

Sand and wave induced mortality in invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels

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Abstract The ability of an invasive species to spread in a new locality depends on its interaction with the indigenous community and on variation in time and space in the environment. The Mediterranean mussel *Mytilus galloprovincialis* invaded the South African coast 30 years ago and it now competes and coexists with the indigenous mussel *Perna perna*. The two species show different tolerances to wave and sand stress, two of the main environmental factors affecting this intertidal community. *P. perna* is more resistant to hydrodynamic stress than *M. galloprovincialis*, while the invasive species is less vulnerable to sand action. Our results show that mortality rates of the two species over a period of 6 months had different timing. The indigenous species had higher mortality than *M. galloprovincialis* during periods of high sand accumulation in mussel beds, while the pattern reversed during winter, when wave action was high. A negative correlation between sand accumulation and attachment strength of the two mussels showed that sand not only affects mussel mortality through scouring and burial, but also weakens their attachment strength, subjecting them to a higher risk of dislodgement. Here we underline the importance of variations in time and

space of environmental stress in regulating the interaction between invasive and indigenous species, and how these variations can create new competitive balances.

Introduction

Biological invasion involves three essential stages: transport of an organism to a new location (Williamson 1996; Mack et al. 2000), establishment in the new locality and then population growth and range expansion (Veltman et al. 1996). The responses of an introduced species to variations in time and space of resource availability, natural enemies and the physical environment determine its ability to invade and the dynamics of co-existence with indigenous species (Moyle and Light 1996; Sher and Hyatt 1999; Davis et al. 2000; Mack et al. 2000).

Invasive species have affected intertidal communities severely in several parts of the world. For example, *Codium fragile*, originally from Japan, has expanded to Europe, Australia, New Zealand, Canada, the United States and Chile (Castilla et al. 2004, 2005), *Perna perna*, probably from Venezuela, has colonised the South Texas coast and its expansion is still in progress (Hicks et al. 2001), *Balanus amphitrite* and *B. glandula* invaded intertidal rocky shores in the Southwest Atlantic and 40 years later have expanded >10° of latitude (Orensanz et al. 2002).

Periodic sand inundation influences diversity and distribution of intertidal species throughout the world (Bally et al. 1984; McQuaid and Dower 1990). Mussel beds can be subjected to high mortality rates generated by sand either through sand burial (Littler et al. 1983) or because the ambient water carries a heavy load of suspended sand (Zardi et al. 2006a). Wave forces also play an important

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role in determining the structure and dynamics of many intertidal communities because they can regulate the supply of food or propagules and break or dislodge organisms, (Menge 1976; Lubchenco and Menge 1978; Paine and Levin 1981; Bustamante and Branch 1996).

The difference in response of indigenous and invasive species to such physical factor has an influence on the success of the invader (Chesson 2000; Shea and Chesson 2002).

The invasive mussel *Mytilus galloprovincialis* arrived in South Africa (about 150 km north of Cape Town) most probably by shipping 30 years ago (Grant and Cherry 1985). Soon after its first detection, it spread to the north at an average rate of 115 km year⁻¹ and to the south at about 25 km year⁻¹ (Hockey and van Erkom Schurink 1992). Now it has colonised the west and south coasts of South Africa. On the south coast, it shows partial habitat segregation with the indigenous *P. perna* in the lower eulittoral zone (referred to here as the mussel zone). *P. perna* dominates the lowest mussel zone and *M. galloprovincialis* the highest, while the two species co-exist in the mid-zone (Bownes and McQuaid 2006). *P. perna* has higher attachment strength than the invasive species and consequently it is able to withstand wave action better (Zardi et al. 2006b). In contrast, *M. galloprovincialis* recolonises free space more rapidly (Erlandsson et al. 2006) and is less vulnerable to the action of sand than the indigenous species (Zardi et al. 2006a). Both wave action and sand accumulation fluctuate seasonally (Zardi et al. 2006a, 2007). Previous studies showed that sand accumulation is at a maximum in autumn with sand covering large portions of mussel populations. Through the end of autumn and winter wave action increases, removing sand and subjecting mussels to higher hydrodynamic stress (Zardi et al. 2007).

We hypothesised that, because the two species show different tolerances to wave action and sand stress, their mortality rates will show different seasonality, with higher mortality for *M. galloprovincialis* during periods of high hydrodynamic stress and for *P. perna* during maximum accumulation of sand. To test this hypothesis we quantified mortality rates of these two species over a period of 6 months and related them to wave and sediment fluctuation over the same period. Support for this hypothesis implies that competitive interaction between these two species will alter on a seasonal basis. Finally we hypothesised that sand affects mussel mortality rates not only directly (through burial or damage caused by sand in suspension), but also through the accumulation of sediments in mussel beds creating a less stable substratum and indirectly weakening the attachment of mussels and making them more vulnerable to dislodgement.

