

Sand stress as a non-determinant of habitat segregation of indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels in South Africa

G. I. Zardi, K. R. Nicastro, F. Porri and C. D. McQuaid

Department of Zoology & Entomology, Rhodes University, 6140 Grahamstown, South Africa

Abstract

Periodical sand inundation influences diversity and distribution of intertidal species throughout the world. This study investigates the effect of sand stress on survival and on habitat segregation of the two dominant mussel species living in South Africa, the invasive *Mytilus galloprovincialis* and the indigenous *Perna perna*. *P. perna* occupies a lower intertidal zone which, monthly surveys over 1.5 years showed, is covered by sand for longer periods than the higher *M. galloprovincialis* zone. Despite this, when buried under sand, *P. perna* mortality rates were significantly higher than those of *M. galloprovincialis* in both laboratory and in field experiments. Under anoxic condition, *P. perna* mortality rates were still significantly higher than those for *M. galloprovincialis*, but both species died later than when exposed to sand burial, underlining the importance of the physical action of sand on mussel internal organs. When buried, both species accumulate sediments within the shell valves while still alive, but the quantities are much greater for *P. perna*. This suggests that *P. perna* gills are more severely damaged by sand abrasion and could explain its higher mortality rates. *M. galloprovincialis* has longer labial palps than *P. perna*, indicating a higher particle sorting ability and consequently explaining its lower mortality rates when exposed to sand in suspension. Habitat segregation is often explained by physiological tolerances, but in this case, such explanations fail. Although sand stress strongly affects the survival of the two species, it does not explain their vertical zonation. Contrary to our expectations, the species that is less well adapted to cope with sand stress maintains dominance in a habitat where such stress is high.

Introduction

Rocky shores throughout the world are periodically disturbed by sand inundation or sand scour; in South Africa, rocky shores that are regularly and extensively inundated by sand are more common than non-inundated rocky shores (31 and 27% of the coastline, respectively; Bally et al. 1984). Despite this, few studies have investigated such ecosystems. Most recent studies have examined the effects of sand on the survival or lifestyle of single species (D'Antonio 1986; Marshall and McQuaid 1989; Pineda and Escofet 1989) or have analysed the effects of sand inundation on species richness and composition (Bally et al. 1984; McQuaid and Dower 1990). Sand can maintain a balance between sand tolerant and sand intolerant competitors (Taylor and Littler 1982; Littler et al. 1983), it can cause a temporary impoverishment of the biota by selective species elimination (Daly and Mathieson 1977; Devlinny and Volsse 1978), and it can explain the habitat segregation of intertidal species (Marshall and McQuaid 1989).

Mussels can be subjected to stress generated by sand either through sand burial or because the ambient water carries a heavy load of suspended sand. They sort filtered material using two pairs of labial palps (Ward et al. 1998) and at very high particle concentrations, the filtration rate can be reduced to zero (Widdows et al. 1979; Richardson 1985; Leverone 1995). Thus, the ability to regulate filter-rejecting mechanisms during sudden changes in sediment load concentration is a prerequisite for survival. In sandy beaches, there is a very rapid decline in oxygen deeper in the sediments (Pearse et al. 1942; Brafield 1964), consequently, when buried under sand, mussels are not only subjected to the negative effects of sand itself, but also to anoxia. In response to periods of depleted oxygen, mussels reduce the valve gape or close the valves (Jørgensen 1990), and switch from aerobic to anaerobic respiration (Taylor 1976), but anaerobic acidic end products can accumulate to lethal levels (Newell 1970).

The invasive mussel *Mytilus galloprovincialis* and the indigenous *Perna perna* coexist and compete in the lower balanoid zone (referred to here as the mussel zone) on the south coast of South Africa (Griffiths et al. 1992; Branch and Steffani 2004). The two species show potential habitat segregation: the upper and the lower areas of the mussel zone are dominated by *M. galloprovincialis* and *P. perna* respectively, while they co-occur in the mid-

mussel zone (Hockey and van Erkom Shurink *1992*; Robinson et al. 2005). *M. galloprovincialis* exhibits several characteristics of an aggressive invasive species: rapid growth rate over a range of water temperatures, high fecundity, high recruitment rate, resistance to desiccation and resistance to parasites (Hockey and van Erkom Shurink *1992*; Van Erkom Shurink and Griffiths *1991, 1993*; Calvo-Ugarteburu and McQuaid *1998*). It is also a strong competitor for primary space, having displaced the indigenous mussel *Aulacomya ater* along the entire west coast of South Africa to Southern Namibia (Griffiths et al. *1992*).

This study investigates the effects of sand stress on the survival of *M. galloprovincialis* and *P. perna*. We hypothesised that, because sand accumulates from the subtidal and has stronger effects low on the shore, sand inundation contributes to habitat segregation (vertical zonation) of the two species. Understanding how the two species behave when subjected to environmental stress helps to predict future interactions and the ecological effects of the invader. Specifically, we tested the hypothesis that *P. perna* has greater tolerance to the effects of sand than *M. galloprovincialis*, so that *M. galloprovincialis* is excluded from the lower shore at least partly through the effects of sand inundation and sand scour. Mortality rates of mussels subjected to sand burial and to sand in suspension were observed in field and laboratory experiments. In order to investigate the possible causes of mortality under sediment load stress, the two species were also subjected to anoxic conditions and the findings were set in the context of field measurements of seasonal fluctuations in sand levels near mussel beds.

