *P. perna* had a negative effect on *M. galloprovincialis* survival (Kruskal–Wallis, $P < 0.05$). Again wave action was important; by the end of the experiment all mussels had been removed from plots stocked only with *M. galloprovincialis*. Thus *P. perna* improves survival of *M. galloprovincialis* on the low shore in the short term, by providing protection against wave action, but excludes it competitively in the longer term. The results show that partial habitat segregation is likely to be a permanent feature on the south coast, with *M. galloprovincialis* unable to dominate the low shore due to the effects of waves and competitive exclusion by *P. perna*. This study is the first attempt to examine the mechanisms of interaction between invasive and indigenous marine mussel species and provides evidence of the importance of environmental conditions in the mediation of this interaction.

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M. Rius · C. D. McQuaid (✉)
Department of Zoology and Entomology, Rhodes
University, Grahamstown 6140, South Africa
e-mail: c.mcquaid@ru.ac.za

Introduction

Alien species are one of the major threats to the maintenance of biodiversity and ecosystem functioning in marine systems (Carlton 1996; Mack et al. 2000; Grosholz 2002). In South Africa, 22 marine alien spe-

cies have been recorded (De Moor and Bruton 1988; Griffiths et al. 1992), but only ten are known to support well-established populations. While the majority of these remain restricted to harbours and sheltered lagoons or estuaries, a single species, the Mediterranean mussel *Mytilus galloprovincialis* (Lamarck), has spread extensively (Robinson et al. 2005) and is now the most abundant alien marine species along the South African coast (Branch and Steffani 2004).

Biological invasions create several interactions between native and invasive species, e.g. predation, competition or parasitism, and these interactions determine the viability of both in any particular situation (Williamson 1996). Many authors have studied how competition affects the interaction between two or more marine species (Branch 1984; Connolly and Roughgarden 1999) and such experiments normally identify a competitive dominant that displaces the competitively inferior species (Harger 1968; Hill 1998). However, because competition can vary over space and time and can be influenced a variety of factors, the dominance of one species over another is not fixed. The intertidal height where organisms interact (Connell 1961; Lubchenco 1980), and the effects of wave action (Paine 1979; Steffani and Branch 2003a) are major factors influencing the outcome of competitive interactions. Two-dimensional space is commonly considered to be a limiting resource on marine rocky shores, but is likely to be a limiting factor only on shores where one or more organisms monopolize the space, occupying 100% of available cover (e.g. Sousa 1984; McGrorty and Goss-Custard 1995).

Mussels are often very successful competitors for space, colonizing extensive intertidal areas and sometimes displacing other intertidal organisms (Paine 1974; Seed and Suchanek 1992). In mussel beds, as mussels grow, space limitation can produce an increase in adult mortality and a decrease in juvenile survival due to intraspecific competition (Griffiths and Hockey 1987). Most of this mortality occurs when the mussels are small (Siegfried et al. 1985). Juvenile mussels are fast growing, intensifying intraspecific competition for space and resulting in massive losses due to self-thinning (Branch and Steffani 2004).

Mytilus galloprovincialis has been described as an invasive species and a competitive dominant in many areas around the world (Lee and Morton 1985; Ramírez and Cáceres-Martínez 1999; Anderson et al. 2002). Along the west coast of South Africa, the indigenous mussel *Aulacomya ater* (Molina) has been largely displaced by *M. galloprovincialis* (Hockey and van Erkom Schurink 1992; Branch and Steffani 2004) and the

limpets *Scutellastra granularis* and *Scutellastra argenvillei* have also been negatively affected (Griffiths et al. 1992; Ruiz Sebastián et al. 2002; Branch and Steffani 2004). For example, *S. argenvillei* competes with the invader for primary space, and their interaction is influenced by the degree of wave force experienced (Steffani and Branch 2003a, b). *M. galloprovincialis* only appeared on the south coast of South Africa in the last fifteen years (McQuaid and Phillips 2000) and there its vertical distribution overlaps with that of the indigenous mussel *Perna perna* (Linnaeus). *P. perna* dominates the lowest zone occupied by mussels and *M. galloprovincialis* the highest, with a middle zone where they co-occur (Phillips 1995; Bownes 2005). However, there is no knowledge of the interaction between the two species or of how these zonation patterns are maintained.

