

Behavioural response of invasive *Mytilus galloprovincialis* and indigenous *Perna perna* mussels exposed to risk of predation

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ABSTRACT: We compared the behavioural responses of an indigenous South African mussel (*Perna perna*) and an invasive mussel (*Mytilus galloprovincialis*) to the risk of predation. Both species were subjected to the specific risk of predation by the native rock lobster *Jasus lalandii* and the general risk of predation simulated by the presence of damaged conspecifics. We hypothesised that, because *M. galloprovincialis* evolved in allopatry from the rock lobster, *P. perna* would respond more strongly to *J. lalandii*, but that there would be less difference between species in their response to damaged conspecifics. The results confirmed our initial hypotheses. *M. galloprovincialis* crawled farther under both predation treatments and generally aggregated more than *P. perna*. *P. perna* has a larger foot, and our results therefore do not reflect morphological differences between the species but imply greater sensitivity in *M. galloprovincialis* to chemical cues. Crawling distance was not enhanced under predation threat relative to the control; therefore, increased clumping due to more rapid random movement cannot explain our results, indicating that chemical attraction among individuals is important. *P. perna* clumping behaviour was significantly greater when exposed to local lobster effluent or damaged conspecifics, whereas *M. galloprovincialis* clumped more when exposed to a general threat of predation but exhibited naïve behaviour to local predator effluent. This lack of responsiveness to a native predator could be due not only to the recent arrival of the European mussel, but also to the relatively low selective effects of predation in South Africa.

KEY WORDS: Clumping behaviour · Invasive species · Risk of predation

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INTRODUCTION

The interaction between an invasive prey species and indigenous predators can play a crucial role in the success of the invader (Settle & Wilson 1990, Torchin et al. 1996, Mack et al. 2000). In particular, when predators are at low abundances or are less effective against new species, escape opportunities arise (Settle & Wilson 1990, Torchin et al. 1996). However, a naïve invader might not be well defended against generalist enemies, in which case escape opportunities are reduced (Mack 1996). Prey respond to predators through physiological, morphological and behavioural adaptations (Endler 1986, Vermeij 1987, Caro & Castilla 2004) and, in sessile and sedentary marine organisms, group living is a common behavioural response

to risk of predation (e.g. Reimer & Tedengren 1997, Côté & Jelnikar 1999). When exposed to water-borne predator effluent in the laboratory, mussels form larger and more clumps more rapidly than mussels under control conditions (Côté & Jelnikar 1999). In the natural environment, mussels clump together to form large, dense beds and are often successful primary space holders in the intertidal habitat (Seed & Suchanek 1992). Several studies have shown that adult mussels are able to move over short distances, making a mussel bed a dynamic structure composed of constantly re-arranging individuals (e.g. Paine & Levine 1981, Schneider et al. 2005). Mussels living at the centre of a bed are more difficult to catch and hold than individuals living at the bed edge or solitary mussels (Petraitis 1987, Svane & Ompi 1993), and are sub-

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jected to lower rates of predation (Okamura 1986). Mussels anchor themselves by means of byssus threads, and under natural conditions produce many byssal threads that may be attached to each other as well as to the substratum. As a result, more force is required to dislodge individuals in the middle of a bed than either those at the edge or solitary animals (Zardi et al. 2006).

