Movement behaviour and mortality in invasive and indigenous mussels: resilience and resistance strategies at different spatial scales

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ABSTRACT: The responses of indigenous and exotic species to environmental factors can differ across spatial and temporal scales, and it is this difference that determines invasion success and the dynamics of co-existence. In South Africa, the indigenous *Perna perna* and the invasive *Mytilus galloprovincialis* are the dominant intertidal mussels on the southern coast, where they co-exist. We compared their movement behaviour over 6 mo at small scales (within and at the edge of mussel beds) and at meso scales (in bays and on the open coast). *M. galloprovincialis* moved more and had higher mortality rates than did *P. perna*. For both species, mortality was greater at the edge than at the centre of beds, and on the open coast than in bays. Mussels at the edge of beds moved more than those within beds, but, while this was true for *M. galloprovincialis* in both habitats, *P. perna* did not show a position effect on the open coast. Cross-correlation analysis showed that movement rates of both species were correlated with mortality rates after a lag of 1 mo. These results suggest that following mortality events, mussels react to increased availability of space and decreased attachment to neighbours by increasing their movement to reorganise into a safer arrangement. However, *P. perna* and *M. galloprovincialis* effectively adopt resistance and resilience strategies, respectively. The effectiveness of each strategy depends on environmental conditions in different habitats, influencing the possibility of co-existence. The higher hydrodynamic stresses experienced in open coast habitats and at the edge of a mussel bed are disadvantageous to the more active, less strongly attached invasive species.

KEY WORDS: Invasive species · Behaviour · Mussel · Open coast · *Mytilus galloprovincialis* · *Perna perna*

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INTRODUCTION

The responses of invasive alien species to variations in time and space of resources, natural enemies and the physical environment of the invaded community are determinants promoting or inhibiting the establishment and the spread of an invader (Moyle & Light 1996, Chesson & Huntly 1997, Davis et al. 2000, Mack et al. 2000). Consequently, differences in responses between native and invasive species can play a crucial role in setting patterns of co-existence (Chesson & Huntly 1997).

The European or Mediterranean mussel *Mytilus galloprovincialis* is a successful invader worldwide, and is

the most successful marine invasive species in South Africa (Branch & Steffani 2004, Robinson et al. 2005). On the south coast of South Africa, it co-exists with the indigenous brown mussel *Perna perna* on the low intertidal zone of rocky shores (referred to here as the mussel zone) and both species are often arranged in very dense single or multilayered mussel beds (authors' pers. obs.). The upper and 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 (Bownes & McQuaid 2006).

Previous studies have shown that these species often respond differently to environmental harshness and that this has ecological effects on their distribution and

partial habitat segregation. Morphological and physiological differences, such as a wider shell shape, a lower attachment strength, poorer tolerance of thermal stress and a higher expression of heat shock proteins of the invasive *Mytilus galloprovincialis* will favour the indigenous species during high hydrodynamic and heat stress (Zardi et al. 2007, authors' unpubl. data). However, the ecological success of *M. galloprovincialis* as an invader is mainly due to high reproductive output and re-colonisation rates (van Erkom Schurink & Griffiths 1991, Erlandsson et al. 2006). Differences in behavioural responses of indigenous species and invaders can also determine whether invasion is promoted or inhibited (Petren & Case 1996, Schneider et al. 2005). Previous laboratory experiments comparing the behavioural responses of *Perna perna* and *M. galloprovincialis* to the risk of predation underlined the greater mobility of the invasive species, which crawled farther and generally aggregated more (Nicastro et al. 2007).

