Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels

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ABSTRACT: The indigenous mussel *Perna perna* and the invasive mussel *Mytilus galloprovincialis* coexist on the low shore of the South African south coast, with partial habitat partitioning. *P. perna* dominates the lower mussel zone, where hydrodynamic stress is higher than in the high mussel zone, where *M. galloprovincialis* dominates. Attachment strength and gonad maturation are highly demanding processes in terms of energy, the former allowing mussels to withstand wave forces, while the latter contributes to recruitment rates. During an 18 mo study, both biological parameters fluctuated seasonally. The invasive and the indigenous species spawned in different periods; gamete maturation was positively correlated with sea surface temperature only for *P. perna*. For both species, attachment strength was negatively correlated with sea surface temperature, but increased in response to wave action through the production of more and thicker threads. Peaks in attachment strength coincided with periods of relatively low gamete production for both species, suggesting that mussels cannot afford to invest simultaneously in both processes. *P. perna* attachment strength was always significantly higher than that of *M. galloprovincialis*, while the latter had a greater reproductive output. We suggest that, although high gamete production improves the ability of *M. galloprovincialis* to colonise free space, it may energetically limit its capacity to invade wave exposed shores.

KEY WORDS: Attachment strength · Reproductive output · Invasive · *Mytilus galloprovincialis* · *Perna perna*

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INTRODUCTION

Wave generated hydrodynamic stress is often the main disturbance factor influencing intertidal communities (e.g. Gaylord et al. 1994, Denny 1995). The ability of an organism to resist the water motion produced by waves is a prerequisite for life in wave-swept environments, and if an organism experiences a force that exceeds its strength of attachment, it will be dislodged. Waves not only dislodge organisms; they can also regulate the supply of food or propagules, playing a crucial role in modelling the structure and dynamics of many intertidal communities (e.g. Paine & Levin 1981,

Sousa 1985). Indeed, the vertical distribution of intertidal community biomass and the trophic composition of that biomass are strongly influenced by wave action (McQuaid & Branch 1985). Wave action can particularly influence filter-feeders, which are often important space-occupiers that influence overall biodiversity by providing niches and increasing spatial complexity.

Mussels are often the major occupiers of primary space on rocky intertidal shores (Seed & Suchanek 1992) and waves can be the major cause of mussel dislodgment (Paine & Levin 1981). Mussels attach firmly to the substratum and to each other by mean of the byssus, an extracellular bunch of collagenous threads,

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secreted in the ventral groove of the foot (Waite 1992). The invasive *Mytilus galloprovincialis* and indigenous *Perna perna* are the 2 dominant mussel species on South African rocky shores. On the south coast of South Africa, the 2 species coexist on the low shore (referred to here as the mussel zone). The upper and the lower areas of the mussel zone are dominated by *M. galloprovincialis* and *P. perna*, respectively, while the 2 species overlap in the mid-mussel zone (Hockey & van Erkom Schurink 1992, Robinson et al. 2005). Hydrodynamic forces affect these 2 species by increasing their growth rates at exposed sites; in addition, *M. galloprovincialis* individuals experiencing high hydrodynamic stress tend to increase shell thickness (Steffani & Branch 2003). Several studies have related differences in the strength of byssal attachment for co-existing mussel species to their preferred flow environment, and generally strong attachment contributes to ecological success on shores subjected to high wave action (e.g. Gardner & Skibinski 1991, Bell & Gosline 1997, Hunt & Scheibling 2001). Zardi et al. (2006b) showed that *P. perna* has a stronger byssal attachment than *M. galloprovincialis* due to the presence of more and thicker threads, and that hydrodynamic stress could be a determinant in the vertical zonation of the 2 species, relegating the less strongly attached *M. galloprovincialis* to the higher mussel zones, where water action is less strong. Interference competition with *P. perna* also contributes to the exclusion of *M. galloprovincialis* from the low shore (Rius & McQuaid 2006b) and the benefit of being more firmly attached to the substratum is especially visible when mussels are subjected to strong winter storms (Zardi et al. 2006b). In addition, the greater tolerance to desiccation of *M. galloprovincialis* could allow this species to colonise the upper mussel zone where the indigenous species is not able to compete (Hockey & van Erkom Schurink 1992).

