

Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa?

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Abstract

The mussel *Mytilus galloprovincialis* is invasive worldwide, has displaced indigenous species on the west coast of South Africa and now threatens *Perna perna* on the south coast. We tested the hypothesis that *Mytilus* will replace *Perna* by examining changes in their distribution on shores where they co-exist. Total cover, adult density, recruit density, recruit/adult correlations and mean maximum lengths of both species were measured in 2001 at two contrasting sites (Plettenberg Bay and Tsitsikamma) 70 km apart, each including two locations 100 m apart. Cover and density were measured again in 2004. Total mussel abundance was significantly lower in Tsitsikamma, and recruit density was only 17% that of Plettenberg Bay. Abundance and cover increased upshore for *Mytilus*, but decreased for *Perna*, giving *Mytilus* higher adult and recruit density and total cover than *Perna* in the upper zones. Low shore densities of recruits and adults were similar between species but cover was lower for *Mytilus*, reflecting its smaller size, and presumably slower growth or higher mortality there. Thus, mechanisms excluding species differed among zones. Recruitment limitation delays invasion at Tsitsikamma and excludes *Perna* from the high shore, while *Mytilus* is excluded from the low shore by post-recruitment effects. Recruitment limitation also shapes population structure. Recruit/adult correlations were significant only where adult densities were low, and this effect was species-specific. Thus, at low densities, larvae settle or survive better near adult conspecifics. After 3 years, these patterns remained strongly evident, suggesting *Mytilus* will not eliminate *Perna* and that co-existence is possible through partial habitat segregation driven by recruitment limitation of *Perna* on the high shore and post-settlement effects on *Mytilus* on the low shore.

1. Introduction

With the global rise in shipping over the last century, coastal marine habitats have been subjected to increasing rates of introduction of alien species (Carlton, 1996 and Grosholz, 2002). Such species can become invasive, with major consequences for community structure, including the elimination of indigenous species (Reusch and Williams, 1999, Branch and Steffani, 2004 and Castilla et al., 2004). Species may become invasive because they have escaped natural enemies such as predators or parasites (Torchin et al., 2002 and Shea and Chesson, 2002) and this may give them a competitive advantage against indigenous species that require the same resources (e.g. Calvo-Ugarteburu and McQuaid, 1998a).

The Mediterranean mussel *Mytilus galloprovincialis* has become invasive in many parts of the world (Lee and Morton, 1985, McDonald et al., 1991 and Anderson et al., 2002) and now has an antitropical distribution, occurring in the temperate zones of the northern and southern hemispheres while absent from the tropics (Hilbish et al., 2000). It was first detected on the upwelling influenced west coast of South Africa in the 1970s (Grant and Cherry, 1985) and has since replaced the indigenous *Aulacomya ater* (Molina) as the dominant mussel on that coast (Van Erkom Schurink and Griffiths, 1990). It has been suggested that invasive species will tend to have more r-selected life-history characteristics (McMahon, 2002) and the ability of *M. galloprovincialis* to replace

Aulacomya presumably stems from of its higher fecundity, recruitment rate and growth rate (Van Erkom Schurink and Griffiths, 1991 and Griffiths et al., 1992). This apparently provides a competitive advantage that allows *M. galloprovincialis* to occupy the entire niche of *Aulacomya*. The primary oceanographic influence on the south coast of South Africa is the Agulhas Current, which is much warmer and more saline than the waters of the west coast. Levels of phytoplankton chlorophyll and the seasonality of primary production are also quite different (Andrews and Hutchings, 1980, Brown, 1992 and Carter et al., 1987) and the two coasts are biogeographically distinct, supporting quite different intertidal biotas (Emanuel et al., 1992). The most abundant mussel on the south coast is *Perna perna*, which is a major occupier of primary space on the lower shore (McQuaid et al., 2000). Since 1990, *M. galloprovincialis* has spread over about 1000 km of the south coast of South Africa (McQuaid and Phillips, 2000 and Robinson et al., 2005). *M. galloprovincialis* on the south coast is immune to the trematode parasites that attack *P. perna* at high infestation rates and collectively castrate female *P. perna* and reduce the growth rates of young mussels (Calvo-Ugarteburu and McQuaid, 1998a and Calvo-Ugarteburu and McQuaid, 1998b). This is likely to provide *M. galloprovincialis* with a competitive advantage over *P. perna*. As *M. galloprovincialis* on the west coast can occupy the entire lower shore to the sublittoral fringe (Bustamante et al., 1997 and Branch and Steffani, 2004), this suggests that *M. galloprovincialis* will replace *P. perna* on this coast as it has done *Aulacomya* on the west coast.

However, *M. galloprovincialis* abundance on the south coast is highly site-specific, with the species becoming well established at some sites, but not others (personal observation). This may be simply an effect of time, with a lag period before *M. galloprovincialis* dominates the whole south coast, but it may also indicate that some degree of habitat segregation is possible between *P. perna* and *M. galloprovincialis*. The ability of a species to become invasive implies that it has an advantage over competing indigenous species, at least at particular times or places (Shea and Chesson, 2002 and With, 2002), but whether the indigenous *P. perna* will be eliminated by *M. galloprovincialis* depends on whether *M. galloprovincialis* can occupy the entire fundamental niche of *P. perna*. If this is not the case, either through physical constraint, or because the competitive balance alters in time or space, then long-term co-existence will be possible. We can phrase this as the question, “What conditions allow the competitive exclusion of an indigenous species and are these conditions met in this case?”

To address such questions, it is necessary to describe the observed patterns quantitatively (Connell, 1974, Underwood and Chapman, 1996 and Underwood et al., 2000). This study examines the structure and dynamics of mixed populations of *P. perna* and *M. galloprovincialis*. We describe co-existence through partial habitat segregation between *M. galloprovincialis* and *P. perna*, examining changes over 3 years in the zonation and population structure of mussels at a site where *M. galloprovincialis* is abundant and one where it is rare.