In the present paper, we attempt to examine competitive interactions between *M. galloprovincialis* and *P. perna* in each of these mussel zones. The intention was to test the hypotheses that *P. perna* excludes *M. galloprovincialis* from the low zone and vice versa in the high zone, with no clear competitive hierarchy in the mid zone. Finally we wished to test if physical factors influence the viability of each species in each zone. Due to disruption of the experiments by waves, the hypothesis on competition was tested effectively only on the low shore.

Materials and methods

Study site

The experiments were set up on the south coast of South Africa, on a sandstone platform with a gentle 1/15 gradient at Old Woman's River (33°30'S, 27°10'E). This coast has equal semi-diurnal tides, with a maximum tidal range of 2–2.5 m. Mussel beds show a clear division between the low, mid and high mussel zones with an overall biomass ratio of 10 *M. galloprovincialis*:1,000 *P. perna* (unpub. data).

Experimental approach and design

The experiment was based on the ability of mussels to re-attach after removal from the shore, by creating new byssus threads (King et al. 1990; Dye and Dyantyi 2002). The experimental treatments involved translocation of mussels to small quadrats at relatively high densities to imitate the confined conditions of natural mussel beds. This allowed different species combinations and densities to be compared

providing insight into intra- and interspecific competition for space. Mussels forced out of the quadrats either laterally or vertically were considered to be mortalities.

The experiment was run three times because of problems with wave action. The first experiment was implemented over 4 months (March 2003–June 2003) covering autumn to winter. The second experiment ran for 8 months (September 2003–April 2004) over spring, summer, and part of autumn. The last experiment covered all seasons over 12 months (April 2004–March 2005).

The experimental design was based on Underwood (1986), who reviewed many published experiments on competition. The first and second experiments used an experimental design with three densities of each species combined, as shown in Table 1, to give nine treatments. Comparisons of the various treatments allow examination of intraspecific competition (effects of increasing density of a species) and interspecific competition (effects of presence of a second species) as shown in Tables 1 and 2. The third experiment was simpler (Table 2), with two densities of each species and a total of five treatments. The density values in each plot were based on earlier observations that, in the most crowded quadrats, mussel growth caused all free space to be filled at an early stage of the experiment.

Fieldwork

First and second experiments

Metal quadrats of 0.1×0.1 m were attached haphazardly to the shore with screws and treatments were assigned randomly to quadrats. Each of the nine treatments had four replicates in each of the three mussel zones, giving 36 quadrats per zone for a total of 108 quadrats and 1,800 individuals per species.

As there were insufficient *Mytilus galloprovincialis* for the experiment at the study site, mussels of 20–30 mm shell length of both species were collected in Plettenberg Bay ($34^{\circ}05'S$, $23^{\circ}20'E$), from a rocky platform very similar to the study site. These mussels were placed in a dry insulated box and transported for 4 h to the laboratory, where they were kept overnight in a 3 m^3 system of high quality seawater, re-circulated through UV sterilisation. The next day the mussels were transported to the study site and placed inside the quadrats. Mussels in the quadrats were covered tightly with soft plastic 2 mm mesh to enable them to re-attach to the rocks. After 4 weeks, the mussels had become firmly attached and the mesh was removed. Mortality was monitored monthly.

The first experiment was disrupted after 4 months by winter storms that removed the mussels from most plots.