Mussel attachment strength responds to spatial and temporal variations in flow; it is correlated with seasonal fluctuations in wave action and increases in winter (Hunt & Scheibling 2001, Carrington 2002). Mussels adjust their attachment strength by varying both the number and the thickness of byssal threads (Bell & Gosline 1997, Carrington 2002, Zardi et al. 2006b). However, Moeser et al. (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. The process of byssal thread production can be energetically expensive, forming 8 to 15% of a mussel's monthly energy expenditure (e.g. Griffiths & King 1979). Reproduction is also energetically expensive and reproductive condition varies season-

ally, usually mirroring temporal fluctuations of sea surface temperature (Seed & Suchanek 1992, Carrington 2002). During gonad development, mussels are subjected to a very high energetic effort, investing up to 90% of their energy budget in gamete production (Seed & Suchanek 1992). Consequently, thread production can be energetically constrained during the reproductive season, making mussels more vulnerable to wave action and thus increasing the risk of dislodgment (Carrington 2002).

The European mussel *Mytilus galloprovincialis* is invasive worldwide and is the most successful invasive marine species in South Africa (Robinson et al. 2005). It has many hallmarks of both a strong competitor and of an opportunistic species. These include rapid growth rate over a range of water temperatures (Griffiths et al. 1992, Hockey & van Erkom Schurink 1992), and resistance to desiccation (Hockey & van Erkom Schurink 1992), parasites (Calvo-Ugarteburu & McQuaid 1998) and sand stress (Zardi et al. 2006a). The invasion of this species on the west coast of South Africa has had major consequences for the overall intertidal community structure, including the elimination of the previously dominant indigenous mussel *Aulacomya ater*. Moreover, it has a very high reproductive capacity, with a total annual output between 20 and 200% greater than that of South African indigenous species, that can result in recruit densities of up to 20000 per 100 cm^2 (van Erkom Schurink & Griffiths 1991, Harris et al. 1998).

Here, we examine attachment strength fluctuations of 2 co-existing mussels, *Mytilus galloprovincialis* and *Perna perna*, and relate them to variations in the hydrodynamic environment and reproductive condition. Thus we tested the hypotheses that (1) strength of attachment is correlated with wave action and is reflected by byssal thread production and (2) strength of attachment is negatively correlated with reproductive effort. The results are discussed in the context of different evolutionary strategies used by the invasive and the indigenous species.

MATERIALS AND METHODS

Mussels were collected monthly between May 2003 and October 2004 from a granite shore in Plettenberg Bay (34° 05′ S, 23° 19′ E), on the south coast of South Africa. The sampling area was small (approximately 20 m^2) and topographically uniform, so all mussels were assumed to be exposed to similar abiotic factors. Samples included only mussels living within a mono-layered bed from the mid-mussel zone.

Attachment strength and reproductive condition. *Mytilus galloprovincialis* and *Perna perna* individuals

(3.5 to 4.5 cm shell length; n = 20 each month for each species) were tested *in situ* for attachment strength (Denny 1987, Bell & Gosline 1997). A 2 mm diameter hole was carefully drilled through the shell valves close to the posterior margin without damaging any byssal threads. A fishhook was inserted through the hole and connected to a recording spring scale via a fishing line. Mussels living within a mussel bed are mainly subjected to lift forces, which act perpendicularly to the substratum (Denny 1987), thus the scale was lifted normal to the rock surface until dislodgment occurred (1 to 3 s) and the force required to detach each mussel was recorded in Newtons (N). All dislodged mussels were at least 20 cm from each other so that attachment strength measurements were not influenced by previous ones. The byssal threads of each dislodged mussel were counted. The diameters of the distal region of 3 randomly chosen byssal threads from each individual were measured using a dissecting microscope with a calibrated micrometer (±1 µm). In addition, the reproductive status of 20 female mussels of each species (3.5 to 4.5 cm shell length) collected at the same site was determined for each month. Reproductive condition status of the 2 sexes cannot be distinguished, therefore female is representative of both sexes (Griffiths & King 1979). A small portion (~0.1 g) of gonad tissue was cut from the middle region of the mantle lobe and fixed in Bouin's solution for histological examination; the remaining gonadal tissue and the rest of the body were dried separately to constant weight (2 d) at 60°C. The fixed gonadal tissues were then dehydrated in ascending concentrations of alcohol, washed in xylene and then embedded in paraffin. Because the reproductive tissues of *Mytilus* spp. (Lowe et al. 1982) and of *P. perna* (Ndzipa 2002) are homogenously distributed throughout the mantle, only a section (6 µm) was cut from each sample and stained with haematoxylin and eosin. A representative section through the gonad tissue was used to determine the reproductive status of each individual using a video microscope system. A grid of 64 points was drawn on the video monitor and the fraction of mantle tissue that was reproductive (mantle gamete fraction) was calculated by dividing the number of points that fell on developing or ripe eggs by the total number of points. This does not provide information on the entire gonad (i.e. gonadal material around the digestive gland is omitted), but does provide a comparative indication of reproductive status. The gonadosomatic index (GSI), a measure of reproductive condition, was calculated by multiplying the mantle gamete fraction by the total mantle dry weight and then dividing it by the dry body weight (including the mantle; Roff 1992).

