Re-colonisation rate differs between co-existing indigenous and invasive intertidal mussels following major disturbance

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ABSTRACT: The potential of introduced species to become invasive is often linked to their ability to colonise disturbed habitats rapidly. We studied the effects of major disturbance by severe storms on the indigenous mussel *Perna perna* and the invasive mussel *Mytilus galloprovincialis* in sympatric intertidal populations on the south coast of South Africa. At the study sites, these species dominate different shore levels and co-exist in the mid mussel zone. We tested the hypotheses that in the mid-zone *P. perna* would suffer less dislodgment than *M. galloprovincialis*, because of its greater tenacity, while *M. galloprovincialis* would respond with a higher re-colonisation rate. We estimated the percent cover of the 2 mussels in the mid-zone from photographs, once before severe storms and 3 times afterwards. *M. galloprovincialis* showed faster re-colonisation and 3 times more cover than *P. perna* 1 and 1.5 yr after the storms (when populations had recovered). Storm-driven dislodgment in the mid-zone was highest for the species that initially dominated at each site, conforming to the concept of compensatory mortality. This resulted in similar cover of the 2 species immediately after the storms. Thus, the storm wave forces exceeded the tenacity even of *P. perna*, while the higher recruitment rate of *M. galloprovincialis* can explain its greater colonisation ability. We predict that, because of its weaker attachment strength, *M. galloprovincialis* will be largely excluded from open coast sites where wave action is generally stronger, but that its greater capacity for exploitation competition through re-colonisation will allow it to outcompete *P. perna* in more sheltered areas (especially in bays) that are periodically disturbed by storms.

KEY WORDS: Invasive species · Spatial co-existence · Exploitation competition · *Mytilus* · *Perna* · Recovery · Disturbance

INTRODUCTION

Alien species have the potential to affect an ecosystem seriously by changing species diversity, community structure and interactions between organisms, sometimes causing extinction of native species (Hobbs & Huenneke 1992, Reusch & Williams 1999, Grosholz 2002, 2005, Castilla et al. 2004, Lee & Klasing 2004, Hoekstra et al. 2005, Schlaepfer et al. 2005). Because shipping and hence the introduction of marine species to non-native localities have increased, coastal marine habitats have become some of the most invaded eco-systems (Grosholz 2002). A species newly introduced to a locality may become invasive if it has some of the following characteristics: a short generation time, high fecundity, a rapid growth rate, a good dispersal ability and large genetic variation (Lee & Klasing 2004). The ways that a non-indigenous species responds (in terms of survival, reproduction and growth) to resource availability, natural enemies and the physical environment determine its ability to invade a new region or area (Shea & Chesson 2002).

Environmental disturbance is usually assumed to release resources (e.g. space) and provide opportuni-

ties for non-indigenous species to invade a new area (Hobbs & Huenneke 1992, Shea & Chesson 2002). However, theory predicts that a successful invader must still 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 & Chesson 2002, With 2002, Hastings et al. 2005). Differences in the response of indigenous and invasive species to variable harsh environmental factors mean that an inferior competitor for a resource could still invade an area if it were a superior coloniser (Shea & Chesson 2002). In accordance with this reasoning, it has been suggested that invaders may be more similar to 'r-selected' species and indigenous species more similar to 'K-selected' species. McMahon (2002) reviewed North American freshwater bivalves and suggested that the indigenous species were more K-selected, giving them adaptations that provide higher resistance against environmental extremes, while invasive species may be more r-selected and have life-history strategies that would allow rapid population recovery.