Table 1 Designs of experiments used to investigate intra- and interspecific competition between *M. galloprovincialis* (*M.*) and *P. perna* (*P.*)

Treatment	1	2	3	4	5	6	7	8	9
<i>M. galloprovincialis</i> (<i>M.</i>)	15	30	45	15	15	30	–	–	–
<i>P. perna</i> (<i>P.</i>)	–	–	–	15	30	15	15	30	45
Comparison	Intraspecific competition 1 vs 2 vs 3 (<i>M.</i> on <i>M.</i>) 7 vs 8 vs 9 (<i>P.</i> on <i>P.</i>)		Interspecific competition <i>M.</i> in 1 vs 4 vs 5 (<i>P.</i> on <i>M.</i>) <i>P.</i> in 4 vs 6 vs 7 (<i>M.</i> on <i>P.</i>)						

Values in cells are number of mussels per $0.1 \times 0.1 \text{ m}^2$ plot

Experimental designs used were for the first and second experiment

Table 2 Designs of experiments used to investigate intra- and interspecific competition between *M. galloprovincialis* (*M.*) and *P. perna* (*P.*)

Treatment	1	2	3	4	5
<i>M. galloprovincialis</i> (<i>M.</i>)	25	50	25	–	–
<i>P. perna</i> (<i>P.</i>)	–	–	25	25	50
Comparison	Intraspecific competition 1 vs 2 (<i>M.</i> on <i>M.</i>) 4 vs 5 (<i>P.</i> on <i>P.</i>)		Interspecific competition <i>M.</i> in 1 vs 3 (<i>P.</i> on <i>M.</i>) <i>P.</i> in 3 vs 4 (<i>M.</i> on <i>P.</i>)		

Values in cells are number of mussels per $0.1 \times 0.1 \text{ m}$ plot

Experimental designs used were for the third experiment

The second experiment was started in summer and the mesh maintained for 4 months to minimize early losses to waves. The mesh was then removed as it could have impeded growth. Wave action again removed mussels from many of the low shore plots while heat/desiccation stress killed many high shore animals. The experiment was terminated 4 months later.

Third experiment

The third experiment included small changes to avoid wave-related losses after removing the mesh. The experiment was set up only in the low mussel zone, where the earlier experiments revealed mussel growth was fastest, and the experimental design was simplified at five treatments, with greater replication ($n = 6$), giving a total of 30 plots, and 600 mussels per species.

The same methodology was used but the lower numbers needed allowed us to collect animals from the study site and place them in the quadrats on the same day.

The mesh was removed after 4 weeks and lids with mesh were placed on top of the quadrats. These lids allowed vertical mussel growth (but little lateral growth) as the mesh was loose. After 3 months, the mesh was replaced with a much looser, coarse mesh (4 mm). This provided some protection, but allowed growth both vertically and laterally. In November, after 8 months, the lids were removed, and the experiment ran until March 2005.

Laboratory work

After each experiment, the remaining mussels were measured to the nearest mm with vernier callipers. The mean final length minus the mean initial length for each species was the estimate of total growth.

To obtain an estimate of the condition of the mussels at the end of the experiments, three mussels were randomly selected from each treatment, replicate, species and zone. The soft tissues were removed and dried at 60°C for 48 h and weighed to 0.1 mg. The shell cavity was measured using the water displacement method. CI was the ratio of dry weight to shell cavity volume (Calvo-Ugarteburu and McQuaid 1998).

Data analysis

All data were tested for normality using Shapiro–Wilk’s W test and for homogeneity of variances using Levene’s test.

For the mortality data, the values collected each month were converted to % mortality to obtain

cumulative % mortality. These data were analysed using parametric 2- and 3-way Model-I Analysis of Variance (ANOVA) with zone, treatment and species as fixed factors. When the data failed to meet the assumptions of ANOVA, and could not be normalized by transformation, the data were analysed using non-parametric Kruskal–Wallis ANOVA tests (Zar 1984). Significant results were followed by Tukey tests (for ANOVA), or Multiple Comparisons Kruskal–Wallis tests (for Kruskal–Wallis ANOVA).

All tests were done using the software STATISTICA version 6.1 for Windows (StatSoft, Inc., 2003) and an α value of 0.05.

