

# Mechanisms of habitat segregation between an invasive and an indigenous mussel: settlement, post-settlement mortality and recruitment

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Received: 22 July 2008 / Accepted: 20 January 2009 / Published online: 12 February 2009  
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**Abstract** The mussel *Mytilus galloprovincialis* is highly invasive worldwide, but displays varying degrees of local and regional coexistence with indigenous mussels through spatial habitat segregation. We investigated the roles of settlement, post-settlement mortality, juvenile growth and recruitment in partial habitat segregation between the invasive *M. galloprovincialis* and the indigenous mussel *Perna perna* on the south coast of South Africa. We used two study locations, Plettenberg Bay and Tsitsikamma, 70 km apart, with two sites (separated by 300–400 m) per location, each divided into three vertical zones. There were no significant effects in Tsitsikamma, where daily settlement and monthly recruitment were significantly lower than in Plettenberg Bay. In Plettenberg Bay, settlement (primary and secondary) and recruitment of both species decreased upshore. Post-settlement mortality was measured over two consecutive 6-day periods during a spring tide and a neap tide. For both species mortality was low on the low-shore. High-shore mortality was consistently low for *M. galloprovincialis*, but increased dramatically for *P. perna* during spring tide. No data were obtained for growth of *P. perna*, but juvenile *M. galloprovincialis* grew more slowly farther upshore. *P. perna* recruited mainly in spring and summer, with a peak in summer far greater than for *M. galloprovincialis*. Recruitment of *M. galloprovincialis* was more protracted, continuing through autumn and winter. Thus local coexistence is due to a combination of pre- and post-

recruitment factors differing in importance for each species. *P. perna* is excluded from the high-shore by recruitment failure (low settlement, high mortality). High survival and slow growth in juveniles may allow large densities of *M. galloprovincialis* to accumulate there, despite low settlement rates. With no differences between species in settlement or mortality on the low-shore, exclusion of *M. galloprovincialis* from that zone is likely to be by post-recruitment processes, possibly strengthened by periodic heavy recruitments of *P. perna*. At larger scales, larval retention and protracted recruitment contribute to the success of *M. galloprovincialis* at Plettenberg Bay, while recruitment limitation may explain why *M. galloprovincialis* is less successful at other sites.

## Introduction

The rising number of non-indigenous species being transported across the world's oceans through shipping and for aquaculture poses a significant threat to marine biodiversity through the elimination or displacement of indigenous species (Carlton and Geller 1993; Occhipinti-Ambrogi 2001). The Mediterranean mussel, *Mytilus galloprovincialis* Lamarck, is one of the most successful marine invasive species and is now globally distributed throughout the temperate zones of the northern and southern hemispheres (Hilbish et al. 2000). From its origin in the Mediterranean it has spread to the northwest Atlantic coast from North Africa to England (Sanjuan et al. 1994; Comesaña et al. 1998) and has successfully colonised shores in Japan, Hong Kong, Korea, Australia and New Zealand (Wilkins et al. 1983; Lee and Morton 1985; McDonald et al. 1990, 1991). However, the most significant invasions of this species are found on the west coasts of North America and South Africa

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Communicated by P. Kraufvelin.

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(McDonald and Koehn 1988; Branch and Steffani 2004; Braby and Somero 2006).

The South African coastline has recently been invaded by the barnacle *Balanus glandula* Darwin (Laird and Griffiths 2008), but *M. galloprovincialis* remains the most extensively widespread non-indigenous marine species, now covering over 2,050 km of coastline (Robinson et al. 2005). Since its introduction on the west coast in the late 1970s, *M. galloprovincialis* has become the dominant intertidal organism from the Cape of Good Hope to southern Namibia, where it has displaced the indigenous mussel *Aulacomya ater* Molina (Griffiths et al. 1992; Branch and Steffani 2004). It has spread onto the south coast of South Africa as far as East London, probably due to a combination of range expansion from the west coast and an independent introduction to Port Elizabeth harbour for mariculture in 1989 (van Erkom Schurink and Griffiths 1990; McQuaid and Phillips 2000). Here, *M. galloprovincialis* has come into contact with a different indigenous mussel, *Perna perna* Linnaeus. It has established large populations at some sites but remains in low densities along most of the coastline (Griffiths et al. 1992; von der Meden unpublished data). It is not infected by parasites that are prevalent in *P. perna* and reduce its growth and fecundity (Calvo-Ugarteburu and McQuaid 1998a, b), so that it seems likely that *M. galloprovincialis* has competitive advantages over *P. perna*. However, where they co-occur at high abundances, the two species show partial vertical segregation. *M. galloprovincialis* dominates the higher mussel zone, where *P. perna* is typically sparse, presumably because it has greater tolerance to desiccation (Hockey and van Erkom Schurink 1992; Nicastro et al. 2008). Although it occurs in high densities across the shore this has not been at the expense of *P. perna*, which remains the dominant species on the low-shore (Bownes and McQuaid 2006). Thus *M. galloprovincialis* has not displaced *P. perna* from its preferred habitat and coexistence seems possible.

Where it has become invasive in other parts of the world, *M. galloprovincialis* exhibits similar local and regional variations in abundance and in its effects on indigenous mussel populations. The same vertical zonation pattern has been described between this species and *Perna canaliculus* Gmelin in New Zealand (Kennedy 1976). In North America, *M. galloprovincialis* has displaced the indigenous mussel *Mytilus trossulus* Gould from most of its former habitat in central and southern California, so that the two species are largely separated regionally (Braby and Somero 2006; Fields et al. 2006). However, it has not displaced another indigenous Californian mussel, *Mytilus californianus* Conrad, which is predominant on wave-exposed shores, while *M. galloprovincialis* appears to be confined to more sheltered shores (Martel et al. 1999).

Most studies have examined habitat segregation between *M. galloprovincialis* and indigenous species from a physiological perspective (Kennedy 1976; Braby and Somero 2006; Fields et al. 2006). In South Africa, differential tolerance to aerial exposure and wave action plays a role in the vertical distributions of *M. galloprovincialis* and *P. perna* (Hockey and van Erkom Schurink 1992; Zardi et al. 2006). However, intertidal community structure is influenced by many factors other than physical stress. For organisms with planktonic larvae, recruitment to the shore is one of the most important factors influencing adult populations. In the past, comparative recruitment studies between sympatric mussel species have been hindered by the difficulty in distinguishing between the larval and post-larval stages, particularly amongst closely related congeneric species that hybridise (Garland and Zimmer 2002). This has been improved by the advent of molecular identification techniques (e.g. Johnson and Geller 2006), but these can be impractical for multivariate studies with large sample sizes. The situation on the south coast of South Africa offers a unique opportunity to examine the role of recruitment in habitat segregation as *M. galloprovincialis* and *P. perna* do not hybridise and their post-larvae can be distinguished morphologically (Bownes et al. 2008). Recruitment limitation is of particular importance on this coast as mussel recruitment rates are orders of magnitude lower than on most temperate boreal shores and the upwelling-dominated west coast of South Africa (Harris et al. 1998).

Recruitment refers to the number of larvae that have settled and survived for a certain period of time, and so includes settlement and a defined period of post-settlement mortality (Keough and Downes 1982). Settlement involves the initial attachment of larvae to the substratum and can significantly influence adult distribution and abundance. Being partly dependent on the delivery of competent larvae to the shore, factors influencing settlement include large-scale oceanographic processes such as upwelling, currents and hydrodynamics associated with shoreline topography (Roughgarden et al. 1988; Bertness et al. 1996; Archambault and Bourget 1999), while closer to shore tidal movements, wave action, substratum availability and tidal height can be important (Gaines and Roughgarden 1985; Bertness et al. 1992; Vargas et al. 2004). Settlement also includes the additional component of larval behaviour and habitat selection, which is widely documented in marine invertebrates (Raimondi 1988; Osman and Whitlatch 1995; Lemire and Bourget 1996), and may be an important mechanism in avoiding detrimental post-settlement interactions (Petersen 1984; Bushek 1988).

