

Differential reproductive investment, attachment strength and mortality of invasive and indigenous mussels across heterogeneous environments

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Abstract Environmental heterogeneity challenges both indigenous species and invaders and can play a defining role in the dynamics of their interactions. We compare bay and open coast habitats to show how environmental heterogeneity and seasonality affect survival and physiological performances of invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) intertidal mussels. *P. perna* had significantly higher attachment strength than *M. galloprovincialis*. Attachment was strongly correlated with hydrodynamic stress and was lower for both species in bays. Both species had a major spawning event when wave action was weakest. In bays, there was no correlation between gonad index (GI) and attachment strength for either species, but on the open coast GI was

negatively correlated with attachment. In bays, maximum GI of *M. galloprovincialis* was 64% higher than for *P. perna*, while on the open coast values did not differ between the two. Thus, on the open coast, both species invest more energy in attachment but *P. perna* can accommodate energetic demands of increased byssal production without altering gonad production, while *M. galloprovincialis* cannot. Mortality was significantly correlated to sand stress, while the correlation with wave action was very weak in bays and non-significant on the open coast probably because sand stress peaked during periods of low wave action. The success of the invader and thus the outcomes of its interaction with the indigenous species are governed by habitat-to-habitat variability. In this case the invasive species is likely to prove a weaker competitor on the more stressful and energetically demanding open coast.

K. R. Nicastro and G. I. Zardi have contributed equally to the work.

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Introduction

Organisms inhabit a highly heterogeneous world. By acting on different temporal and spatial scales, environmental conditions vary in intensity, frequency and suddenness shaping species dynamics, creating a mosaic of structures, modifying interactions between organisms and affecting competition outcomes

(e.g. Levins 1968; Paine and Levin 1981; Chesson and Huntly 1997; Zardi et al. 2008). Short- or long-term stressful changes in abiotic conditions, which impair or threaten to impair homeostasis, can trigger physiological and/or behavioural responses by an individual (Sapolsky 1992; Broom and Johnsen 1993; Buchanan 2000). However, a sudden or intense stress event can have lethal consequences and is known to affect space allocation, recruitment and subsequent inter-specific competition and species composition (e.g. Connell and Keough 1985; Chesson 1994; Sousa 2001).

By interacting with the diverse biological attributes of species, environmental heterogeneity plays a defining role in invasion and coexistence dynamics (Hu and Tessier 1995; Gerlach and Rice 2003; Leicht-Young et al. 2007). As both indigenous species and invaders respond to environmental variations, it is the difference in their responses that determines the success of the invader and how it interacts with native species (Chesson 2000; Shea and Chesson 2002). If environmental conditions change, the well adapted indigenous species may lose its prior advantage over non-indigenous species (Byers 2002; Pranovi et al. 2006). However, changes of environment can also challenge established invasive species and possibly limit their distribution (Sheley et al. 1997; Shea and Chesson 2002; Zardi et al. 2008).

Here, we examined the responses of competing indigenous and invasive mussels to environmental factors that show strong seasonality and spatial variability and we discuss how this affects the potential for co-existence. The Mediterranean mussel *Mytilus galloprovincialis* is a successful invader worldwide. It is the most successful marine invasive species in South Africa (Robinson et al. 2005; Hanekom 2008) where it 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 indigenous species (Erlandsson et al. 2006). On the south coast of South Africa, *M. galloprovincialis* co-exists with the indigenous mussel *Perna perna* with partial habitat segregation in the lower eulittoral zone (Bownes and McQuaid 2006). Among the most important physical factors shaping rocky intertidal populations are wave exposure and the effects of scouring or burial by sand (e.g. Marshall and McQuaid 1989; Gaylord et al. 1994; Denny 1995; Zardi et al. 2006a). Both abiotic

components can cause a temporary impoverishment of the biota by selective species elimination (Devlinny and Volse 1978; McQuaid and Branch 1985; Petes et al. 2007), explain the habitat segregation of some intertidal species (Marshall and McQuaid 1989; Zardi et al. 2006a, b; Petes et al. 2007) and, when intense and sudden, they can be responsible for non-selective mass mortality (Denny and Wetthey 2000; Denny et al. 2003). *M. galloprovincialis* and *P. perna* show different tolerances to wave and sand stress. *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* is less vulnerable than the indigenous species to the scouring and anoxic stresses induced by sand inundation and burial (Zardi et al. 2006a).

The response of an organism to a particular environmental factor can also be affected by other energy demanding physiological processes. Both byssal thread production (Hawkins and Bayne 1985; Seed and Suchanek 1992) and seasonal gonad development (e.g. Griffiths and King 1979) impose very high energetic demands on mussels. Attachment strength can be energetically constrained during the reproductive season, making mussels more vulnerable to wave action and thus increasing the risk of dislodgment (Carrington 2002a; but see Lachance et al. 2008). These trade-offs can be a result of habitat and seasonal differences in the availability of energy and in the partitioning of this energy into different physiological performances. Two of the most commonly observed differences between invasive and native species are that invaders do better than the natives when stress is low and that the ability of invader to outperform natives is reduced when stress is high (Baker 1986; Dukes and Mooney 1999). There is also evidence that habitat heterogeneity promotes invasion and coexistence mechanisms that are not possible in homogeneous environments (Melbourne et al. 2007). Thus, high stress should lessen the vulnerability of habitats to invasion, or modify the interaction between invasion and resident community. Here we hypothesize that the invasive and indigenous species react to a changing environment by adapting their performances over different spatial and temporal scales, and this plasticity provides them with different degrees of success. In particular we tested the following hypotheses:

- (1) Attachment strength of both species will fluctuate seasonally and will be higher on the open coast where hydrodynamic stress is greater.
- (2) Reproductive output of both species will be reduced under more wave exposed conditions because of conflict with the need for stronger byssal attachment, but the consequences of this trade off will be greater for the invasive species because of its higher investment in gamete production.
- (3) Because the two species show different tolerances to wave action and sand stress, their mortality rates will differ spatially and seasonally, with higher mortality for *M. galloprovincialis* when and where hydrodynamic stress is high, and for *P. perna* during periods and at sites of maximum accumulation of sand.