Spatial diversity and temporal fluctuations of environmental factors can occur across large or small patches and over short and long time scales, respectively (Levins 1968). Bays are a common feature of the world's coastlines, and bay habitats usually differ physically from adjacent coastal habitats (Stauber 1950, Loosanoff & Nomejka 1951). Intertidal organisms in bays often face lower flow velocities and physical disturbance in contrast to individuals in open coast habitats (Ricketts & Calvin 1968, Castilla et al. 2002, Largier 2004). At a smaller scale, breaking waves can expose intertidal mussels to different forces due to the water's velocity, drag and lift (Denny 1995). Lift force is the main hydrodynamic force exerted on mussels living tightly packed in mussel beds (Denny 1987), while mussels living outside beds are mainly subjected to drag forces acting in the direction of flow (Bell & Gosline 1997). Wave exposure can influence the structure of mussel beds (Hammond & Griffiths 2004), and mussels react to different hydrodynamic forces by varying their attachment strength, while individuals sheltered within a bed have lower attachment strength than those living outside the bed or at its fringe (Witman & Suchanek 1984, Bell & Gosline 1997, Zardi et al. 2006). However, the greater strength of attachment of individuals living outside a bed is usually not enough to compensate for the higher hydrodynamic load, making this position less secure (Zardi et al. 2006). Mussels clump together to form large dense beds that play a major role as primary space holders in the intertidal habitat (Seed & Suchanek 1992). Adult mussels are able to move over short distances, making a mussel bed a dynamic structure composed of constantly rearranging individuals (e.g. Paine & Levine 1981, Schneider et al. 2005), and laboratory studies have suggested that different movement strategies could

influence species-specific mortality rates (Schneider et al. 2005).

Movement of *Mytilus galloprovincialis* and *Perna perna* was investigated in the field over a period of 6 mo, comparing mussel behaviour in sheltered bays and on the more wave-exposed open coast. Within each of these habitats, we compared mussels at the edge and at the centre of beds. We tested the hypotheses that (1) due to generally higher hydrodynamic stress, mussels at open coast sites will experience higher mortality rates and, consequently, they will continuously adjust their position, looking for a protected, more secure arrangement; (2) mussels at the centre of a clump will be subjected to lower mortality rates and will move less than mussels at the edge of a clump, where individuals are less constrained by other mussels; (3) the indigenous mussel will move less than the invasive species, adopting a less dynamic strategy, as previous studies have shown that *P. perna* has a higher attachment strength than *M. galloprovincialis*.

MATERIALS AND METHODS

Mussel movement. Mussel movement was measured in 2 bays, Plettenberg Bay (34° 00′ 17″ S, 23° 27′ 17″ E) and Algoa Bay (33° 58′ 47″ S, 25° 39′ 30″ E), and at 2 open coast sites, Robberg (34°06′14″S, 23°23′07″E) and Cape Recife (34° 02′ 27″ S, 25° 32′ 01″ E). Each site had 2 locations 200 m apart at which digital pictures of 12 quadrats (20 × 20 cm) were taken monthly for 6 mo. In each quadrat, 6 individuals of each species (identified by shell shape and colouring) were selected from mussels in the centre of monolayer mussel beds and another 6 individuals from mussels living at the edge (4 to 5 cm in shell length). For each selected mussel, the net displacement (crawling distance) was recorded every month by superimposing photographs of fixed quadrats. Data on the total distances crawled by mussels in 6 mo fulfilled the pre-requisites for parametric analysis (Cochran's test) and were analysed using separate 5-factor nested ANOVA (GMAV5 software) to investigate the effects of Species (*Perna perna* or *Mytilus galloprovincialis*, fixed factor) and Position in the bed (centre or edge, fixed factor) on movement. In both cases the other 4 factors were Habitat (bays or open coast, fixed factor), and Sites nested within Habitat, Location nested within Sites and Quadrat nested within Location (all random factors).

Mussel mortality. Mortality rates of *Perna perna* and *Mytilus galloprovincialis* were measured at the same 2 locations at the same sites, based on the digital pictures of quadrats described above. Every month, in each quadrat, 10 individuals were selected from mussels in the centre of mussel beds and another 10 mussels from

those living at the edge. Mortality was assessed by comparing digital pictures for consecutive months. The mortality data for quadrats fulfilled the requirements for parametric analysis (Cochran's test) and were analysed using nested ANOVA (GMAV5 software) with Position, Species and Habitat as fixed factors, and Site and Location as nested random factors.

Cross-correlation. Mean monthly movement of each species in bays and on the open coast was cross-correlated with mean monthly mussel mortality rate using various lags from +6 to –6 mo for movement.