2. Materials and methods

2.1. Study sites

Tides in South Africa are semi-diurnal, with tidal ranges of 2–2.5 m over spring tides and 1 m over neap tides (Field and Griffiths, 1991). On the south coast, the area occupied by mussels is generally clearly divided into three vertical zones, characterised by different taxa and different patterns of mussel cover. The sites were chosen to represent sites where *M. galloprovincialis* is relatively abundant (Plettenberg Bay) and where it is relatively scarce (Tsitsikamma). Plettenberg Bay (34°05'S; 23°19'E) is typical of a series of half-heart or log-spiral bays found on this coast. It includes a long stretch of sandy beach, with patches of sand-influenced granite rock. The two locations at this site, Lookout Beach (A) and Beacon Isle (B), are ca. 400 m apart near the middle of the bay (Fig. 1B, C). Both are wave exposed, and mussel beds at this site are multilayered, particularly in the mid- and high mussel zones.

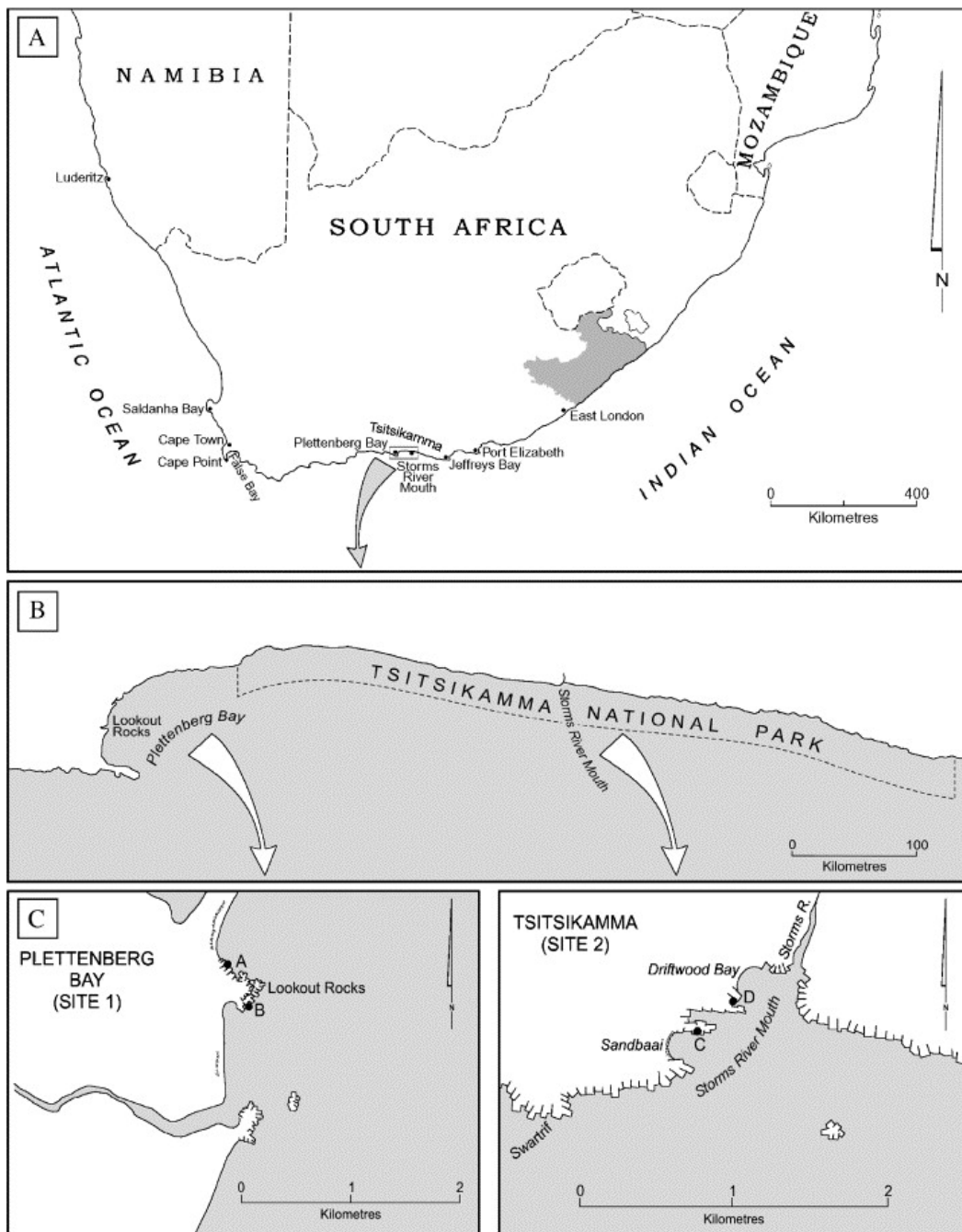


Fig. 1. (A) Position of study sites on the south coast of South Africa; (B) coastal topography of Plettenberg Bay and Tsitsikamma; (C) position of locations within each site. A—Lookout Beach, B—Beacon Isle, C—Sandbaai, D—Driftwood Bay.

The Tsitsikamma site ($33^{\circ}1'S$; $23^{\circ}53'E$) is formed by sandstone rocks and is virtually beachless. The two locations, Sandbaai (C) and Driftwood Bay (D), are ca. 300 m apart in a slight embayment. They receive some protection from southwesterly winds (Fig. 1C) and are moderately exposed/exposed to wave action. Mussels form fairly continuous, monolayered beds on the mid-shore and occur in isolated patches in the low and high mussel zones.