Materials and methods

Physiological parameters

Along the south coast of South Africa, rocky headlands bound large “half heart” bays. The measurements were run monthly between November 2006 and October 2007 in two of these bays (Plettenberg Bay 34°00'17"S, 23°27'17"E; Algoa Bay 33°58'47"S, 25°39'30"E) and at two open coast sites at headlands (Robberg 34°06'14"S, 23°23'07"E; Cape Recife 34°02'27"S, 25°32'01"E).

Each site had two locations 200 m apart, approximately 20 m² in area and topographically uniform, so all mussels in the same site were assumed to be exposed to similar abiotic factors (Fig. 1). Samples included only mussels living within a monolayered bed (i.e. all mussels attached directly to the substratum) from the mid-mussel zone where the two species co-exist.

Attachment strength

Mytilus galloprovincialis and *Perna perna* individuals (3.5–4.5 cm; $n = 12$ each month for each species at each location) were tested in situ for attachment strength as previously described in Zardi et al. (2006b). All dislodged mussels were at least 20 cm from each other so that attachment strength measurements were

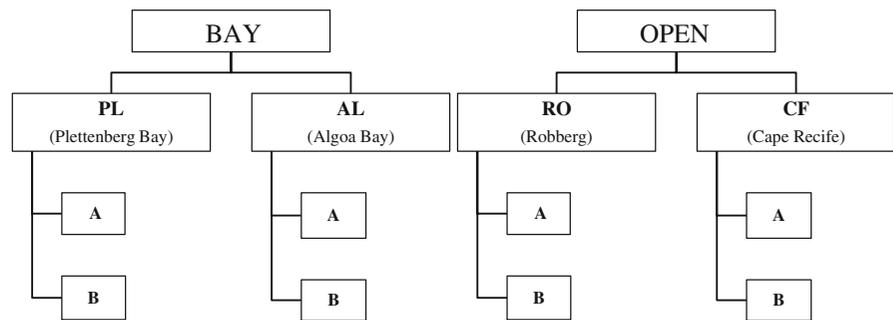
not influenced by previous ones. Data fulfilled the pre-requisites for parametric analysis (Cochran's Test) thus were analysed using nested ANOVA (GMAV5 software) to investigate the effects of species (*P. perna* or *M. galloprovincialis*, fixed factor) and time (12 months, fixed factor) on attachment strength with habitat (bays or open coast, fixed factor), sites nested within habitat (random factor) and locations nested within sites (random factor). All statistical interactions were considered in the analysis.

Reproductive condition

Because reproductive effort is strongly linked to size in mussels, we restricted ourselves to animals of a narrow size range. The wet mantle was dissected from each mussel (shell length 3.5–4.5 cm; $n = 25$ each month for each species at each location) and both body and mantle were dried at 60°C to a constant weight. Samples were weighed to the nearest 0.001 g and Gonad Index (GI) was then calculated as the dry mantle weight divided by the dry body weight (Carrington 2002a). For the cross-correlations (see below) seasonal fluctuations were used in the analysis. For the comparison between species in the two habitats only peaks of GI were used because the aim was to compare maximum reproductive output rather than fluctuations of gonad tissue development. These peaks occurred in January 2007 for both species. These values fulfilled the pre-requisites for parametric analysis (Cochran's Test) and were analysed using nested ANOVA (GMAV5 software) to investigate the effects of species (*P. perna* or *M. galloprovincialis*, fixed factor) on maximum GI with habitat (bays or open coast, fixed factor), sites nested within habitat (random factor), locations nested within sites (random factor). All statistical interactions were considered in the analysis.

Mortality

At each site, digital pictures of 12 quadrats (20 × 20 cm) were taken monthly, and new quadrats were selected each month (i. e. each quadrat was photographed twice only). In each quadrat, 20 individual mussels were identified and mortality was estimated every month as disappearance or death of identified individuals between consecutive photographs. Data were analysed as for attachment strength,

Fig. 1 Diagram of the study design

with mortality as the dependent factor. Note that because mortality is based on differences between successive months, the number of time period is one less than attachment strength and GI (i. e. from December 2006 to October 2007).

Environmental factors

Seasonal sand depth

Digital photographs of mussel beds populating vertical rocks were taken every month at four locations 200 m apart at each of the four sites (Plettenberg Bay, Robberg, Algoa Bay, Cape Recife). Seasonal sand depth was determined by analysing digital images of 3 m wide transects running c. 15 m horizontally across a vertical rock face at each site. Sand depth tended to be uniform across the vertical width of each transect and the lowest level recorded was the benchmark from which all other levels were measured. The data fulfilled the pre-requisites for parametric analysis (Cochran's Test) and were analysed using nested ANOVA (GMAV5 software) to investigate the effects of habitat (bays or open coast, fixed factor) and time (12 months, fixed factor) on sand depth, with sites nested within habitat (random factor). All statistical interactions were considered in the analysis.

Off-shore wave heights

Off-shore wave heights were obtained from a virtual buoy located at 34°51'S, 23°53'E, as recorded by the USA National Data Buoy Centre (www.ndbc.noaa.gov). A virtual buoy gives a wave model prediction based on a real buoy report. Wave height, wave direction, wave period, wind speed and wind

direction were extracted from the NOAA WAVEWATCH III model (Tolman 1999). Estimated mean daily wave heights were calculated from hourly values and then used to calculate mean monthly values.

Cross-correlation analyses

Mean attachment strengths of *M. galloprovincialis* and *P. perna* were cross-correlated with GI, using GI as the lagged variable. Wave forces were cross-correlated with mean attachment strengths of each species, using attachment strength as the lagged variable. Mortality rates of each species were cross-correlated with seasonal sand elevation and wave force, using mortality as the lagged variable. Cross-correlations had a lag interval of 1 month and were performed with the computer program Statistica 7. Seasonal bay and open coast wave force data were obtained by converting offshore wave height values according to the regression equation derived in Nicastro et al. (2008).