Shapiro's and Levene's tests were used to assess normality and homogeneity of variances respectively.

All data failed the requirements for parametric analysis, and transformation was not successful, therefore non-parametric analysis was used.

Kruskal-Wallis tests were used to evaluate the effects of species and month on attachment strength, number of byssal threads and diameter of the distal region. For each month, data were further analysed for significant differences between the 2 species using Kruskal-Wallis tests and a post-hoc analysis with Bonferroni correction.

Oceanographic data. 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). A virtual buoy gives a wave model prediction of a buoy report. Wave heights, wave direction, wave period, wind speed and wind direction were extracted from the NOAA WAVE-WATCH III model (Tolman 1999). Estimated mean daily wave heights were calculated from hourly values and then used to calculate mean monthly values. Daily sea surface temperature (SST) data were recorded at Tsitsikamma (32° 21′ S, 26° 58′ E, approximately 70 km from the study site) by the South African Weather Service, and were used to determine mean monthly values.

Cross-correlation. Mean attachment strengths of *Mytilus galloprovincialis* and *Perna perna* were cross-correlated with wave height, GSI and SST. GSI of each species was cross-correlated with SST using the computer program Statistica 7.

RESULTS

Attachment strength and reproductive condition

Mean attachment strength varied seasonally (Fig. 1a), showing exactly the same pattern for both species. There was a rapid decrease in late winter/early spring (between August and October) and a more gradual increase in summer (beginning in December/January). Maximum attachment strength values were recorded in August 2003 (73.4 N) and in September 2004 (96.6 N) for *Mytilus galloprovincialis* and *Perna perna* respectively. The 2 species showed the weakest attachment in November 2003 (32.2 N) and in December 2003 (43.6 N) for *M. galloprovincialis* and *P. perna*, respectively. A Kruskal-Wallis test showed that *P. perna* was significantly (p < 0.0001) more strongly attached than *M. galloprovincialis*. Mean thread number followed the same seasonal pattern, decreasing between August and October and increasing between December and February (Fig. 1b). Mean thread diameter also seasonally fluctuated but lagged behind attachment strength and thread number, decreasing in
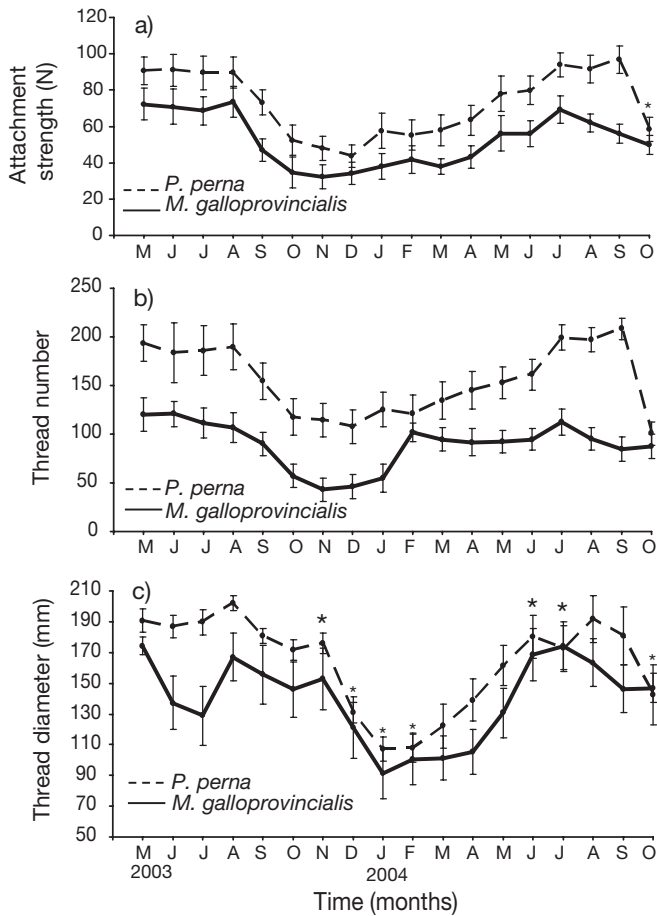
Fig. 1. *Mytilus galloprovincialis* and *Perna perna*. Physiological characteristics of *M. galloprovincialis* and *P. perna* in Plettenberg Bay, S. Africa, from May 2003 to October 2004. (a) Mean (±SD) monthly attachment strength, (b) mean (±SD) monthly thread number, (c) mean (±SD) monthly thread diameter. *: month when species **did not** differ significantly. For thread diameter: November (p = 0.0071), December (p = 0.3507), January (p = 0.0699), February (p = 0.4488), June (p = 0.0531), July (p = 0.0924) and October 2004 (p = 0.6072); for attachment strength: October 2004 (p = 0.0131)