Materials and methods

Laboratory experiments

For all laboratory experiments, adult mussels (3–5 cm shell length) of both species were collected from the mid mussel zone of a rocky shore at Plettenberg Bay on the south coast of South Africa (34° 22' S, 23° 22' E; Fig. 1). Before each laboratory experiment all individuals were acclimated in oxygenated seawater for 24 h. All experiments were run in a controlled environment chamber at 19°C under a 12:12 h light:dark regime (high output fluorescent light). Salinity was maintained at 35‰. Experimental aquaria were aerated and the water was replaced daily. Mussel mortality was assessed as failure to close the valves when disturbed. Mortality rates were calculated as means of three aquaria for each treatment and analysed using repeated measures ANOVA with treatment as a fixed factor.

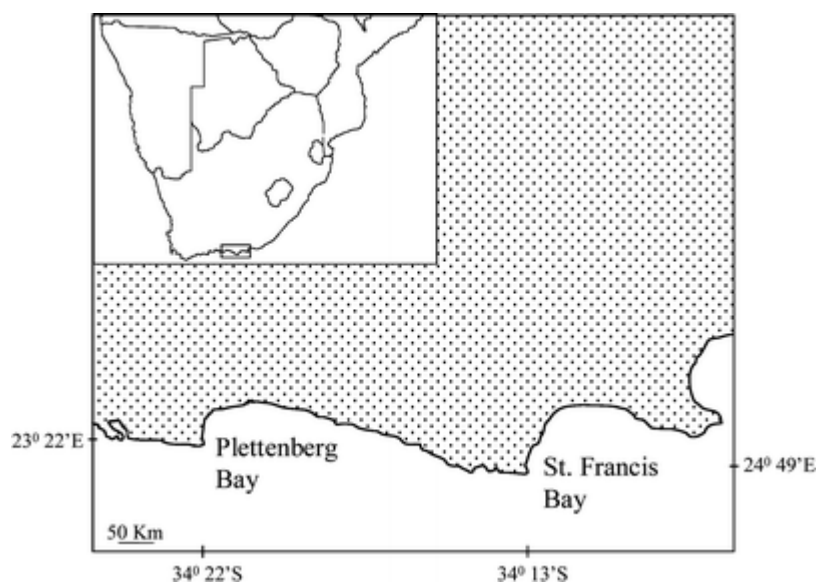


Fig. 1 Location of study areas

Sand burial and suspended sand

Mussels ($n=360$ for each species) were placed in nylon net bags (6 mm mesh) containing 10 mussels each, and subjected to three different sand load conditions in aquaria:

1. Sand in suspension: 12 g l^{-1} of fine sand. This concentration was based on the average load of resuspended sand measured in the sea at high tide near the study mussel bed.
2. Buried: covered with sand to a depth of 10–15 cm.
3. Control: aerated seawater, no sand.

Each experimental condition was replicated three times (three aquaria). In order to keep sand in suspension in treatment 1, compressed air was pumped through perforated tubes placed on the floor of the aquaria. For treatment 2, air was pumped through the water above the level of the sand. Dead mussels were counted and removed daily.

Anoxia

For each species, 15 individuals were placed in each of three aquaria containing 5 l of anoxic sea water. Anoxic conditions ($0.01\text{--}0.03 \text{ ml O}_2 \text{ l}^{-1}$) were prepared by bubbling Instrumental Grade N_2 gas into the aquaria, and then sealing them. Anoxic seawater was replaced daily and oxygen tension was checked every 12 h and readjusted if necessary. Dead mussels were counted and removed daily.

Labial palp length

A dissecting microscope was used to measure the lengths of the labial palps of 20 mussels (25–67 mm shell length) of each species to the nearest millimetre. Regression analysis was used to test the dependence of labial palp length on animal shell length for each species and a Student's t test was used to test equality of the two regression coefficients.

Sand content

M. galloprovincialis and *P. perna* ($n=60$ for each) were placed in six nylon net bags. Twenty mussels of each species were placed in each of three aquaria. The bags were then buried under sand to a depth of 10–15 cm. The experiment was run for 72 h and mortality was checked daily. Every 24 h, five live individuals were taken from each bag. Sand content of the animals was removed by opening the mussels and carefully washing the tissues. The water used to rinse the internal parts of the animal was drawn through a glass fibre filter, which was then dried at 60°C to constant weight. After the first day, the shell volume of each animal was measured by comparing the weight of NaCl required to fill one valve, to the weight of a known volume of NaCl.