Results

Physiological parameters

Attachment strength

Perna perna consistently had significantly higher attachment strengths than *Mytilus galloprovincialis*, with attachment strength always being higher on the open coast for both species (Fig. 2a). There were two three-way interactions between time and species \times site (habitat) or species \times location (habitat, site) because the degree of difference between species changed through time at some locations and at some sites ($P < 0.01$ and $P < 0.05$, respectively).

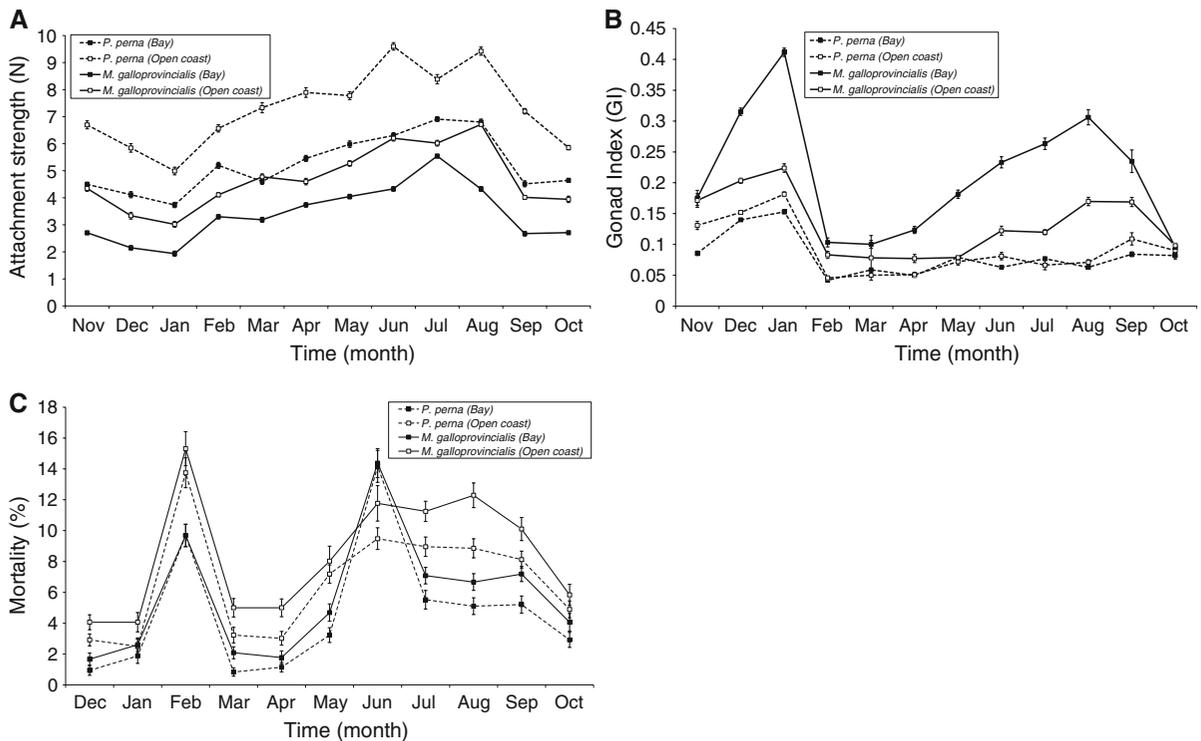


Fig. 2 Physiological parameters from November 2006 to October 2007 of *P. perna* and *M. galloprovincialis* in bay and open coast habitats: **a** mean (\pm SE of sites) monthly

attachment strength, **b** mean (\pm SE of sites) monthly gonad index (GI), **c** mean (\pm SE of sites) monthly percentage mortality rates

Reproductive condition

While in bays *M. galloprovincialis* had a significantly higher (64%; Fig. 2b) maximum GI than *P. perna*, the difference between species was not significant on the open coast (species \times habitat, $P < 0.01$). There was also a species \times location (site, habitat) interaction because at one location on the open coast maximum GI for *M. galloprovincialis* $>$ *P. perna* ($P < 0.05$).

M. galloprovincialis had two spawning events. The highest GI values were reached in January followed by a sudden decrease indicating strong summer spawning. A weaker, more protracted spawning event was observed in spring between August and October. There was only a single clear spawning event in summer for *P. perna*, with maximum gonad index values in January followed by spawning till February.

Mortality

M. galloprovincialis mortality rates were higher than those of *P. perna* ($P < 0.01$; Fig. 3c).

There was a significant time \times habitat interaction ($P < 0.05$). In general, the open coast locations had higher monthly mussel mortality rates than bays but in June this pattern was reversed and in January no differences between habitats were recorded. A time \times location (habitat, site) interaction is explained by location differences recorded in December, March, September and October ($P < 0.001$).