The European mussel *Mytilus galloprovincialis* is a successful invader worldwide, and is the most successful marine invasive species in South Africa (Robinson et al. 2005). On the south coast of South Africa, it co-exists with the indigenous mussel *Perna perna* and both species are often arranged in very dense mono- or multilayered mussel beds (authors' pers. obs.). The invasion of this coast by the European mussel has major consequences for community structure and strongly affects the faunal assemblages found within mussel beds; moreover, it extends the vertical distribution of mussel beds further upshore, increasing intertidal biomass and consequently food sources for predators (van Erkom Schurink & Griffiths 1990, Hammond & Griffiths 2004). On South African rocky shores, predators have much weaker effects on prey populations than in other parts of the world (Castilla et al. 1994, Bustamente & Branch 1996), but one of the most important predators is the rock lobster *Jasus lalandii*. *J. lalandii* is the most important commercial lobster in southern Africa and, in South Africa, it co-occurs with both *P. perna* and *M. galloprovincialis* mussel species (Griffiths & Seiderer 1980, authors' pers. obs.). Studies of *J. lalandii* stomach contents have shown that it feeds mainly on mussels; however, sea urchins, algae, polychaetes and crustaceans are also taken (Newman & Pollock 1974, Pollock 1978). In areas where it is abundant, *J. lalandii* is capable of eliminating standing stocks of prey species (e.g. the mussels *Aulacomya ater* and *Choromytilus meridionalis* on the west coast of South Africa; Griffiths & Seiderer 1980).

The aim of this study was to investigate clumping behaviour of the invasive *Mytilus galloprovincialis* and indigenous *Perna perna* when subjected to predatory risk as indicated by water-borne cues from the generalist predator *Jasus lalandii* and damaged conspecifics, the latter being a signal of a nearby attack by a crushing predator. It has been shown that, among mussels, damaged conspecifics induce increased byssus production (Cheung et al. 2004) and thicker and mechanically stronger shells (Leonard et al. 1999). Here we tested the following hypothesis: (1) the interaction between the European *M. galloprovincialis* and the South African rock lobster is recent, and therefore the invasive mussel will exhibit a less pronounced reaction to the risk of this predator than will the indigenous *P. perna*; (2) the difference between the 2 mussel species

will be less pronounced when subjected to the general risk of predation simulated by the presence of damaged conspecifics, rather than to the specific risk induced by effluent from the South African crushing predator.

MATERIALS AND METHODS

Mussel collection. Adult mussels (4 to 5 cm shell length) of both species were collected from a rocky shore at Plettenberg Bay on the south coast of South Africa (34°22'S, 23°22'E). Before each laboratory experiment, all individuals were acclimated in oxygenated seawater for 48 h. All experiments were run in a controlled environment chamber at 19°C under a 12:12 h light:dark regime. Salinity was maintained at 35‰. Experimental aquaria were aerated and the water was replaced daily. Before the start of each experiment, byssus threads were carefully cut with a pair of scissors to separate the mussels from each other and individual mussels were numbered using white correction fluid.

Predator effluent and damaged conspecifics. Two days before the start of the experiment, 2 lobsters (*Jasus lalandii*, cephalothorax length approximately 30 cm) collected from Plettenberg Bay were placed individually in tanks containing 50 l of seawater and not fed. Oxygen was bubbled via an air stone and a biological filter was placed in each of the tanks. After 48 h the seawater from these aquaria was used as effluent for experiments involving lobster effluent. In the damaged conspecifics treatment, 4 damaged mussels were arranged symmetrically at the edge of each container for the duration of the experiment; for the mixed species groups, we used 2 damaged individuals of each species. Mussels used for this purpose were 4 to 5 cm long; they were damaged by cutting the adductor muscle and placed in the containers with the shell valves open.

Clumping behaviour and crawling distance. Experimental treatments were administered to each of 3 species combinations in round plastic containers (35 cm diameter) containing 5 l of oxygenated seawater. Mussels were arranged in a grid. Two containers each held 16 mussels from a single species (1 container for each species studied) and a third held a mixed group of 16 mussels (8 of each species arranged alternately). Each species treatment was replicated 3 times (3 containers). Two experiments were carried out using different individual mussels.

In the first experiment, mussels were placed in plastic tanks containing control seawater or lobster effluent and subjected to 1 of 4 experimental treatments: (1) mussels in control seawater arranged in a grid

1.5 cm apart; (2) mussels in control seawater 4.5 cm apart; (3) mussels in lobster effluent seawater 1.5 cm apart; and (4) mussels in lobster effluent seawater 4.5 cm apart. The 2 distances were such that the extended mussel foot could cover the near but not the far distance.

