

# Mechanisms of habitat segregation between an invasive (*Mytilus galloprovincialis*) and an indigenous (*Perna perna*) mussel: adult growth and mortality

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## Abstract

The invasive mussel *Mytilus galloprovincialis* and the indigenous mussel *Perna perna* coexist intertidally on the south coast of South Africa through partial vertical habitat segregation: *M. galloprovincialis* dominates the upper shore and *P. perna* the lower shore. Recruitment patterns can explain the zonation of *P. perna*, but not the invasive species. We examined the role of post-recruitment interactions by measuring spatial and temporal differences in adult growth and mortality rates of the two species. Specifically, we tested the hypothesis that interspecific differences in growth and mortality reflect adult distribution patterns. The two study locations, Plettenberg Bay and Tsitsikamma, are 70 km apart with two sites (separated by 300–400 m) per location, each divided into three vertical zones. Growth was measured seasonally using different marking methods in 2001 and 2003. Cumulative adult mortality was measured through summer in 2003/2004. Both species generally grew more slowly upshore, but they showed different effects of season. For *P. perna*, growth was significantly reduced in winter in the low zone, but unaffected by season in the high zone. For *M. galloprovincialis*, growth was either unaffected by season or increased in winter, even in the high zone. Thus, growth of *P. perna* and *M. galloprovincialis* was reduced under cool winter and warm summer temperatures, respectively; and while growth was more similar between species in summer, *M. galloprovincialis* grew much faster than *P. perna* in winter. Mortality of *P. perna* increased upshore. For *M. galloprovincialis*, mortality was not zone-dependent and was significantly greater than for *P. perna* on the low-shore and (generally) across the shore in Tsitsikamma. Both species had higher growth and mortality rates in Plettenberg Bay than in Tsitsikamma. Thus, *P. perna* seems able to maintain spatial dominance on the low-shore and at certain sites because of higher mortality of *M. galloprovincialis*. We conclude that seasonality in growth of the two species reflects their biogeographic affinities and that coexistence is possible through pre-recruitment effects that limit the vertical distribution of *P. perna* and post-recruitment effects that limit *M. galloprovincialis*.

## Introduction

Physical stresses and interspecific interactions such as competition play a significant role in intertidal community dynamics and the coexistence of competing species (Connell [1961](#); Dayton [1971](#); Suchanek [1978](#)) but are also important to the success of biological invasions. One of the main concerns with invasive species is that they can replace or reduce the number of native ones, and many studies have shown how invasive species outcompete local residents due to superior competitive abilities and physiological tolerances (Holway [1999](#); Byers [2000](#); Steffani and Branch [2005](#)). However, interactions with the environment and native species make the invasiveness of non-indigenous species unpredictable, and competitive ability can be equally important to the resistance of a community to invasion (Sans et al. [2004](#); Paini et al. [2008](#)).

In mussels, growth and mortality are good indicators of competitive ability (Barkai and Branch [1989](#); Petraitis [1995](#)). Superior growth rates can lead to mortality or reduced fitness over slower-growing individuals either directly through overgrowing, undercutting and crushing, or indirectly through exploitation of important resources such as food and space (Harger [1972](#); Wootton [1993](#)). Differential growth and mortality rates between species can reflect physiological tolerances to external factors such as temperature, salinity, sedimentation, desiccation and wave action (van Erkom Schurink and Griffiths [1993](#); McQuaid and Lindsay [2000](#); Westerbom et al. [2002](#); Thielges et al. [2004](#)), in addition to biological pressures such as predation, competition and reproductive demands (Harger [1972](#); Menge et al. [1994](#); Zardi et al. [2007](#)). Recruitment can strongly influence the prevalence of interspecific interactions. High recruitment rates are usually correlated with high adult abundances leading to stronger competition for resources and density-dependent mortality (Connolly and Roughgarden [1998](#)).

These factors may vary spatially e.g., with tidal height, different levels of wave exposure or coastal topography (Griffiths 1981; Archambault et al. 1999; McQuaid and Lindsay 2000), with important consequences for the distributions of competing species. On the Pacific coast of North America, the mussel *Mytilus californianus* Conrad has a growth advantage over *Mytilus trossulus* Gould at higher water velocities, which may explain its dominance on wave-exposed shores (Ackerman and Nishizaki 2004). Temporal fluctuations in environmental or biological variables can also alter the competitive advantage enjoyed by different species so that the competitive hierarchy is continually changing (Harger 1972; Sousa 1979; Paine 1984).

The Mediterranean mussel *Mytilus galloprovincialis* Lamarck is a highly successful invasive species that is now widespread in temperate zones worldwide (Hilbish et al. 2000). In many invaded localities, *M. galloprovincialis* is more successful in the upper intertidal zones than native species due to a superior tolerance of high temperatures and aerial exposure (Kennedy 1976; Petes et al. 2007; Schneider and Helmuth 2007), and its ability to maintain growth in these zones (van Erkom Schurink and Griffiths 1993). It has largely displaced the indigenous *Mytilus trossulus* from most of its southern habitats on sheltered shores in California, likely due to a greater tolerance of high water temperatures than the native mussel, but it appears to be largely absent from wave-exposed shores, where the indigenous *Mytilus californianus* predominates (Ackerman and Nishizaki 2004; Braby and Somero 2006; Fields et al. 2006). However, on the Atlantic coast of Ireland, *M. galloprovincialis* favours wave-exposed shores and is virtually absent from sheltered shores where *Mytilus edulis* Linnaeus is abundant (Gosling and Wilkins 1981), and on the cold-temperate west coast of South Africa, it outcompetes indigenous limpets on moderately exposed shores, where it is most abundant and growth and condition of mussels are highest (Steffani and Branch 2003, 2005; Hammond and Griffiths 2004). *M. galloprovincialis* therefore appears to be highly adaptable to different environments, demonstrating a wide physiological tolerance that is typical of many invasive species. On South African shores, it has spread over 2,050 km of coastline, although 88% of standing stock is concentrated on the west coast where it was first introduced (Robinson et al. 2005) and where its ecological impacts have been most severe. It has displaced the indigenous mussel *Aulacomya ater* Molina intertidally and has significantly altered the population structure and abundance of local mussel and limpet populations there (Griffiths et al. 1992; Branch and Steffani 2004; Steffani and Branch 2005).