Material and methods

Field measurements were carried out on granite shores in the mid-mussel zone to allow comparison between the two species in Plettenberg Bay (34°05'S, 23°19'E), on the south coast of South Africa, for a 6-month period (May–October 2003) covering maximum stress in terms of sand accumulation and winter storm action. The study sites were topographically uniform, so all mussels were assumed to be exposed to similar abiotic conditions. This area is exposed in terms of wave action, particularly to south-easterly swells. Only monolayered mussel beds were investigated.

Mortality

Twenty areas (15 cm × 15 cm) were haphazardly chosen from the mid-mussel zone where the two species co-exist. In each area, 20 *M. galloprovincialis* and 20 *P. perna* (3.5–4.5 cm) were marked with a paint dot (~3 mm diameter), which was fixed to the shell by covering it with superglue. Mortality rates of the two species were recorded monthly and each month 20 new areas were chosen and 20 new individuals of each species were marked, so that *n* was 20 (areas) at the beginning of each month. The experiment was replicated at two sites, Robberg and Keurbooms, about 8 km apart in Plettenberg Bay.

Attachment strength and sediment amount

To quantify the average amount of sediment present in mussel beds, five samples (15 cm × 15 cm) of monolayered mussel bed were collected monthly at Robberg and Keurbooms, removing all material in quadrats by scraping. Samples were transported to the laboratory and all mussels ≥2 mm were removed. The remaining sediments were dried separately to constant weight (2 days at 60°C) and their weight was determined.

In May, mussel strength of attachment and sediment accumulation within mussel beds were recorded at three sites in Plettenberg Bay: Robberg Beach, Keurbooms Beach and Look-Out Beach. Before removing the samples, the strength of attachment of one individual (3.5–4.5 cm) of each species was determined in five quadrats, to relate it to the amount of sediment present in that quadrat. To measure attachment strength, a 2-mm diameter hole was drilled through the shell valves close to the posterior margin using a hand-held battery operated drill (Denny 1987). A fish hook, connected to a recording spring scale, was inserted through the hole. The scale was steadily and uniformly lifted normal to the rock surface until

dislodgment occurred (after 1–3 s). The force required to detach each mussel was recorded in Newtons.

Wave height

Estimated wave heights were obtained from data for a virtual buoy located at 34°51'S, 23°53'E as recorded by the USA National Data Buoy Centre (www.ndbc.noaa.gov; NOAA WAVEWATCH III model; Tolman 1999). Mean daily wave heights were calculated from hourly values, and then used to calculate mean monthly values.

Statistical analysis

Shapiro's and Levene's tests were used to assess normality and homogeneity of variances respectively. Mortality data failed the requirements for parametric analysis, therefore non-parametric Kruskal–Wallis tests were performed to evaluate species differences in each month.

Correlation analysis was used to test for significant relationship between monthly mortality of each species and mean monthly values for wave height and sediment amount.

Linear regression analysis was also used to test for significant relationship between sediment amount in May and attachment strength for each species in the same month.

Results

Mortality

Mortality rates of both species at Robberg and Keurbooms fluctuated seasonally during the sampling period. At both sites *M. galloprovincialis* mortality attained a clear peak in winter (July and August) and *P. perna* showed peaks in autumn (May) and another in winter (August). When analysing each month separately, mortality of *P. perna* was significantly (Kruskal–Wallis test, $P < 0.001$; Fig. 1) higher than that for *M. galloprovincialis* in autumn (May and June), except for Keurbooms in June ($P = 0.8$). In contrast, winter (July and August) mortality rates were significantly higher for *M. galloprovincialis* than for *P. perna* ($P < 0.01$). Spring (September and October) mortality rates did not differ significantly between species (in September $P = 0.4$ and $P = 0.1$ and in October $P = 1$ and $P = 0.6$ for Robberg and Keurbooms respectively). High variability of mortality rates was recorded, especially in August.