However, many species are capable of relocating after initial settlement. In mussels initial attachment (primary settlement) can be followed by detachment and re-attachment (secondary settlement) in different zones or on different

substrata (Beukema and de Vlas 1989; Alfaro 2006), which may occur many times before juveniles permanently enter the adult population (Bayne 1964). Mussel larvae frequently settle initially on algae (e.g. McQuaid and Lindsay 2005). While for some species the fate of such larvae is uncertain (Reaugh et al. 2007), settlement onto algae may be followed by secondary settlement to the mussel bed (Bayne 1964; Alfaro 2006). Thus primary and secondary settlement can affect adult population structure in different ways. Mortality in juvenile invertebrates is often determined within the first few days after settlement, due to the physiological stress associated with metamorphosis, and a greater vulnerability to physical stress in smaller individuals (Gosselin and Qian 1997; Garcia-Esquivel et al. 2001). Variations in post-settlement mortality can therefore obscure patterns of settlement, leading to large-scale differences in community structure and composition (Osman and Whitlatch 2004).

Here we examine the factors controlling habitat segregation and coexistence in *Perna perna* and *Mytilus galloprovincialis* and whether zonation is a result of primarily pre- or post-recruitment events. We investigate the role of settlement, early post-settlement mortality, juvenile growth and recruitment to test specific hypotheses based on the population structure of *P. perna* and *M. galloprovincialis* at two locations with different mussel abundances on the south coast (Bownes and McQuaid 2006): (1) *P. perna* is excluded from the high-shore by recruitment failure, either through lack of settlement or through post-settlement mortality; (2) high densities of *M. galloprovincialis* in this zone reflect the accumulation of successive settlements of slow-growing individuals that show good survival; (3) recruitment limitation is responsible for the difference in mussel abundance between these locations, and may delay invasion by *M. galloprovincialis* at other locations with low recruitment.

## Materials and methods

### Study sites

Sampling took place at two locations 70 km apart on the south coast of South Africa: Plettenberg Bay (34°05'S; 23°19'E), where *M. galloprovincialis* is abundant, and Tsitsikamma (33°1'S; 23°53'E), where it is rare. Two randomly chosen sites were selected at each location. The shore at each site was divided into three vertical zones characterised by different taxa and different patterns of mussel cover. Plettenberg Bay is typical of a series of half-heart bays on this coast. It includes a long sandy beach interspersed with patches of sand-swept granite rocks. The two sites, Lookout Beach and Beacon Isle, were ca. 400 m apart

near the middle of the bay, and both were exposed in terms of wave action. Mussel beds were multilayered, particularly in the mid and high zones. The indigenous mussel *Choromytilus meridionalis* Krauss was present only on the low-shore at Lookout Beach. Mussels dominated the lower intertidal zones at this location, while barnacles (*Chthamalus dentatus* Krauss) were most abundant on the high-shore. Tsitsikamma has sandstone shores and little sand. The two sites, Sandbaai and Driftwood Bay, were ca. 300 m apart and lay in a slight embayment that was moderately exposed or exposed to wave action. Mussels formed fairly continuous monolayered beds on the mid-shore and occurred in isolated patches in the low and high mussel zones. The low-shore was characterised by a band of encrusting coralline algae and the limpet *Scutellastra cochlear* Born, while barnacles (*Octomeris angulosa* Sowerby, *Tetraclita serrata* Darwin) and the snail, *Littorina africana knysnaensis* Philippi were abundant in the high zone.

### Post-larval identification

Post-larvae (0.28–5.0 mm) of the three mussels *Perna perna*, *Mytilus galloprovincialis* and *Choromytilus meridionalis* were identified to species under a dissecting microscope based on diagnostic morphological features described in Bownes et al. (2008).

### Distinguishing primary and secondary settlers

In mussels, there is a clear demarcation between the larval and adult shell regions, allowing size at settlement to be determined (Martel et al. 1995). Settlers were collected from randomly selected settlement pads (see below) retrieved after 24 h on the shore from all zones and both locations. Size at settlement was measured under a light microscope fitted with an ocular micrometer.

### Settlement and recruitment

Settlers were collected using plastic scouring pads soaked in sea water for 24 h before use (see Gilg and Hilbish 2003). Six screws were drilled into the rocks in each zone, about 1.0 m apart, and individual pads were attached to each screw using washers and cable ties. All mussels collected from settlement pads on a daily basis will be referred to as settlers (primary or secondary) and those collected at monthly intervals as recruits. Recruitment was measured monthly from July 2000 to July 2001 and daily settlement samples were collected concurrently in April 2001. However, samples could not be collected every day due to sea conditions, preventing estimation of post-settlement mortality. Settlement and post-settlement mortality were therefore measured again in March 2003.

### Settlement

Daily settlement was measured from 27 March to 26 April 2001 in Plettenberg Bay and Tsitsikamma. There were three pads per zone at each site that were replaced every 24 h upon collection. The remaining three pads were collected at the end of the month to estimate recruitment. Both settlement and recruitment were very poor in Tsitsikamma, so that the repetition of the experiment was only done at the two sites in Plettenberg Bay. This took place from 17 to 28 March 2003, although rough seas prevented sampling at Beacon Isle after 24 March. Six pads per zone were replaced daily upon collection.

Settlement pads were frozen immediately after collection. In the laboratory, settlers were removed by vigorously shaking the pad in water, which was then filtered through two sieves of 1 mm and 0.15 mm mesh size. This process was repeated three to four times. The contents of each sieve were washed into a Petri dish and examined under a dissecting microscope. Settlers were transferred to a piece of filter paper (using a pipette for the smaller individuals), identified to species and measured using a micrometer. Juveniles were distinguished as either “dead” (no tissue in the valves) or “alive” at the time of collection. For settlement, all mussels were counted. Samples were stored in 70% alcohol.

### Post-settlement mortality

Post-settlement mortality was measured over the same period in March 2003, covering two consecutive periods of 6 days over a spring and a neap tide. An additional six pads were attached to each screw giving six pairs per zone. One pad of each pair was replaced daily, while the second was left on the shore for 6 days. In this way we hoped to minimise variation in settlement between the daily and 6-day pads. Due to interrupted sampling, mortality could not be measured at Beacon Isle over neap tide.

Mortality for each pair was calculated by subtracting the total number of “live” recruits in the 6-day pads from the cumulative daily settlement that occurred during that time. Mortality was expressed as a percentage of the cumulative daily settlement. There are shortcomings to this method, but due to the large number of variables being measured it was the only feasible method of measuring mortality in situ, while keeping an adequate sample size.

### Recruitment

Recruitment samples were collected monthly from June 2000 to July 2001 at both sites in Plettenberg Bay, and from August 2000 and October 2000 to July 2001 at Sandbaai and Driftwood Bay in Tsitsikamma, respectively. Logistic

problems resulted in sampling intervals of 2 weeks on rare occasions and one interval of 6 weeks. The number of recruits in each pad was averaged for the two time periods over which they were in the field. The data were grouped into months and then standardised by converting to recruitment in 30 days.

Recruitment samples with exceptionally high numbers were sub-sampled using a plankton splitter. Smaller (<1.0 mm) and larger juveniles were sub-sampled separately, and this was usually only necessary for the smaller sizes. The efficiency of this technique was confirmed by comparing subsamples statistically. Juveniles were again distinguished as either dead or alive upon collection and only live mussels were counted as recruits.