*Mytilus galloprovincialis* is now invasive on the south coast of South Africa where it coexists with the indigenous mussel *Perna perna* Linnaeus. As in other parts of the world, it reaches its greatest abundance in the upper intertidal zones, while the indigenous mussel dominates the lower shore (Bownes and McQuaid 2006). *P. perna* is excluded from the high-shore by low settlement and high post-settlement mortality, but recruitment failure does not explain the exclusion of *M. galloprovincialis* from the low-shore (Bownes and McQuaid 2009). Although the same vertical zonation pattern is always evident, the abundance of *M. galloprovincialis* is also highly variable between locations, with low densities along most of the coastline. This study examines the role of post-recruitment factors in habitat segregation and coexistence between *P. perna* and *M. galloprovincialis* on the south coast, by measuring spatial and temporal differences in their growth and mortality rates at two locations with different mussel abundances: one where *M. galloprovincialis* is abundant and one where it is rare. We propose that growth and mortality vary with shore height, favouring each species in the zone where it is dominant, by testing the following hypotheses: (i) that *M. galloprovincialis* is excluded from the low-shore as adults by poor growth rates and high mortality rates subsequent to successful recruitment; (ii) given that *P. perna* is the better interference competitor on the low-shore (Rius and McQuaid 2006), it will show superior growth rates and reduced mortality there compared to the invasive; (iii) that on the high-shore, where settlement of both species is reduced (Bownes and McQuaid 2009), *M. galloprovincialis* is able to maintain high densities through higher growth and lower adult mortality than *P. perna*. We also expect that *P. perna* will show better survival and growth than *M. galloprovincialis* at the location where the invasive is less abundant.

## Growth

For the study species, maximum growth is achieved at sizes of approximately 10–20 mm in length, after which growth begins to decrease with increasing size (Bownes 2006). Mussels on the south coast reach sexual maturity at 20–30 mm in length (Lawrie and McQuaid 2001). The stage of rapid growth before the onset of maturity (10–30 mm in length) is likely to be important to adult interactions and competition for space. Differences in response to environmental conditions are also greatest, and therefore likely to be most evident, where growth is faster i.e., in smaller, sub-adult mussels (Seed 1969). We therefore aimed to incorporate both sub-adult and adult growth by measuring length-specific growth rates from a broad size spectrum of the population at each shore level using ANCOVA.

It was not logistically possible to include patch as a variable nested within zone. Therefore, in each experiment, approximately 80 haphazardly chosen mussels (40 per species, 10–80 mm in length) were marked in each zone at each site so that individual mussels form the sample units. There can be considerable horizontal variation in growth within zones, due to the effects of shading and sun exposure, or position within the mussel bed (Okamura 1986; Schneider and Helmuth 2007). As we were only interested in the variability associated with tidal height and location, conditions were controlled by only marking individuals that were surrounded by other mussels to avoid edge effects (usually from the middle of the mussel bed at each shore level), and only in sun-exposed areas, typical conditions for most mussels at these sites. Marked individuals in each zone were scattered throughout the mussel bed but were generally ca. 1 m apart for ease of recovery. In Tsitsikamma, mussels in the low and high zones occurred in isolated patches rather than in continuous beds, therefore marked mussels were scattered among several haphazardly chosen patches in each zone.

Growth was measured using the fluorochrome growth marker calcein ( $125 \text{ mg l}^{-1}$ ) (Kaehler and McQuaid 1999) in summer (February/March) and winter (June/July) of 2001. Mussels were marked over a single spring tide in each zone at each site in Plettenberg Bay and Tsitsikamma. Samples were collected after 1 month and kept frozen. In the laboratory, mussel length was measured to the nearest mm using Vernier calipers. One valve of each mussel was set in polyester resin, sectioned sagittally using a diamond saw, and then examined under an Olympus fluorescence microscope. Using a micrometre, growth was measured as the distance between the green fluorescent mark and the growing tip (Kaehler and McQuaid 1999).

The recovery rate of marked mussels using this technique was sometimes poor, especially for *Mytilus galloprovincialis*. The experiment was therefore repeated using an alternative method in late summer (March/April) and late winter (July/August) of 2003. Mussels were marked using small triangular paper tags that were glued to the shell using quick-drying superglue, with the longest point of the triangle at the tip of the growing edge (adapted from Millstein and O'Clair 2001). In the laboratory, growth was measured as the distance from the tip of the triangle to the new growing edge using a dissecting microscope fitted with a micrometre.

## Mortality

Mortality was measured during summer (November 2003–March 2004) when desiccation and heat stress are greatest. Ten patches of twenty adult mussels (ten of each species) were marked in each zone at each site. Marked mussels were 30–50 mm in length in the lower zones, and 20–40 mm on the high-shore. Mussel shells were dried and marked with yellow paint, which was sealed with glue once dry. Mortality was measured several times over a period of 4 months by counting the number of mussels remaining.

## Analyses

### Growth

Growth rates of different-sized mussels were analysed simultaneously using analysis of covariance (ANCOVA), which accounts for the variation associated with initial size (General Linear Models, Statistica 6.1–8.0). However, in some cases the assumption of homogeneous slopes was not met. As an alternative, a subset of the data within the size range 10 to 40 mm shell length was analysed using ANOVA. This was possible where growth within this size range showed no relationship with initial shell length. These results were almost identical to those from the ANCOVA; therefore only the latter are presented.