November and reaching minimum values between January and February, with maximum values in winter and early spring (Fig. 1c). Kruskal-Wallis tests showed that *P. perna* had significantly more (42.5%) and thicker (14.4%) threads than *M. galloprovincialis* (p < 0.0001 in both cases). Statistical analysis using Kruskal-Wallis tests and Bonferroni corrected post-hoc tests (α = 0.0028) revealed that mean monthly attachment strength and thread number were significantly different between the 2 species during all months except October 2004 for attachment strength (p = 0.0131). In contrast, mean monthly thread diameter was not significantly different in November (p = 0.0071), December (p = 0.3507), January (p = 0.0699), February (p = 0.4488), June (p = 0.0531), July (p =
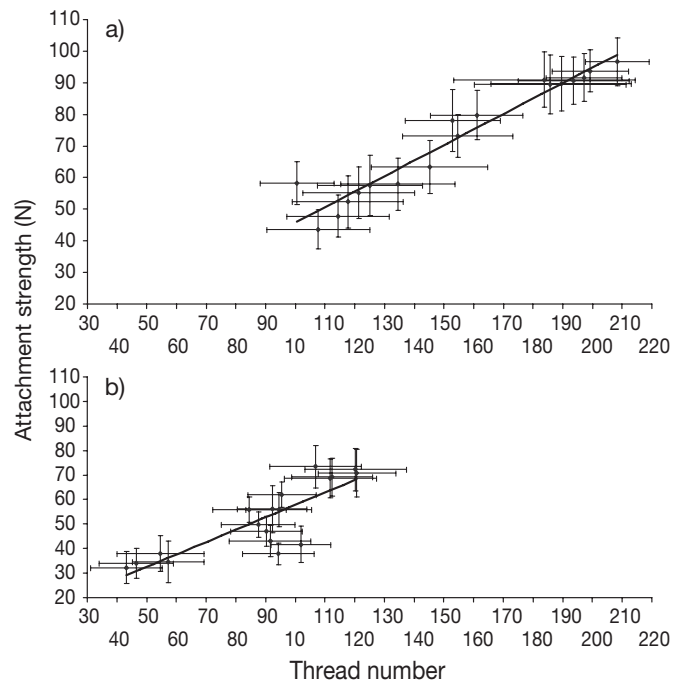

Fig. 2. *Mytilus galloprovincialis* and *Perna perna*. Correlation between mean monthly attachment strength and mean monthly threads numbers for (a) *P. perna* (p < 0.001; $y = 0.4905x - 3.3182$, $r^2 = 0.9381$) and (b) *M. galloprovincialis* (p < 0.001; $y = 0.5054x + 7.2668$, $r^2 = 0.7002$)

0.0924) and October 2004 (p = 0.6072). For each species, mean attachment strength was significantly correlated with thread number (p < 0.001; Fig. 2a,b) and diameter (p < 0.05 for *M. galloprovincialis* and p < 0.001 for *P. perna*; Fig. 3a,b), but r^2 values were much lower for *M. galloprovincialis* than for *P. perna* in both cases.

Fluctuations in gamete maturation and release showed that both *Mytilus galloprovincialis* and *Perna perna* have 2 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 (Fig. 4). Maximum GSI was much higher (60%) for *M. galloprovincialis* than for *P. perna*.