Field experiments

Sand burial

Adult mussels of both species (3–5 cm shell length) were collected in November 2004 in the intertidal zone at St. Francis Bay ($34^\circ 13' \text{ S}$, $24^\circ 49' \text{ E}$; Fig. 1), about 140 km west of Plettenberg Bay. Three experimental sites, approximately 100 m apart, were selected in sand covered areas adjacent to rocks with mussel populations and at approximately the same vertical height as the mussel zone. Mussels ($n=240$ for each species) were immediately placed in nylon net bags and buried in situ under 30–40 cm of sand. Each bag contained 20 individuals of the same species; bags were equally distributed among sites. Bags were attached by fishing line to nearby rocks, so that they could be found easily. A table tennis ball was left beside each mussel bag; its presence at the next low tide confirmed that the samples had not been exhumed during high tide. Every day, bags were recovered and the

mortality of each species was checked. Dead animals were removed. Mortality rates were calculated as means for each site and analysed using repeated measurements ANOVA.

Seasonality of sand level fluctuation

Digital photographs of mussel beds populating vertical rocks were taken every month at two intertidal sites (Keurbooms and Robberg, 10 km apart) in Plettenberg Bay (Fig. 1) for a period of 18 months. *M. galloprovincialis* and *P. perna* zones were defined as the areas of the mussel bed that were covered by at least 90% ($\pm 5\%$) of one of the two mussel species. The mid-mussel zone was the area of co-existence between the *M. galloprovincialis* and *P. perna* zones. The lowest level of sand recorded at each site during the monitoring period was taken to be the reference level from which all other levels were measured. Percentage cover of mussels was determined by analysing digital images of 3 m wide transects running c. 15 m horizontally in each zone at each site.

Results

Laboratory experiments

Mortality rates under conditions of sand burial, sand suspension and anoxia

Repeated measures ANOVA showed that mortality rates were higher for *P. perna* than for *M. galloprovincialis* under all sand stress and anoxic treatments ($P < 0.0001$ in all cases). During the entire experiment, under control conditions, *P. perna* suffered 2.5% mortality compared to 4.2% for *M. galloprovincialis*. When subjected to sand burial in the laboratory, mortality for both species began after 2 days (12.5 and 4.2% for *P. perna* and *M. galloprovincialis*, respectively). Lethal time for 50% mortality ($L_T 50$) was reached after 4 days for *P. perna* and 6 days for *M. galloprovincialis* (Fig. 2, Table 1). When subjected to sand suspension, mortality was much lower for both species. Mortality for *P. perna* started after 5 days (0.8%), while the first dead *M. galloprovincialis* were found only after 9 days (1.7%). $L_T 50$ was reached after 10 and 14 days for *P. perna* and *M. galloprovincialis*, respectively (Fig. 3). Under anoxic conditions, mortality for both species began later than when buried under sand (after 4 days, 2.2% for *M. galloprovincialis* and 4.4% for *P. perna*). $L_T 50$ was reached after 9 and 12 days for *P. perna* and *M. galloprovincialis*, respectively (Fig. 4).

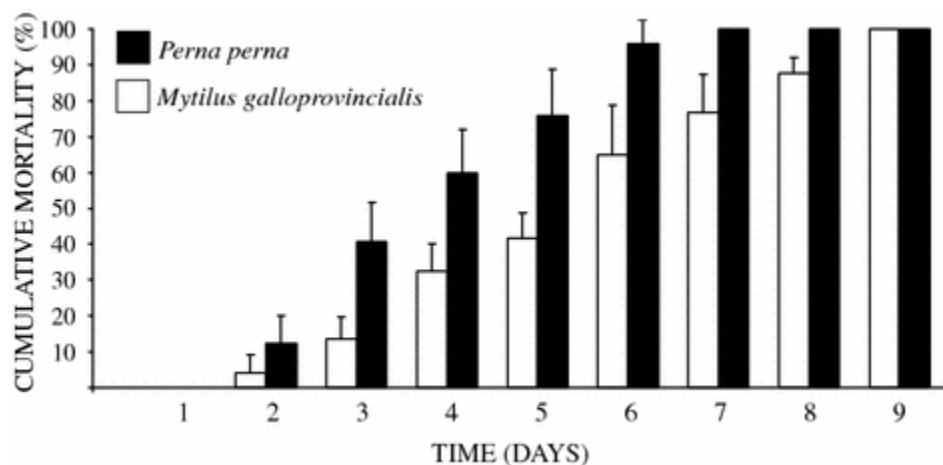


Fig. 2 Mean cumulative percentage mortality for three aquaria (+SD) of *P. perna* and *M. galloprovincialis* when exposed to sand burial in the laboratory. Mortality rates were significantly ($P < 0.0001$) higher for *P. perna* than for *M. galloprovincialis*