Due to missing data we did not have replicate sites at both locations in either year, thus a nested ANCOVA, with site nested in location, was not possible. We therefore used factorial ANCOVA with one or more of the following variables: season, zone and species as fixed factors and site as a random factor. While we have discussed location effects based on comparisons of sites from each location, significant results must be interpreted with caution. Sample sizes were also unbalanced (see Table 1). Post hoc comparisons were made using Newman–Keuls multiple range tests. The data did not require transformation to reach the assumptions of homogeneity of variances and normality.

Table 1 Number of marked individuals (*n*) of *P. perna* (*P.p*) and *M. galloprovincialis* (*M.g*) recovered from each zone at each site for the growth experiments in summer and winter, 2001 and 2003

Loc	Site	Summer						Winter					
		Low		Mid		High		Low		Mid		High	
		<i>P.p</i>	<i>M.g</i>	<i>P.p</i>	<i>M.g</i>	<i>P.p</i>	<i>M.g</i>	<i>P.p</i>	<i>M.g</i>	<i>P.p</i>	<i>M.g</i>	<i>P.p</i>	<i>M.g</i>
2001													
Plett	BI	20	14	26	16	8	7	25	11	11	12	10	20
Tsi	SB	25	–	15	10	13	12	45	10	54	60	45	21
Tsi	DB	19	–	28	10	9	10	9	–	16	18	–	–
2003													
Plett	LB	28	38	17	9	7	7	24	43	27	61	12	35
Plett	BI	32	20	25	16	22	15	21	26	18	60	20	23
Tsi	DB	20	12	35	12	–	–	15	26	15	28	23	31

*Sites and locations* Lookout Beach (LB) and Beacon Isle (BI) in Plettenberg Bay (Plett); and Sandbaai (SB) and Driftwood Bay (DB) in Tsitsikamma (Tsi)

– No data recovered

### Mortality

Over the 4-month experiment, whole patches were lost due to wave action, and no samples were retrieved from the lower zones in Plettenberg Bay after the 2-month sample. As repeated measures ANOVA was not possible, mortality was analysed after 2 and 4 months separately. For the 2-month analysis, we had a sample size of only three patches in some zones in Plettenberg Bay. Rather than excluding large numbers of samples, the test was performed using unbalanced sample sizes ( $n = 3–10$ ). We used a four-way mixed-model nested ANOVA (General Linear Models, Statistica 6.1–8.0) with site as a random factor nested within location. Sample sizes were higher in Tsitsikamma. For the 4-month analysis, we therefore used a three-way balanced factorial

ANOVA ( $n = 5$ ) to examine the effects of site, zone and species on mortality at this location. The data did not require transformation to reach the assumptions of homogeneity of variances and normality.

Results  
Growth

**2001**

Results were only obtained from three of the study sites in 2001: Beacon Isle in Plettenberg Bay, and Sandbaai and Driftwood Bay in Tsitsikamma. Analyses were further complicated by missing data from zones within each site (see sample sizes in Table 1). Due to the fragmented nature of the data, several different analyses were performed to examine the effects of site (and location), zone and season on the growth of each species. This meant that there was some overlap in the data being analysed, and therefore some repetition in the results.

A comparison of growth of both species between seasons and in all three zones was only possible for one site: Beacon Isle in Plettenberg Bay. All three main effects were significant, with a highly significant interaction among them ( $P < 0.001$ , Table 2). In summer, growth of both species decreased upshore, and *Perna perna* grew significantly faster than *Mytilus galloprovincialis* on the low-shore (Fig. 1a). Winter affected the two species differently. On the low and mid-shore, *P. perna* growth decreased significantly with no change from summer for *M. galloprovincialis*. The reverse was true on the high-shore where growth of *P. perna* remained low, but growth of *M. galloprovincialis* increased significantly. Consequently, *M. galloprovincialis* had significantly faster growth than *P. perna* in the low and high zones in winter.

Table 2 ANCOVA of growth of *P. perna* and *M. galloprovincialis* at Beacon Isle (BI), Plettenberg Bay, in summer and winter of 2001

	Effect	df	MS	F	P
Length	Fixed	1	122.558	134.302	<0.001
Season	Fixed	1	13.544	14.842	<0.001*
Zone	Fixed	2	41.688	45.683	<0.001*
Species	Fixed	1	4.180	4.580	0.03*
Season × zone	Fixed	2	10.239	11.220	<0.001*
Season × species	Fixed	1	31.867	34.921	<0.001*
Zone × species	Fixed	2	5.486	6.012	0.003*
Season × zone × species	Fixed	2	7.701	8.439	<0.001*
Error		167	0.913		