Seven species of marine molluscs have been introduced to South Africa by accident (Griffiths et al. 1992). Of these species, the Mediterranean blue mussel *Mytilus galloprovincialis* (Lamarck, 1819) became invasive (Griffiths et al. 1992) after its introduction to the west coast of South Africa in the late 1970s (Grant & Cherry 1985). It has since become the most abundant mussel on the west coast (>70% of mussel biomass), having outcompeted the indigenous mussel *Aulacomya ater* (Molina, 1782) because of its higher fecundity, recruitment and growth rates (van Erkom Schurink & Griffiths 1990, 1991, 1993, Griffiths et al. 1992, Steffani & Branch 2003a, Branch & Steffani 2004). *M. galloprovincialis* has spread ca. 1000 km along the south coast of South Africa since 1990 (McQuaid & Phillips 2000, Robinson et al. 2005). There it is a threat to the indigenous brown mussel *Perna perna* (Linnaeus, 1758), the dominant mussel on the south and east coasts, which has generally lower fecundity, recruitment and growth rates than other mytilid mussels (Lasiak & Barnard 1995, Harris et al. 1998). While *P. perna* is infested by many different trematodes, *M. galloprovincialis* is free of these parasites both in one of its native regions (north of Spain) and in South Africa (Calvo-Ugarteburu & McQuaid 1998a). Survival and competitive ability are negatively affected in infested *P. perna*, which may give parasite-free *M. galloprovincialis* a competitive advantage (Calvo-Ugarteburu & McQuaid 1998b).

The abundance of *Mytilus galloprovincialis* is highly variable and site specific on the south coast. At sites where *M. galloprovincialis* is abundant, it dominates the upper mussel zone, and *Perna perna* dominates the lower mussel zone, with an overlap in distribution in the mid mussel zone (Bownes & McQuaid in press). Mortality is higher for *M. galloprovincialis* on the low shore, both with storms and under normal wave conditions (Bownes 2005, Rius & McQuaid 2006). Furthermore, field experiments have shown that *P. perna* has higher tenacity than *M. galloprovincialis*, because it produces more and thicker byssus threads (Zardi et al. in press). This appears to give *P. perna* higher resistance against wave disturbance. Settlement rates of *P. perna* are less consistent through the year, and, in the upper mussel zone, it suffers greater post-settlement mortality of recent recruits than *M. galloprovincialis* (Bownes 2005). These factors may explain the differences in zonation between the 2 species.

Storm waves that generate strong lift forces can have severe effects on intertidal organisms, especially in mussel beds on exposed rocky shores, where large, distinct gaps of bare space are often formed (Paine & Levin 1981, Denny 1987). This has been observed on the west coast of North America, where *Mytilus californianus* (Conrad, 1837) in the later stages of succession following a disturbance by storm waves shows almost complete domination over *Mytilus trossulus* (Gould, 1850) in mature mussel beds (Paine & Levin 1981, Paine 1984, Suchanek 1985). It has been suggested that *M. californianus* has a higher competitive ability than *M. trossulus* (but see also Wootton 2002) in the competition for space, which is often the limiting resource on intertidal rocky shores. Natural disturbances such as strong waves and storms are also quite frequent on South African shores, and have the potential to dislodge large areas of mussel bed on the south coast.

In the present paper, we test the model that an indigenous species (*Perna perna*) has higher resistance to environmental disturbance (less easily dislodged by storm waves) and an invader (*Mytilus galloprovincialis*) has higher colonisation ability following such disturbances.

MATERIALS AND METHODS

Study area and sampling design. We studied 2 sites where *Mytilus galloprovincialis* occurs at high densities on the south coast of South Africa. These sites are rather uncommon, as there are very few localities where these 2 species occur in sympatry with a high cover of *M. galloprovincialis*. The sites, Look-Out Beach and Robberg, are rocky shores separated by ca. 5 km in Plettenberg Bay (34° 05′ S, 23° 20′ E; Fig. 1). Intertidal mussel beds in this wave-exposed region occur on the lower shore and can be divided into low, mid and upper mussel zones. The width of each mussel
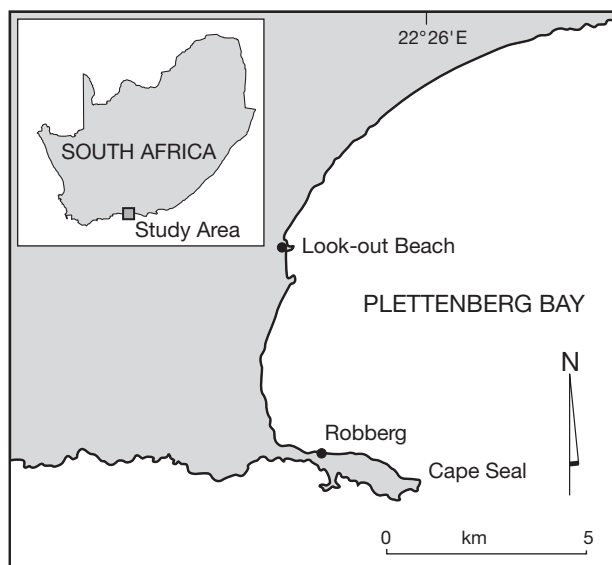
Fig. 1. Map of study area and 2 sampling sites (•) on the south coast of South Africa