RESULTS

Mussel movement

Crawling distance varied monthly, showing a similar pattern for both species. There was a rapid increase in mean crawling distance in March (autumn) and a decrease in the following months (Fig. 1a,b). *Mytilus galloprovincialis* generally crawled farther than *Perna perna*, but in the analysis of effects of species (Table 1) there was a significant Species × Site interaction, as the difference was non-significant at one site. In bays, *M. galloprovincialis* crawled 75 and 56% more than *P. perna* for individuals living at the edge and in the centre of mussel beds, respectively, while on the open coast, the equivalent values were 65 and 61%.

Position also had a strong effect on movement (Table 2). There was a Position × Site effect and a Position × Location effect, but in both cases the interaction reflected a difference of degree. At all sites edge had a greater effect than centre, but the effect was stronger at some sites than others, while at all locations edge also had a greater effect than centre, but again the effect was stronger at some locations. Movement was greater for both species in bays than on the open coast, but the ef-
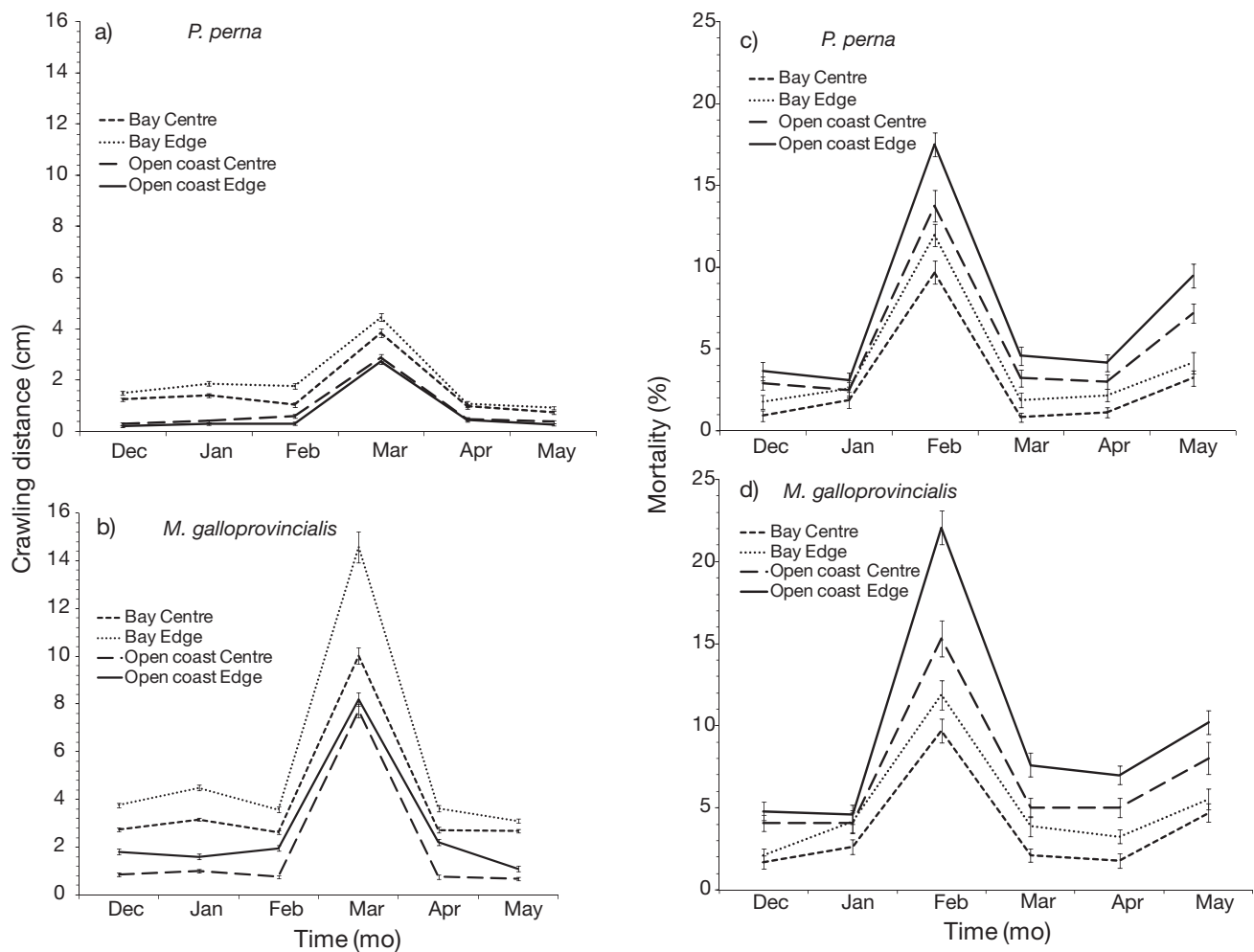