2.2. Population structure

Samples were collected from each location over spring tides in April 2001 and May 2004. The percentage cover of each species was estimated visually using ten quadrats (25×25 cm) placed randomly in each zone. Density was measured by removing all mussels from three quadrats in areas of 100% mussel cover in each zone. In 2001 only, all mussels ≥ 2 mm were identified to species and their lengths measured (1 mm precision) using Vernier calipers. Mussels of each species were arranged into 10 mm size groups and those < 10 mm long were classified as recruits. Densities of recruits and individuals ≥ 10 mm were analysed separately. *P. perna* and *M. galloprovincialis* appear to become sexually mature at 20–30 mm (unpublished data), thus, in examining adult/recruit correlations, adult density only included individuals > 30 mm.

2.3. Analyses

A third species, *Choromytilus meridionalis* was almost entirely restricted to the low shore at Lookout Beach and was therefore excluded from most statistical analyses. However, low-shore cover and density at Lookout Beach in 2001 were compared among all three species using One-way ANOVA with Species as a fixed factor. The abundances of all three species were also compared between years using a factorial ANOVA with Year as a fixed factor. All aspects of population structure of *P. perna* and *M. galloprovincialis* (cover, density, recruit density and maximum lengths) were analysed using mixed model ANOVA with a combination of nested and factorial factors (Statistica 6.0, Advanced General Linear Model). Site, Zone and Species were fixed factors, Location was random and nested within Site. To examine changes in cover and density between years, Year was included as a fifth factor, which was fixed. Significant results were examined using Newman–Keuls multiple range tests ($\alpha = 0.05$). Variations in the maximum sizes of mussels were analysed using the maximum lengths of the ten largest individuals (quadrats pooled). The relationship between recruit and adult density was investigated using Pearsons Product Moment correlation analysis. The maximum length and percentage cover data did not require transformation. However, the density data were significantly heterogeneous with non-normal distributions, and sample sizes were small ($n = 3$). Data were therefore square root transformed (Underwood, 1997). All post-hoc results for density were plotted using transformed data.

3. Results

3.1. Population structure in 2001

3.1.1. Percentage cover

Fig. 2A–D shows percentage cover of mussels in each zone at each location. *C. meridionalis* was only found on the low shore at Lookout Beach, where its cover was significantly greater than that of *P. perna* and *M. galloprovincialis* ($F = 4.95$; $p = 0.01$). As a result, cover of *P. perna* and *M. galloprovincialis* was lower there than at Beacon Isle.

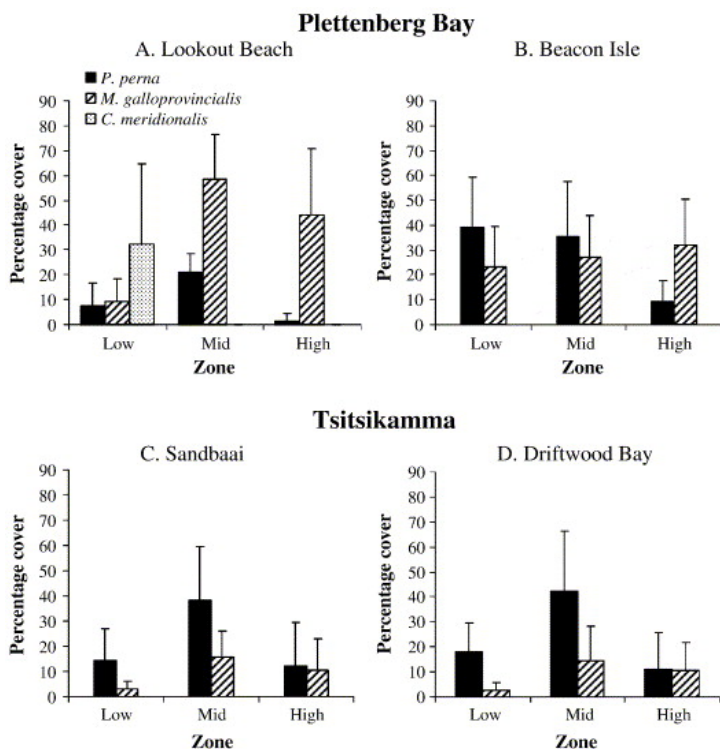


Fig. 2. *Mytilus galloprovincialis* and *Perna perna*. Mean percentage cover of mussels at different tidal heights at locations in Plettenberg Bay and Tsitsikamma in 2001. A—Lookout Beach; B—Beacon Isle; C—Sandbaai; D—Driftwood Bay. Error bars indicate standard deviations.

Mussel cover in Tsitsikamma was significantly lower than in Plettenberg Bay (Table 1; $p < 0.05$). There were also significant location (site) \times species and zone \times species interactions. Cover of *P. perna* was greatest in the mid-zone and lowest in the high zone (Fig. 3). *M. galloprovincialis*, however, had significantly greater cover in the upper two zones than the low zone. *P. perna* cover was significantly greater than *M. galloprovincialis* cover in the low zone, and vice versa in the high zone, with no significant difference in the mid-zone. However, this is an artifact. *P. perna* cover was much greater than *M. galloprovincialis* cover in the mid-zone in Tsitsikamma while the pattern was reversed at Lookout Beach (Fig. 2). The only location where cover of the two species was similar in this zone was at Beacon Isle (36% for *P. perna* and 27% for *M. galloprovincialis*). The interaction between location (site) and species revealed that cover of *M. galloprovincialis* was significantly greater at Lookout Beach than at Beacon Isle, while the opposite was true for *P. perna*. There were no significant differences between locations in Tsitsikamma.