Results

First experiment

Mortality

In early June 2003 there were severe storms (personal observation and wave height data from “<http://www.buoyweather.com>”) that destroyed most of the plots, leaving only patches of byssus threads in the quadrats. In the months before and after the storms, total mortality remained low, between 2 and 9% per month, with minimal differences evident between species or among zones. However, in June, 67.7 and 37.8% of all *M. galloprovincialis* and *P. perna* respectively were lost. Mortality decreased upshore, but in all zones mortality of *M. galloprovincialis* was higher than that of *P. perna* (Fig. 1).

Second experiment

Mortality

Total cumulative mortality (treatments and zones pooled) during the 4 months when the quadrats were covered by mesh was 6.7% for *M. galloprovincialis* and 5.9% for *P. perna*. One month after the removal of the mesh, the total accumulated mortality was 52.7% for *M. galloprovincialis* and 49.6% for *P. perna*. At the end of the experiment these values had risen to 72.2 and 58.7% respectively.

The data from every month failed normality and homoscedasticity tests ($P < 0.05$) and no transformation allowed the data to satisfy the assumptions of parametric tests. Significant effects were found between species and zones (Kruskal–Wallis ANOVA tests, $P < 0.05$ and $P < 0.01$ respectively). The effect of species was only significant in the low zone (Multiple

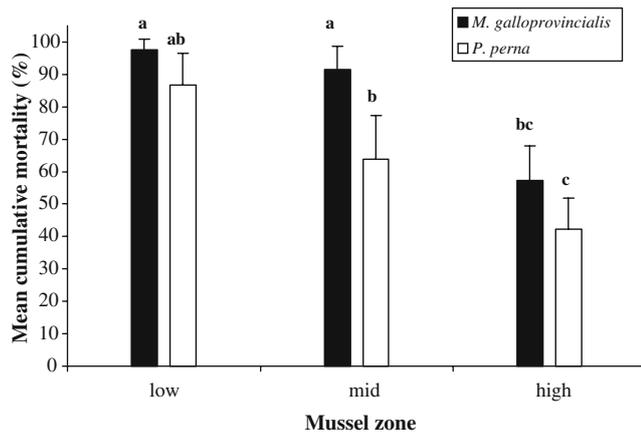


Fig. 1 First experiment. Mean cumulative mortality (%) by the end of the experiment for *M. galloprovincialis* and *P. perna* in each zone (treatments pooled). Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Multiple Comparisons Kruskal–Wallis tests

Comparisons Kruskal–Wallis test, $P < 0.05$), where mean mortality of *M. galloprovincialis* was much higher than that of *P. perna* (Fig. 2). Mortality of *M. galloprovincialis* was not affected by zone, while for *P. perna*, mortality was statistically greater in the high zone than in the mid and low zones. The treatment effect was weak; treatment four differed from treatments 2 and 3 (Table 1, Multiple Comparisons Kruskal–Wallis test, $P < 0.05$).

Condition

Log-transformed condition index data were analysed using 3-way ANOVA (species, zone and treatment). The results (Fig. 3) showed a significant interaction among species, treatment and zone ($F = 2.6$, $P < 0.01$), the effect of treatment being the only non-significant main effect ($F = 0.9$, $P > 0.05$). Mean CI for *P. perna* was higher than for *M. galloprovincialis* in all zones, but the difference was significant (Tukey test, $P < 0.05$) only in the low and mid zones (Fig. 3).