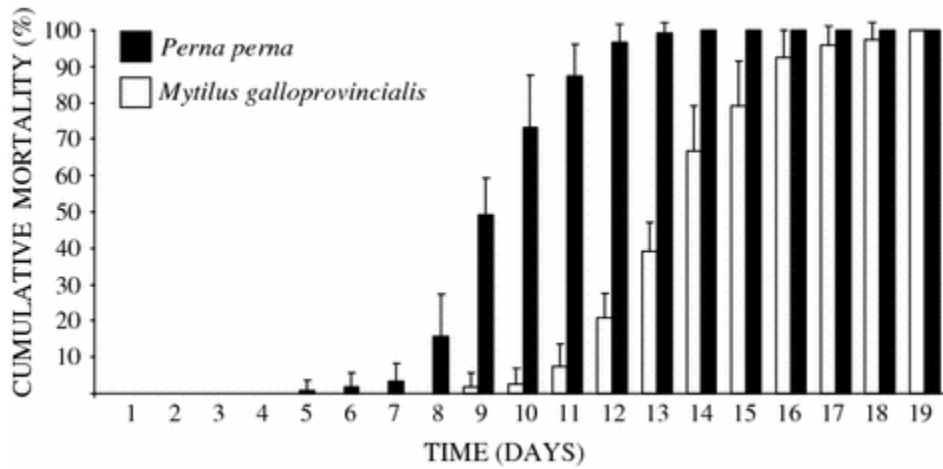


Fig. 3 Mean cumulative percentage mortality for three aquaria (+SD) of *P. perna* and *M. galloprovincialis* when exposed to sand in suspension (12 g l^{-1}) in the laboratory. Mortality rates were significantly ($P < 0.0001$) higher for *P. perna* than for *M. galloprovincialis*

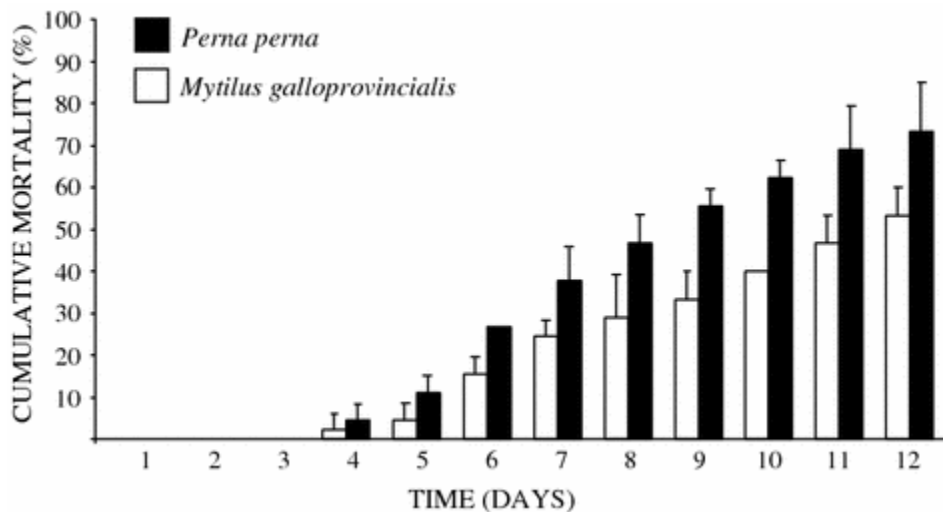


Fig. 4 Mean cumulative percentage mortality for three aquaria (+SD) of *P. perna* and *M. galloprovincialis* when exposed to anoxic conditions in the laboratory. Mortality rates were significantly ($P < 0.0001$) higher for *P. perna* than for *M. galloprovincialis*

Labial palp length

Labial palp length increased with animal size for both species (regression analysis $R^2 = 0.8607$ for *M. galloprovincialis* and $R^2 = 0.6071$ for *P. perna*; $n = 20$, $P < 0.001$ in both cases). *M. galloprovincialis* had significantly ($P < 0.0001$) longer labial palps than *P. perna* over the whole size range, averaging 28.3% longer overall (Fig. 5).

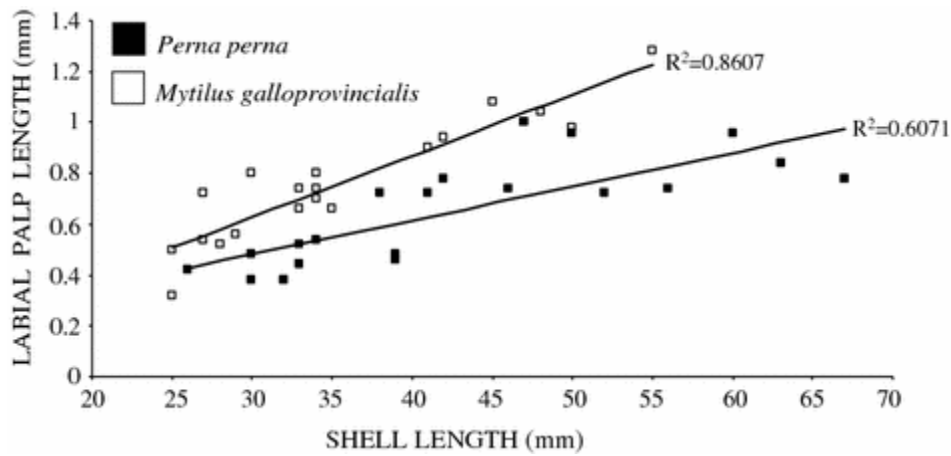


Fig. 5 Relationship between shell length and labial palp length for *P. perna* ($y=0.0133x+0.0824$; $P<0.001$) and *M. galloprovincialis* ($y=0.0241x+0.0948$; $P<0.001$)

Sand content

Correlation analysis showed no relation between volume of the animal and sand content. Subsequently a two-way model 1 ANOVA was used to analyse the data, with species and day as factors. Two-way ANOVA showed that the amount of sand present in live mussels buried under sand was significantly ($P<0.0001$) higher for *P. perna* than for *M. galloprovincialis*, with no significant time--species interaction. Within the first 24 h, 47.8 and 8.4 mg of sand were found in *P. perna* and *M. galloprovincialis*, respectively. The amount of sand increased slightly during the following days, up to 98.8 mg for *P. perna* and 16.9 mg for *M. galloprovincialis*, though the effect of time was just non-significant ($P = 0.055$).