zone depends on the slope of the shore and the degree of wave action, but generally each zone is 2 to 3 m wide. Mussel beds are usually monolayered, with the byssus threads of adults attached directly to the rock surface (McQuaid et al. 2000). However, in the mid-zone of Robberg some mussels are attached to other individuals, often creating more than 1 layer. At the 2 study sites, *Perna perna* and *M. galloprovincialis* overlap in distribution in the mid mussel zone, creating a patchy mosaic of the 2 species, while *P. perna* dominates the lower and *M. galloprovincialis* the upper mussel zone.

Two sub-sites, separated by ca. 25 m, were sampled at each site. Within each sub-site, 15 non-overlapping photographs were taken haphazardly within a 5 m stretch in the mid mussel zone. In each photograph, the percent cover of each mussel species was estimated in a 10 × 10 cm quadrat. Cover was estimated visually using a transparent frame of 16 small quadrats (each small quadrat constituting 6.25% of the total frame area) placed over the larger quadrat within the photograph. Discrimination between species was made by the following procedure: (1) we made sure that we analysed percent cover of the mussels from clear, good-quality photographs; (2) we identified the 2 mussel species mainly by shell colour, *Mytilus galloprovincialis* having darker and blue colours (sometimes black) and *Perna perna* having brown (usually light brown) and more purple colours (see Branch et al. 1994); (3) we followed the characterisation of subtle shell colour differences (e.g. narrow blue lines indicate that it is *M. galloprovincialis*) outlined by Bownes (2005) in a study of the morphology and habitat segregation between these 2 mussel species in this region.

This procedure was first performed at the end of July and the beginning of August 2000, spending 1 d (spring low tide) taking photographs at each site. The procedure was then repeated 3 different times (December 2000, September 2001, April 2002) to monitor the percent cover after severe storm waves removed large patches of mussels in mid-October 2000, and to monitor subsequent re-colonisation by the 2 species.

Mussels had re-colonised empty space in the mussel beds to pre-disturbance levels after about 8 mo (by May 2001), but we could not separate juveniles or recruits of the 2 species in the photographs until a few months later.

Hypotheses. The specific hypotheses for the mid-zone that we tested were: (1.1) storms affect *Perna perna* and *Mytilus galloprovincialis* differently, i.e. dislodgment of *P. perna* is lower than for *M. galloprovincialis*; (1.2) dislodgment depends on the percent cover of the 2 species before the storms, i.e. higher cover before the storms will result in higher dislodgment and lower cover just after storms; (2) re-colonisation of free space following storms occurs at a higher rate for *M. galloprovincialis* than for *P. perna*; (3) with different dislodgment and/or re-colonisation rates, the relative cover of the 2 species will be different after recovery from the disturbance (i.e. 1 and 1.5 yr after the storms) compared to before the storms.

Statistical analyses. A 4-factor ANOVA was done with the percent cover of mussels in the mid-zone as the dependent variable. There were 2 fixed factors: species (2 levels — *Mytilus galloprovincialis* and *Perna perna*) and time (4 levels — 2 mo before [July/August 2000], 2 mo after [December 2000]; 11 mo after [September 2001] and 18 mo after [April 2002] the storms). Thus, the different levels of the factor time represented the situation before storms, just after storms, after recovery of mussel populations and ca. 1 yr after population recovery, respectively. The remaining 2 factors were random: site (2 levels: Look-out Beach and Robberg) and sub-site (2 levels: nested in site).