\* Highlights significant effects and interactions

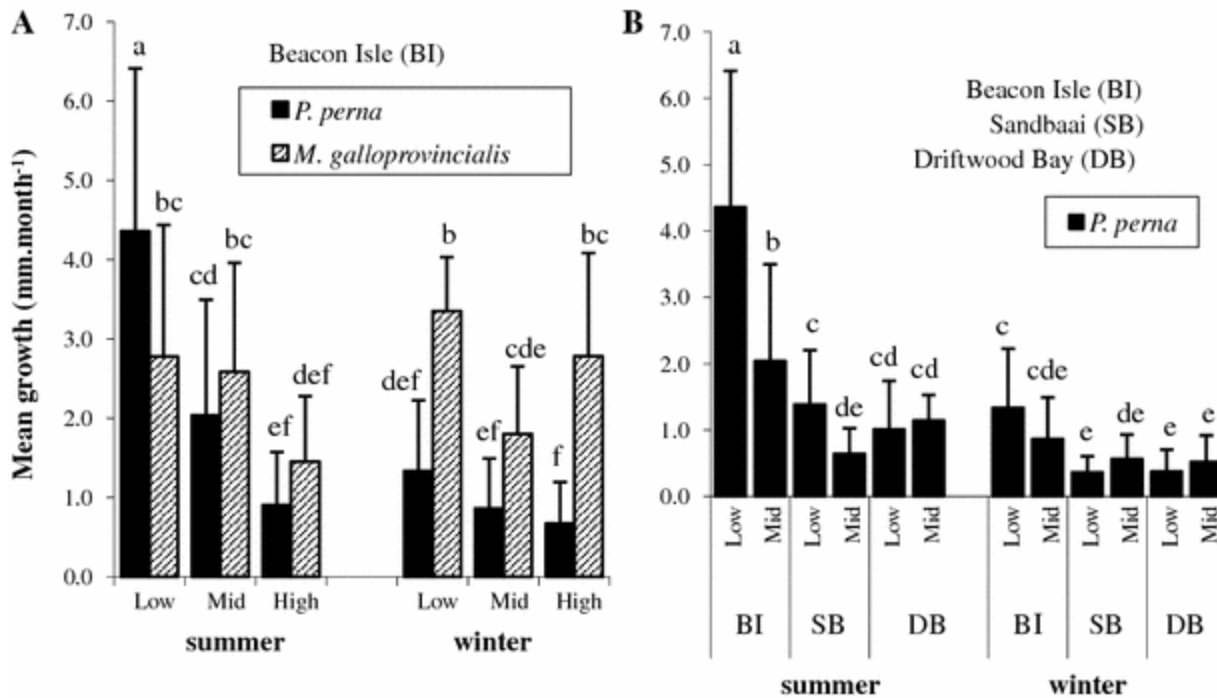


Fig. 1 2001, post hoc comparisons of **a** the season  $\times$  zone  $\times$  species interaction on growth of *P. perna* and *M. galloprovincialis* in summer and winter at Beacon Isle (BI), Plettenberg Bay; and **b** the season  $\times$  site  $\times$  zone interaction on growth of *P. perna* in the low and mid-zones only at Beacon Isle (BI), Plettenberg Bay, and Sandbaai (SB) and Driftwood Bay (DB), Tsitsikamma. Letters indicate homogeneous groups (Newman-Keuls test,  $\alpha < 0.05$ ). Values in this and subsequent figures are means + SD

Growth of both species could only be compared between sites from both locations and in all three zones for two of the sites and for winter only: Beacon Isle in Plettenberg Bay and Sandbaai in Tsitsikamma. Three-way ANCOVA revealed a significant interaction among site, zone and species ( $F_{2,257} = 5.78$ ;  $P < 0.01$ ). The results showed that winter growth of *Mytilus galloprovincialis* was faster than for *Perna perna* across locations, with significant differences in all zones in Plettenberg Bay, but only the mid-shore in Tsitsikamma. *M. galloprovincialis* also grew faster in Plettenberg Bay than Tsitsikamma in all zones, while this difference was only significant for *P. perna* on the low-shore. For both species, growth was significantly higher on the low-shore than the high-shore in Plettenberg Bay, with no differences between zones in Tsitsikamma.

Growth from all three sites could only be compared for *Perna perna* alone, and only for the low and mid zones. Three-way ANCOVA showed a significant interaction between season, site and zone ( $F_{2,280} = 9.41$ ;  $P < 0.001$ ). The effect of season on growth of *P. perna* was consistent across sites and locations, with significantly slower growth in winter than summer in both the low and mid zones (Fig. 1b). In summer, growth in both zones was significantly faster in Plettenberg Bay than in either site in Tsitsikamma, with no difference between the two Tsitsikamma sites. In winter, the difference between locations was only significant on the low-shore, again with no difference between either of the Tsitsikamma sites. The effect of zone differed between sites, with either significantly faster growth on the low-shore than the mid-shore or no difference between these zones.

## 2003

Results were again only obtained from three of the study sites: Lookout Beach and Beacon Isle in Plettenberg Bay, and Driftwood Bay in Tsitsikamma. In Tsitsikamma, no data were recovered from the high-shore in summer (Table 1). Growth of both species could be compared between seasons and at all three sites, but only for the low and mid-zones. The only significant interaction was that between season and species ( $P = 0.015$ ,

Table 3). The two species had similar growth rates in summer, but while growth of *Perna perna* decreased significantly in winter, growth of *Mytilus galloprovincialis* increased significantly, with faster growth than *P. perna* (Fig. 2).

Table 3 ANCOVA of growth of *P. perna* and *M. galloprovincialis* in the low and mid zones at Lookout Beach (LB) and Beacon Isle (BI), Plettenberg Bay, and Driftwood Bay (DB), Tsitsikamma, in summer and winter of 2003

	Effect	df	MS	F	P
Length	Fixed	1	115.403	247.182	0.000
Season	Fixed	1	0.715	0.396	0.593
Site	Random	2	17.396	1.455	0.457
Zone	Fixed	1	41.257	2.948	0.228
Species	Fixed	1	6.353	2.915	0.229
Season × site	Random	2	1.828	0.656	0.655
Season × zone	Fixed	1	8.318	2.302	0.268
Site × zone	Random	2	14.074	2.733	0.243
Season × species	Fixed	1	24.554	61.442	0.015*
Site × species	Random	2	2.212	1.161	0.585
Zone × species	Fixed	1	0.357	0.130	0.753
Season × site × zone	Random	2	3.652	2.898	0.257
Season × site × species	Random	2	0.399	0.317	0.759
Season × zone × species	Fixed	1	4.333	3.490	0.201
Site × zone × species	Random	2	2.765	2.196	0.314
Season × site × zone × species	Random	2	1.255	2.688	0.069
Error		603	0.467		

\* Highlights significant effects and interactions

Fig. 2 2003, post hoc comparisons of the season × species interaction on summer and winter growth of *P. perna* and *M. galloprovincialis* (low and mid-zones; Lookout Beach and Beacon Isle, Plettenberg Bay, and Driftwood Bay, Tsitsikamma). Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )

A comparison of growth of both species in all three zones and across sites was possible for winter only. There was a significant interaction between site, zone and species ( $F_{4, 489} = 3.88$ ,  $P = 0.004$ ). The important differences here were that winter growth of *Mytilus galloprovincialis* was faster than for *Perna perna* in all zones (across sites), including the high-shore, although the difference between species in this zone was only significant at Beacon Isle. Growth decreased upshore for both species at both sites in Plettenberg Bay and the difference between the low and high zones was usually significant, with no differences between zones in Tsitsikamma. Both species grew faster in Plettenberg Bay (both sites) than in Tsitsikamma in the lower zones, but for *P. perna* the difference was only significant on the low-shore.