### Juvenile growth

Juvenile growth was measured in situ at the two sites in Plettenberg Bay, in November 2003 using the fluorochrome growth marker calcein (Kaehler and McQuaid 1999). Eighteen pads were placed on the low-shore at each location for 48 h to collect settlers. The pads were then removed and immersed in a calcein-sea water solution ( $200 \text{ mg l}^{-1}$ ) for 2 h. After immersion, six pads were placed in each zone. Samples were collected after 2 weeks and kept frozen. In the laboratory juveniles were extracted and measured individually under a light microscope fitted with an ocular micrometer. Once measured, each mussel was examined under an Olympus fluorescence microscope and growth was measured as the distance between the growing edge of the shell and the calcein mark (Kaehler and McQuaid 1999).

### Analyses

#### Settlement

Settlement was averaged for each day, and date was used as the replicate. Date was not included as a factor due to poor sample sizes on some days and because substantial variation in daily settlement rates might have masked the effects of those factors that were more relevant to our questions. In 2001, samples could not be collected over the two neap tides due to sea conditions, therefore only dates with pads that had been on the shore for 24 h were used in the analyses ( $n = 22$ ). We examined the effects of site, zone and/or species on settlement using factorial ANOVA with unbalanced sample sizes, where site was a random factor and zone and species were fixed. Post hoc comparisons were made using Newman–Keuls multiple range tests. The data were log-transformed when the assumptions of parametric analysis were not met. For 2001 no transformation was required and for 2003 all data were transformed except for

the comparison of secondary settlement amongst zones at Beacon Isle.

#### Post-settlement mortality

Mortality was analysed using factorial ANOVA with unbalanced sample sizes and site, zone or species as factors. The data did not require transformation.

#### Recruitment

The recruitment data were grouped into seasons defined as follows: October–November (spring), December–February (summer), March–May (autumn) and June–July (winter). The months from June to September 2000 were excluded as we did not have data for all four sites. A mixed model Nested ANOVA was performed with season, location, site, zone and species as factors, where site was random and nested within location.

#### Juvenile growth

Due to poor recovery of marked individuals, virtually no results were obtained for *P. perna*. There was a strong positive relationship between initial length and growth of *M. galloprovincialis*, which was generally significant. *M. galloprovincialis* growth was analysed using a two-way ANCOVA with initial length as a covariate and site and zone as factors. The data did not require transformation.

## Results

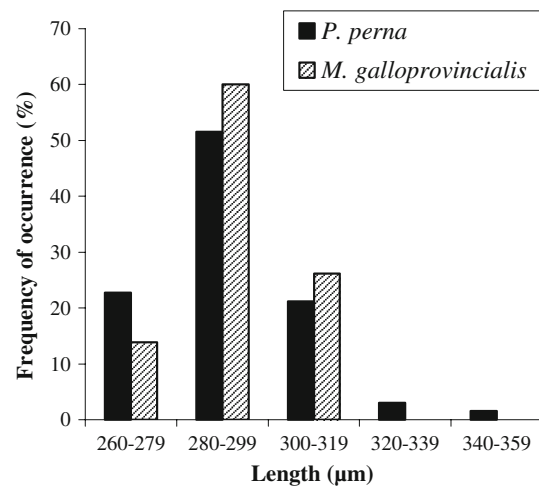
### Categorising primary and secondary settlers

*Perna perna* and *M. galloprovincialis* settlers had similar size distributions, generally ranging from 270 to 320  $\mu\text{m}$ , with the largest percentage of larvae settling at approximately 290  $\mu\text{m}$  (Fig. 1). The majority of newly settled post-larvae were <330  $\mu\text{m}$  in length, with a maximum size of 340  $\mu\text{m}$  for *P. perna*. Primary settlers were therefore categorised as post-larvae of <340  $\mu\text{m}$  in length and all individuals  $\geq 340$   $\mu\text{m}$  were regarded as secondary settlers.

### Settlement

#### April 2001

There was no primary settlement in Tsitsikamma. In Plettenberg Bay, primary settlement for *P. perna* was very low with only a few individuals settling during this time. Therefore, only *M. galloprovincialis* settlement was analysed and only for 5 April onwards, as there was virtually no settle-



**Fig. 1** Size frequency distributions of newly settled post-larvae from randomly chosen samples collected in Tsitsikamma and Plettenberg Bay in April 2001 and March 2003:  $n = 66$  and  $65$  for *P. perna* and *M. galloprovincialis*, respectively

**Table 1** ANOVA of (a) primary settlement of *M. galloprovincialis* only and (b) secondary settlement of *P. perna* and *M. galloprovincialis* in April 2001, Plettenberg Bay

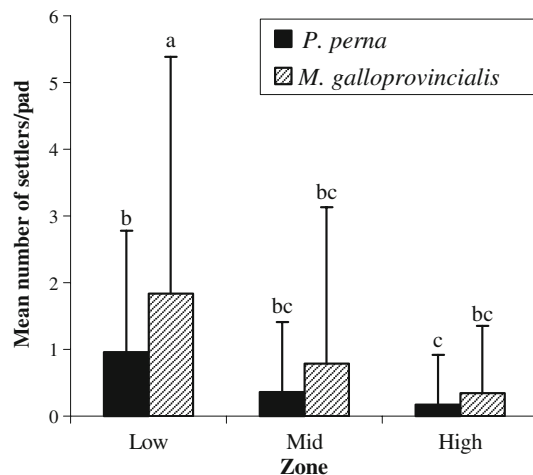
	Effect	df	MS	F	P
(a)					
Site	Random	1	121.41	1.50	0.344
Zone	Fixed	2	127.61	1.57	0.389
Site $\times$ zone*	Random	2	81.25	3.42	0.034*
Error		233	23.76		
(b)					
Site	Random	1	12.79	5.652	0.165
Zone*	Fixed	2	70.20	114.475	0.009*
Species	Fixed	1	39.87	23.505	0.129
Site $\times$ zone	Random	2	0.61	14.110	0.066
Site $\times$ species*	Random	1	1.70	26.864	0.006*
Zone $\times$ species*	Fixed	2	6.37	146.647	0.007*
Site $\times$ zone $\times$ species	Random	2	0.04	0.011	0.989
Error		655	3.80		

\* Significant differences

ment before this ( $n = 16$ ). There was a significant interaction between site and zone (Table 1a), the difference between sites being significant only on the low-shore, with higher settlement at Beacon Isle. *M. galloprovincialis* also settled in significantly greater numbers on the low-shore than in the upper zones at this site. Although settlement decreased upshore at Lookout Beach, the effect of zone was not significant.

Secondary settlement in Tsitsikamma was very low and intermittent and was only 3% of that in Plettenberg Bay. The Tsitsikamma data were therefore excluded from the analysis so that location effects were not examined in either year. The ANOVA of secondary settlement in Plettenberg





**Fig. 2** April 2001, post hoc comparison of the zone  $\times$  species interaction on secondary settlement of *P. perna* and *M. galloprovincialis* in Plettenberg Bay. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ ). Values in this and subsequent figures are mean  $\pm$  SD

Bay revealed significant interactions between site and species and between zone and species (Table 1b). Secondary settlement of *M. galloprovincialis* was significantly greater than for *P. perna* at Lookout Beach, with no difference between species at Beacon Isle. *M. galloprovincialis* settlement was significantly greater at Lookout Beach than at Beacon, Isle while *P. perna* settlement did not differ between sites. *M. galloprovincialis* also settled in significantly greater numbers than *P. perna* on the low-shore across sites (Fig. 2). Both species showed an upshore decrease with similar, low settlement on the high-shore.