Oceanographic data

Mean monthly wave height increased in late autumn-winter and decreased in late spring with minima in summer (i.e. January, February; Fig. 5a). Mean monthly sea surface temperature showed a seasonal cycle with a peak in late summer (21.8°C, February) and 2 minima in early spring 2003 (15.6°C, September) and winter 2004 (16.2°C, July; Fig. 5b).
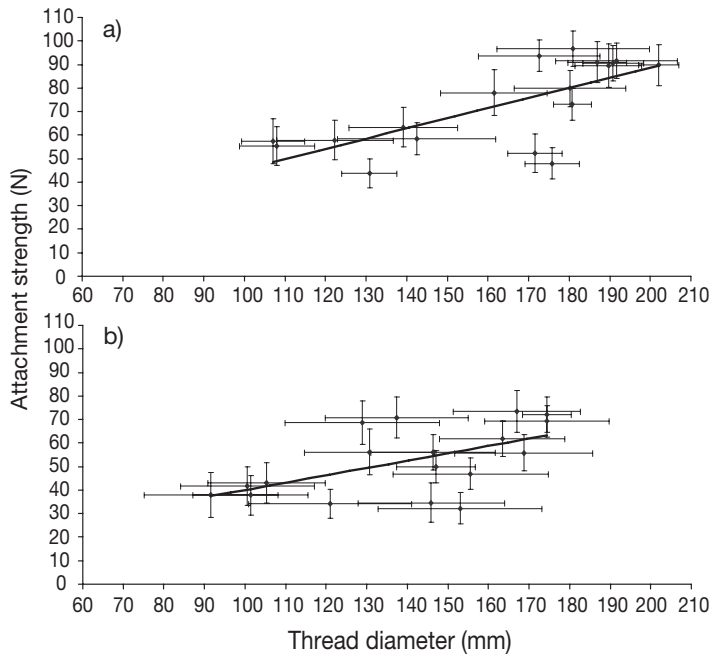
Fig. 3. *Mytilus galloprovincialis* and *Perna perna*. Correlation between mean monthly attachment strength and mean monthly thread diameter for (a) *P. perna* (p < 0.001; $y = 0.4334x + 2.118$, $r^2 = 0.5199$) and (b) *M. galloprovincialis* (p < 0.05; $y = 0.3115x + 8.8785$; $r^2 = 0.3313$)
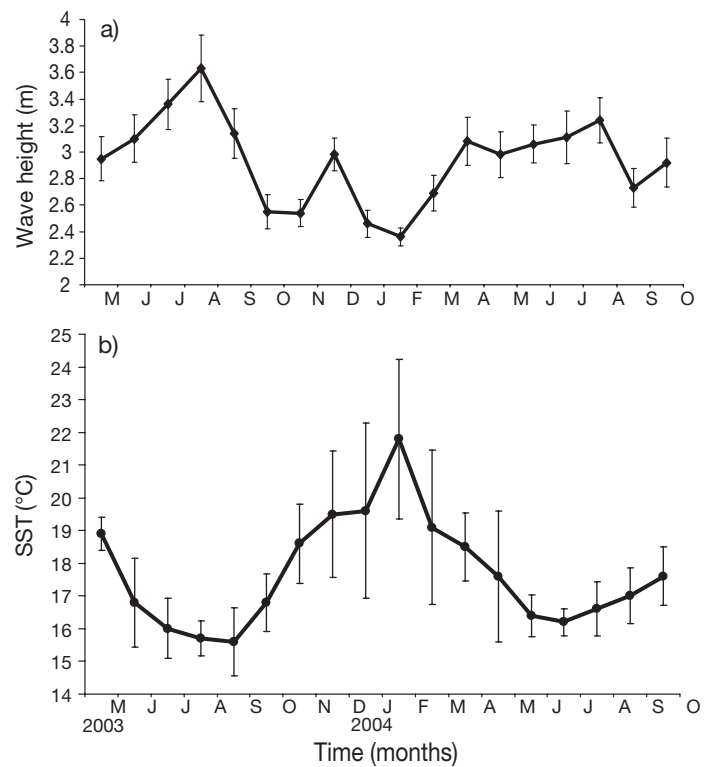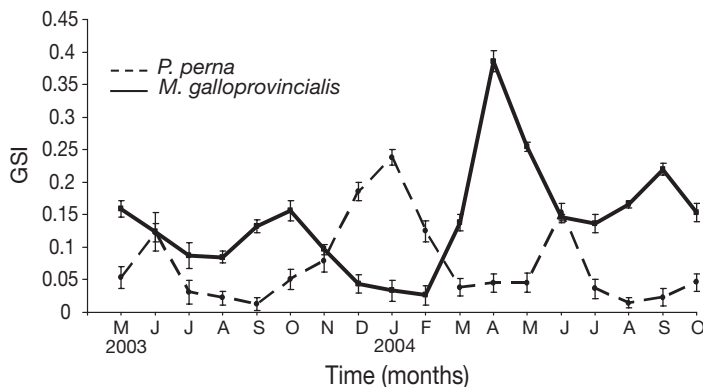

Fig. 4. *Mytilus galloprovincialis* and *Perna perna*. Mean (±SD) monthly gonadosomatic index in (GSI) Plettenberg Bay from May 2003 to October 2004

Cross-correlation analyses

The highest positive correlation between attachment strength and mean wave height was observed at zero lag for both species, and when attachment strength lagged 1 mo behind (lag = –1; *Perna perna*) or preceded wave height by 1 mo (lag = +1; both species; Fig. 6a,b). Attachment strength was negatively correlated with GSI 1 to 2 mo earlier (lag = +1, +2 mo) for *P. perna* and 6 mo earlier (lag = +6) for *Mytilus gallo-*

Fig. 5. Environmental characteristics in Plettenberg Bay from May 2003 to October 2004. (a) Mean (±SD) monthly wave height, (b) mean (±SD) monthly SST

provincialis (Fig. 6c,d). Attachment strength of both species was negatively correlated with SST with zero lag and when it preceded SST by 1 or 2 mo (lag = +1, +2; Fig. 7a,b). *P. perna* gonad index showed significant positive correlations with SST at lag of zero and +1; for *M. galloprovincialis* GSI was not significantly correlated with SST (Fig. 7c,d).