Table 1
Results of mixed model ANOVA on the percentage cover of *P. perna* and *M. galloprovincialis* in 2001

	Effect	Df	MS	F	p
Site*	Fixed	1	5645.4	19.328	0.048*
Zone	Fixed	2	7036.3	5.096	0.079
Species	Fixed	1	1.1	0.000	0.987
Site \times Zone	Fixed	2	46.5	0.034	0.967
Site \times Species	Fixed	1	10666.7	3.621	0.197
Zone \times Species*	Fixed	2	3822.8	11.786	0.021*
Site \times Zone \times Species	Fixed	2	1618.9	4.991	0.082
Location (Site)	Random	2	292.1	0.073	0.931
Location (Site) \times Zone	Random	4	1380.7	4.257	0.095
Location(Site) \times Species*	Random	2	2945.8	9.082	0.033*
Location(Site) \times Zone \times Species	Random	4	324.3	1.398	0.236
Error		216	232.0		

Significant effects are marked with an asterisk (Df=degrees of freedom; MS=mean squares).

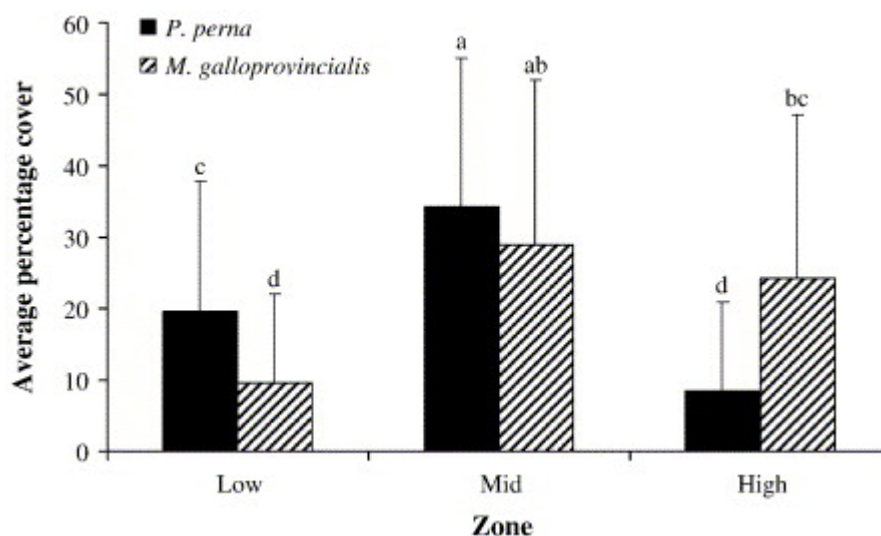


Fig. 3. *Mytilus galloprovincialis* and *Perna perna*. Results of post-hoc comparison of the effects of the interaction between Zone and Species on percentage cover in 2001. Letters indicate homogeneous groups. Error bars indicate standard deviations.

3.1.2. Size structure and density

The size distribution of mussels in Plettenberg Bay was skewed to the left irrespective of zone or species (Fig. 4). There was a peak in the average density of mussels among recruits (< 10 mm) after which density decreased with increasing size. *M. galloprovincialis* showed the same pattern in Tsitsikamma, however, the size distribution of *P. perna* there was bimodal, with similar-sized peaks among recruits (< 10 mm) and adults (30–50 mm).