Fig. 1. *Mytilus galloprovincialis* and *Perna perna*. Mean (±SE) monthly (a,b) crawling distance and (c,d) mortality for (a,c) *P. perna* and (b,d) *M. galloprovincialis* at the centre and at the edge of a mussel bed, in bays and on the open coast

Table 1. *Mytilus galloprovincialis* and *Perna perna*. Results of 5-factor nested ANOVA to investigate the effects of Species (*P. perna* or *M. galloprovincialis*) on movement after 6 mo

Source of variation	df	MS	*F*	p
Habitat	1	58994.34	11.94	0.0745
Site (Habitat)	2	4939.88	32.75	<0.01
Location (Habitat × Site)	4	150.86	7.19	<0.0001
Species	1	110722.56	144.23	<0.01
Quadrat (Habitat × Site × Location)	88	20.99	1.3	<0.05
Habitat × Species	1	10416.75	13.57	0.0664
Species × Site (Habitat)	2	767.67	47.68	<0.01
Species × Location (Habitat × Site)	4	16.1	1.27	0.2067
Species × Quadrat (Habitat × Site × Location)	88	12.65	0.78	0.067
Residual	2112	16.19		

fect of Habitat was non-significant (p = 0.0745) in both analyses. When movement was analysed separately for each species, each showed a non-significant habitat effect (p = 0.07 for *M. galloprovincialis* and p = 0.08 for *Perna perna*), with individuals in bays crawling farther than mussels on the open coast, regardless of their position in the bed. *M. galloprovincialis* at the edges of beds always crawled significantly farther than mussels within beds, but the effect was stronger at some sites and locations than others (Position × Site, p < 0.05; Position × Location, p < 0.01). *P. perna* showed the same effect of position, but only in bays (Position × Habitat, p < 0.05).

Mussel mortality

Mussel mortality fluctuated seasonally and the highest mortality rates were reached in February (late summer) for both species, both on the open coast and in bays (Fig. 1c,d).

There were strong effects of both Species (*Mytilus galloprovincialis* mortality > *Perna perna* mortality) and Habitat (open coast > bays), with a significant Species × Habitat interaction as the species difference was greater on the open coast (Table 3). Mortality rates were generally higher on the edge of mussel beds than at the centre, but the difference was not significant at 4 locations (Location × Position, p < 0.05).

Cross-correlation

The highest (and only significant) correlations between movement and mortality rates were positive and were observed when movement lagged 1 mo behind mortality (lag = –1; Fig. 2).

DISCUSSION

In general, *Mytilus galloprovincialis* moved significantly more than *Perna perna* over a period of 6 mo. Previous studies on mussel movement (Hunt & Scheibling 2002) and on colonization and patch dynamics (Hunt & Scheibling 1998, 2001, Schneider et al. 2005) showed that adult crawling can play a crucial role in the dynamics and structure of intertidal mussel beds. Under some circumstances space made available by mortality may be occupied by new settlers, or even

Table 2. *Mytilus galloprovincialis* and *Perna perna*. Results of 5-factor nested ANOVA to investigate the effect of Position in the bed (centre or edge) on movement after 6 mo