DISCUSSION

Our results showed that *Perna perna* is, on average, 28% more strongly attached than the invasive *Mytilus galloprovincialis*, and that this difference was maintained during the 18 mo of the survey, with an increase in attachment strengths of 40% for both species in winter compared to summer. Thread number strongly influences mussel tenacity and seasonal changes of attachment strength are mirrored by fluctuation in thread number (Seed & Suchanek 1992, Bell & Gosline 1997, Carrington 2002). Although Moeser et al. (2006) found that seasonal fluctuation of attachment strength can be explained by variation in the material properties of byssal threads, rather than their quantity, our results showed a positive correlation between
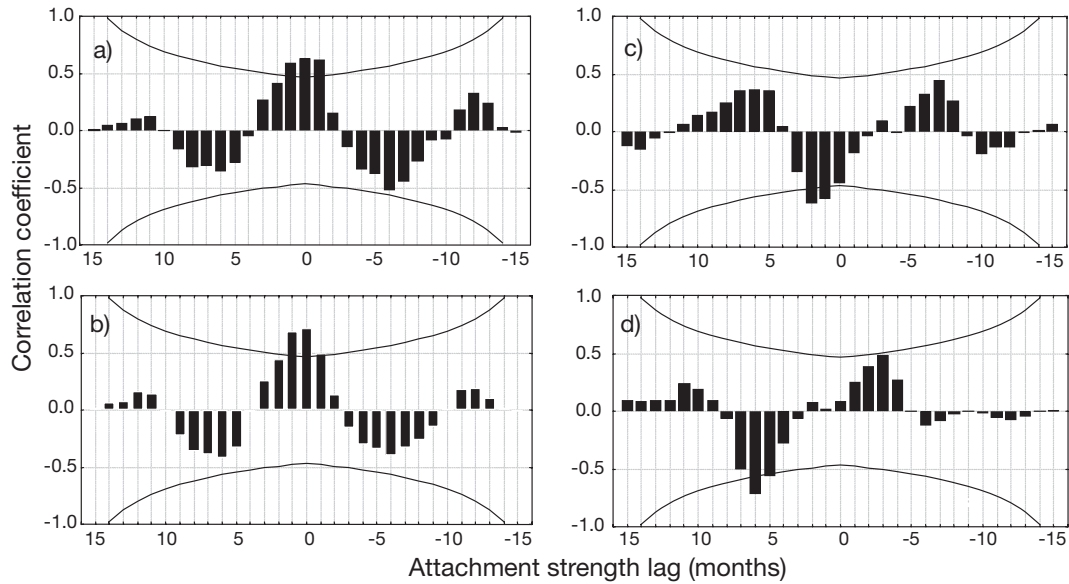
Fig. 6. *Mytilus galloprovincialis* and *Perna perna*. Cross-correlation analyses of monthly mean attachment strength with wave height for (a) *P. perna*, (b) *M. galloprovincialis* and with GSI for (c) *P. perna*, (d) *M. galloprovincialis*. Bars are correlation coefficients; curved lines are approximate 95% confidence levels for the significance of each correlation
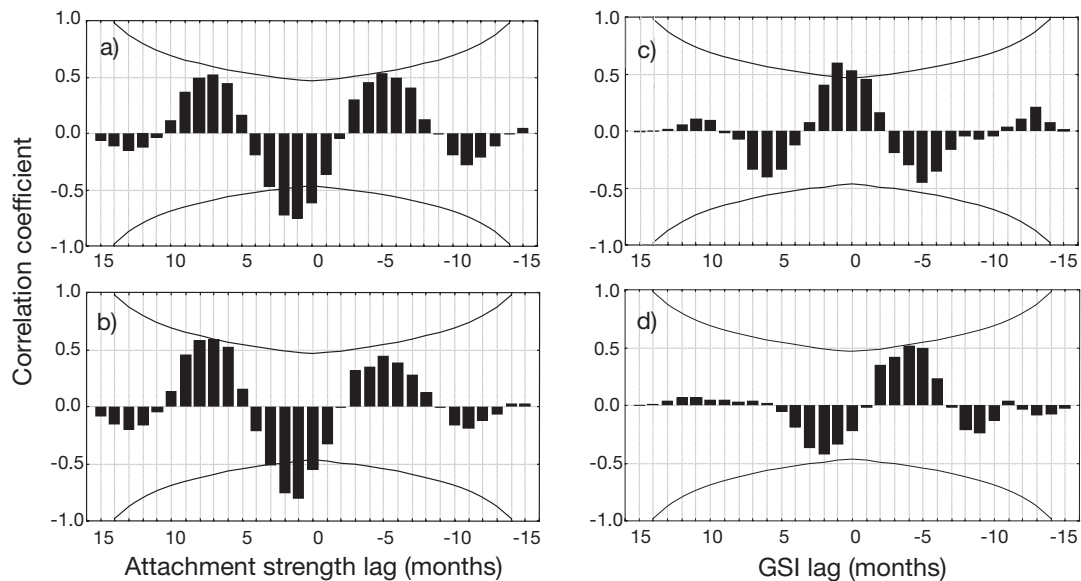