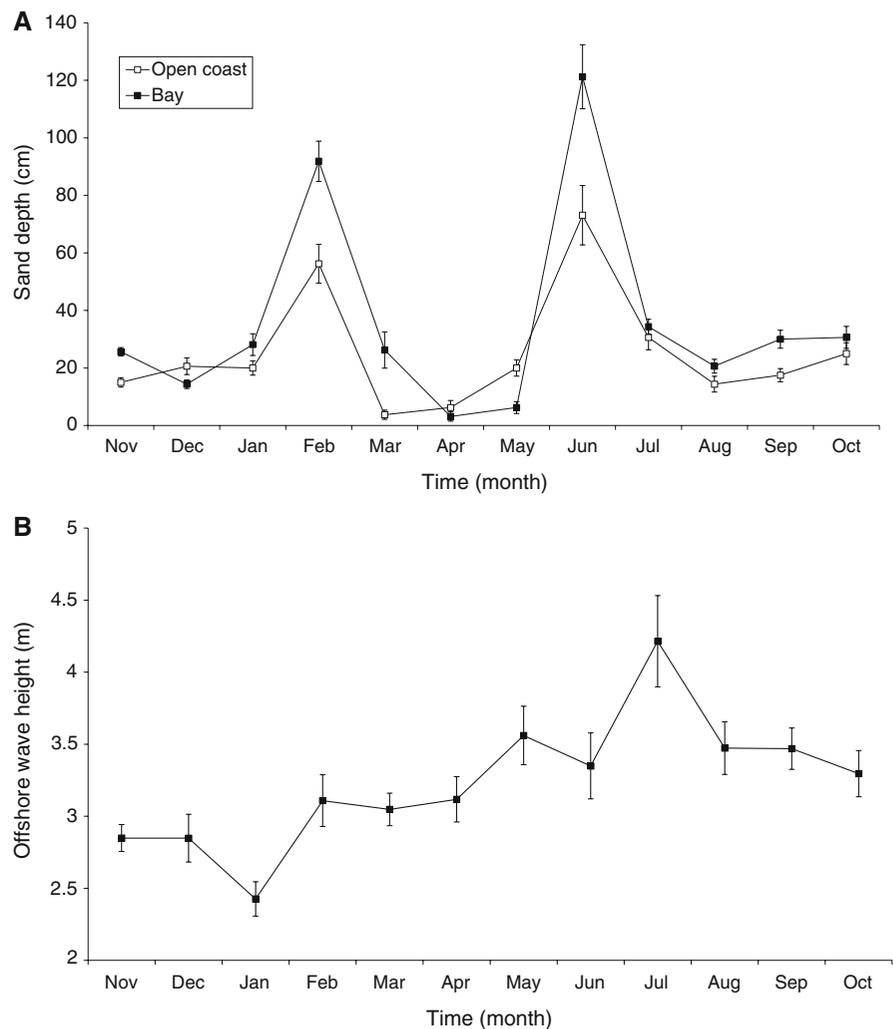
In bays, two peaks in mortality occurred at the end of summer (February) and in winter (June), with much lower rates for the rest of the year. On the open coast there was a peak in mortality again in late summer (February), but no such peak in June. Instead there was a protracted period of relatively high mortality over winter/spring (June–October).

Environmental parameters

Seasonal sand depth

In February and in June, bays had a significantly greater range between maximum and minimum sand

Fig. 3 Environmental parameters from November 2006 to October 2007: **a** mean (\pm SE of sites) monthly sand depth in bay and open coast habitats; **b** mean (\pm SE of sites) monthly offshore wave height, data from a virtual buoy located at 34°51'S, 23°53'E, as predicted by the USA National Data Buoy Centre (www.ndbc.noaa.gov)



depth than did the open coast ($P < 0.01$; Fig. 3a). There was a time \times site (habitat) interaction due to high variability among sites for 9 out of 11 months ($P < 0.05$). In both habitats, sand accumulation increased towards the end of summer (February) and the beginning of winter (June), followed by massive removal in the subsequent months. Sand levels then remained low through spring/early summer and autumn. The lowest sand level ($y = 0$) occurred in March for the open coast and in April in bays and fluctuation of sand coverage showed mean vertical changes of up to 122 cm.

Wave force measurements

Mean monthly offshore wave height increased in late autumn–winter with a peak in July, and decreased in

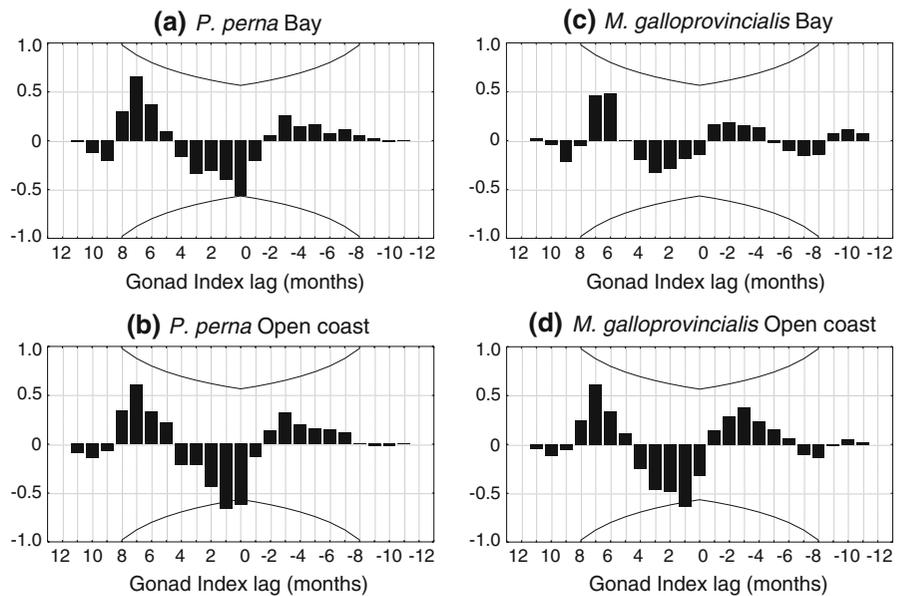
spring and summer with a minimum in January (Fig. 3b).

Cross-correlation analyses

No significant correlation was observed between attachment strength and GI for bays, but there was a significant negative correlation on the open coast for both species where GI coincided with attachment strength or preceded it by 1 month (lag = +1 for *M. galloprovincialis* and lag = +1 and 0 for *P. perna*; Fig. 4).

For both species, significant positive correlations between attachment strength and wave force were observed at lags of zero and +1 in the bays and at lags of zero and ± 1 on the open coast (Fig. 5). This means that, depending on the habitat, the highest

Fig. 4 Cross-correlation analyses of monthly mean attachment strength with monthly mean gonad index for **a** *P. perna* in bays, **b** *P. perna* open coast and **c** *M. galloprovincialis* in bays, **d** *M. galloprovincialis* open coast. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation. A positive lag indicates that the highest correlation between the two variables occurs when the lagged variable GI precedes attachment strength in time



correlations between attachment strength and wave action occur with no lag (lag = 0), so that they are in phase, or with a lag of plus or minus 1 month (lag = +1 or -1) so that one follows the other by 1 month.

Significant positive correlations between mortality rates and sand elevation were observed at zero lag for both species in both habitats, but with a higher correlation at bay sites (Fig. 6), meaning that maximum mortality occurs as sand accumulates.