Source of variation	df	MS	*F*	p
Habitat	1	58994.34	11.94	0.0745
Site (Habitat)	2	4939.88	32.75	<0.01
Location (Habitat × Site)	4	150.86	7.19	<0.0001
Position	1	9000.47	25.13	<0.05
Quadrat (Habitat × Site × Location)	88	20.99	0.3	<0.0001
Habitat × Position	1	1811.21	5.06	0.1535
Position × Site (Habitat)	2	358.11	7.71	<0.05
Position × Location (Habitat × Site)	4	46.42	7.57	<0.0001
Position × Quadrat (Habitat × Site × Location)	88	6.13	0.09	<0.0001
Residual	2112	69.03		

Table 3. *Mytilus galloprovincialis* and *Perna perna*. Results of 5-factor nested ANOVA applied to mortality rates after 6 mo

| Source of variation	df	MS	*F*	p
Habitat	1	0.6388	67.3	<0.05
Site (Habitat)	2	0.0095	0.81	0.5063
Location (Habitat × Site)	4	0.0117	7.07	<0.0001
Position	1	0.1693	229.28	<0.01
Species	1	0.1211	491.66	<0.01
Habitat × Position	1	0.0103	13.92	0.0649
Habitat × Species	1	0.0152	61.67	<0.05
Position × Site (Habitat)	2	0.0007	0.19	0.8373
Species × Site (Habitat)	2	0.0002	0.07	0.9347
Position × Location (Habitat × Site)	4	0.004	2.4	<0.05
Species × Location (Habitat × Site)	4	0.0036	2.16	0.0725
Position × Species	1	0.0044	9.27	0.0931
Habitat × Position × Species	1	0.2243	0.0014	3.02
Species × Position × Site (Habitat)	2	0.0005	0.14	0.8709
Species × Position × Location (Habitat × Site)	4	0.033	1.98	0.0966
Residual	352	0.0017		
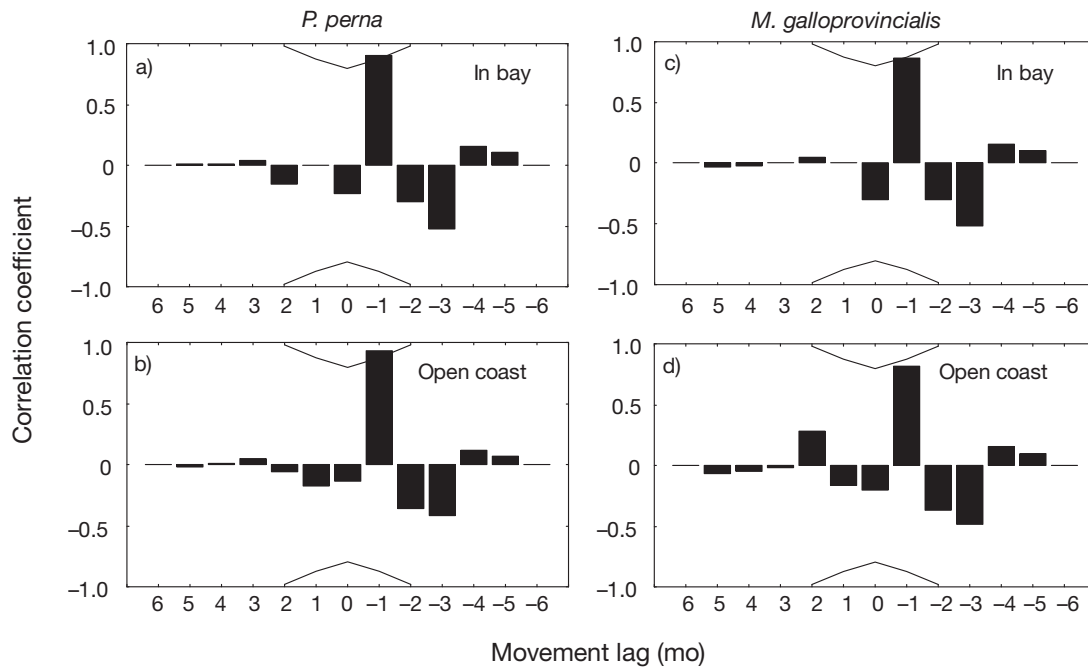
Fig. 2. *Mytilus galloprovincialis* and *Perna perna*. Cross-correlation analyses of monthly mean movement with mortality rates for (a,b) *P. perna* and (c,d) *M. galloprovincialis* in (a,c) bays and (b,d) on the open coast. Bars are correlation coefficients; curved lines are approximate 95 % confidence levels for the significance of each correlation