### March 2003

Primary settlement was generally very low at both Plettenberg Bay sites, except for one peak in settlement of *M. galloprovincialis* at Lookout Beach on 28 March (low-shore mean  $33.5 \pm 27.09$  settlers/pad). Sites could only be compared for the first 8 days (17–24 March) and there were significant site-zone and site-species interactions (Table 2a). For the site-zone interaction, settlement decreased upshore with a significant difference between the low and high zones at both sites (Fig. 3a). Only mid-shore settlement varied between sites with greater settlement at Lookout Beach. For the site-species interaction there was little difference in primary settlement between species at Lookout Beach, while *P. perna* had significantly higher settlement than *M. galloprovincialis* at Beacon Isle (Fig. 3b). Primary settlement of *M. galloprovincialis* was significantly greater at Lookout Beach than Beacon Isle, with no site differences for *P. perna*.

For secondary settlement *P. perna* and *M. galloprovincialis* showed a significant site-species interaction

**Table 2** ANOVA of (a) primary settlement and (b) secondary settlement of *P. perna* and *M. galloprovincialis* in March 2003, Plettenberg Bay

	Effect	df	MS	F	P
(a)					
Site	Random	1	0.45	1.338	0.369
Zone	Fixed	2	1.07	9.491	0.095
Species	Fixed	1	0.33	1.473	0.439
Site $\times$ zone*	Random	2	0.11	35.015	0.0278*
Site $\times$ species*	Random	1	0.23	65.157	0.009*
Zone $\times$ species	Fixed	2	0.01	2.188	0.314
Site $\times$ zone $\times$ species	Random	2	0.003	0.063	0.939
Error		507	0.05		
(b)					
Site	Random	1	21.06	8.501	0.134
Zone	Fixed	2	5.61	9.463	0.096
Species	Fixed	1	0.31	0.161	0.757
Site $\times$ zone	Random	2	0.59	9.859	0.092
Site $\times$ species*	Random	1	1.95	32.180	0.028*
Zone $\times$ species	Fixed	2	0.14	2.333	0.300
Site $\times$ zone $\times$ species	Random	2	0.06	0.464	0.629
Error		507	0.13		

Dates were pooled

(Table 2b). Both species had fewer secondary settlers at Beacon Isle and settlement was significantly greater for *M. galloprovincialis* than *P. perna* at Lookout Beach (Fig. 4).

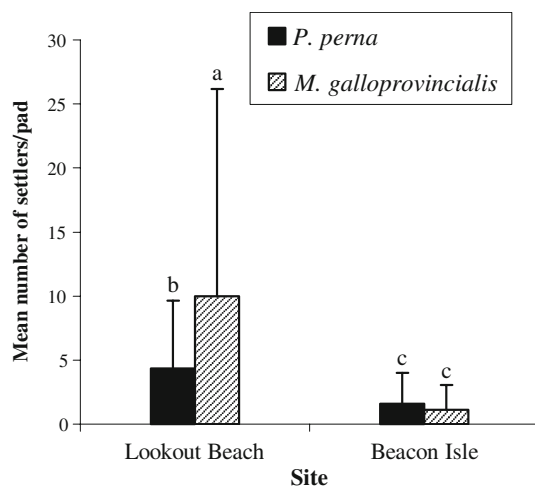
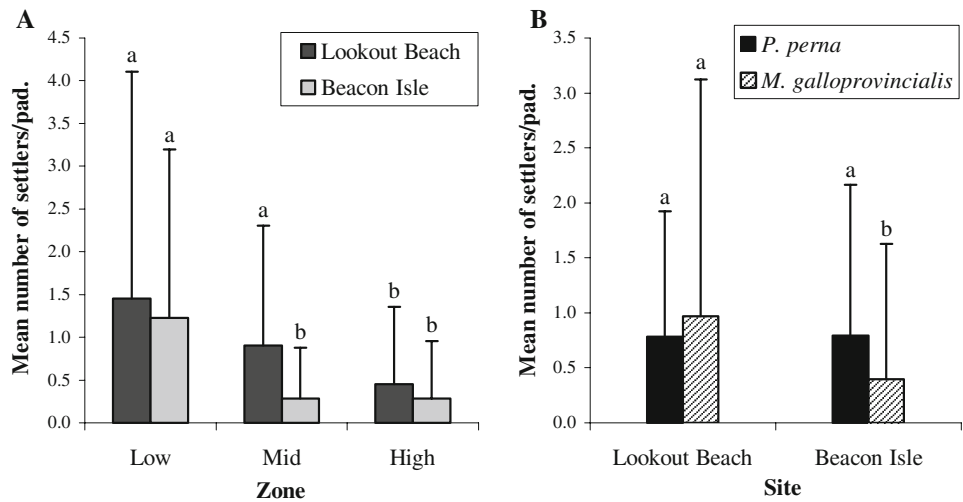
Although settlement was measured over relatively short time-scales and direct comparisons between years were not possible, the overall pattern was clear. Both primary and secondary settlement of *P. perna* and *M. galloprovincialis* decreased upshore, with no zone-dependent differences between species. This occurred irrespective of site and year in Plettenberg Bay. Settlement also varied among sites and locations. Settlement in Plettenberg Bay was substantially greater than in Tsitsikamma.

### Post-settlement mortality

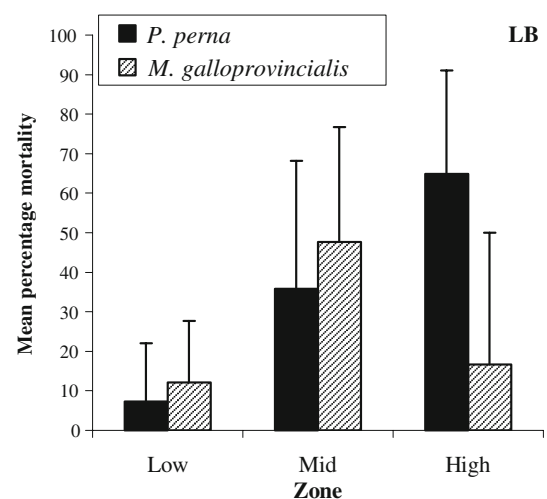
Mortality of *P. perna* and *M. galloprovincialis* in March 2003 was compared between zones and sites over spring tide, but there were no significant effects or interactions. There was a marked difference in settlement rates between the two sites in the first 6 days of sampling. We therefore examined post-settlement mortality over spring tide at each site separately.

At Lookout Beach, mortality was significantly greater in the upper zones than the low shore ( $F_{2,20} = 3.85$ ,  $P = 0.038$ ), with no effect of species. The interaction between zone and species was not quite significant ( $F_{2,20} = 3.17$ ,  $P = 0.064$ ), but some zone-specific differences

**Fig. 3** March 2003, post hoc comparisons of: **a** the site × zone interaction and **b** the site × species interaction on primary settlement of *P. perna* and *M. galloprovincialis* in Plettenberg Bay. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )



**Fig. 4** March 2003, post hoc comparison of the site × species interaction on secondary settlement of *P. perna* and *M. galloprovincialis* in Plettenberg Bay. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )



**Fig. 5** March 2003, post-settlement mortality of *P. perna* and *M. galloprovincialis* at different tidal heights over a spring tide at Lookout Beach, Plettenberg Bay. Values are mean + SD

between species were important. Mortality of *P. perna* and *M. galloprovincialis* was similar in the two lower zones and significantly higher on the mid-shore than on the low-shore for both species (Fig. 5). However, on the high-shore mortality of *P. perna* increased dramatically, while mortality of *M. galloprovincialis* decreased (65 and 17%, respectively). There was no significant difference in mortality between zones or species at Beacon Isle where settlement rates were significantly lower.