Fig. 7. *Mytilus galloprovincialis* and *Perna perna*. Cross-correlation analyses of monthly mean attachment strength with SST for (a) *P. perna*, (b) *M. galloprovincialis* and cross-correlation analyses of monthly mean GSI with SST for (c) *P. perna*, (d) *M. gallo-provincialis*. Bars are correlation coefficients; curved lines are approximate 95% confidences levels for the significance of each correlation

attachment strength and thread number. In addition, although the relationship was weaker, thread thickness was also significantly correlated with seasonal strength of attachment.

The time required for mussels to react to changes in hydrodynamic stress can vary even within the same species; *Mytilus edulis* attachment strength can both precede or react to increasing wave height (Carrington 2002). In the cross-correlation analysis, the highest correlation of attachment strength with wave height was observed at zero lag for both species, but other high correlations were also observed (at +1 lag for *M. galloprovincialis* and ±1 lag for *P. perna*). Consequently, there is an increased production of byssal threads to

withstand wave action, but it is not clear if this reacts to or precedes increased hydrodynamic stress. Despite the ability of mussels to produce a byssal thread in less than 5 min (G. I. Zardi pers. obs.) and thus to adjust their attachment strength in a relatively short time, there were periods when high hydrodynamic stress did not coincide with high strength of attachment (e.g. December 2003). Mussel dislodgements are sporadic events that occur unpredictably throughout the year, but strong storms during winter render mussels particularly prone to hydrodynamic disturbances (Brundrit & Shannon 1989). Rius & McQuaid (2006) showed that, under experimental conditions in the field, mortality of *M. galloprovincialis* during a storm was higher than that of *P. perna* in the same zones, highlighting the ability of the indigenous mussel to better withstand hydrodynamic stress.

A variety of other environmental variables, such as temperature, sand stress and food supply, could affect byssal thread production. Sea surface temperature is known to affect byssal thread production (e.g. Clarke & McMahon 1996, Moeser et al. 2006), and our results show that attachment strength increased with decreasing sea surface temperature. In addition, South African rocky shores are regularly and extensively inundated by sand, with highest sand accumulations in autumn (Zardi et al. 2006a), coinciding with high hydrodynamic stress. Sand inundation can increase the amount of sediment (sand, shell fragments etc.) within a mussel bed, making the substratum less stable and mussels more prone to dislodgement (Zardi et al. 2006a). Water flow at wave-exposed shores not only puts mussels at risk of dislodgement and damage to their shells, it also delivers more food than at sheltered sites (e.g. Bustamante & Branch 1996, Dhalhoff & Menge 1996). Food provides energy for metabolically costly processes such as byssal thread replacement, somatic growth, increases in shell thickness and gamete synthesis (Griffiths & King 1979, Seed & Suchanek 1992). Consequently, attachment strength could not only react to the direct effect of wave forces, but also be influenced by energetic constraints due to energy investment in other physiological needs. The relatively low investment in attachment strength compared to the high investment in reproduction implies that mussels may divert a relatively small amount of energy from reproduction to attachment strength when necessary, without a substantial decrease in the former. Nevertheless, thread production is influenced by food supply and the observation of Carrington (2002), that co-occurring high levels of attachment strength and reproduction followed unusually high phytoplankton abundance, indicates the need to balance these 2 energetic requirements. Our results also offer indirect support for the concept of needing to balance reproduction