Field experiments

Sand burial

Repeated measures ANOVA showed that mortality rates for *P. perna* were significantly higher than for *M. galloprovincialis* ($P<0.0001$) with sand burial. Mortality rates followed the same pattern as for the laboratory sand burial experiment. After 48 h, mortality was 14.6 and 3.3% for *P. perna* and *M. galloprovincialis*, respectively; $L_T 50$ was reached after 5 days for *P. perna* and 6 days for *M. galloprovincialis* (Fig. 6).

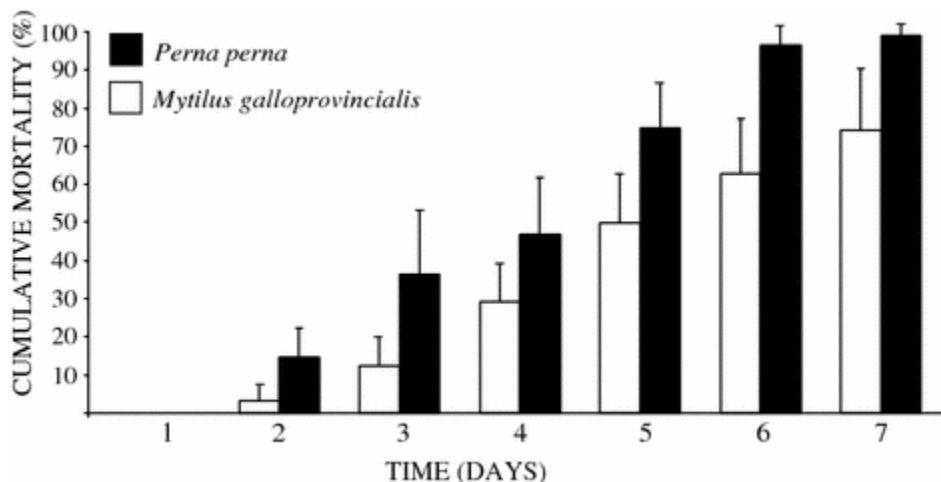


Fig. 6 Mean cumulative percentage mortality for three sites (+SD) of *P. perna* and *M. galloprovincialis* when exposed to sand burial in the field. Mortality rates were significantly ($P<0.0001$) higher for *P. perna* than for *M. galloprovincialis*

Seasonality of sand level fluctuation

Monthly pictures of mussel beds taken at Plettenberg Bay showed strong seasonal fluctuation of sand coverage with vertical changes of up to 175 cm. Sand accumulation increased towards the end of summer and the beginning of autumn (particularly April and March), followed by massive removal at the end of autumn. A hundred percent mortality for both species was observed once sand level decreased to uncover the mussel beds one month later in May. Sand levels then remained low until the following summer. The lowest sand level ($y=0$ in Fig. 7 a, b) occurred during winter between August and September. At its greatest depth (April--May 2004 in Robberg, April--May 2003 in Keurbooms), sand completely covered the *Perna* and the mid-zones, while the *Mytilus* zone was covered 35 and 21.4% at Robberg and Keurbooms, respectively (Fig. 7).