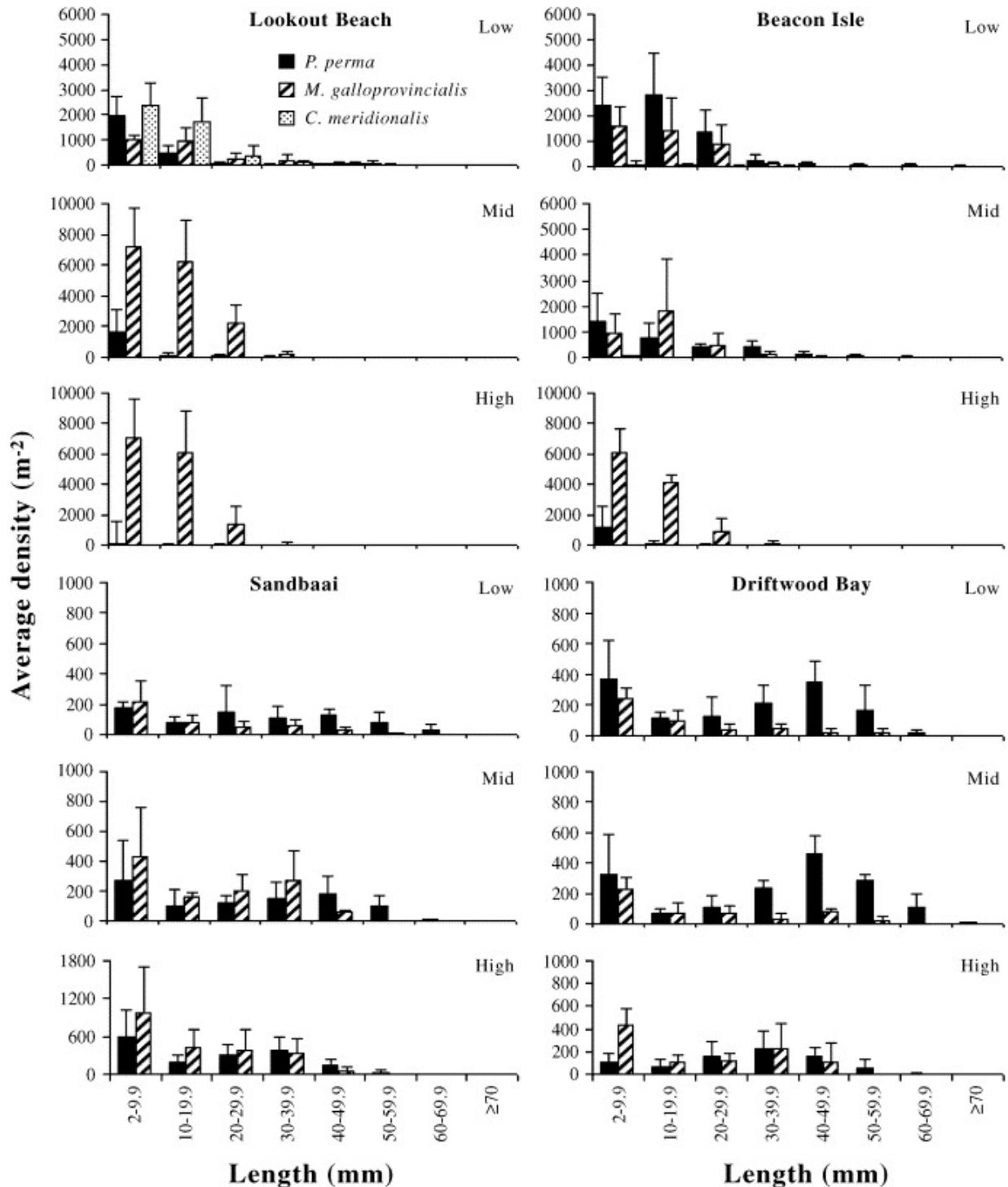


Fig. 4. *Mytilus galloprovincialis*, *Perna perna* and *Choromytilus meridionalis*. Size structure and density of mussels in different zones at Lookout Beach and Beacon Isle (in Plettenberg Bay) and Sandbaai and Driftwood Bay (in Tsitsikamma) in 2001. Error bars indicate standard deviations.

Density of *C. meridionalis* in Plettenberg Bay mirrored percentage cover. This species was abundant on the low shore at Lookout Beach and very low numbers of small individuals were found on the low shore at Beacon Isle. No significant differences in the density of the three species were found at Lookout Beach ($F = 2.23$; $p = 0.19$). Analysis of the densities of *P. perna* and *M. galloprovincialis* > 10 mm revealed a significant difference between sites (Table 2; $p = 0.01$). Average densities were 2923 m^{-2} and 696 m^{-2} in Plettenberg Bay and Tsitsikamma respectively. Density also varied with height on the shore with a different pattern between species ($p = 0.03$). *P. perna* density decreased upshore, and was significantly greater on the low shore than on the high shore, while *M. galloprovincialis* displayed the opposite pattern (Fig. 5). Density of *M. galloprovincialis* was significantly greater than that of *P. perna* in the upper two zones, but was slightly lower than *P. perna* on the low shore.

Table 2
Results of mixed model ANOVA on the density of *P. perna* and *M. galloprovincialis* in 2001

	Effect	Df	MS	F	p
Site*	Fixed	1	7324.83	78.543	0.012*
Zone	Fixed	2	137.82	0.2377	0.799
Species	Fixed	1	3534.79	1.5365	0.341
Site × Zone	Fixed	2	110.94	0.1913	0.833
Site × Species	Fixed	1	8332.16	3.6218	0.197
Zone × Species*	Fixed	2	2816.21	10.0911	0.027*
Site × Zone × Species	Fixed	2	1504.72	5.3918	0.073
Location (Site)	Random	2	93.26	0.0358	0.965
Location (Site) × Zone	Random	4	579.93	2.078	0.248
Location (Site) × Species*	Random	2	2300.58	8.2435	0.038*
Location (Site) × Zone × Species	Random	4	279.08	2.263	0.076
Error		48	123.32		

Significant effects are marked with an asterisk (Df =degrees of freedom; MS=mean squares).

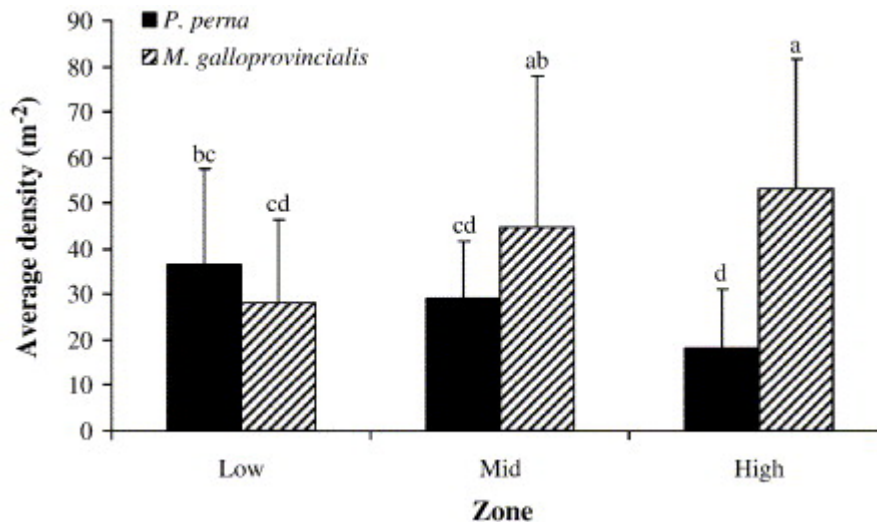


Fig. 5. *Mytilus galloprovincialis* and *Perna perna*. Results of post-hoc comparison of the effects of the interaction between Zone and Species on the density of mussels ≥ 10 mm in 2001. Error bars indicate standard deviations.

As with cover, densities differed between locations within sites ($p = 0.04$). There were no significant differences in density between *P. perna* and *M. galloprovincialis* in Tsitsikamma regardless of location. However, in Plettenberg Bay the density of *M. galloprovincialis* was significantly greater at Lookout Beach than at Beacon Isle, while the opposite was true for *P. perna*. *M. galloprovincialis* also had a significantly greater density than *P. perna* at both locations.