## Summary

Among the different analyses, we have repetition of the broad patterns both within and between years. This includes the effects of seasonality and location on both species. Although growth generally decreased further

upshore, this effect was not consistent between seasons and sites, particularly at times or places where growth was slower. *Perna perna* generally grew fastest on the low-shore in summer with consistently poor growth on the high-shore. Growth was more similar between species in summer, but they responded differently in winter, when *P. perna* growth decreased significantly in the lower zones. In contrast, growth of *Mytilus galloprovincialis* was either similar between seasons or increased so that winter growth of *M. galloprovincialis* was consistently and substantially higher than for *P. perna* in all zones. Both species had faster growth rates in Plettenberg Bay than Tsitsikamma in the lower zones.

### Mortality

Cumulative mortality rates of *Perna perna* and *Mytilus galloprovincialis* are shown in Fig. 3. In Plettenberg Bay, mortality could not be measured on the low-shore at Lookout Beach after 2 weeks or on the low and mid-shores at either site after 3 and 4 months. After 2 months, mortality in Plettenberg Bay ranged from 30 to 70% in all zones; and after 4 months, it was nearly 100% on the high-shore. Mortality of both species appeared to be lower at Tsitsikamma, with less than 60% mortality across zones after 4 months, except for the low-shore at Driftwood Bay, where *M. galloprovincialis* experienced 80% mortality.

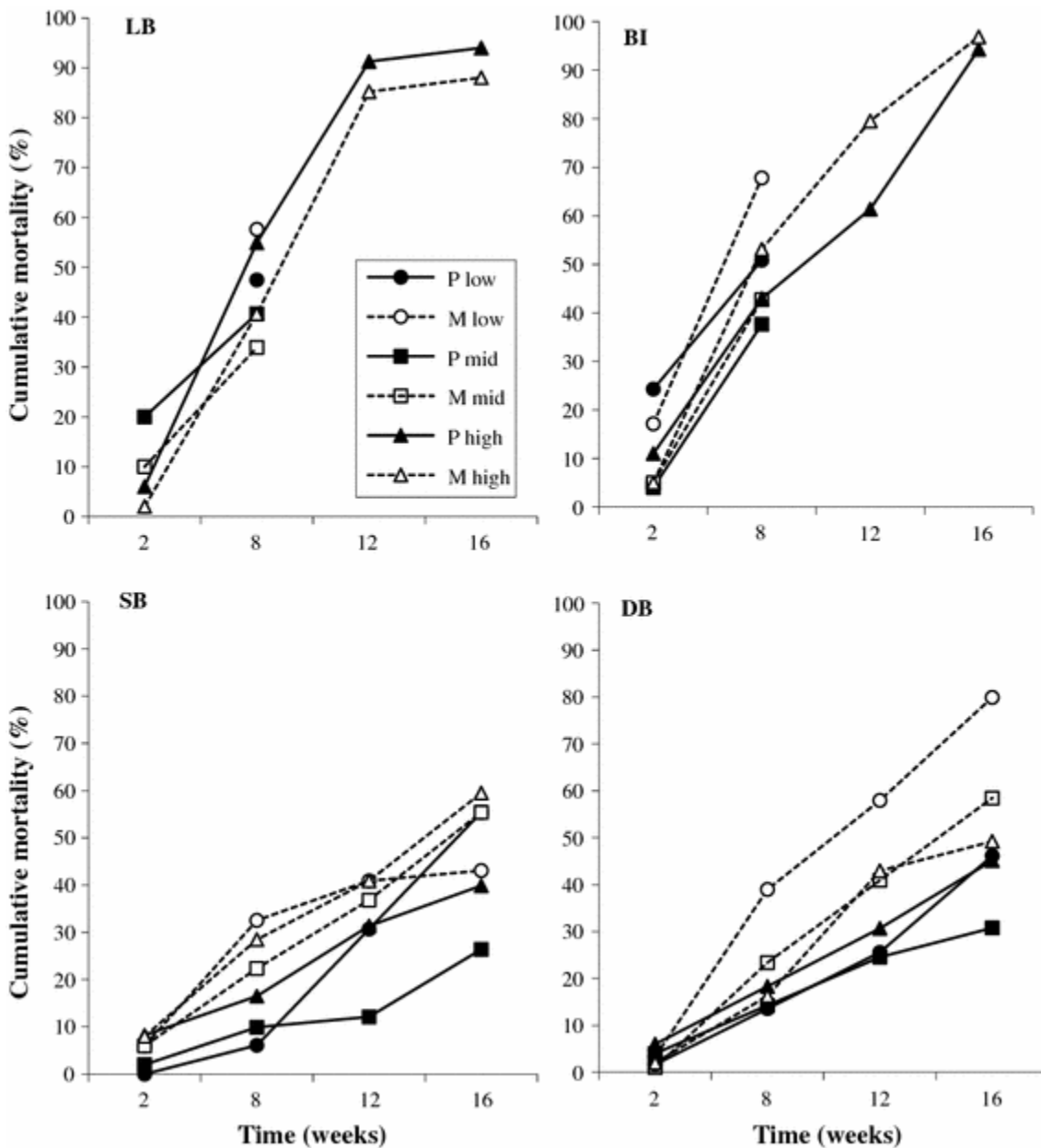




Fig. 3 Cumulative mortality of *P. perna* and *M. galloprovincialis* at Lookout Beach (LB) and Beacon Isle (BI), Plettenberg Bay, and Sandbaai (SB) and Driftwood Bay (DB), Tsitsikamma, over 4 months in summer from November 2003 to March 2004

A nested ANOVA of mortality after 2 months, with location, site (location), zone and species as factors, showed that the effect of location was significant ( $P < 0.05$ , Table 4): total mortality (both species) was higher in Plettenberg Bay than Tsitsikamma. There was a significant interaction between zone and species (both locations;  $P < 0.01$ ). Mortality of *Perna perna* increased upshore and was significantly greater on the high-shore than the low and mid-shores (Fig. 4a). Mortality of *Mytilus galloprovincialis* was similar between zones and was significantly greater than for *P. perna* on the low-shore, with no difference between species in the upper zones. There were also species-specific differences in mortality between sites nested within locations ( $P < 0.03$ ). Post hoc comparisons revealed that overall mortality of the two species (across zones) was similar in Plettenberg Bay and did not differ between sites. However, in Tsitsikamma, mortality of *M. galloprovincialis* was greater than for *P. perna* at both sites, with a significant difference at Sandbaai (Fig. 4b).