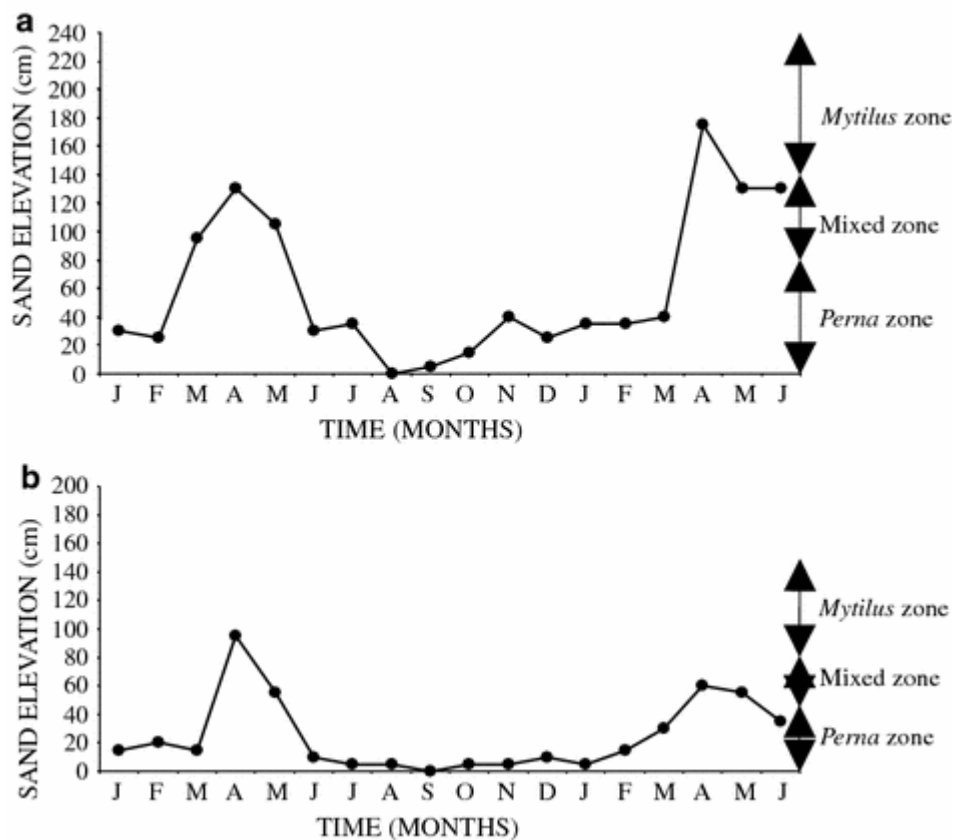


Fig. 7 Seasonal sand elevation at Robberg (a) and at Keurbooms (b). The lowest level of sand recorded at each site was taken to be the reference level ($y=0$). The vertical limits of the three mussel zones at each site are indicated

Discussion

To become successful, an invasion depends both on the characteristics of the invaders and on the degree of invasion resistance provided by the invaded environment (Kolar and Lodge 2001). Fluctuation in space and time of resources (Davis et al. 2000), natural enemies (Calvo-Ugarteburu and McQuaid 1998; Keane and Crawley 2002) and physical factors (Moyle and Light 1996) can favour alien species with broad environmental tolerances. The ability of invasive and indigenous species to respond to environmental fluctuations in time and space regulates the dynamics of their competition, coexistence and habitat segregation (Chesson 2000).

Our digital photographs showed considerable movement of sand, which seasonally covers mussel beds, with enormous effects on mussel survival and consequently on the community. The maximum accumulation of sand to a depth of 175 cm should be seen in the context of a maximum tidal range on this coast of 2–2.5 m (Field and Griffiths 1991). The dramatic effects of sand inundation are obvious from the total mortality of mussels in natural beds covered for one month, while mass mortality of mussels not buried, but exposed to high sediment loads, are observed periodically (personal observation).

In this study we tested the hypothesis that habitat segregation of *P. perna* and *M. galloprovincialis* could be explained by a greater physiological tolerance of sediment load of the indigenous species. The results were very clear cut and consistent, but rejected this hypothesis.

When exposed to suspended sand in the laboratory, *M. galloprovincialis* showed much greater tolerance than *P. perna*. The greater ability of the invasive species to withstand this stress could be a daily competitive advantage when sediment is brought in suspension during high tide. Mussels are suspension feeding bivalves and consequently they are very vulnerable to high levels of sediment loads in the water (Bricelj and Malouf 1984; MacDonald et al. 1998; Cheung and Shin 2005). The two pairs of labial palps are responsible for rejecting non-food material that has been filtered out (Morton 1987; Seed and Richardson 1999). The material rejected by the palps, together with some large particles rejected directly by the gills, forms mucoid aggregates or pseudofeces that are expelled by both inhalant and exhalant siphons (Foster-Smith 1975). At high levels of sediment the sorting mechanism may become overloaded and the equilibrium between filtration and rejection of material is altered; consequently increasing proportions of filtered material are rejected as pseudofeces until the filtration rate reaches a maximum and then declines to zero (Widdows et al. 1979; Newell et al. 1989).

Ward et al. (1998) showed that, in heterorhabdic bivalve species (ctenidia possessing two type of cilia beating in opposing directions), most of the particle sorting takes place on the ctenidia, while homorhabdic species, including marine mussels, have ctenidia possessing only one type of cilia and rely predominantly on the labial palps for particle selection. The significantly longer labial palps measured in *M. galloprovincialis* could be a morphological explanation for higher mortality rates of *P. perna* under conditions of sand suspension (Kjørboe and Møhlenberg 1981). In late summer and autumn, massive quantities of sand are moved by storms, covering large portions of the mussel zone on rocky shores. Both laboratory and field experiments showed that *P. perna* is less resistant than *M. galloprovincialis* to sand burial conditions. On sandy beaches, there is a very rapid decline in oxygen deeper in the sediment; at a depth of 2 cm the oxygen content is generally about 1.4 ml l^{-1} , while at a depth of 5 cm there is frequently only about 0.3 ml l^{-1} (Pearse et al. 1942; Brafield 1964). When buried under sand, mussels are exposed to both the abrasive action of the sand itself and to anoxic conditions. Some bivalves live under conditions not only of low oxygen, but also of high sulphide conditions (e.g. Kraus and Doeller 2004) and it can be difficult, or perhaps impossible to separate the effects of hypoxia from increases in hydrogen sulphide under natural conditions (Wu 2002). However, there is no evidence of hydrogen sulphide leading to mortality in the system studied here.