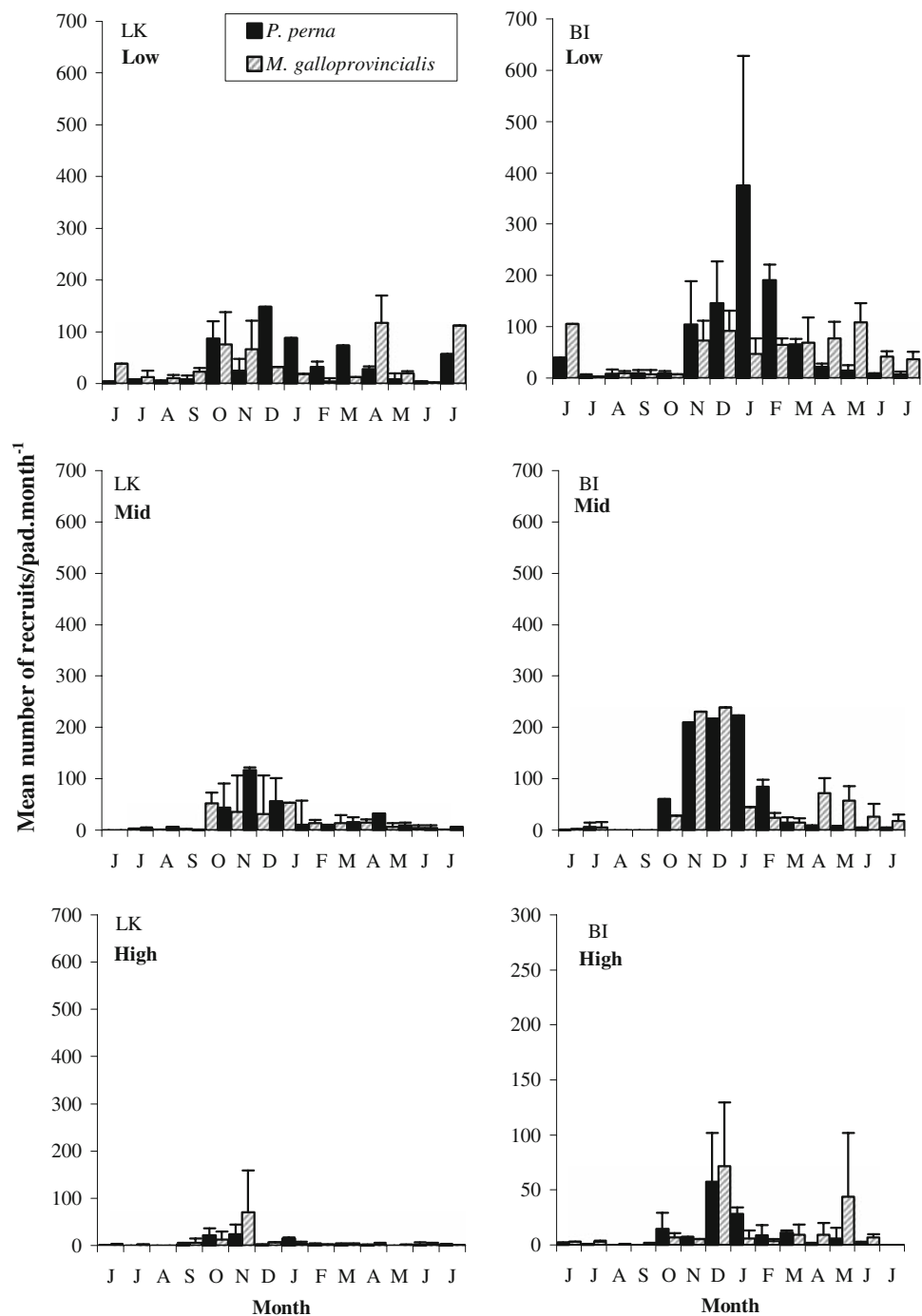
Mortality over a neap tide at Lookout Beach showed a significant effect of zone ( $F_{2,26} = 4.06$ ,  $P = 0.029$ ) but not of species or the interaction term. Mortality of both species was significantly greater on the mid-shore than either the low or high-shore. *P. perna* exhibited different patterns of high-shore mortality between tides, with 65% mortality over spring tide and only 6% over neap tide. In contrast,

*M. galloprovincialis* displayed the same zone mortality pattern during both tides.

Recruitment

*Perna perna* and *M. galloprovincialis* exhibited different patterns of recruitment in Plettenberg Bay (Fig. 6). *P. perna* recruited mainly in spring and summer (October–March) with very little recruitment in the autumn and winter months. There was a major recruitment peak at Beacon Isle in January, with a smaller peak on the mid-shore only in November and December (spring/early summer) that was observed for *M. galloprovincialis* as well. However, recruitment of *M. galloprovincialis* was more protracted, continuing through autumn and winter. Both species had very poor recruitment from July to

**Fig. 6** June 2000–July 2001, monthly recruitment of *P. perna* and *M. galloprovincialis* at different tidal heights at Lookout Beach (LB) and Beacon Isle (BI), Plettenberg Bay. Values are mean + SD



September 2000. Recruitment rates were reduced higher up the shore.

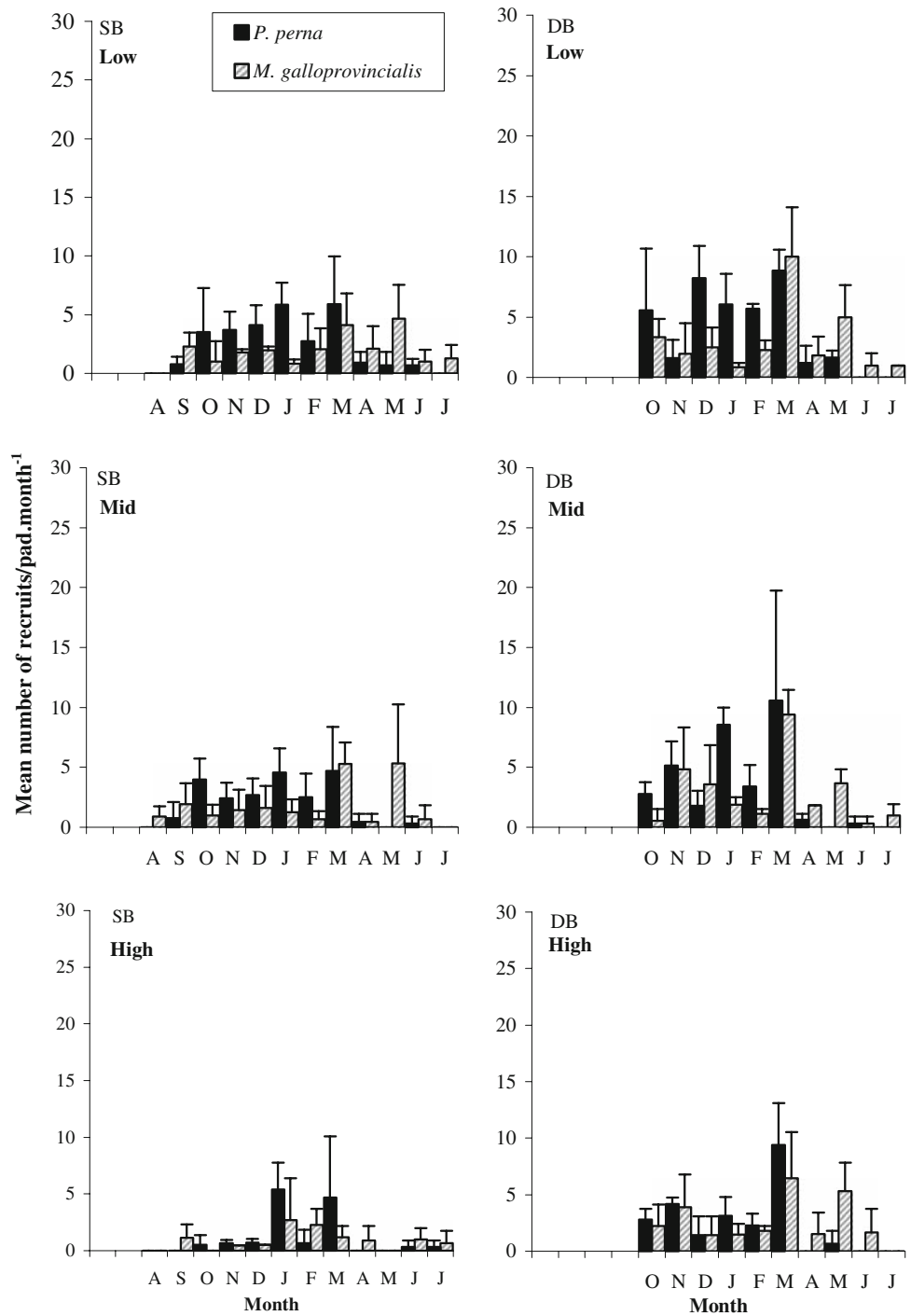
Recruitment rates were substantially lower in Tsitsikamma. The seasonal patterns of recruitment for *P. perna* and *M. galloprovincialis* were similar to those observed in Plettenberg Bay, though there were no obvious peaks (Fig. 7; note difference in scale from that in Fig. 6). The effect of zone was not as apparent here, although recruitment appeared to be reduced on the high-shore.