3.1.3. Recruit density and adult/recruit correlations

Recruit density in Plettenberg Bay was six times greater (2636 m^{-2} and 362 m^{-2} respectively) than in Tsitsikamma ($p < 0.01$). There was also a significant interaction between Zone and Species ($p = 0.02$). *M. galloprovincialis* recruit density increased upshore, while *P. perna* recruit density decreased upshore (Fig. 6). Within zones, recruit density between species only differed significantly on the high shore where *M. galloprovincialis* had a greater density of recruits than *P. perna*.

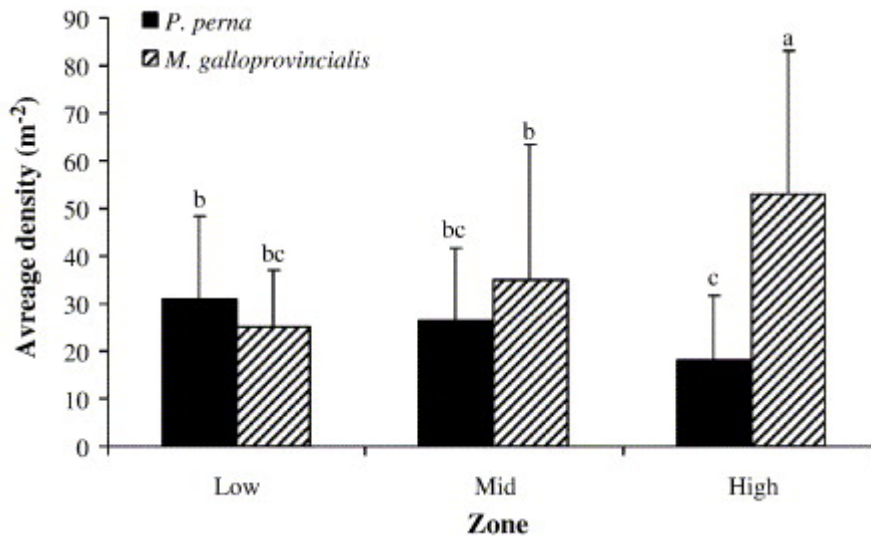


Fig. 6. *Mytilus galloprovincialis* and *Perna perna*. Results of post-hoc comparisons of the effects of the interaction between Zone and Species on the density of recruits (2–9.9 mm) in 2001. Error bars indicate standard deviations.

The relationship between recruit and adult density at different tidal heights was examined at each site (Table 3). Significant positive correlations were found for *M. galloprovincialis* on the low and mid-shore in Tsitsikamma only, and on the high shore at both sites and the low shore in Tsitsikamma for *P. perna*. These results indicate that where adult density is low, recruit density is low and that within mixed populations this effect may be species-specific.

Table 3
Correlations between recruit and adult density in each zone

Zone	Site	<i>P. perna</i>	<i>M. galloprovincialis</i>
Low	Plettenberg Bay	$r^2=0.19$ $p=0.39$	$r^2=0.02$ $p=0.79$
	Tsitsikamma	$r^2=0.96$ $p=0.001$	$r^2=0.81$ $p=0.01$
Mid	Plettenberg Bay	$r^2=0.08$ $p=0.59$	$r^2=0.03$ $p=0.37$
	Tsitsikamma	$r^2=0.05$ $p=0.68$	$r^2=0.73$ $p=0.03$
High	Plettenberg Bay	$r^2=0.98$ $p<0.001$	$r^2=0.24$ $p=0.32$
	Tsitsikamma	$r^2=0.75$ $p=0.03$	$r^2=0.43$ $p=0.16$

Locations at each site are pooled ($n=6$). Significant correlations are in bold.

3.1.4. Maximum lengths

There were significant Site \times Zone \times Species ($p = 0.02$) and Location (Site) \times Zone \times Species interactions ($p < 0.001$). In Plettenberg Bay, mean maximum length (MML) of *P. perna* decreased significantly upshore at both locations (Fig. 7A). MML of *M. galloprovincialis* also decreased upshore at Lookout Beach, but not at Beacon Isle, where MML was greatest on the mid-shore (Fig. 7B). Both species generally attained larger maximum sizes at Beacon Isle than at Lookout Beach. *P. perna* attained significantly larger sizes than *M. galloprovincialis* on the low shore, while the opposite was true on the high shore, regardless of location.

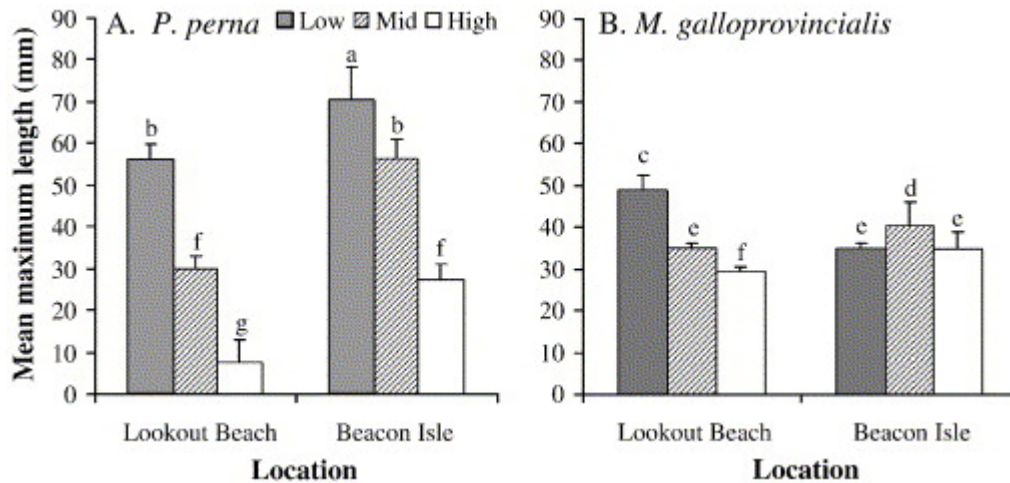


Fig. 7. Mean maximum lengths of (A) *Perna perna* and (B) *Mytilus galloprovincialis* in Plettenberg Bay in 2001: post-hoc test on the Location (Site) \times Zone \times Species interaction. Letters indicating homogeneous groups apply to both graphs. Error bars indicate standard deviations.