To understand how much anoxia influences mortality during sand burial, mussels were kept in anoxic seawater without sand. *P. perna* was more sensitive to this condition, and this is in accord with published values for oxygen tolerances. *P. perna* and *M. galloprovincialis* can regulate oxygen uptake down to concentrations of approximately 2–2.5 (Marshall and McQuaid 1993) and 3.4 ppm (De Zwaan et al. 1991), respectively. However, both species began to die later than when buried under sand, indicating that the physical action of sand is a crucial factor influencing mortality. Recent studies show that sediment load stress is strongly correlated to irreversible damage to gill structure in *Perna viridis* (Cheung and Shin 2005). Seriously damaged gill filaments could reduce the effective gill surface area and affect the pumping rate of the organism, leading to hypoxic stress (Jones et al. 1992; Au et al. 2004). When buried, both species accumulated sand within the shell valves while still alive, but the quantities were much higher for *P. perna*. This suggests that *P. perna* gills are more severely damaged and could explain its higher mortality rates, though histological analysis of sand damaged gill tissue of the two species is needed to confirm this. Under control conditions of oxygenated water, mussels in aquaria use the foot to rearrange their position and aggregate in clumps. Valve closure in anoxic water prevents this (personal observation). Moreover, in anoxic water, mussels were not able to replace decayed byssal threads to maintain a constant attachment strength (personal observation). These physical limitations could be an important disadvantage when uncovered by sand after temporary burial and re-exposed to hydrodynamic stress.

Although all the results indicate that *P. perna* is less resistant to sand stress, it occupies the lower mussel zone and so, at least at some sites, it is more exposed to the periodic effects of suspended sand and sand burial. Our survey showed that the *Perna* zone at the study sites was covered by sand for long periods of the year and digital photographs showed that buried mussel beds were completely removed when sand levels dropped again in summer. In addition, the absence of *M. galloprovincialis* juveniles on the lower shore and of *P. perna* juveniles

on the higher mussel zone (personal observation) suggests that interspecific differences in reaction to abiotic stress are not restricted to adults.

We conclude that, despite the fact that *M. galloprovincialis* should have the competitive advantage of being less vulnerable to sand on the low shore, sand is not involved in habitat segregation of *P. perna* and *M. galloprovincialis* and that other biotic or abiotic factors are responsible for preventing the invasive species from colonising the lower mussel zone. In particular there is experimental evidence that combinations of wave action (G. I. Zardi, unpublished data) and competitive displacement by *P. perna* (Rius and McQuaid, submitted) effectively exclude *M. galloprovincialis* from the lower parts of the mussel zone. Moreover, our results show that a species that is morphologically and physically less well adapted than a competitor can nevertheless maintain dominance.

Table 1 Summary of number of individuals per species, replicates and L_T 50 (days) for *Mytilus galloprovincialis* and *Perna perna* when subjected to sand and anoxic stress

Treatment	Number of individuals per species	Replicates	L_T 50 (days) ^a	
			<i>Mytilus galloprovincialis</i>	<i>Perna perna</i>
Suspended sand in laboratory	120	3 aquaria	14	10
Sand burial in laboratory	120	3 aquaria	6	4
Sand burial in field	80	3 sites	6	5
Anoxia in laboratory	15	3 aquaria	12	9

^aLethal time for 50% mortality expressed in days

Acknowledgements

We thank A.N. Hodgson for his very helpful advice and M.J. Roberts for providing excellent facilities during field experiments. This research was funded by Rhodes University and the National Research Foundation of South Africa.

References

- Au DWT, Pollino CA, Wu RSS, Shin PKS, Lau STF, Tang JYM (2004) Chronic effects of suspended solids on gills structure, osmoregulation, growth, and triiodothyronine in juvenile green grouper *Epinphelus coioides*. Mar Ecol Prog Ser 266:255–264
- Brafield AE (1964) The oxygen content of interstitial water in sandy shores. J Anim Ecol 33:97–116
- Branch GM, Steffani CN (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). J Exp Mar Biol Ecol 300:189–144
- Bricelj VM, Malouf RE (1984) Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar Biol 84:155–165
- Calvo-Ugarteburu G, McQuaid CD (1998) Parasitism and invasive species: effects of digenetic trematode on mussels. Mar Ecol Prog Ser 169:149–163
- Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366
- Cheung SG, Shin PKS (2005) Size effects of suspended particles on gill damage in green-lipped mussel *Perna viridis*. Mar Pollution Bull (in press)