Post hoc tests (Student-Neuman-Keuls [SNK]; see Underwood 1997) were also carried out for the ANOVA. The assumption of homogeneous variances was tested using Cochran's test (see below).

RESULTS

Cover of *Perna perna* and *Mytilus galloprovincialis* before and after storms

ANOVA showed a strong interaction of all 4 factors (Table 1). Variances were slightly heterogeneous (Cochran's test: $C = 0.11$; $C_{crit} = 0.08$; see Underwood

Table 1. *Perna perna* and *Mytilus galloprovincialis*. A 4-factor ANOVA of the percent cover of the 2 mussels in the mid-zone. Species (Sp) and time (Ti) are fixed factors, while site (Si) and sub-site (Ss) (nested in site) are random factors

Source of variation	df	MS	F	p	Error term
Species	1	69790	4.49	0.28	Sp × Si
Time	3	6508	6.77	0.08	Ti × Si
Site	1	1599	8.21	0.10	Ss (Si)
Sub-site (Site)	2	195	2.46	0.09	Residual
Sp × Ti	3	15730	2.23	0.26	Sp × Ti × Si
Sp × Si	1	15550	21.33	0.044	Sp × Ss (Si)
Sp × Ss (Si)	2	729	9.21	0.0001	Residual
Ti × Si	3	961	2.64	0.14	Ti × Ss (Si)
Ti × Ss (Si)	6	364	4.60	0.0001	Residual
Sp × Ti × Si	3	7067	19.45	0.0017	Sp × Ti × Ss (Si)
Sp × Ti × Ss (Si)	6	363	4.59	0.0002	Residual
Residual	448	79			

1997, Quinn & Keough 2002), but this could not be rectified by data transformation. However, slightly heterogeneous variances are not a problem when the numbers of different groups and degrees of freedom (df) are as high as in the present study, i.e. 32 groups and 14 df in each (Underwood 1997, Quinn & Keough 2002). Although sub-site was involved in significant interactions, the differences between sub-sites were relatively minor, involving the strength of effects, rather than different effects (see Fig. 2).

At Look-out Beach, *Perna perna* dominated the mid-zone before the storms occurred, while immediately after the storms its abundance was reduced to almost half (to the same percent cover as *Mytilus galloprovincialis*). Its cover then continued to decline for the following 18 mo (Fig. 2a, Table 2). In contrast, *M. galloprovincialis* showed low cover both before and just after the storms, but increased dramatically in abundance over the rest of the study period (Fig. 2a, Table 2).

At Robberg, the percent cover of *Perna perna* was rather low on all occasions, but there was no visible effect of the storms (Fig. 2b, Table 2). *Mytilus galloprovincialis* dominated the mid-zone at Robberg before the storms, with a decrease of more than half immediately afterwards, reaching a cover similar to that of *P. perna*. However, as at Look-out Beach, *M. galloprovincialis* showed rapid recovery, while *P. perna* abundance declined slightly with time (Fig. 2b, Table 2). Thus, at both sites the initially dominant species suffered drastic losses during the storms and cover of both species converged on approximately 20 to 30 % in its immediate aftermath. Hence, the storms most strongly affected the species that had highest initial cover, but at both sites *M. galloprovincialis* re-

colonised the freed space faster and by the end of the study dominated the mid-zone, with about 3 times as much cover as *P. perna*.

DISCUSSION

The present study showed that 11 mo after the storms, when populations had recovered to predisturbance levels, cover of *Mytilus galloprovincialis* was 3 or more times greater than that of *Perna perna* in the mid-zone, and the difference was even greater 7 mo later. Particularly notable was the change from *P. perna* to *M. galloprovincialis* as the species with greater cover at Look-out Beach.