immigrants from nearby patches. Nevertheless, our results indicate that during the study period resident survivors responded to freeing of space by increased movement. Due to the extreme spatial and temporal heterogeneity in environmental conditions of rocky intertidal habitats, even the small-scale movements observed during the field experiment are likely to subject mussels to different micro-environmental conditions (Helmuth & Denny 2003) and could be important in regulating population dynamics. For example, Schneider et al. (2005) suggested that differences in the movement between conspecific *M. edulis* and *M. galloprovincialis* could account for observed species-specific differences in their survival. In our study, the more dynamic strategy adopted by *M. galloprovincialis*, together with lower attachment strength than *P. perna* (Zardi et al. 2006), could explain the higher mortality rates experienced by *M. galloprovincialis* during the 6 mo survey.

Mussels anchor themselves to the substratum by means of byssal threads (Waite 1992). When subjected to higher hydrodynamic stress, both *Mytilus galloprovincialis* and *Perna perna* increase the production of byssal threads to attach more firmly to the substratum (Zardi et al. 2007). For both species, movement was higher at bay sites than at open coast sites, possibly because the lower hydrodynamic stress experienced at bay sites allows mussels to be less strongly attached to the substratum. Furthermore, in all cases

except *P. perna* on the open coast, total movement over 6 mo was higher for mussels at the edge of a bed than for mussels deep within a bed. This can be explained by tight packing and lower availability of space within beds, and by the fact that mussels inside patches are bound to the substratum by the byssal threads of their neighbours as well as their own threads.

Due to their orientation and position on the rocks, mussels in beds and solitary individuals are primarily subjected to lift and drag forces, respectively. Laboratory experiments have shown that solitary mussels tend to arrange the posterior–anterior axis parallel to the substratum and perpendicular to prevailing water flow, thus exposing a smaller area and decreasing the hydrodynamic load (Dolmer & Svane 1994). In the field, because the flow of breaking waves is variable and unpredictable, this ideal arrangement is difficult to maintain. Zardi et al. (2006) showed that the orientation of solitary mussels to wave force is critical. On average, a solitary mussel of 4.5 cm (*Perna perna* or *Mytilus galloprovincialis*) in the worst position (broadside to the flow, i.e. posterior–anterior axis perpendicular to the water flow) exposes 60 % more surface area than a similarly sized mussel positioned with the posterior–anterior axis parallel to the water flow, and will experience proportionally greater hydrodynamic stress. In contrast, mussels in beds lie vertical to the substratum, exposing the smallest shell area to lift, which is independent of the direction of water flow

(Denny 1987). Consequently mussels in beds are subjected to a more predictable hydrodynamic environment (Denny 1987). Individuals living outside a mussel bed generally have higher attachment strength than those inside a bed (Witman & Suchanek 1984, Bell & Gosline 1997). However, this greater attachment strength is usually not enough to compensate for the higher and more variable hydrodynamic regime, making mussels outside beds more prone to dislodgement (Zardi et al. 2006). This prediction of dislodgement is confirmed in the present study: over 6 mo mortality rates for mussels at the edge of mussel beds were greater than for mussels at the centre of beds.

Unexpectedly, at the open coast sites movement rates of *Perna perna* did not show any significant differences between individuals at the edges and within beds. This may be explained by the higher wave action of the open coast, which would lead to higher attachment strength. Together with the low movement rates typical of *P. perna*, this could alter the general pattern, helping to explain this result. The relatively weak attachment strength of *Mytilus galloprovincialis* allows greater freedom of movement, but prevents the approach of resisting wave dislodgement, especially under the more extreme conditions of the open coast.