Growth

Growth data showed significant effects of species and zone (Kruskal–Wallis ANOVA test, $H = 5.5$, $P < 0.05$ and $H = 88.7$, $P < 0.01$, respectively) but not treatment ($H = 0.8$, $P > 0.05$). The overall data showed that maximum growth for both species occurred in the low zone, minimum growth on the high zone for *P. perna* and in the mid zone for *M. galloprovincialis*. Growth in the mid zone was higher for *P. perna* than for *M. galloprovincialis*, and vice versa in the high zone, but the differences were not significant. Multiple Comparisons

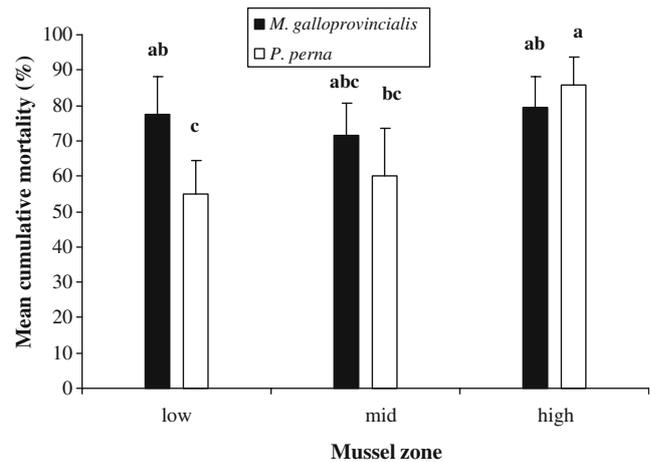


Fig. 2 Second experiment. Mean cumulative mortality (%) by the end of the experiment for each species in each zone (treatments pooled). Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Multiple Comparisons Kruskal–Wallis tests

Kruskal–Wallis tests showed significant differences ($P < 0.05$) among all zones for *P. perna*, while the low zone differed from the mid and high zones for *M. galloprovincialis*. Again, differences between species were non-significant in each zone.

Third experiment

Mortality

Total mortality before the mesh was removed after 8 months was 7.2% for *P. perna* and 11.8% for *M. galloprovincialis*. One month after mesh removal, the values were 9.7% for *P. perna* and a remarkable

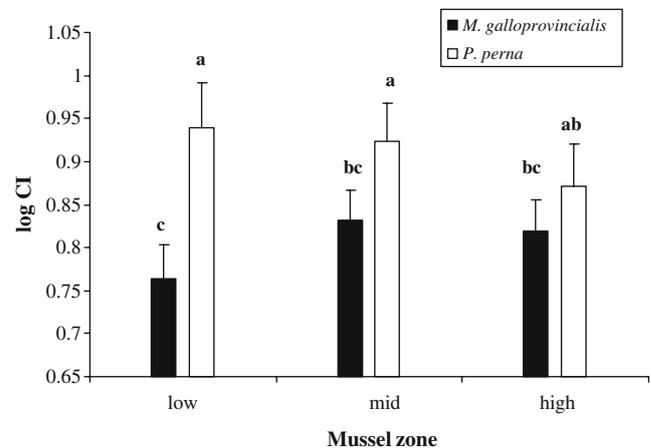


Fig. 3 Second experiment. Mean log CI values for each species in each zone. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Multiple Comparisons Kruskal–Wallis tests

74.2% for *M. galloprovincialis*. Of total *M. galloprovincialis* mortality, 91.2% were lost from monospecific quadrats. At the end of the experiment, total losses had increased to 15.7% for *P. perna* and 91.5% for *M. galloprovincialis*. Two analyses were performed, using only data from the first eight months to separate the effects of competition and the entire data set for the effects of competition combined with wave action.

The accumulated mortality data showed slightly non-normal distribution ($P < 0.05$) and heteroscedasticity for the first 3 months (Levene's test, $P < 0.05$) but homoscedasticity in the last 9 months ($P > 0.05$). No transformation could satisfy the assumptions of parametric tests. Kruskal–Wallis ANOVA was run using species and treatments as factors. For the first 8 months, both factors showed significant effects (Kruskal–Wallis ANOVA test: species $P < 0.01$ and treatment $P < 0.05$). *M. galloprovincialis* showed higher mortality than *P. perna* in treatment 3 (Multiple Comparisons Kruskal–Wallis, $P < 0.05$; Fig. 4). Treatments 1 and 3 for *M. galloprovincialis* differed significantly ($P < 0.05$), indicating interspecific competition, with a negative effect of *P. perna* on *M. galloprovincialis* mortality. In the other treatments, mortality was slightly higher for *M. galloprovincialis* than for *P. perna*, but the differences were not significant ($P > 0.05$).