Table 4 Nested ANOVA of mortality of *P. perna* and *M. galloprovincialis* after 2 months at Lookout Beach (LB) and Beacon Isle (BI) in Plettenberg Bay, and Sandbaai (SB) and Driftwood Bay (DB) in Tsitsikamma, in summer 2003/2004

	Effect	df	MS	F	P
Location	Fixed	1	12962	19.109	0.046*
Zone	Fixed	2	431	0.534	0.622
Species	Fixed	1	2616.8	5.043	0.149
Location × zone	Fixed	2	532.8	0.660	0.564
Location × species	Fixed	1	642.6	1.239	0.378
Zone × species	Fixed	2	996	13.126	0.006*
Location × zone × species	Fixed	2	16.2	0.214	0.813
Site (location)	Random	2	692.1	0.546	0.608
Site (location) × zone	Random	4	836.1	13.167	0.014*
Site (location) × species	Random	2	526.8	7.184	0.027*
Site (location) × zone × species	Random	4	63.5	0.213	0.931
Error		124	298.1		

\* Highlights significant effects and interactions

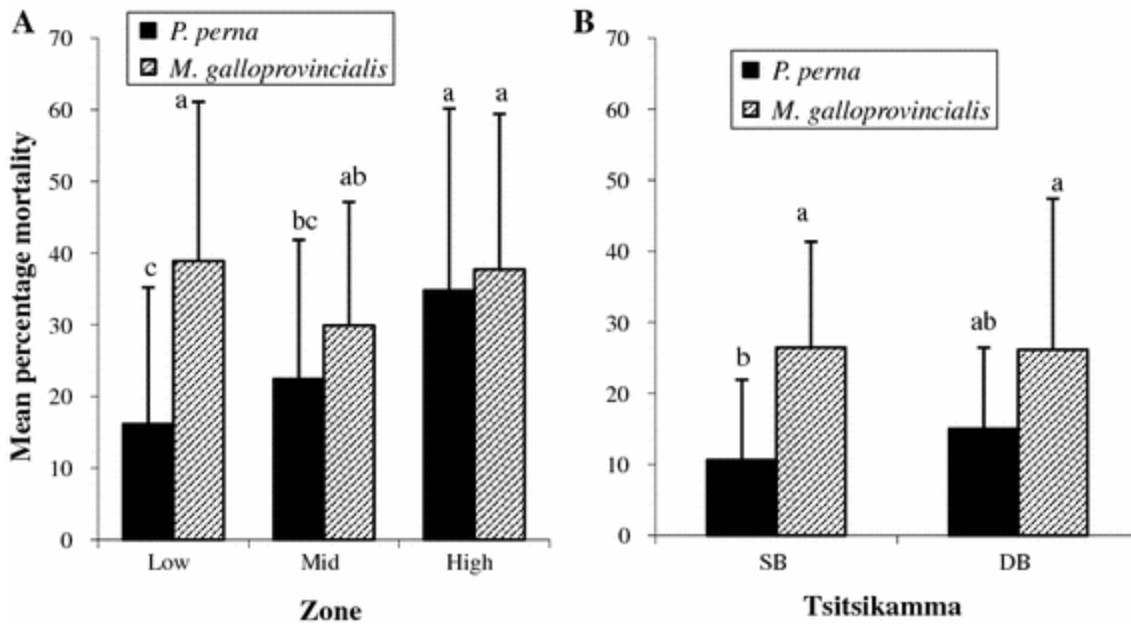


Fig. 4 Mortality after 2 months: post hoc comparisons of **a** the zone  $\times$  species interaction on summer mortality of *P. perna* and *M. galloprovincialis* (Plettenberg Bay and Tsitsikamma); and **b** the site (location)  $\times$  species interaction on summer mortality of *P. perna* and *M. galloprovincialis* at Sandbaai (SB) and Driftwood Bay (DB), Tsitsikamma. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )

After 4 months, a three-way ANOVA on mortality in Tsitsikamma, with site, zone and species as factors, revealed a significant interaction among them ( $F_{2, 48} = 4.06$ ,  $P = 0.024$ ). Mortality of *Perna perna* did not differ significantly among zones regardless of site, but was lowest on the mid-shore (Fig. 5). Except for the low-shore at Sandbaai, mortality was higher for *Mytilus galloprovincialis* than for *P. perna* across sites, with a significant difference in the low and mid zones at Driftwood Bay. Low-shore mortality of *M. galloprovincialis* was also significantly greater than on the high-shore at this site.