The Nested ANOVA revealed a significant interaction between season, location, zone and species ( $F_{6,575} = 4.819$ ,  $P < 0.01$ ). Recruitment of both species was significantly greater in Plettenberg Bay than in Tsitsikamma in the lower zones, regardless of season (Fig. 8), with no difference in high-shore recruitment. There were no significant differences in recruitment between seasons, zones or species in Tsitsikamma.

In Plettenberg Bay, recruitment decreased higher up the shore and the difference between the low and high zones



**Fig. 7** August 2000–July 2001, monthly recruitment of *P. perna* and *M. galloprovincialis* at different tidal heights at Sandbaai (SB) and Driftwood Bay (DB), Tsitsikamma. Gaps indicate months where no samples were collected. Values are mean + SD

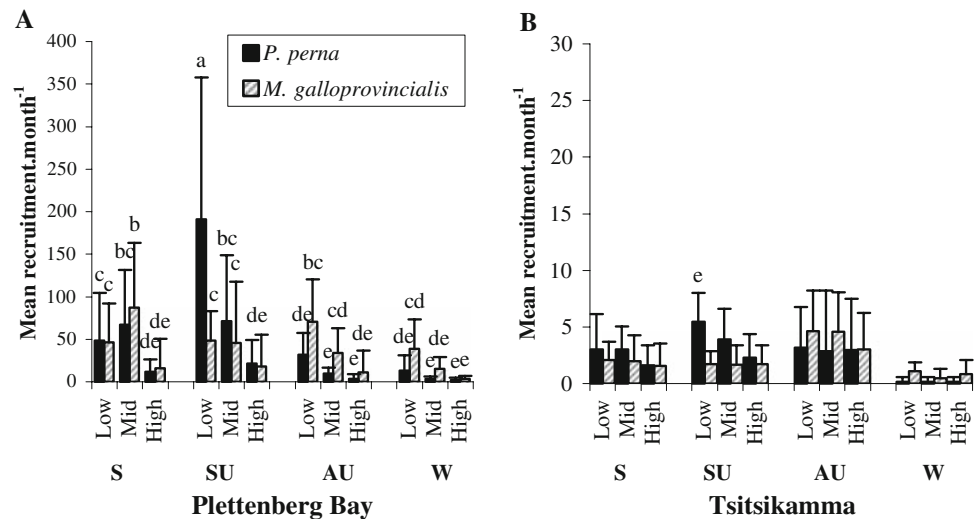


was generally significant for both species (Fig. 8). High-shore recruitment did not differ significantly between species or seasons. The effect of zone was most apparent for *P. perna* in summer due to a peak in low-shore recruitment, which was far greater than that of *M. galloprovincialis* at any other time. Recruitment of *P. perna* was significantly greater in spring and summer than autumn and winter in the lower zones. There was a smaller peak in recruitment of *M. galloprovincialis* on the mid-shore in spring, but

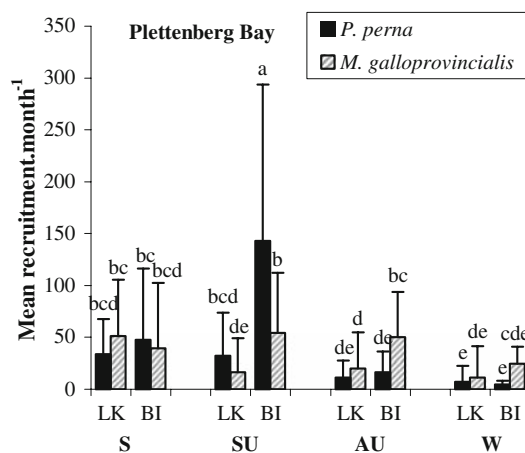
otherwise recruitment was more similar between seasons. Recruitment in the lower zones was greater than for *P. perna* in autumn and winter with a significant difference in autumn.

There was also a significant interaction between site (location), season and species ( $F_{6,575} = 4.302, P = 0.014$ ). Again there were no significant differences in recruitment between sites in Tsitsikamma. In Plettenberg Bay, the seasonal patterns described for each species were broadly the

**Fig. 8** Post hoc comparison of the season  $\times$  location  $\times$  zone  $\times$  species interaction on recruitment of *P. perna* and *M. galloprovincialis* in **a** Plettenberg Bay and **b** Tsitsikamma. *S* spring, *SU* summer, *AU* autumn, *W* winter. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ ). All bars in Tsitsikamma are signified by homogeneous group *e*



same, but with some important site-specific differences. *P. perna* recruited mainly in spring and summer at both sites but the large summer recruitment peak was only observed at Beacon Isle (Fig. 9). At Lookout Beach, recruitment of *M. galloprovincialis* was significantly greater in spring than the other seasons, while at Beacon Isle, recruitment was similar from spring to autumn, but was lower in winter. The species-specific differences between seasons were only significant at Beacon Isle (i.e. *P. perna* > *M. galloprovincialis* in summer and *M. galloprovincialis* > *P. perna* in autumn). Both species had significantly greater recruitment at Beacon Isle than at Lookout Beach in summer and for *M. galloprovincialis* in autumn.