- D'Antonio CM (1986) Role of sand in domination of hard substrata by the intertidal alga *Rhodomela larics*. *Mar Ecol Prog Ser* 27:263–275
- Daly MA, Mathieson AC (1977) The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Mar Biol* 43:45–56
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- Devlinny JS, Volse LA (1978) Effect of sediments on the development of *Macrocystis pyrifera* gametophytes. *Mar Ecol* 48:343–348
- De Zwaan A, Cortesi P, van den Thillart G, Roos J, Storey KB (1991) Differential sensitivities to hypoxia by two anoxia-tolerant marine molluscs: A biochemical analysis. *Mar Biol* 111:343–351
- Field JG, Griffiths CL (eds) (1991) Littoral and sublittoral ecosystems of southern Africa. In: Mathieson AC, Nienhus PH (eds) *Ecosystems of the world*. Elsevier, Amsterdam, pp 323–346
- Foster-Smith RL (1975) The effect of concentration of suspension on filtration rates of pseudofaecal production for *Mytilus edulis* (L), *Cerastoderma edule* (L) and *Venerupis pullastra* (Montagu). *J exp mar Biol Ecol* 17:1–22
- Griffiths CL, Hockey PAR, Van Erkom Schurink C, Le Roux PJ (1992) Marine invasive aliens on South African shores: Implications for community structure and trophic functioning. *S Afr J Mar Sci* 12:713–722
- Hockey CL, van Erkom Schurink C (1992) The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *T Roy Soc S Afr* 48:123–139
- Jones HD, Richards OG, Southern TA (1992) Gill dimension, water pumping rate and body size in the mussel *Mytilus edulis* L. *J Exp Mar Biol Ecol* 155:213–237
- Jørgensen CB (eds) (1990) *Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology*. Olsen and Olsen, Fredensborg, Denmark
- Keane RM, Crawley MG (2002) Exotic plant invasion and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Kjørboe T, Møhlenberg F (1981) Particle selection in suspension-feeding bivalves. *Mar Ecol Prog Ser* 5:291–296
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16:199–204
- Leverone GR (1995) Growth and survival of caged adult bay scallops (*Argopecten irradians concentricus*) in Tampa Bay with respect to levels of turbidity, suspended solids and chlorophyll *a*. *Florida Sci* 58:216–227
- Littler MM, Martz DR, Littler DS (1983) Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Mar Ecol Prog Ser* 11:129–139
- MacDonald BA, Beacon GS, Ward JE (1998) Physiological response of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles II. Absorption efficiency and scope of growth. *J Exp Mar Biol Ecol* 219:127–141
- Marshall DJ, McQuaid CD (1989) The influence of the respiratory response on the tolerance to sand inundation of the limpets *Patella granularis* (L) (Prosobranchia) and *Siphonaria capensis* (Q et G) (Pulmonata). *J exp mar Biol Ecol* 129:191–201

- Marshall DJ, McQuaid CD (1993) Differential physiological and behavioural responses of the intertidal mussels, *Choromytilus meridionalis* (Kr.) and *Perna perna* L., to exposure to hypoxia and air: a basis for spatial separation. *J Exp Mar Biol Ecol* 171:225–237
- McQuaid CD, Dower KM (1990) Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia* 84:142–144
- Morton B (1987) The functional morphology of the organs of the mantle of *Perna viridis* (L 1758) (Bivalvia: Mytilacea). *Am Malacol Bull* 5:159–169
- Moyle PB, Light T (1996) Fish invasions in California: do abiotic factors determine success. *Ecology* 77:1666–1670
- Newell CR, Shumway SE, Cucci TL, Selvin R (1989) The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resources availability for the mussel *Mytilus edulis* L., 1758 at bottom culture sites in Maine. *J Shellfish Res* 8:187–196
- Newell RC (eds) (1970) *Biology of intertidal animals*. Logos, London
- Pearse AS, Humm HJ, Wharton GW (1942) Ecology of beaches at Beauford, NC. *Ecol Monogr* 12:135–90
- Pineda J, Escofet A (1989) Selective effects of disturbance on populations of sea anemones from northern Baja California, Mexico. *Mar Ecol Prog Ser* 55:55–62
- Richardson BA (1985) The impact of forest road construction on the benthic invertebrate fauna of a coastal stream in southern New South Wales. *Bull of Aust Soc Limnol* 10:65–88
- Robinson TB, Griffiths CL, McQuaid CD, Rius M (2005) Marine alien species of South Africa – status and impacts. *S Afr J Mar Sci* (in press)
- Seed R, Richardson CA (1999) Evolutionary traits in *Perna viridis* (L) and *Septifer virigatus* (Weigmann) (Bivalvia: Mytilidae). *J Exp Mar Biol Ecol* 239:273–287
- Suchanek TH (1985) Mussels and their role in structuring rocky shores communities. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder and Stoughton, London, pp 70–96
- Taylor AC (1976) Burrowing behaviour and anaerobiosis in the bivalve *Artica islandica* (L). *J Mar Biol Ass UK* 56:95–109
- Taylor PR, Littler MM (1982) The role of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. *Ecology* 63:135–146
- Van Erkom Schurink C, Griffiths CL (1991) A comparison of reproductive cycles and reproductive output in four southern African mussel species. *Mar Ecol Prog Ser* 76:123–134
- Van Erkom Schurink C, Griffiths CL (1993) Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109:253–273
- Ward JE, Levinton JS, Shumway SE, Cucci TL (1998) Particle sorting in bivalves: in vivo determination of the pallial organs of selection. *Mar Biol* 131:283–292
- Widdows J, Fieth P, Worrall CM (1979) Relation between seston, available food and feeding activity, in the common mussel *Mytilus edulis*. *Mar Biol* 50:195–207