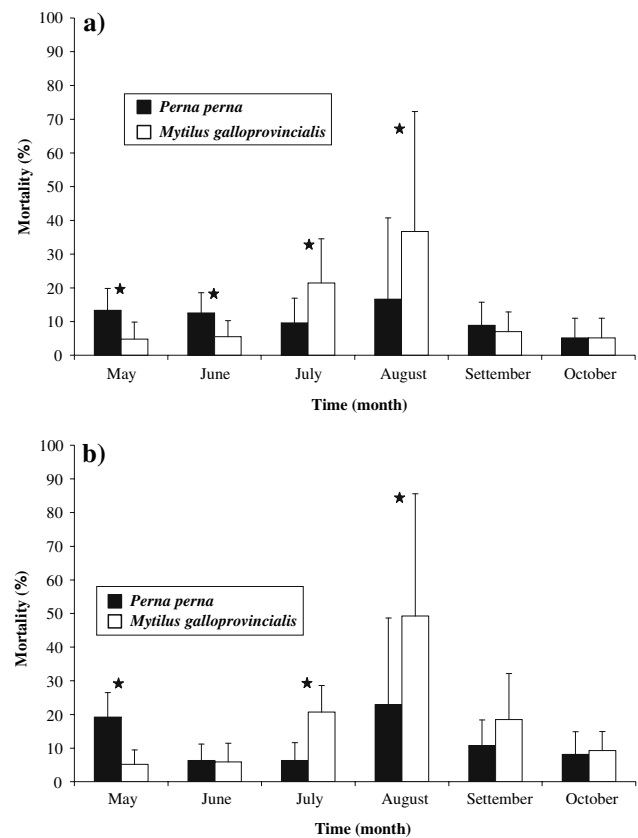


Fig. 1 Mean percentage monthly mortality rates (+SD) of *Perna perna* and *Mytilus galloprovincialis* at **a** Robberg, **b** Keurbooms. Filled star When mortality rates are significantly different between the two species

Attachment strength and sediment amount

Both sites showed similar seasonality of sediment accumulation, with a decline from a maximum in May (Fig. 2). There was a significant ($P < 0.05$, $r^2 = 0.8413$ for *M. galloprovincialis* and $r^2 = 0.9974$ for *P. perna*; Fig. 3) negative correlation between amount of sediment and strength of attachment for each species. Mean monthly mortality was not correlated with sediment amount for either species ($P > 0.05$, $n = 12$, $r = -0.26$ for *M. galloprovincialis* and $r = 0.47$ for *P. perna*).

Wave height

Mean monthly wave height increased in late autumn–winter, with a peak in August, and decreased in spring (Fig. 2). Mean monthly mortality of *M. galloprovincialis* was significantly correlated with wave height ($P < 0.05$, $n = 12$, $r = 0.79$), but not for *P. perna*.

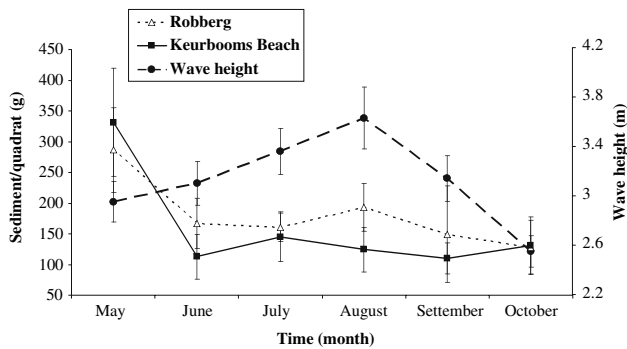


Fig. 2 Mean (\pm SD) monthly amount of sediment in quadrats at Robberg and Keurbooms and mean (\pm SD) monthly wave height from May to October 2003

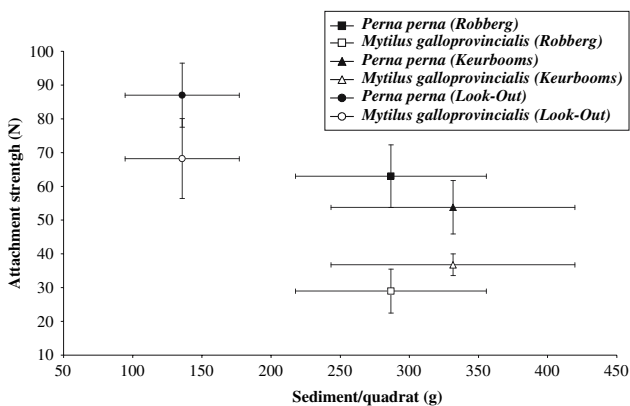


Fig. 3 Correlation between mean (\pm SD) monthly amount of sediment in quadrats and mean (\pm SD) monthly attachment strength for *Perna perna* ($n = 15$, five quadrats for each of the three locations, $y = -0.1669x + 109.88$, $r^2 = 0.9974$) and *Mytilus galloprovincialis* ($n = 15$, five quadrats for each of the three locations, $y = -0.1856x + 91.298$)

Discussion

The two forms of stress measured were out of phase. Sand accumulation reached a maximum when wave action was minimal, with sand being removed as wave stress increased through winter. Sand inundation or sand scour and wave action are two of the primary causes of disturbance on rocky shores (Paine and Levin 1981; Zardi et al. 2006a, b). Sand can maintain a balance between sand tolerant and sand intolerant competitors (Taylor and Littler 1982; Littler et al. 1983), while both waves and sand can cause a temporary impoverishment of the biota by selective species elimination (Daly and Mathieson 1977; Devlinny and Volsse 1978), and can also explain habitat segregation of intertidal species (Marshall and McQuaid 1989).