against attachment strength. Both species showed a major and a minor spawning event each year. In each case, the highest gonad index peak was preceded by gamete production during periods of relatively low hydrodynamic stress. In contrast, minor peaks in GSI followed periods of relatively high wave height. This suggests that channelling more energy into attachment strength limits gonad tissue development. The major gamete production was more protracted for *Perna perna* (4 mo) than for *Mytilus galloprovincialis* (2 mo) and maximum GSI was much greater for the invasive species. It has been shown that *M. galloprovincialis* has a very high reproductive output (van Erkom Schurink & Griffiths 1991, Harris et al. 1998), which, together with fast growth, and the ability to colonise free space very rapidly (Erlandsson et al. 2006) could be responsible for allowing it to become the most abundant alien marine species in South Africa (Robinson et al. 2005).

Many attempts have been made to determine the factors controlling mussel gametogenesis and spawning. Of these, temperature and food supply seem to be particularly important. Rising, falling and fluctuating temperatures have all been reported to stimulate spawning in *Mytilus* spp. (e.g. Wilson 1987, Seed & Suchanek 1992). A few studies have suggested that spawning occurs only within a critical temperature range (e.g. Sprung 1983), while others did not find any relation between spawning and temperature (Sunila 1981).

Reproduction can be influenced by several other environmental factors, such as rough weather, phase of the moon, tidal fluctuations, salinity and endogenous factors (e.g. Wilson 1987, Seed & Suchanek 1992). In South Africa, different spawning periods are reported in different regions for *Perna perna* and *Mytilus galloprovincialis* (Berry 1978, van Erkom Schurink & Griffiths 1991). Mussels analysed in this study were sampled from the same restricted area at the same time, and consequently are presumed to be exposed to the same environmental factors. Despite this, the 2 species showed different reproductive timing, suggesting that species–specific endogenous factors or responses to environmental conditions play a crucial role in regulating gametogenesis and spawning. *P. perna* gonad index values mirrored fluctuations in sea surface temperature, while the gonad index of *M. galloprovincialis* was not significantly cross-correlated with sea surface temperature. If we consider mussel spawning periods as sudden decreases of gonad index from relatively high values, *M. galloprovincialis* spawning events always took place at temperatures ranging between 16.4 and 19.5°C, while *P. perna* spawned at the highest and the lowest temperatures recorded in the 18 mo of the survey.

The negative correlation between attachment strength and GSI for *Mytilus galloprovincialis* was at a maximum with a lag of 6 mo. Given that mussels can adjust attachment strength within minutes and that *M. galloprovincialis* can reach maximum GSI values within 2 to 3 mo, this correlation between GSI and attachment probably has little biological meaning. Note that the correlation refers only to attachment strength and gonad index and does not take into consideration other factors that could have a seasonal influence on either. However, for both species maximum GSI always coincided with relatively low attachment strength, indicating that mussels could not afford energetically to maintain high levels of both biological parameters simultaneously.

Surprisingly, on the cold water, upwelling-dominated west coast, where *Perna perna* is absent, *Mytilus galloprovincialis* extends to the low shore (G. I. Zardi pers. obs.). This is possible partly because *P. perna* does not exclude *M. galloprovincialis* through competition, but also because *M. galloprovincialis* must be able to withstand the higher wave forces of the low shore, something it cannot do on the south coast (Rius & McQuaid 2006). Resisting low shore wave action on the west coast may be possible because frequent upwelling leads to higher phytoplankton availability (Brown 1992, Bustamante et al. 1995), allowing attachment strength to be increased even during reproduction.

In conclusion, it is possible that attachment strength and reproductive status are independently driven by environmental factors such as wave action or sea surface temperature that are themselves negatively correlated, so that any apparent relationship between these biological variables is coincidental. Nevertheless, our results support the initial hypotheses and suggest that attachment and reproduction are linked as competing energetic demands. Attachment strength of the 2 mussels constantly tracked fluctuations in wave height and was correlated with byssal thread production. Moreover, both species seem to alternate the investment of their energy into either attachment strength or gametogenesis. However, while the invasive *Mytilus galloprovincialis* adopts an evolutionary approach that emphasises reproduction over attachment strength, the indigenous *Perna perna* seems to ensure individual survival of wave action at the expense of lower reproductive output.

This suggests that gamete production is energetically constrained by the energy needed to increase attachment strength during periods of high wave action. *Perna perna* attachment strength was higher than *Mytilus galloprovincialis* through all seasons, while the invasive species had a higher reproductive effort. The present study shows that 2 coexisting species can maintain different energetic strategies. Although high gamete production improves the ability of *M. galloprovincialis* to colonise free space, at the same time it could energetically limit its ability to invade wave exposed shores.

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