In Tsitsikamma, MML of *P. perna* decreased upshore at Sandbaai (Fig. 8A), while MML of *M. galloprovincialis* did not differ among zones (Fig. 8B). At Driftwood Bay, MML of both species was greater in the mid-zone than in the other two zones. *P. perna* had a significantly greater MML than *M. galloprovincialis* at this site, regardless of zone or location. Post-hoc results of the interaction between Site, Zone and Species are not presented, but both species had greater maximum sizes in the upper two zones in Tsitsikamma than in Plettenberg Bay. In the low zone, MML of *P. perna* was greater in Plettenberg Bay while there was no difference in MML of *M. galloprovincialis* between sites in this zone.

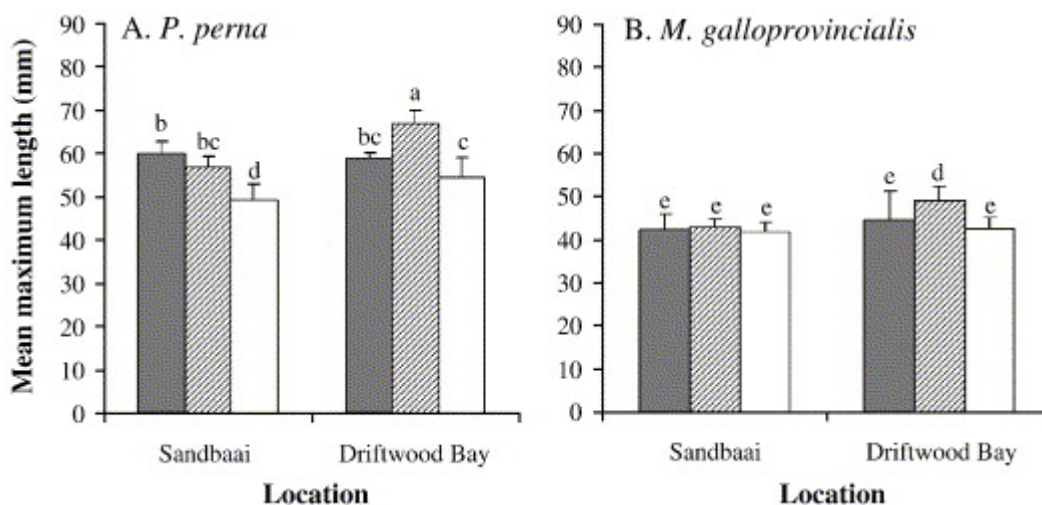


Fig. 8. Mean maximum lengths of (A) *Perna perna* and (B) *Mytilus galloprovincialis* in Tsitsikamma in 2001: post-hoc test on the Location (Site) \times Zone \times Species interaction. Letters indicating homogeneous groups apply to both graphs. Error bars indicate standard deviations.

3.2. Percentage cover and density in 2004

3.2.1. Percentage cover

On the low shore at Lookout Beach, cover of *C. meridionalis* had decreased significantly after 3 years, while cover of *P. perna* and *M. galloprovincialis* had increased significantly. ANOVA of *P. perna* and *M. galloprovincialis* cover indicated a significant increase of both in 2004 (Year effect, $F = 70.58$; $p = 0.01$), with no significant interactions of any factor with Year. Cover of *M. galloprovincialis* had increased on the mid-shore at both sites. Thus *M. galloprovincialis* had extended its distribution onto the mid-shore in Tsitsikamma where cover had increased by 41%. However, this was not at the expense of *P. perna*, and the same vertical zonation patterns between species were still strongly evident, i.e. *P. perna* cover was still significantly greater than *M. galloprovincialis* cover on the low shore regardless of site, with the opposite pattern on the high shore.

3.2.2. Density

The densities of *C. meridionalis*, *M. galloprovincialis* and *P. perna* had increased significantly by 2004 ($F = 5.7$; $p = 0.03$) on the low shore at Lookout Beach, with no significant differences between species. Thus, although the cover of *C. meridionalis* had decreased, it was still abundant in this area. Densities of *P. perna* and *M. galloprovincialis* (> 10 mm) had increased significantly in 2004 ($F = 87.99$; $p = 0.01$), and there were no significant interactions with Year. As with percentage cover, the same vertical patterns of density were still evident and the difference in density between sites was still significant ($F = 450.1$; $p = 0.002$).

4. Discussion

We posed the question “What conditions allow the competitive exclusion of an indigenous species and are these conditions met in this case?” Displacement of an indigenous species will require that the invasive can occupy and exhibit competitive dominance over the entire fundamental niche of the former. This appears not to be the case here, as our study demonstrated clear vertical separation of the two, with an area of overlap and co-existence in the mid-zone. After 3 years the basic pattern of zonation was unchanged, so that the vertical distributions of these species appear stable at least in the short to medium term, allowing co-existence through partial habitat segregation. Our findings allow us to erect several hypotheses about the processes that maintain this pattern, and these processes differ between zones. Recruitment limitation seems to be important on the high shore and post-recruitment factors on the lower shore.