We also noted that the cover of mussels was higher in the upper zone than in the mid-zone just after storms had occurred, even though percent cover was close to 100 % in both mussel zones before the storms, especially at Robberg (authors' pers. obs.). This difference may be because mussels in the mid-zone often form more than 1 layer at Robberg, so that mussels may not be attached directly to the substratum and so are easier to dislodge. In the mid-zone, the storms affected primarily the most abundant species, which differed between the sites, reducing both species at both sites to approx-

Table 2. *Perna perna* and *Mytilus galloprovincialis*. Student-Newman-Keuls test (post hoc test) of the ANOVA in Table 1, showing the sampling occasions at which the mussel cover of the 2 species differed at Look-out Beach and Robberg. Same letters indicate no significant differences between means (p > 0.05), while different letters show significant differences (p < 0.05)

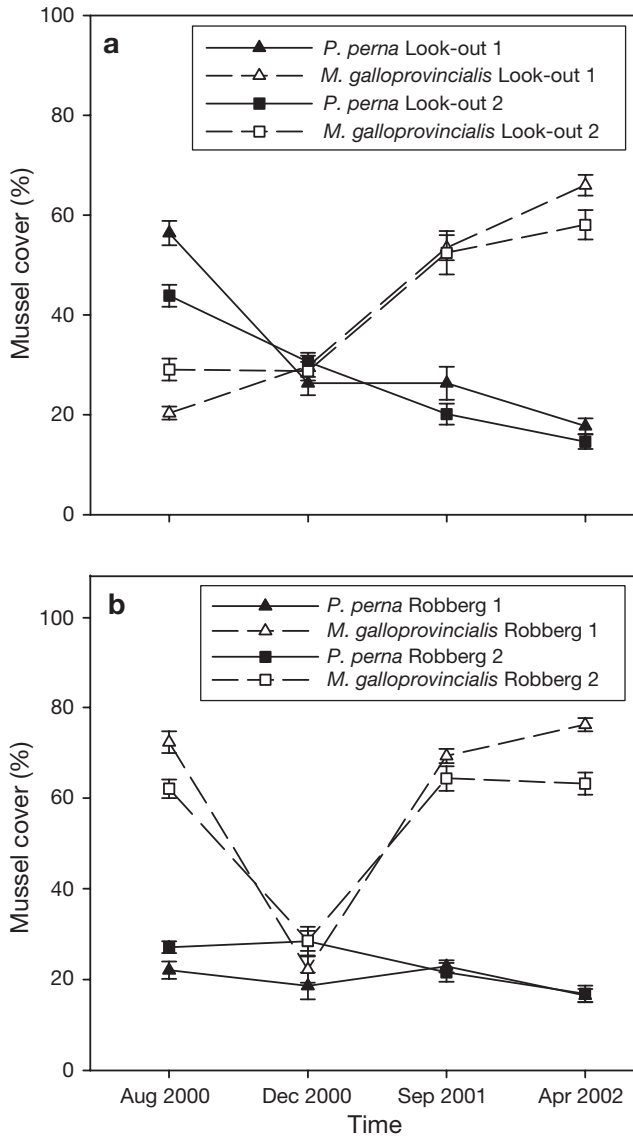|	Date	Homogenous groups
Look-out Beach		
P. perna	Aug 2000	c
	Dec 2000	b
	Sep 2001	b
	Apr 2002	a
M. galloprovincialis	Aug 2000	b
	Dec 2000	b
	Sep 2001	c
	Apr 2002	d
Robberg		
P. perna	Aug 2000	b
	Dec 2000	b
	Sep 2001	b
	Apr 2002	a
M. galloprovincialis	Aug 2000	c
	Dec 2000	b
	Sep 2001	c
	Apr 2002	c

Fig. 2. *Perna perna* and *Mytilus galloprovincialis*. Mean percent cover of the 2 mussel species in the mid-zone at different times (before storms, just after storms, after recovery to pre-disturbance levels, and 7 mo later) and sub-sites at (a) Look-out Beach and (b) Robberg. Mean ± SE

imately 30% cover. This conforms to the concept of compensatory mortality (Connell 1978), possibly because the more abundant species is more densely packed, forming patches that are less well attached. As a result, it was straightforward to determine differences in re-colonisation rate between species.