**Fig. 9** Post hoc comparison of the site (location)  $\times$  season  $\times$  species interaction on recruitment of *P. perna* and *M. galloprovincialis* at Lookout Beach (LB) and Beacon Isle (BI) in Plettenberg Bay. There were no significant differences between sites in Tsitsikamma. *S* spring, *SU* summer, *AU* autumn, *W* winter. Letters indicate homogeneous groups (Newman–Keuls test,  $\alpha < 0.05$ )

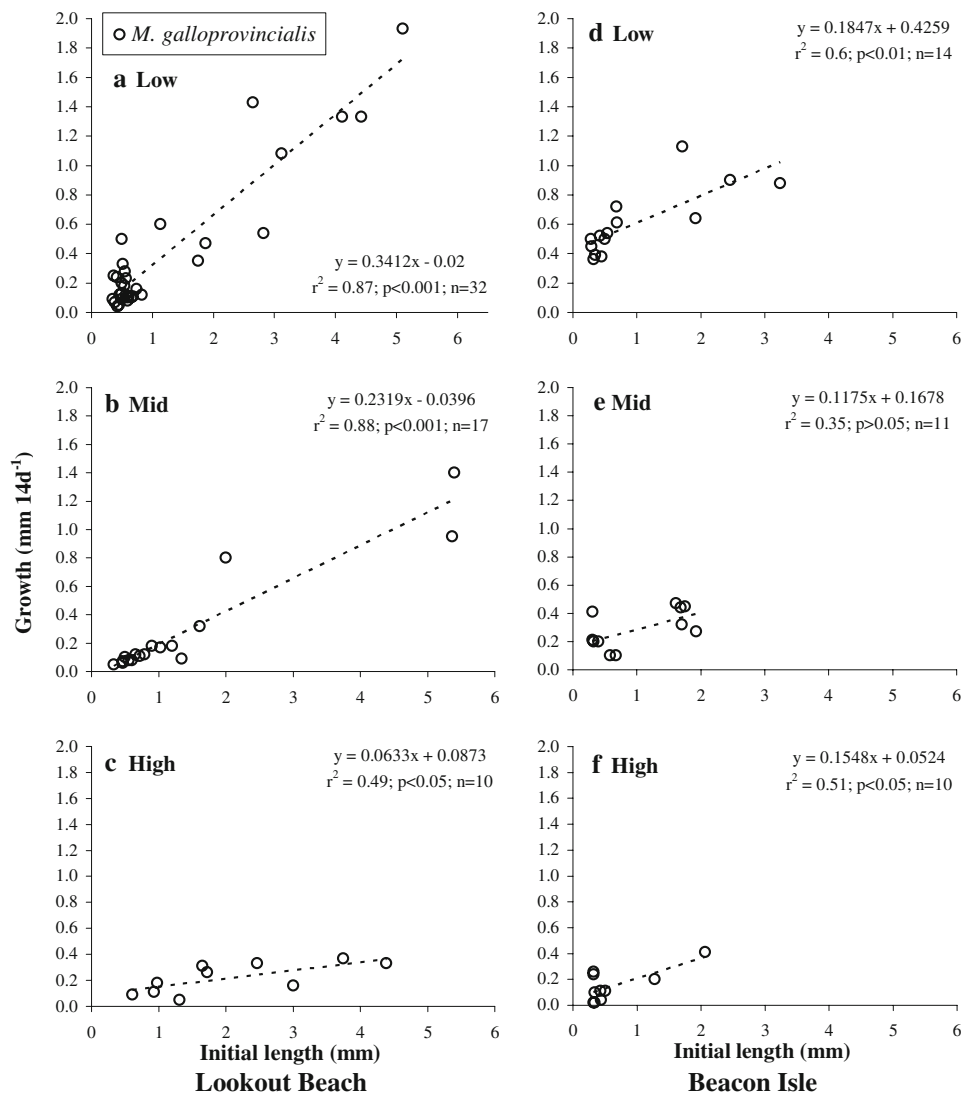
### Juvenile growth

No data were obtained for the growth of juvenile *P. perna*, but post-larval growth of *M. galloprovincialis* increased with increasing size, although less obviously so on the high-shore where growth of larger juveniles was slower (Fig. 10). Growth appeared to decrease with increasing height on the shore, as seen by the flattening of the growth curve; however, the differences were marginally non-significant (Table 3).

### Discussion

Primary settlement is often a strong determinant of adult community structure in intertidal invertebrates, but for mussels its effects can be modified by the dispersal and resettlement of post-larval stages. In this study, there were site effects but the two settlement phases did not appear to differ between tidal heights for either *P. perna* or *M. galloprovincialis*; the abundances of both primary and secondary settlers decreased upshore for both species. The effect of site on the abundance of primary and secondary settlers varied between species and in years. Invertebrate post-larvae have been recorded from offshore plankton samples suggesting that large-scale secondary dispersal does occur; however, most evidence indicates that it is a more localised process, often triggered by disturbance (Olivier et al. 1996; Cáceres-Martínez et al. 1994, Cáceres-Martínez and Figueras 1998). In contrast, planktonic larvae can be dispersed over scales of 10s to 100s of km (McQuaid and Phillips 2000; Becker et al. 2007). Primary and secondary settlement are therefore likely to be influenced by different processes. Local physical conditions such as coastal morphology, wind, currents, internal tidal waves and larval patchiness in the water column are likely to result in the

**Fig. 10** November 2003, juvenile growth of *M. galloprovincialis* at different tidal heights at Lookout Beach (a–c) and Beacon Isle (d–f), Plettenberg Bay



**Table 3** ANCOVA on growth of juvenile *M. galloprovincialis* in November 2003, Plettenberg Bay

	Effect	df	MS	F	p
Length	Fixed	1	7.83	234.990	<0.001
Site	Random	1	0.88	12.423	0.0638
Zone	Fixed	2	1.07	14.212	0.0672
Site × zone	Random	2	0.075	2.244	0.112
Error		87	0.03		

differential delivery of larvae among sites 300–400 m apart (Vargas et al. 2004; McQuaid and Lindsay 2005; Porri et al. 2006), while local hydrodynamics and disturbance regimes may be more important to secondary relocation and settlement of post-larvae (Olivier et al. 1996).

In terms of their vertical distributions it is clear that adult populations of *M. galloprovincialis* do not reflect differential settlement, while vertical patterns of settlement were

consistent with the adult distribution of *P. perna*. This effect of zone has been observed for *M. galloprovincialis* and *P. perna* elsewhere (Cáceres-Martínez and Figueras 1997; McQuaid and Lindsay 2005). Intertidal invertebrates often experience reduced settlement at higher shore levels (e.g. Bertness et al. 1992), which may be due to the greater submergence time in the lower zones that allows more time for settlement (Menge 1991; Miron et al. 1995). For *P. perna*, greater settlement on the low-shore could be interpreted as a response to adult conspecifics (Barnett et al. 1979; Raimondi 1988), but recent manipulative experiments indicate that it is an effect of tidal emersion (Porri et al. 2007).

In California, the invasive *M. galloprovincialis* settled abundantly where adults were rare, while the indigenous *M. californianus* settled mostly in its adult habitat (Johnson and Geller 2006). Post-settlement mortality was considered to be responsible for adult distribution of the invasive. Our results showed that post-settlement survival of both species

on the low-shore was very good (>80%). Both species also recruited more successfully in the lower zones, indicating that low-shore populations are regulated primarily by adult interactions. However, there were significant variations in seasonal recruitment rates between sites and species on the low-shore. For example, at Beacon Isle, *P. perna* exhibited strong summer recruitment on the low-shore that was significantly greater than for *M. galloprovincialis*. This is likely to reflect differences in reproductive season between species (Zardi et al. 2007), but the effects of post-settlement mortality may also be important.