Mortality rates of both species varied seasonally, and were particularly high in February 2007, probably due to sand and/or wave stress (authors' pers. obs.); these 2 factors are often responsible for mass mortality in the intertidal zone and can generate gaps within mussel beds (Paine & Levine 1981, Carrington 2002, Zardi et al. 2008). Thus, the availability of free space, diminished attachment to neighbours and the necessity of finding safer arrangements are likely explanations for the high movement rates observed in March 2007. This is supported by the cross-correlation analysis between monthly mean movement and mortality rates, which showed that high mortality was followed over the next month by high movement rates. Our study did not extend to cover the winter period when mortality, particularly through wave action, is likely to be especially high, but we predict that this effect will be even stronger in stormy months.

Clumping behaviour and the search of a safer arrangement can strongly influence mussel survival rates; a mussel living in a densely packed bed exploits the physical protection from hydrodynamic stress and predation offered by nearby mussels. Individuals living at the centre of a bed are more difficult for predators to catch and hold than individuals living at the bed edge or solitary mussels (Petraitis 1987, Svane & Ompi 1993), and are, thus, subjected to lower rates of predation (Okamura 1986). In addition, mussels living outside or at the edge of a bed are subjected to higher hydrodynamic stress and a higher probability of dislodgement (Zardi et al. 2007). However, in a mussel bed, reduced

food availability leads to slower growth and lower reproductive output (Okamura 1986, Fréchette et al. 1989, O'Riordan et al. 1993, Butman et al. 1994). Moreover, mussel beds can form a very dense and intricate matrix of byssal threads attaching to the substratum and linking mussels to each other. When mussel density is very high, the byssal matrix can lose contact with the substratum, resulting in a slight elevation of the mussel bed, i.e. a hummock. These hummocks are relatively easily dislodged by wave action, forming gaps (e.g. Seed & Suchanek 1992, authors' pers. obs.).

Our hypotheses were only partially confirmed by our results: mussels at the edges of beds moved more and suffered higher mortality than individuals within a bed. However, despite higher mortality rates, mussels living on the open coast moved less than individuals in bays. It is likely that the high wave regime on the more exposed open coast drives mussels to produce large numbers of byssal threads, resulting in a safer attachment, but obliging them to be less mobile. This appears particularly to be the case for *Perna perna* at the edge of beds. Moreover, the comparatively wave-sheltered conditions within bays are associated with lower mortality rates. This accords with the observation of higher cover of adult mussels in bays than at open coast sites (C. von der Meden unpubl. data).

However, our results confirm that position is important, with mussels at the edge of a mussel bed having more freedom of movement than the more constrained individuals within a bed. Also, as initially hypothesised, *Perna perna* moved less than *Mytilus galloprovincialis*, adopting a resistance strategy that favours safety against wave action through higher attachment strength and lower movement rates.

Mytilus galloprovincialis is a very aggressive invasive species. Within South Africa, it exhibits resistance to trematode parasites (Calvo Ugarteburu & McQuaid 1998a,b), but also rapid growth rates over a range of water temperatures (Griffiths et al. 1992, Hockey & van Erkom Schurink 1992), high fecundity (van Erkom Schurink & Griffiths 1991), high recruitment rates (Harris et al. 1998) and resistance to desiccation (Hockey & van Erkom Schurink 1992, authors' unpubl. data). These features have high energy demands that come at the cost of reduced attachment strength (Zardi et al. 2007). Waves can be the major cause of mussel stress and mortality in the intertidal zone (Paine & Levine 1981, Steffani & Branch 2003), and the ability to resist dislodgement is an important attribute for a potentially invasive species.

Although the reproductive strategy of *Mytilus galloprovincialis* has played a crucial role in its ability to invade rocky shores worldwide, for example by allowing it to recolonise free space more quickly than *Perna perna* (Erlandsson et al. 2006), the energetic costs render it more vulnerable to wave-induced mortality

(Zardi et al. 2007). The high hydrodynamic stresses experienced at open coast sites and at the edges of mussel beds are problematic for the more dynamic and less strongly attached invasive species. In terms of wave action, *P. perna* and *M. galloprovincialis* effectively adopt resistance and resilience strategies, respectively, the effectiveness of each strategy depending on environmental conditions. Consequently, coastal topography (i.e. bays versus the open coast) and, at smaller scales, position within a mussel bed can play a crucial role in limiting the invasive potential of *M. galloprovincialis* and setting patterns of co-existence with indigenous species.

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