No significant correlations between mortality rates and wave force were observed on the open coast, but there was a significant positive correlation in bays for both species when mortality rates preceded wave force by 1 month (lag = +1; Fig. 7).

Discussion

Environmental heterogeneity challenges invasive and native coexisting species and can alter the exploitative ability of the invader (Melbourne et al. 2007). Here, we show that physiological performances of co-existing mussels are affected by spatial and temporal fluctuations of environmental conditions. Because these species respond differently to abiotic stresses, the invasiveness of *Mytilus galloprovincialis* and thus the outcomes of interactions between the two mussels are likely to vary along environmental gradients.

Previous studies have described *M. galloprovincialis* and *Perna perna* as species with different evolutionary strategies. *M. galloprovincialis* emphasises reproduction over attachment strength, and adopts a more dynamic response to disturbance, seeking aggregation or a safer arrangement as a mechanism of coping with hydrodynamic stress. In contrast, *P. perna* has higher attachment strength at the expense of lower reproductive output (van Erkom Schurink and Griffiths 1991; Harris et al. 1998; Zardi et al. 2007). Interestingly, our results only partially confirm these findings. Previous findings show that GI in both species is proportionate to the number of eggs, so that a higher GI value indicates greater egg production (Zardi et al. 2007). While in bay habitats the maximum GI of *M. galloprovincialis* was 64% higher than that of *P. perna*, on the open coast, maximum values for GI were not significantly different between the two species. *M. galloprovincialis* has a second spawning peak in August, however, the strong negative effect of a more stressful environment is evident in both spawning peaks. Attachment strength also varied spatially, mirroring the degree of wave action (see Nicastro et al. 2008 for measurements of maximum wave force at these sites), with higher values on the open coast than at bay sites for both species, and higher values for the indigenous species than *M. galloprovincialis*. The open coast habitat reduces *M. galloprovincialis*' traits of high fecundity probably because of the need

Fig. 5 Cross-correlation analyses of monthly mean wave force with monthly mean attachment strength for **a** *P. perna* in bays, **b** *P. perna* open coast and **c** *M. galloprovincialis* in bays, **d** *M. galloprovincialis* open coast. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation. A positive lag indicates that the highest correlation between the two variables occurs when the lagged variable attachment strength precedes wave force in time

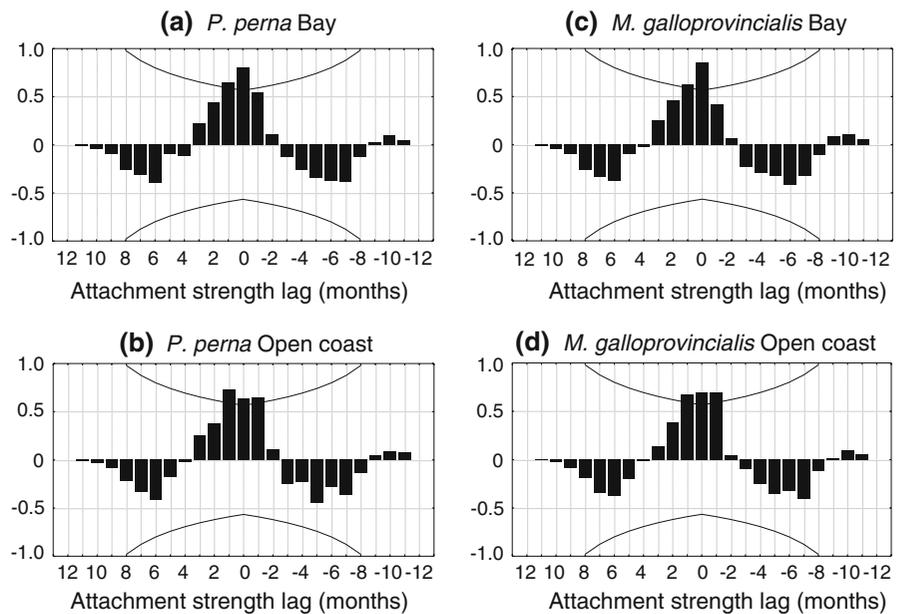
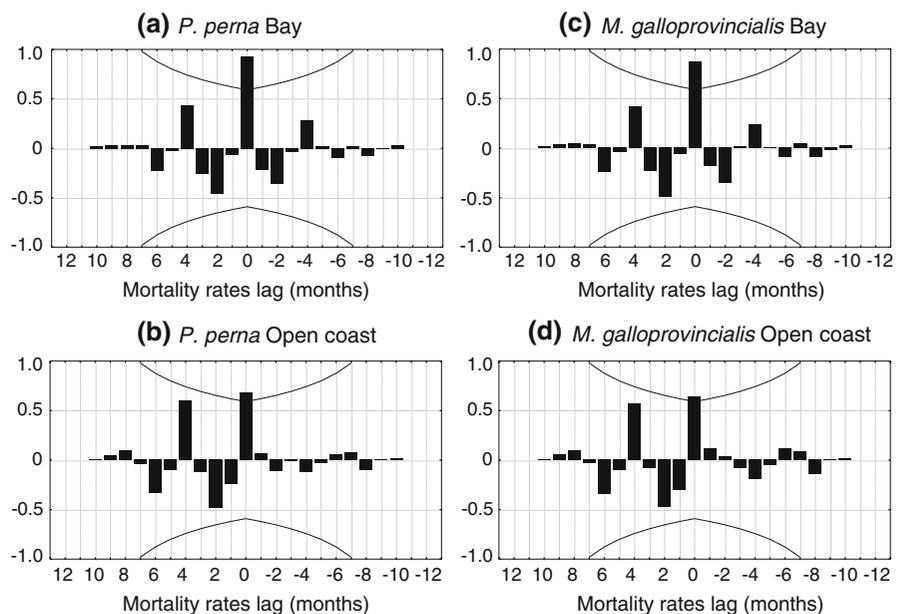


Fig. 6 Cross-correlation analyses of monthly mean mortality rates with monthly mean sand depth for **a** *P. perna* in bays, **b** *P. perna* open coast and **c** *M. galloprovincialis* in bays, **d** *M. galloprovincialis* open coast. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation. A positive lag indicates that the highest correlation between the two variables occurs when the lagged variable mortality precedes sand depth in time