Mortality after 12 months also showed significant effects of both factors (Kruskal–Wallis ANOVA test, $P < 0.01$). Multiple Comparisons Kruskal–Wallis tests (Fig. 5) showed significant differences between treatments 4 and 5, indicating intraspecific competition in *P. perna*, with higher mortality at higher densities. In treatment three, the differences between species increased, with fewer *P. perna* dying than *M. galloprovincialis* in the last 4 months (Figs. 4, 5), reinforcing

the suggestion of interspecific competition. The comparison of treatments 1 and 3 for *M. galloprovincialis* is misleading with regard to competition as it indicates that *P. perna* improves survival of *M. galloprovincialis*. This reflects the fact that all monospecific plots of *M. galloprovincialis* suffered 100% mortality due to wave action.

Condition

Condition index data showed normal distribution and homoscedasticity. 2-way ANOVA showed a strong species effect ($F = 25.6$, $P < 0.001$) with *P. perna* being superior to *M. galloprovincialis* in all treatments. The effects of treatment and its interaction with species were not significant ($P > 0.05$).

Growth

Growth data were missing for treatments 1 and 2, as all animals had been removed by waves. Data showed non-normality ($P > 0.001$) and heteroscedasticity ($P > 0.001$). Kruskal–Wallis ANOVA showed significant species and treatment effects ($P < 0.001$). Multiple Comparisons Kruskal–Wallis tests showed no significant differences among treatments for *P. perna*, while *P. perna* in all treatments had faster growth than *M. galloprovincialis* in the only treatment for which data were available.

Discussion

An unexpected result of this study was the influence of wave action on the experiments. Physical disturbance

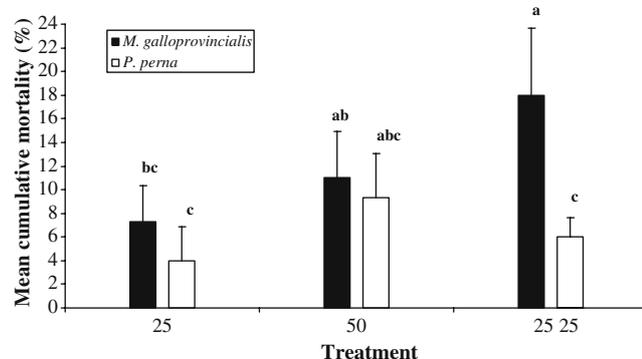


Fig. 4 Third experiment, results after 8 months. Mean cumulative mortality (%) for each species in each treatment. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Multiple Comparisons Kruskal–Wallis tests

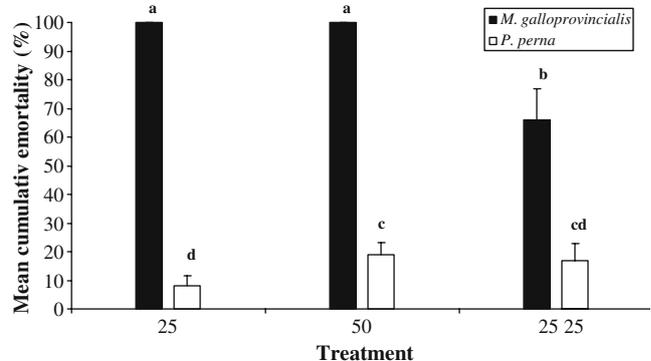


Fig. 5 Third experiment, results after 12 months. Mean cumulative mortality (%) for each species in each treatment. Vertical bars denote 95% confidence intervals. Letters indicate homogenous groups as determined by Multiple Comparisons Kruskal–Wallis tests

may act in the same way as predation, maintaining non-equilibrium conditions under which competition is reduced (Branch 1984) and retarding the process of competitive elimination (Connell 1978). By removing individuals that can competitively exclude other organisms, the system is maintained in a state of biological undersaturation (Hockey and Bosman 1986; Steffani and Branch 2003a). Wave action is one of the primary causes of disturbance on rocky shore, preventing dominant competitors from monopolizing primary space and preserving diversity (Paine and Levin 1981; Sousa 1984).