Mortality of both species fluctuated over the study period but *M. galloprovincialis* mortality showed more pronounced variation. The different abilities of the invasive and indigenous species to withstand sand and wave stress

indicate that the dynamics of co-existence and competition are not constant but vary in time.

In May, when amounts of sediment reached maximum levels, *P. perna* mortality rates were significantly higher than for the invasive species. During periods of maximum hydrodynamic stress (August), more *M. galloprovincialis* than *P. perna* died. These results accord with previous findings that *M. galloprovincialis* is less resistant to wave action and less affected by sand stress than *P. perna* (Zardi et al. 2006a, b).

Despite the fact that the effect of sand inundation is more pronounced on the indigenous species than on *M. galloprovincialis*, there was no correlation between sand accumulation and mortality rates of both species. This lack of correlation is probably due to the masking effect of wave action, which is particularly high during periods of low sand accumulation (mortality of *P. perna* due to sand decreases in the transition to winter, but by midwinter mortality due to waves increases).

Rocky intertidal habitats often exhibit high spatial and temporal heterogeneity because of the complex interaction between breaking waves and rocky shore organisms (Paine and Levin 1981; Erlandsson et al. 2006). The magnitude of hydrodynamic forces acting upon intertidal organisms can be extremely variable over scales of cm–m (Helmuth and Denny 2003, Denny et al. 2004) and it has been suggested that movement of sedentary intertidal organisms between microhabitats can lead to significant changes in mortality rates (Schneider et al. 2005). Adult mussels are able to move over short distances, making a mussel bed a dynamic structure composed of constantly re-arranging individuals (Paine and Levin 1981). The high variability of physical disturbance over small scales can thus explain the high variability of mortality rates we measured (especially during August), even when comparing quadrats that were only a few cm apart.

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. High levels of sand in suspension can damage internal tissues through abrasion (Cheung and Shin 2005), while anoxia, through accumulation of anaerobic acidic end-products, leads to massive mortality rates of mussels when buried (Newell 1970; Marshall and McQuaid 1989; Zardi et al. 2006a). The negative correlation between attachment strength and amount of sediment shows that the less stable secondary substratum of sand and shell fragments weakens the attachment strength of mussels living within a bed. Previous studies performed in Plettenberg Bay between May 2003 and October 2004, showed that both *M. galloprovincialis* and *P. perna* have two major spawning events each year: the former from October to December 2003 and from April to June 2004, the latter from June to July 2003

and 2004 and from January to March 2004 (Zardi et al. 2007). *P. perna* gamete release reaches highest levels during periods of maximum sand stress. A weaker attachment strength, sand inundation and burial cause mass or even total mortality of mussels, potentially having a large effect on population reproductive output and consequently on the dynamics of adult populations (Zardi et al. 2006a, 2007).

Mussels are an important group among marine invaders (Nalepa and Schloesser 1993; Carlton 1999) and, despite its recent arrival, *M. galloprovincialis* is the most abundant alien marine species in South Africa (Robinson et al. 2005). It shows several characteristics of an aggressive species that make it an effective competitor. These include high recruitment rates (Harris et al. 1998) resistance to desiccation (Hockey and van Erkom Schurink 1992), parasites (Calvo-Ugarteburu and McQuaid 1998) and sand stress (Zardi et al. 2006a) rapid growth rate over a range of water temperatures (Griffiths et al. 1992; Hockey and van Erkom Schurink 1992), and high fecundity (van Erkom Schurink and Griffiths 1993). However, when investigating alien species, it is also necessary to consider the recipient community and environment. The coastline of South Africa offers a wide variety of environmental conditions, but most of it is exposed to strong wave action. Growth, condition and recruitment of *M. galloprovincialis* are high in wave-exposed habitats but reduced under very exposed conditions (Steffani and Branch 2003; Branch and Steffani 2004). Wave action also generates free space. *M. galloprovincialis* has very high recruitment rates and reproductive output (van Erkom Schurink and Griffiths 1991; Harris et al. 1998) and it is a better exploitation competitor, occupying freed space more effectively than *P. perna* (Erlandsson et al. 2006). However, the positive influence of wave action on the invasive species is not constant; our study shows that periods of intense hydrodynamic stress (winter) favour the indigenous species, resulting in a seasonal shift in the competitive balance between *M. galloprovincialis* and *P. perna*.

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