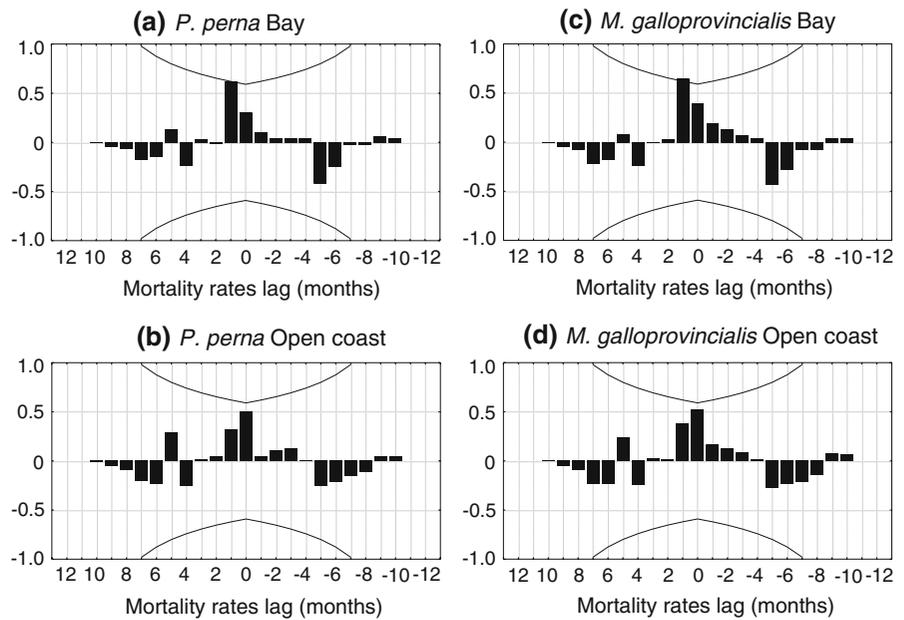
to channel energy into attachment strength. Thus gonad development of the invasive species is affected by coastal topography, while the spawning rate of the indigenous species is preserved. Therefore abiotic stress in the form of wave action appears to reduce the ability of *M. galloprovincialis* to be invasive as it loses its advantage over the native species in terms of reproductive output.

This correlates well with the observation of von der Meden et al. (2008) that the two species have

significantly greater % cover within bays than on the open coast, and the effect of bay is stronger for *M. galloprovincialis* than for *P. perna*.

Besides spatial disparities, attachment strength also showed strong temporal variation, generally decreasing in summer and increasing in winter, and was strongly positively correlated (with little lag) with seasonal fluctuations in wave force in the two habitats. While this appears to be yet another manifestation of the ability of mussels to sense and

Fig. 7 Cross-correlation analyses of monthly mean mortality rates with wave force for **a** *P. perna* in bays, **b** *P. perna* open coast and **c** *M. galloprovincialis* in bays, **d** *M. galloprovincialis* open coast. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation. A positive lag indicates that the highest correlation between the two variables occurs when the lagged variable mortality precedes wave force in time



respond to their flow environment, they are not always precise in their response, for example low attachment strength values relative to wave height were observed in September and October 2007 and it is well known that other factors affect the strength of attachment. These include sea surface temperature, food supply, predator cues, endolithic infestation and the molecular structure of the byssus (Lucas et al. 2002; Ishida and Iwasaki 2003; Moeser et al. 2006; Babarro et al. 2008, Zardi et al. 2009). For example, a previous study at Plettenberg Bay (Zardi et al. 2007) showed that the attachment strength of both *M. galloprovincialis* and *P. perna* is negatively correlated with sea surface temperature. In addition, rocky shores are regularly and extensively inundated by sand increasing the amount of sediment (sand, shell fragments etc.) within a mussel bed and making the substratum less stable and mussels more prone to dislodgement (Zardi et al. 2008). The hydrodynamic stress experienced by intertidal organisms depends partly on their shape (Denny 1995). Previous studies on the west coast of South Africa showed that the shell of *M. galloprovincialis* tends to be lower and narrower at exposed sites, perhaps reducing the effect of hydrodynamic forces (Steffani and Branch 2003). It is possible that this allows mussel populations on the open coast to reduce higher hydrodynamic stress. However, regardless of intraspecific differences in

shell shape, our data showed that mortality rates are higher on the open coast than in bays.

At bay sites, there was no correlation between GI and attachment strength for either species. This lack of correlation suggests that the relatively low hydrodynamic stress in bays allows mussels to invest less energy in attaching to the substratum and to maintain high levels of GI and survival simultaneously. In contrast, on the open coast, GI was negatively correlated with attachment strength at a lag of +1 and (only for *P. perna*) with zero lag, indicating that, for both species, attachment strength was high when, or 1 month after, GI was low. Alternatively, high GI coincided with or preceded (*P. perna*) low attachment strength. Note that the analysis refers to correlations between attachment strength and GI, which appear despite the effects of other energetically demanding factors such as shell growth, which may also show seasonality (Griffiths and King 1979). Thus, major spawning events occurred during periods of low wave action, when limited investment was required in attachment strength. In addition, the minor spawning for *M. galloprovincialis* coincided with periods of intense wave action and very high attachment strength. Hence, it seems that channelling more energy into attachment strength limits gonad tissue development, indirectly supporting the concept of trade off between reproduction and attachment

strength (Carrington 2002a, b; Moeser et al. 2006; Zardi et al. 2007). Moeser and Carrington (2006) found that seasonal variation in attachment strength is not related to increased thread production in response to hydrodynamic stress, and that the material properties of byssal threads and thread decay rates could be determinants of attachment strengths; whatever the mechanism a trade off between gamete production and attachment strength is always maintained. However, this is not true for *Mytilus edulis* in suspended culture (Lachance et al. 2008). Intertidal mussels experience a more heterogeneous environment than when cultured in suspension especially in terms of temperature, food availability and hydrodynamic stress. Differences in environmental conditions could explain these contrasting results.