Mussels are prone to removal by waves, leaving bare patches within mussel beds (Harger and Landenberger 1971; Denny 1995). Dislodgements are sporadic events, which can occur unpredictably throughout the year, but strong storms during winter are particularly important (Brundrit and Shannon 1989). A storm destroyed most of the first experiment in June 2003. Predators have relatively little influence on mussel populations in South Africa (Griffiths and Hockey 1987) and it was clear from both the meteorological data and the presence of large patches of byssus threads attached to the rocks (personal observation) that virtually all this mortality was due to wave action. A clear species effect was found and mortality was higher for *M. galloprovincialis* than *P. perna* in all zones. The same species effect occurred in the second experiment and again in the third experiment, when the removal of the mesh resulted in an increase of 2.5 and 62.3% in the mortality of *P. perna* and *M. galloprovincialis* respectively. Clearly when translocated, *M. galloprovincialis* is more vulnerable to waves than *P. perna* on the south coast. This accords with Zardi et al. (2006) who found that *M. galloprovincialis* has fewer and thinner byssus threads than *P. perna*. *M. galloprovincialis* survives well on exposed shores on the west coast of South Africa (Branch and Steffani 2004), where sea temperatures are much lower (9–14°C) than in the study area (12–21°C). This suggests that tenacity of *M. galloprovincialis* is influenced by sea temperature, which could contribute to the fact that it is a weaker invader on the south coast, despite being immune to the parasites that reduce *P. perna* fecundity and growth (Calvo-Ugarteburu and McQuaid 1998). Another hypothesis is that the re-attachment of the invader is not as good as that of *P. perna*.

In the third experiment, *M. galloprovincialis* was entirely removed from all monospecific control quadrats, while individuals in quadrats with both species, showed higher survival rates. This suggests that the invader survives better on this coast when it is found intermingled with the indigenous mussel, which pre-

sumably provides protection against dislodgement by wave action.

The first experiment also showed a strong zone effect with a marked upshore decrease in mortality (Fig. 1). Comparison of the first and second experiments suggests that *M. galloprovincialis* and *P. perna* survived differentially in each mussel zone resulting in spatial segregation (see Figs. 1, 2). The invader did not show a very clear pattern in mortality between mussel zones, the only strong difference being found in the first experiment when the final mortality in the high zone was very low. This suggests higher viability in this zone than in the others. These results are in accordance with Bownes (2005), who analysed aspects of settlement, recruitment, growth and mortality of both species, and found that *M. galloprovincialis* performed better in higher zones than *P. perna*, and vice versa. In contrast, *P. perna* showed very clear but opposite patterns in the first and second experiments. In the first experiment, mortality was primarily due to storm disturbance during winter and clearly diminished from the low to the high mussel zone. In the second experiment, mortality in the mid and low zones was lower than in the high zone. In this last zone, during the summer months, empty shells were found still attached to the rocks in the quadrats, indicating that the mussels had not been killed by wave action. This suggests that *P. perna* in the high mussel zone was strongly affected by heat and desiccation during summer. These experiments showed that wave action is capable of removing mussels throughout the year, mostly in the low zone, and especially during storms. In contrast, storms did not affect mussels in the high zone, but mortality due to factors such as desiccation was important during summer. Mortality in the mid zone was intermediate in both experiments.