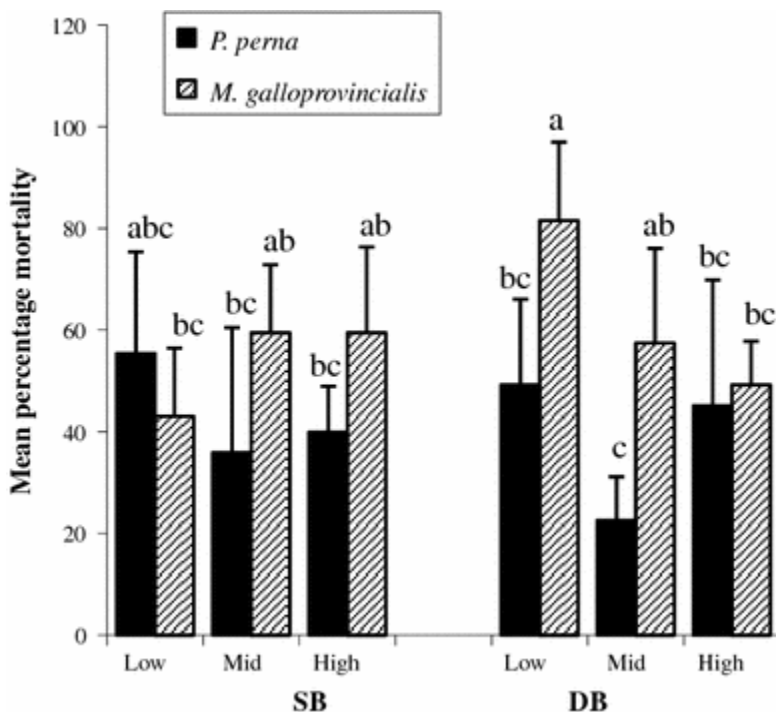


Fig. 5 Mortality after 4 months: post hoc comparisons of the site  $\times$  zone  $\times$  species interaction on summer mortality of *P. perna* and *M. galloprovincialis* at Sandbaai (SB) and Driftwood Bay (DB), Tsitsikamma. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )

## Summary

Mortality of *Mytilus galloprovincialis* was generally higher than for *Perna perna*. This difference was strongest (and usually significant) on the low-shore, with no difference between species in the high zone. Mortality was higher in Plettenberg Bay than Tsitsikamma for both species. In Plettenberg Bay, mortality was similar between species but was higher for *M. galloprovincialis* than *P. perna* in Tsitsikamma.

## Discussion

Earlier work (Bownes and McQuaid [2009](#)) showed that settlement and recruitment correlate well with the adult distribution of *Perna perna*, but this was not true for *Mytilus galloprovincialis*. We therefore proposed that within-shore distribution of *M. galloprovincialis* is better explained by post-recruitment effects and that growth and mortality rates (a proxy for competitive ability) of the two species would vary with shore height in a way that reflects their adult distribution patterns. Despite significant spatial and temporal variability, our results show that each species gains an advantage either through growth or mortality of adults in the zone where it is dominant.

## Growth

For the growth experiments, individual mussels were treated as independent sample units for each shore height. Since adult mussels grow more slowly, the likelihood of observing differences due to the independent variables being measured is reduced, particularly where or when growth is slower (e.g., high intertidal zone). We therefore measured growth across a broad size range to incorporate younger, faster-growing mussels (see Materials and Methods). Due to the number of variables being measured and the size range required, it was not feasible to include patch as a variable nested within zone. This is not problematic in this case, as individuals were chosen randomly (but with the same horizontal spacing across shore heights) and were scattered in the mussel bed or among multiple patches where these occurred. Although recovery was sometimes poor, surviving samples showed reasonable dispersion. Our hypotheses also concerned the effects of vertical variation rather than of patches within zones, which is why conditions on the shore were controlled to minimise horizontal variability.

Growth of both species generally decreased with increasing tidal height, although this effect was less clear at times or in places where growth was slow. Reduced growth at higher tidal levels is common in bivalves (e.g., Griffiths [1981](#), Vincent et al. [1994](#), Bartol et al. [1999](#)) and has been reported for *Perna perna* and *Mytilus galloprovincialis* elsewhere on this coast (Rius and McQuaid [2006](#)). This is generally attributed to a reduction in feeding time higher up the shore (Griffiths and Griffiths [1987](#), Marsden and Weatherhead [1999](#)), which may be augmented by desiccation and high temperatures reducing the energy available for growth, as more is required for metabolic maintenance (Bartol et al. [1999](#)). *M. galloprovincialis* grows better than *P. perna* at higher shore levels on the south west coast of South Africa, probably because it is more tolerant of desiccation stress (van Erkom Schurink and Griffiths [1993](#)). Our results show that, on the south coast, this difference is seasonal. *M. galloprovincialis* is more resistant to desiccation, but it is also more sensitive to high temperatures than *P. perna* (Nicastro et al. submitted); thus, while *P. perna* grew poorly on the high-shore regardless of season, growth rates of *M. galloprovincialis* generally improved in winter, even on the high-shore.

The effect of season on growth was equally important in the lower intertidal zones. *Perna perna* grew fastest on the low-shore in summer, but in contrast to *Mytilus galloprovincialis*, growth decreased significantly in the lower zones in winter (reducing the effect of tidal height). Consequently, growth was more similar between species in summer, but *M. galloprovincialis* grew substantially faster than *P. perna* in all zones in winter. Many benthic invertebrates experience depressed winter growth rates, which can be due to decreased temperature or

food supply (Dekker and Beukema 1999, Beal et al. 2001, Menge et al. 2008) or to reproductive seasonality (Kautsky 1982, Cranford and Hill 1999).

On the north African coast of Algiers, where the two species are also in contact, *Perna perna* shows similarly strong seasonality, but *Mytilus galloprovincialis* shows more consistent growth throughout the year (Abada-Boudjema and Dauvin 1995), suggesting that our study area offers more marginal habitat than Algiers for *M. galloprovincialis*. The difference in response of these species to seasonality presumably reflects their biogeographic affinities. *P. perna* is essentially a warm-water species, while *M. galloprovincialis* has relatively wide temperature tolerances. *P. perna* is widely distributed in tropical and subtropical regions of the Indian and Atlantic Oceans (Berry 1978). In South Africa, it thrives on the sub-tropical east coast but was absent from the cold water Benguela upwelling system of the west coast even before the invasive species arrived there (van Erkom Schurink and Griffiths 1990). Both the study species can have a winter spawning event in South Africa (van Erkom Schurink and Griffiths 1991, Zardi et al. 2007), and poor tolerance of low temperatures coupled with winter spawning is likely to be the main cause of reduced winter growth in *P. perna*. In contrast, *M. galloprovincialis* is highly successful in the cool-temperate conditions of the west coast of South Africa. However, its occurrence in the subtropical waters of Hong Kong (Lee and Morton 1985) and its displacement of *Mytilus trossulus* in central and southern California (Fields et al. 2006) suggests that it is also well-adapted to warm habitats.