Wave action (Nicastró et al. 2008) and sand fluctuation are greater on the open coast and in bays, respectively. Cross-correlations between mortality rates and sand elevation showed a high positive correlation at bay sites, indicating that sand inundation is a major stress affecting survival in mussel populations in bays. The lag period here was zero, underlining the immediate effects of sand, as mortality and sand accumulation peaked simultaneously. Although wave induced hydrodynamic stress often plays a crucial role in regulating mortality rates of intertidal organisms, the correlation between wave action and mortality rates of *P. perna* and *M. galloprovincialis* was very weak in bay habitats and non-significant on the open coast. Probably, this was due to the masking effect of sand stress. Our results show that these two stresses operate out of phase with one another. In particular, in February sand level was extremely high, coinciding with periods of relatively low wave action. Consequently, a sand-induced peak in mortality decreases the correlation between wave and mortality. In addition, wave stress is more prolonged over the year and is usually characterized by a relatively gradual seasonal increase. Contrary to sand stress, mussels have the potential to adapt to higher wave action by increasing their attachment to the substratum. This could also form part of the explanation for mortality being less well correlated to wave force than to sand stress. It is also possible that mussels on the open coast adjust to the continuously intense hydrodynamic stress typical of this habitat, giving them higher resistance to sudden increases in wave action during storms. Thus,

the consequence of chronically higher wave action is a reduction in gonad output for *M. galloprovincialis*, rather than mortality. Unexpectedly, in February, despite greater sand accumulation in bays, more mussels died on the open coast. Carrington (2002a) showed that *M. edulis* on Rhode Island shores is slow to build up attachment strength following summer, perhaps due to energetic constraints on thread production during the reproductive season. Waves of equivalent magnitude arriving later in the storm season pose less risk of dislodgment because attachment strength steadily increases. In our study, the effect of greater wave action on the open coast could have been further enhanced by the concurrent sand inundation and a sudden increase in hydrodynamic stress acting on mussels weakened by a major spawning event in January. Regardless of the causes, the high mortality rates experienced by mussel populations on the open coast increase population turnover rates in this habitat, freeing space for new colonizers and allowing more frequent and intense gene pool replenishment (Nicastró et al. 2008).

To become a successful invader, an introduced species must have some advantage over an indigenous species, at least at particular times or places, or in a certain life-history trait, such as colonising ability (Shea and Chesson 2002; Hastings et al. 2005). A high reproductive output (van Erkom Schurink and Griffiths 1991; Harris et al. 1998; Zardi et al. 2007), together with fast growth (Griffiths et al. 1992; Hockey and van Erkom Schurink 1992) and the capacity to colonise free space very rapidly, make *M. galloprovincialis* a very strong competitor in terms of re-colonization of free space (Erlandsson et al. 2006). However, disturbance often prevents local competitive exclusion by dominant competitors because species usually exhibit trade-offs between competitive ability and colonization ability or between competitive ability and stress tolerance (Wilson 1984; Petraitis et al. 1989; Chesson and Huntly 1997). Our results partially confirm the initial hypotheses. *P. perna* is attached to the substratum more strongly than *M. galloprovincialis*. In both species, strength of attachment fluctuates spatially and during the year in response to wave action changes. However, probably because of the confounding effect of other environmental stressors (especially sand accumulation) a significant correlation between hydrodynamic stress and mortality rates

was not observed. In addition, our results show that the reproductive output of *M. galloprovincialis* is generally lower on the open coast than in bays, and that on the open coast maximum GI values for the two species are not significantly different. Less stressful conditions in terms of wave action in bay habitats (Nicastro et al. 2008), allows *M. galloprovincialis* to maintain a low strength of attachment and invest more energy in gonad development.

The observed inter- and intra-specific differences in responses to the environment stress highlight the need of *M. galloprovincialis* and *P. perna* to optimize resource allocation and help explain patterns of adult abundance in these two habitats (von der Meden et al. 2008). This study shows that, by observing the responses of coexisting species to a wide range of environmental conditions, it is possible to identify characteristic differences in relative performance and ecological plasticity which are known to be crucial factors in dynamics of coexistence between competing indigenous and invasive species (Davis et al. 2000; Mack et al. 2000; Pranovi et al. 2006).

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References

- Babarro JMF, Fernandez-Reiriz MJ, Labarta U (2008) Secretion of byssal threads and attachment strength of *Mytilus galloprovincialis*: the influence of size and food availability. *J Mar Biol Assoc UK* 88:783–791
- Baker HG (1986) Patterns of plant invasion in North America. In: Mooney HA, Drake JA (eds) *Ecology of biological invasions of North America and Hawaii*. Springer, New York, pp 44–57
- Bownes S, McQuaid CD (2006) Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa? *J Exp Mar Biol Ecol* 338:140–151
- Broom DM, Johnsen KG (1993) *Stress and animal welfare*. Chapman & Hall, New York
- Buchanan KL (2000) Stress and the evolution of condition-dependent signals. *Trends Ecol Evol* 15:156–160
- Byers JE (2002) Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* 130:146–156
- Carrington E (2002a) Seasonal variation in the attachment strength of the blue mussel: causes and consequences. *Limnol Oceanogr* 47:1723–1733
- Carrington E (2002b) The ecomechanics of mussel attachment: from molecules to ecosystems. *Integr Comp Biol* 42:846–852
- Chesson P (1994) Multispecies competition in variable environment. *Theor Popul Biol* 45:227–276
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Chesson P, Huntly N (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* 150:519–553
- Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett STA, White PS (eds) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, pp 125–151
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- Denny MW (1995) Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol Monogr* 65:371–418
- Denny MW, Wethey D (2000) Physical processes that generate patterns in marine communities. Chapter 1. In: Bertness M, Hay M, Gaines S (eds) *Marine community ecology*. Sinauer Press, NY
- Denny MW, Miller LP, Stokes MD, Hunt LJH, Helmuth BST (2003) Extreme water velocities: topographical amplification of wave-induced flow in the surf zone of rocky shores. *Limnol Oceanogr* 48:1–8
- Deviny JS, Volsse LA (1978) Effect of sediments on the development of *Macrocystis pyrifera* gametophytes. *Mar Biol* 48:343–348
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends Ecol Evol* 14:135–139
- Erlandsson J, Pal P, McQuaid CD (2006) Re-colonisation rate differs between co-existing indigenous and invasive intertidal mussels following major disturbance. *Mar Ecol Prog Ser* 320:169–176
- Gaylord B, Blanchette CA, Denny MW (1994) Mechanical consequences of size in wave-swept algae. *Ecol Monogr* 64:287–813
- Gerlach JD, Rice KJ (2003) Testing life history correlates of invasiveness using congeneric plant species. *Ecol Appl* 13:167–179
- Griffiths CL, King JA (1979) Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. *Mar Biol* 53:217–222
- 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
- Hanekom N (2008) Invasion of an indigenous *Perna perna* mussel bed on the south coast of South Africa by an alien mussel *Mytilus galloprovincialis* and its effect on the associated fauna. *Biol Inv* 10:233–244
- Harris JM, Branch GM, Elliott BL, Currie B, Dye AH, McQuaid CD, Tomalin BJ, Velasquez C (1998) Spatial an

- temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *S Afr J Zool* 33:1–11
- Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A et al (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecol Lett* 8:91–101
- Hawkins AJS, Bayne BL (1985) Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*: budgets, conversion efficiencies and maintenance requirements. *Mar Ecol Prog Ser* 25:181–188
- Hockey PAR, Van Erkom Schurink C (1992) The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Trans R Soc S Afr* 48:123–139
- Hu SS, Tessier AJ (1995) Seasonal succession and the strength of intra- and interspecific competition in a *Daphnia* assemblage. *Ecology* 76:2278–2294
- Ishida S, Iwasaki K (2003) Reduced byssal thread production and movement by the intertidal mussel *Hormomya mutabilis* in response to effluent from predators. *J Ethol* 21:117–122
- Lachance AA, Myrand B, Tremblay R, Koutitonsky V, Carrington E (2008) Biotic and abiotic influences on the attachment strength of blue mussels (*Mytilus edulis*) from suspended culture. *Aquat Biol* 2:119–129
- Leicht-Young SA, Silander JA Jr, Latimer AM (2007) Comparative performance of invasive and native *Celastrus* species across environmental gradients. *Oecologia* 154:273–282
- Levins R (1968) Evolution in changing environments. Princeton University Press, Princeton
- Lucas JM, Vaccaro E, Waite JH (2002) A molecular, morphometric and mechanical comparison of the structural elements of byssus from *Mytilus edulis* and *Mytilus galloprovincialis*. *J Exp Biol* 205:1807–1817
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- 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
- McQuaid CD, Branch GM (1985) Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Mar Ecol Prog Ser* 22:153–161
- Melbourne BA, Cornell HA, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol Lett* 10:77–94
- Moerer GM, Carrington E (2006) Seasonal variation in mussel byssal thread mechanics. *J Exp Biol* 209:1996–2003
- Moerer GM, Leba H, Carrington E (2006) Seasonal influence of wave action on thread production in *Mytilus edulis*. *J Exp Biol* 209:881–890
- Nicastro KR, Zardi GI, McQuaid CD, Teske PR, Barker NP (2008) Coastal topography drives genetic structure in marine mussels. *Mar Ecol Prog Ser* 368:189–195
- Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol Monogr* 51:145–178
- Petes LE, Menge BA, Murphy GD (2007) Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *J Exp Mar Biol Ecol* 351:83–91
- Petraitis PS, Latham RE, Niesenbaum RA (1989) The maintenance of species diversity by disturbance. *Q Rev Biol* 64:393–418
- Pranovi F, Franceschini G, Casale M, Zucchetto M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: the Manila clam in the Venice Lagoon. *Biol Inv* 8:595–609
- Robinson TB, Griffiths CL, McQuaid CD, Rius M (2005) Marine alien species of South Africa—status and impacts. *S Afr J Mar Sci* 27:297–306
- Sapolsky RM (1992) Neuroendocrinology of the stress response. In: Becker JB, Breedlove SM, Crews D (eds) Behavioral endocrinology. Massachusetts Institute of Technology Press, Cambridge, pp 287–324
- Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling EG (ed) The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier, New York, pp 87–169
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Sheley RL, Olson BE, Larson LL (1997) Effect of weed seed rate and grass defoliation level on diffuse knapweed. *J Range Manage* 50:39–43
- Sousa WP (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines S, Hay ME (eds) Marine community ecology. Sinauer Assoc., Sunderland, pp 85–130
- Steffani CN, Branch GM (2003) Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Mar Ecol Prog Ser* 246:197–209
- Tolman HL (1999) User manual and system documentation of WAVEWATCH-III version 1.18. NOAA/NWS/NCEO/OMB technical note 166, pp 110
- 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
- von der Meden CEO, Porro F, Erlandsson J, McQuaid CD (2008) Coastline topography affects the distribution of indigenous and invasive mussels. *Mar Ecol Prog Ser* 372:135–145
- Wilson JB (1984) The intermediate disturbance hypothesis of species coexistence is based on patch dynamics. *N Zeal J Ecol* 18:176–181
- Zardi GI, Nicastro KR, McQuaid CD, Rius M, Porri F (2006a) Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. *Mar Biol* 150:78–88
- Zardi GI, Nicastro KR, Porri F, McQuaid CD (2006b) Sand stress as a non-determinant of habitat segregation of indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels in South Africa. *Mar Biol* 148:1031–1038
- Zardi GI, McQuaid CD, Nicastro KR (2007) Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous

Perna perna and invasive *Mytilus galloprovincialis* mussels. Mar Ecol Prog Ser 334:155–163

Zardi GI, Nicastro KR, McQuaid CD, Erlansson J (2008) Sand and wave induced mortality in invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels. Mar Biol 153:853–858

Zardi GI, Nicastro KR, McQuaid CD, Gektidis M (2009) Effects of endolithic parasitism on invasive and indigenous mussels in a variable physical environment. PloS ONE 4:e6560