The general model that the indigenous *Perna perna* would have lower dislodgment and the invasive *Mytilus galloprovincialis* higher re-colonisation rates was supported only regarding the prediction of differences in recovery. Hence, regardless of which species was initially more abundant at a site, the end result

was the same, with *M. galloprovincialis* dominating 1 and 1.5 yr after a major storm disturbance.

The higher re-colonisation rate and recovery of *Mytilus galloprovincialis* in the mid-zone following disturbance can be explained by its r-selected traits of higher fecundity, recruitment and growth rates (van Erkom Schurink & Griffiths 1991, 1993, Lasiak & Barnard 1995, Harris et al. 1998, Steffani & Branch 2003a, Branch & Steffani 2004). Settlement rates (in our definition, settlement does not encompass post-settlement mortality while recruitment does) in the Plettenberg Bay area are also generally lower and more inconsistent for *Perna perna* than for *M. galloprovincialis* (Bownes 2005), which can explain the differences in re-colonisation rates after the storms. Explaining why there were no differences in dislodgment between the 2 species is more difficult. The theory of K- (indigenous) and rselected (invasive) species predicts that indigenous species would have higher resistance against disturbance (McMahon 2002), and *P. perna* indeed has more byssus threads and a higher tenacity under normal wave conditions (Zardi et al. in press). There are at least 2 explanations for our results. Firstly, there may be seasonal variation in the attachment strength of mussels, e.g. the tenacity of *M. edulis* (Linnaeus, 1758) at Rhode Island increased 2-fold in winter compared to summer (Carrington 2002). Perhaps the tenacity of *P. perna* is lower in October (when the storms occurred) than during the winter months (June to August). Mussels may also attach more strongly when predators are present, and this effect can vary both temporally and spatially in the field (see e.g. Reimer & Tedengren 1997). Secondly, the results can be more simply explained by the strength of the storms. The waves were so strong that even the higher tenacity of *P. perna* was not sufficient to prevent dislodgment of many individuals. Thus, the effects of the storms were related more to the density (or perhaps layering) of mussels than to the tenacity of the 2 species.

Environmental disturbance may create resource opportunities for non-indigenous species (e.g. storms creating extra space), but the differences in response of indigenous and non-indigenous species determine whether or not invasion is promoted by disturbance, as is the case for some ant communities in America (Zettler et al. 2004). The spatio-temporal resource competition theory predicts that fluctuations of environmental disturbance in time and space may also have major but different effects on indigenous and non-indigenous species, favouring them at different times and places (Shea & Chesson 2002, Hastings et al. 2005). Thus, it is possible that there was a differential temporal response in re-colonisation between *Perna perna* and *Mytilus galloprovincialis*, e.g. seasonality in

recruitment may differ. However, recruitment of these species occurs roughly during the same seasons, and the recovery of these mussel populations took ca. 8 mo. During this period (October to May) *P. perna* normally has at least 1 peak in its recruitment (Harris et al. 1998, McQuaid & Lawrie 2005). Furthermore, there was no spatial variability at local scales (within and between shores in the Plettenberg Bay area) in the differential responses (re-colonisation rate) by *P. perna* and *M. galloprovincialis* following the storms. This may, however, differ between bays and the open coast.

Intermediate disturbance or moderate frequencies of disturbance in a community can prevent competitive exclusion of organisms, thus promoting species co-existence (Connell 1978, Shea et al. 2004). For example, on rocky shore mussel beds, intermediate disturbance by storm waves or intermediate stages in the succession would promote a higher species diversity of algae, barnacles and mussels (Paine & Levin 1981, Suchanek 1985, Sebens 1991). This co-existence may also increase competition for space between certain organisms, e.g. between *Perna perna* and red algae on the south-east coast of South Africa (Erlandsson et al. 2005). However, as disturbance may also affect biodiversity negatively by promoting invasions by non-indigenous species, the effects of disturbance cause a dilemma (Hobbs & Huenneke 1992). The present study certainly shows that disturbance by severe storms can promote invasion by *Mytilus galloprovincialis*. The question is whether this pattern exists only on short time-scales or also on longer ones and larger spatial scales. In other words, will co-existence of *P. perna* and *M. galloprovincialis* be maintained on some shores of the south coast, or will *M. galloprovincialis* eventually displace *P. perna* and dominate along this coast, as it has done on the west coast? The answer to this question will depend on the strength and frequency of storms and other disturbances (e.g. mussel harvesting) in the future.