## Mortality

While we did not examine seasonality in mortality, restricting ourselves to the high-stress summer period, there were clear effects of both tidal height and location. Mortality of *Perna perna* increased higher upshore after 2 months, but did not differ between zones in Tsitsikamma after 4 months. Mortality of *Mytilus galloprovincialis* was relatively high in all zones and was significantly higher than for *P. perna* on the low-shore. The similar mortality between species in the high zone was unexpected and contrary to published information for these species, where *P. perna* has shown greater mortality than *M. galloprovincialis* on the high-shore, and than at lower tidal heights, due to emersion stress (van Erkom Schurink and Griffiths 1993, Rius and McQuaid 2009). *M. galloprovincialis* also shows better survival in upper intertidal areas compared to other native species e.g., *Perna canaliculus* Gmelin in New Zealand and *Mytilus trossulus* in California (Kennedy 1976, Petes et al. 2007, Schneider and Helmuth 2007). Our results can partly be explained by a severe storm and unusually rough sea conditions throughout the mortality study. The high mortalities recorded in Plettenberg Bay were mostly caused by the removal of mussel clumps by wave action (pers obs. SB). *M. galloprovincialis* has weaker byssal attachment than *P. perna* (Zardi et al. 2006) and forms densely packed beds in the upper zones at this site, particularly further upshore where mussels are smaller (Bownes and McQuaid 2006). Attachment in multilayered clumps of smaller mussels is weaker (Petraitis 1995), so that these high-shore beds would be particularly susceptible to dislodgement under extreme conditions. Both species would be equally vulnerable when whole patches are dislodged, and these species exhibit compensatory mortality (*sensu* Connell 1978) in that the more abundant species shows higher wave-induced mortality during storms (Erlandsson et al. 2006). *M. galloprovincialis* reaches its greatest densities in the high zone at these sites, which could not be sustained by consistently high levels of mortality, especially since settlement there is low (Bownes and McQuaid 2006, 2009). Storms of this severity are rare, and it is expected that under normal conditions, *M. galloprovincialis* would show better survival in this zone.

The two species have similar recruitment rates in the low zone, but *Mytilus galloprovincialis* has significantly lower cover and smaller maximum sizes than *Perna perna*, suggesting either slower growth or higher adult mortality (Bownes and McQuaid 2006, 2009). Our results show that *M. galloprovincialis* is excluded from the low-shore as adults by mortality. This reflects a combination of greater vulnerability to wave action due to a lower attachment strength than *P. perna* (Zardi et al. 2006) and the fact that *P. perna* is a better competitor for space on the low-shore (Rius and McQuaid 2006).

## Location

We proposed that *Perna perna* would have superior growth and survival rates in Tsitsikamma, where *Mytilus galloprovincialis* was less abundant. This was not the case for growth. Although mussel growth was generally slower in Tsitsikamma, presumably reflecting differences in nearshore conditions of production and food advection (Menge et al. [2003](#)), the effects of species, zone and season were similar to those at Plettenberg Bay. In contrast to growth, overall mortality (across zones) was relatively similar between species in Plettenberg Bay but was higher for *M. galloprovincialis* than *P. perna* in Tsitsikamma. Consistently higher mortality, combined with low recruitment rates (Bownes and McQuaid [2009](#)), may therefore limit the success of the invasive species there.

Both species had faster growth and higher mortality in Plettenberg Bay, where sand inundation is more frequent, than Tsitsikamma, therefore sand stress is unlikely to have been important in this study (see also Zardi et al. [2008](#)). Competition and wave action may explain the difference in mortality between locations. Plettenberg Bay is one of several semi-enclosed bays on the south coast, which generally support much higher mussel abundances than open coast sites such as Tsitsikamma (Bownes and McQuaid [2006](#), von der Meden et al. [2008](#)). The higher mortality rates there are typical of high density populations where recruitment rates are high and space is limited, as competition for food and space is increased. Mussel beds in Tsitsikamma are also monolayered and therefore less vulnerable to removal by wave action so that a combination of reduced competition (linked to slower growth) and higher tenacity may account for the lower mortalities of mussels there.

## Conclusions

Mortality differed between species on the low-shore and between locations (*Mytilus galloprovincialis* showed higher mortality in that zone and at Tsitsikamma where it is rare), but not on the high-shore. In contrast, differences in growth were strong in both the low and high zones, though the strength of this difference depended on season. Seasonality in the two species appears to reflect their adaptation to low temperatures and may modify the competitive hierarchy between them. Like their growth patterns, recruitment of *Perna perna* appears to be seasonal, while *M. galloprovincialis* has more steady recruitment throughout the year (Bownes and McQuaid [2009](#)). In the lower zones, *P. perna* therefore has the advantage in summer, with high recruitment and growth rates, and lower adult mortality rates. While *P. perna* experiences reduced activity in winter, *M. galloprovincialis* shows the reverse, so that its growth is significantly faster, and its recruitment rates are slightly higher, though it remains vulnerable to high mortality in winter storms (Erlandsson et al. [2006](#)). Thus, *M. galloprovincialis* gains an advantage through growth in winter, which may contribute to its dominance in the upper intertidal zones. However, despite being able to recruit and grow successfully in places where it is rare as adults, it is limited by adult mortality, which appears to be a strong force controlling its distribution and abundance on the south coast (see Rius and McQuaid [2006](#), Erlandsson et al. [2006](#), Zardi et al. [2007](#)) and suggests that the indigenous *P. perna* is likely to persist as the dominant species in low-shore habitats.

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