Settlement therefore fails to explain the large densities of *M. galloprovincialis* in the high zone and the vast difference in relative species abundances there. We proposed that slow growth in juveniles would minimise intra-specific competition for space and, combined with good survival, would allow the accumulation of large densities of *M. galloprovincialis* in this zone despite low rates of settlement, while low settlement and/or post-settlement mortality would limit the abundance of *P. perna*. Our results support this hypothesis. Growth of juvenile *M. galloprovincialis* tended to decrease further upshore, particularly in larger individuals (>1.0 mm). Most intertidal bivalves experience slower growth further upshore due to reduced feeding time and increased physiological stress at higher shore levels (Griffiths 1981; Griffiths and Griffiths 1987; Vincent et al. 1994; Bartol et al. 1999). However, the influence of tidal height on juvenile mussel (*M. galloprovincialis*) growth may not become apparent for several weeks post-settlement (Phillips 2002), which may account for the (marginally) non-significant results in our study.

A shortcoming of the mortality method used is that it cannot distinguish between mortality and emigration of mussels (if any) from the recruitment pads, nor can it account for immigration of larger individuals. Also, mortality estimates could be biased between species, for example, if one species is dislodged more easily after death. As adults, *P. perna* has greater attachment strength than *M. galloprovincialis* (Zardi et al. 2007), so that dislodgement of dead *M. galloprovincialis* juveniles might occur more quickly than for *P. perna*. We have not measured this, but large numbers of dead individuals of both species were found in the monthly recruitment samples, suggesting that the risk of losing individuals within 24 h of settlement is minimal. Nevertheless, the results should be treated cautiously. Post-settlement mortality of *M. galloprovincialis* on the high-shore remained low over both the spring and neap tides and at both sites. However, mortality of *P. perna* increased markedly upshore over the spring tide at Lookout Beach, so that high-shore mortality of *P. perna* far exceeded that of *M. galloprovincialis* (65 and 17%, respectively). In other juvenile invertebrates, increased mortality upshore has been attributed to increased desiccation stress

with greater aerial exposure (Kennedy 1976; Roegner and Mann 1995; Chan and Williams 2003). Conditions during neap tide were often too rough to sample, indicating that high-shore areas are more wave splashed during neap than spring low tides (personal observation), which presumably reduces desiccation. *M. galloprovincialis* is more tolerant of desiccation stress than *P. perna* as adults (Hockey and van Erkom Schurink 1992), and the better post-settlement survival of *M. galloprovincialis* in the high zone implies the same dissimilarity in the early settlement stages, at least at certain times.

*Perna perna* recruited mainly in spring and summer, with a strong summer peak on the low-shore that was significantly greater than for *M. galloprovincialis* at any other time. *M. galloprovincialis* experienced a small peak in recruitment in spring/early summer, but otherwise recruitment was more protracted for this species, continuing through autumn and winter. Strong pulses of recruitment of *P. perna* over *M. galloprovincialis* may contribute to the persistence of *P. perna* as the dominant species on the low-shore. However, the absence of a significant seasonal peak for *M. galloprovincialis* could have been an anomaly, as it experiences seasonal recruitment peaks on the west coast of South Africa (Harris et al. 1998) and strong variations in recruitment rates among years are common in many invertebrates (Siegel et al. 2008); but on face value the data suggest a more protracted reproductive season for this species on the south coast. Protracted recruitment can be advantageous for invasive species as the process is repeated under differing conditions (Crawley 1986). In Plettenberg Bay, disturbance caused by winter storms creates free space in the mid-intertidal zone that *M. galloprovincialis* is able to exploit better than *P. perna* due to its greater colonisation ability (Erlandsson et al. 2006). This could reflect the prolonged recruitment of *M. galloprovincialis* through winter, at a time when *P. perna* recruits are virtually absent. Recovery of *P. perna* was poor, which raises the concern that *M. galloprovincialis* may eventually be able to out-compete *P. perna* at this location (Erlandsson et al. 2006).

Settlement and recruitment were consistently and substantially greater in Plettenberg Bay than Tsitsikamma, supporting our hypothesis that poor settlement and recruitment limitation are responsible for the differences in adult abundances between locations. Wind-induced upwelling is common along the Tsitsikamma coast (Schumann et al. 1982), and may cause larvae to be transported offshore, resulting in poor recruitment rates there (Roughgarden et al. 1988; Connolly and Roughgarden 1998). The south coast in general experiences low, trickle recruitment (Lasiak and Barnard 1995; McQuaid and Phillips 2006), which has been linked to low spawning intensity (McQuaid and Phillips 2006). Larval dispersal and mortality may also result in heavier recruitment losses on the open coast

compared to bays, which frequently act as larval retention sites (Archambault and Bourget 1999; Helson and Gardner 2004; McQuaid and Phillips 2006). This has important implications for the success of *M. galloprovincialis* at certain sites and its spread on the south coast.

In marine environments, many non-indigenous species have disjointed distributions that are restricted to semi-enclosed systems such as harbours, bays and estuaries (Robinson et al. 2005; Wasson et al. 2005). This may be influenced by larval retention, which promotes successful establishment and population expansion of a colonising species. For example, the success of the invasive barnacle *Elminius modestus* Darwin in Lough Hyne was attributed to a high degree of water retention, which led to it forming a self-perpetuating population (Lawson et al. 2004; Watson et al. 2005). However, larval retention can also limit larval dispersal and hence the spread of non-indigenous species out of these systems. There is likely to be some exchange with the open coast so that high density populations may act as a source for nearby coastal sites (McQuaid and Phillips 2006). This may have affected the increase in abundance of *M. galloprovincialis* in Tsitsikamma during this study (Bownes and McQuaid 2006). However, this effect diminishes with distance from the source population (McQuaid and Phillips 2000). The rate of spread of *M. galloprovincialis* on this coast appears to be decreasing (Rius and McQuaid 2006) and the evidence suggests that recruitment limitation plays a role.

## Conclusions

Local coexistence between *P. perna* and *M. galloprovincialis* on the south coast seems to be due to a combination of pre- and post-recruitment events that differ in importance between species. Our results show that the relative contributions of settlement, post-settlement mortality and recruitment to the determination of adult distributions are complex, and none could explain habitat segregation entirely. As hypothesised, *P. perna* is largely excluded from the high-shore by recruitment failure. *M. galloprovincialis* is able to dominate the high intertidal zone, most likely because of the absence of a dominant competitor and the high physiological tolerance of *M. galloprovincialis* to desiccation stress (Nicastro et al. 2008). In other parts of the world, *M. galloprovincialis* displays a similar superiority to indigenous species in the upper intertidal zones, which has been explained by its enhanced tolerance of high temperatures and aerial exposure (Kennedy 1976; Petes et al. 2007; Schneider and Helmuth 2007). High survival and slow growth in juveniles may allow large densities of *M. galloprovincialis* to accumulate there, despite low settlement rates. Both *P. perna* and *M. galloprovincialis* had

strong settlement and recruitment on the low-shore and high post-settlement survival. Low adult abundance of *M. galloprovincialis* in this zone must therefore be determined primarily by post-recruitment events, including greater vulnerability to wave action and competitive exclusion by *P. perna* (Rius and McQuaid 2006; Zardi et al. 2006). At larger scales, larval retention and protracted recruitment are likely to have contributed to the success of *M. galloprovincialis* in Plettenberg Bay. However, recruitment is strongly limited on the south coast, and this appears to have restricted the spread of *M. galloprovincialis* and its ability to establish viable populations at most sites.

**Acknowledgments** We would like to extend special thanks to the Tsitsikamma National Park for allowing us to sample within the reserve and specifically J. Allen, S. Brouwer and E. Bester for organising permits and for their hospitality during field trips. In addition, thank you to Dr. S. Kaehler, Dr. J. Erlandsson, N. Wilson, Dr. G. Zardi and B. Hayward for their help in the field; Dr. M. Villet, Prof. S. Radloff and Dr. F. Porri for their help and advice with statistics and Mr. and Mrs. R.S. Bownes for their support. Our gratitude also goes to the National Research Foundation for funding this research.

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