M. galloprovincialis had higher density and cover than *P. perna* in the upper zones and this is most easily explained by the factors controlling early recruitment. We hypothesise that either *P. perna* does not readily settle on the high shore, or it experiences significantly higher post-settlement mortality than *M. galloprovincialis*. *M. galloprovincialis* had its greatest recruit density on the high shore and this could be due to patterns of settlement. However, settlement and growth are often reduced on the high shore due to shorter immersion times (Seed, 1969 and Cáceres-Martínez and Figueras, 1997), and we suggest that the higher recruit density of *M. galloprovincialis* in this zone reflects the accumulation of successive settlements of slow-growing individuals.

On the low shore, recruit and adult densities of the two species were similar, but *M. galloprovincialis* cover was lower because of its smaller size. The smaller size of *M. galloprovincialis* must reflect either slower growth or higher mortality rates than for *P. perna*. Experimental evidence indicates that mortality is indeed greater, due to the combined effects of wave action and interference competition by *P. perna* (Rius and McQuaid, in press).

In the absence of *M. galloprovincialis*, *P. perna* on this coast typically forms large, continuous beds from low to mid-shore levels, and decreases in abundance higher on the shore (McQuaid et al., 2000). Where it is excluded from low-shore areas by dense bands of the limpet *Scutellastra cochlear*, as in Tsitsikamma, it reaches maximum abundance on the mid-shore (Stephenson and Stephenson, 1972 and Van Erkom Schurink and Griffiths, 1990). On the other hand, *M. galloprovincialis* is frequently more abundant at mid- to high shore levels on the west coast (Van Erkom Schurink and Griffiths, 1990, Griffiths et al., 1992 and Hockey and Van Erkom Schurink, 1992), although it is capable of dominating the low shore under exposed conditions (Bustamante et al., 1997 and Branch and Steffani, 2004).

P. perna and *M. galloprovincialis* also overlap in their geographic distributions on the Atlantic coast of North Africa and the Mediterranean coast of Algeria (Abada-Boudjema and Dauvin, 1995). There, as here, both are towards the limits of their geographic distributions (Berry, 1978, Siddall, 1980 and Hilbish et al., 2000) and demonstrate vertical separation. In fact, *M. galloprovincialis* shows similar patterns of zone segregation with *Perna viridis* in Hong Kong (Lee and Morton, 1985) and *Perna canaliculus* in New Zealand (McDonald et al., 1991).

In addition to vertical zone effects, there were very strong horizontal effects of both location and site. *P. perna* was generally more abundant than *M. galloprovincialis* at Beacon Isle, but not 400 m away at Lookout Beach, where *C. meridionalis* dominated the low shore. Intertidally, *C. meridionalis* characteristically occupies low-shore rocks subject to sand scour or siltation (Van Erkom Schurink and Griffiths, 1990 and Hockey and Van Erkom Schurink, 1992), and is able to survive burial under sand for months (Marshall and McQuaid, 1993). Both *M. galloprovincialis* and especially *P. perna* are less tolerant of sand stress (Marshall and McQuaid, 1993 and Zardi et al., 2006). This may have prevented these species, especially *P. perna*, from reaching high numbers on the low shore at Lookout Beach, which was periodically buried by sand in 2001. Three years later, density of all three species had increased, as had cover of *P. perna* and *M. galloprovincialis*, though cover of *C. meridionalis* decreased. This followed the removal of large quantities of sand by the sea during 2003, with the low shore remaining largely free of sand until at least February 2004. This allowed *P. perna* and *M. galloprovincialis* to colonize this zone, forming a multilayered bed with *C. meridionalis* persisting in the lower layers, where some sand accumulated. Two months later the lower shore was again completely buried by sand. Many rocky shores in South Africa and elsewhere are strongly influenced by sand (Bally et al., 1984) and clearly the dynamics of low-shore mussel populations at Lookout Beach are driven largely by sand inundation.

Overall mussel abundance was significantly greater in Plettenberg Bay than in Tsitsikamma. Recruitment is an important contributor to large-scale differences in community structure (Roughgarden et al., 1988, Connolly and Roughgarden, 1998 and Archambault and Bourget, 1999) and recruit density of both *P. perna* and *M. galloprovincialis* was six times greater in Plettenberg Bay than in Tsitsikamma in 2001. Cover and density of *P. perna* and *M. galloprovincialis* generally increased in 2004, and the fact that *M. galloprovincialis* extended its distribution onto the mid-shore in Tsitsikamma by the end of the study implies that this site is also susceptible to invasion by this species, but that where recruitment is poor this process may be slower. While the cover of *M. galloprovincialis* increased on the mid-shore at both sites, this was not at the expense of *P. perna*.

Correlations of recruit and adult densities were significant only where adult densities were low, and this effect was species-specific. Connell (1985) and Menge (1991) found that recruit density was positively correlated with adult density when recruitment was low. This has been attributed to density-dependent mortality at high recruitment levels (Connell, 1985). The fact that this correlation seems to be species-specific in mixed populations indicates that larvae either settle or survive better near adult conspecifics when their densities are low.

The study makes two main points. (1) Recruitment limitation helps to exclude *P. perna* from the high shore, appears to delay invasion at Tsitsikamma, and is correlated with major differences in population structure between the two study sites (2) *M. galloprovincialis* appears not to be excluded from the low shore by recruitment limitation, but by post-settlement effects. Thus it is likely that *M. galloprovincialis* and *P. perna* will continue to co-exist through habitat segregation and that the indigenous *P. perna* will not be entirely displaced. How the two species co-occur on the mid-shore and whether this situation is stable in the long-term is unclear.

Acknowledgements

The authors gratefully acknowledge financial support from The National Research Foundation of South Africa and from Rhodes University.

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