Organisms with high colonisation rates following disturbances can be successful invaders, even if they are weaker competitors (Shea & Chesson 2002), i.e. they may be successful at exploitation competition, if not at interference competition. *Mytilus galloprovincialis* appears to have both a high competitive ability, e.g. due to its growth dynamics (Griffiths et al. 1992) and lack of parasites (Calvo-Ugarteburu & McQuaid 1998a,b), and a high colonisation ability following disturbance (present study). This suggests that *M. galloprovincialis* will come to dominate and perhaps form mono-cultures (at the expense of *Perna perna*) on the shores of the south coast, as it has on the west coast of South Africa, or as *M. californianus* has on the west coast of North America (Paine 1984). However, the situation is not simple. Experimental evidence from the

lower, mid and upper mussel zones of the open coast indicates that artificially created monospecific patches of *M. galloprovincialis* suffer 100% mortality due to normal wave action (i.e. not storms). *M. galloprovincialis* in mixed patches with *P. perna* show much better survival than those in monospecific patches, but still suffer mortality due to interspecific competition (Rius & McQuaid 2006). Thus, the results of interactions between these 2 species may be site specific. For example, only some sites along the south coast have relatively high cover of *M. galloprovincialis*, and it appears to be more abundant in bays than on the open coast (C. D. McQuaid pers. obs.). On the west coast, *M. galloprovincialis* has higher growth and recruitment on semi-exposed shores (Steffani & Branch 2003a, Branch & Steffani 2004), which may suggest why there is much interaction between *M. galloprovincialis* and *P. perna* in large bays, such as Plettenberg Bay. For example, interactions between *P. perna* and *M. galloprovincialis* are likely to be influenced by conditions of wave action, as is the case for interactions between *M. galloprovincialis* and the limpet *Scutellastra argenvillei* (Krauss, 1848) described by Steffani & Branch (2003a,b). It is also possible that *M. galloprovincialis* has a higher re-colonisation rate than *P. perna* on bare space, but that *P. perna* will recover its population density by recruiting onto *M. galloprovincialis* patches after some time has passed. It is common for some benthic organisms to avoid colonising bare space and instead settle onto established colonies of particular species (Dunstan & Johnson 2004). To our knowledge, there has been no observation of *P. perna* naturally re-colonising a cleared area where it is otherwise dominant; instead this results in algae and barnacles taking over the empty habitat (Hockey & Bosman 1986). In fact, the vast majority of *P. perna* recruits are found either among algae or among adult mussels (Erlandsson & McQuaid 2004, McQuaid & Lindsay 2005), so that colonisation of free space is likely to be by encroachment rather than settlement.

Advantages to invaders can arise through disruption of the historical pattern of resource supply and consumption, often created by anthropogenic disturbances such as alteration of fire patterns, harvesting of biomass, nutrient enrichment, habitat destruction and climate change (Shea & Chesson 2002). Indigenous species may not be adapted to the changed environmental conditions, which could provide resource opportunities for non-indigenous species and enhance their invasion success (Byers 2002, Shea & Chesson 2002). For example, the frequency of severe storms and strong waves may increase in the future as a result of global warming. In the South African context, disturbances, such as the exploitation of mussels as food, as well as storms, are very common on the south and east

coasts (Harris et al. 1998, Erlandsson & McQuaid 2004), and increased intensity and frequency of these disturbances could favour *Mytilus galloprovincialis* rather than *Perna perna* in the colonisation of rocky shores.

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