Condition index is an important measure of the physiological status of mussels and of the relative allocation of resources to tissue or shell growth (Raubenheimer and Cook 1990; Seed and Suchanek 1992). The second and third experiments showed strong species effects, with higher CI values for *P. perna* than *M. galloprovincialis* in the low and mid zones, but no significant differences in the high zone. Thus *P. perna* performed better than *M. galloprovincialis* in the lower zones, while in the high zone, *M. galloprovincialis* performance improved so that growth and condition were similar for both species (Fig. 3).

On the south coast, *P. perna* grows much faster under exposed than sheltered conditions (McQuaid and Lindsay 2000), and on the west coast marked differences in growth and condition of *M. galloprovincialis* were detected among sites straddling a gradient

of wave exposures (Steffani and Branch 2003c). *M. galloprovincialis* grew faster and had higher condition values at moderately exposed sites than at sheltered sites (van Erkom Schurink and Griffiths 1993) but both growth and condition diminished at extremely exposed sites (Steffani and Branch 2003c).

M. galloprovincialis is an aggressively invasive alien species in South Africa (Hockey and van Erkom Schurink 1992; Griffiths et al. 1992) and is perceived as a strong competitor for intertidal space (Hockey and van Erkom Schurink 1992). However, our third experiment gave evidence of competitive exclusion of *M. galloprovincialis* by *P. perna* on the low shore (comparisons of treatments 1 and 3, Table 2). In addition, higher mortality was found in all quadrats with 50 individuals than in quadrats with 25 individuals. Further, after 12 months, significant differences were found between the monospecific treatments of *P. perna*, indicating the occurrence of intraspecific competition in this species (Fig. 5). Although most examples of intraspecific competition demonstrate effects on growth or fecundity (e.g. Branch 1975; Underwood 1976), in this case there is no evidence of such sublethal effects, but only of mortality through displacement from the substratum.

The fact that byssus attachment of *P. perna* is much stronger than *M. galloprovincialis*, and that the latter appeared to survive better in mixed than in monospecific beds, suggests that *M. galloprovincialis* survival is enhanced by the presence of *P. perna*. However, at the same time that *P. perna* confers protection against dislodgement by wave action, it competitively excludes *M. galloprovincialis*. Thus, *M. galloprovincialis* individuals that survive wave removal by being in mixed species beds may eventually be removed by interspecific competition.

Some studies have described higher performance of pernids than other mytilids (Vakily 1989) and have described *P. perna* as a successful invasive species (Hicks et al. 2001). A clear example of *M. galloprovincialis* disadvantage on this coast is its weaker byssus tenacity in relation to *P. perna* (Zardi et al. 2006). On the west coast, peak biomass, maximum size of *M. galloprovincialis*, its greatest percent cover and depth of mussel beds are all attained at intermediate levels of wave exposure (Branch and Steffani 2004). Our study site, Old Woman's River was defined as semi-sheltered (McQuaid and Lindsay 2000), which should provide ideal conditions for *M. galloprovincialis*. However our results suggest that the assumption that *M. galloprovincialis* will inevitably displace *P. perna* from the south coast, as *P. perna* is an inferior competitor, should be recon-

sidered on the basis that the presence of *P. perna* increases mortality of *M. galloprovincialis* on the low shore.

From the results in Figs. 4 and 5, it was concluded that on the low shore, *P. perna* is a better competitor for space than *M. galloprovincialis* (Figs. 4, 5). However, *P. perna* showed better performance, CI and growth values in lower than higher mussel zones, while *M. galloprovincialis* followed the opposite trend. Thus we were able to test our hypothesis on competition on the low shore only and conclude that *M. galloprovincialis* is excluded from this zone by the combined effects of wave action and interspecific competition. The data also suggest that *P. perna* may be excluded from the upper shore by abiotic stress during summer. This implies that *M. galloprovincialis* extends higher up the shore to parts of the shore previously unoccupied by *P. perna*, but we have no data on this.

The findings suggest that the invasion of the south coast by *M. galloprovincialis* may have reached a limit set by unfavourable environmental conditions and that the competitive effects of this invasive on the indigenous species are less intense than on the west coast, allowing co-existence through partial habitat segregation.

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