The second experiment was run with the following treatments: (1) mussels in control seawater 1.5 cm apart; and (2) mussels with damaged conspecifics 1.5 cm apart. The position of each mussel was recorded after 1, 3, 6, 12, 18, 24 h with digital photographs, and clumps were defined as 2 or more mussels attached to each other by 1 or more byssal threads. Clumping behaviour was quantified as number of mussels forming clumps, and crawling distance was recorded for the first 3 h of each experiment.

For Expt 1 (lobster effluent), data on the number of mussels forming clumps after 24 h were analysed using 3-way ANOVA, with distance, treatment and species as fixed factors. Expt 2 (damaged conspecifics) was run using 1 distance only, and data on the number of mussels forming clumps after 24 h were analysed using 2-way ANOVA, with species and treatment as fixed factors. Significant effects were examined using Tukey's post hoc test.

Data on the total distances crawled by mussels in the first 3 h of Expt 1 failed the requirements of Shapiro's test and Levene's test. Data were analysed using Kruskal-Wallis tests to investigate the effects of species (*Perna perna* or *Mytilus galloprovincialis*) and treatment (lobster effluent or control) in separate analyses. Data on crawling distances in Expt 2 failed the requirements of Shapiro's test, but Levene's test showed homogeneity of the data. Parametric analysis was used on the assumption that ANOVA is relatively robust to the effects of non-normality (Zar 1999); therefore, data were analysed using 2-way ANOVA with species (*P. perna* or *M. galloprovincialis*) and treatment (damaged conspecifics or control) as fixed factors.

Table 1. Results of 3-way ANOVA applied to number of mussels forming clumps after 24 h in Expt 1 (lobster effluent) with treatment, species and distance as fixed factors

Source of variation	df	MS	F	p
Treatment	1	17.36	6.44	0.02
Species	2	48.03	17.82	<0.0001
Distance	1	650.25	241.33	<0.0001
Treatment × Species	2	11.86	4.4	0.02
Treatment × Distance	1	17.36	6.44	0.02
Species × Distance	2	4.75	1.76	0.19
Treatment × Species × Distance	2	5.03	1.87	0.18
Error	24	2.69		

Foot measurements. Shell lengths of individuals of *Mytilus galloprovincialis* and *Perna perna* (n = 30 for each species), covering a wide size range (3.1 to 6.1 cm), were determined after any encrusting organisms had been removed. These mussels were then opened by carefully slicing through the adductor muscle, and the maximum width of the fully contracted foot was measured. This is proportional to, but more accurately measurable than, maximum foot length (Seed & Richardson 1999). A 1-way ANCOVA was used to evaluate the effects of species (fixed factor) and shell length (co-variate) on the maximum width of the contracted foot.

RESULTS

Clumping behaviour

Perna perna clumping behaviour was significantly greater when exposed to predator effluent or damaged conspecifics, whereas *Mytilus galloprovincialis* exhibited significantly more clumping when exposed to damaged conspecifics, but not lobster effluent.

Expt 1 (lobster effluent)

There were significant effects of all 3 factors, with significant treatment × distance and treatment × species interactions (Fig. 1, Table 1). All species showed greater clumping when separated by 1.5 cm than when separated by 4.5 cm, and none exhibited a treatment effect when separated by 4.5 cm (Tukey's test: p = 1). The percentage of mussels forming clumps differed significantly among species (Tukey's test: p < 0.05, in the order *Mytilus galloprovincialis* > mixed groups > *Perna perna*), but when separated by 1.5 cm, only *P. perna* exhibited a significant treatment effect (Tukey's test: p < 0.05). Because clumping behaviour was more pronounced with spacing of 1.5 cm, the greater distance was not investigated further.

Expt 2 (damaged conspecifics)

Both factors had significant effects, with no significant interaction (Fig. 2, Table 2). A significantly higher percentage of *Mytilus galloprovincialis* formed clumps relative to *Perna perna* (Tukey's test: p < 0.05), but mixed groups did not differ significantly from either of the 2 species (p = 0.1 with *M. galloprovincialis*, and p = 0.8 with *P. perna*).

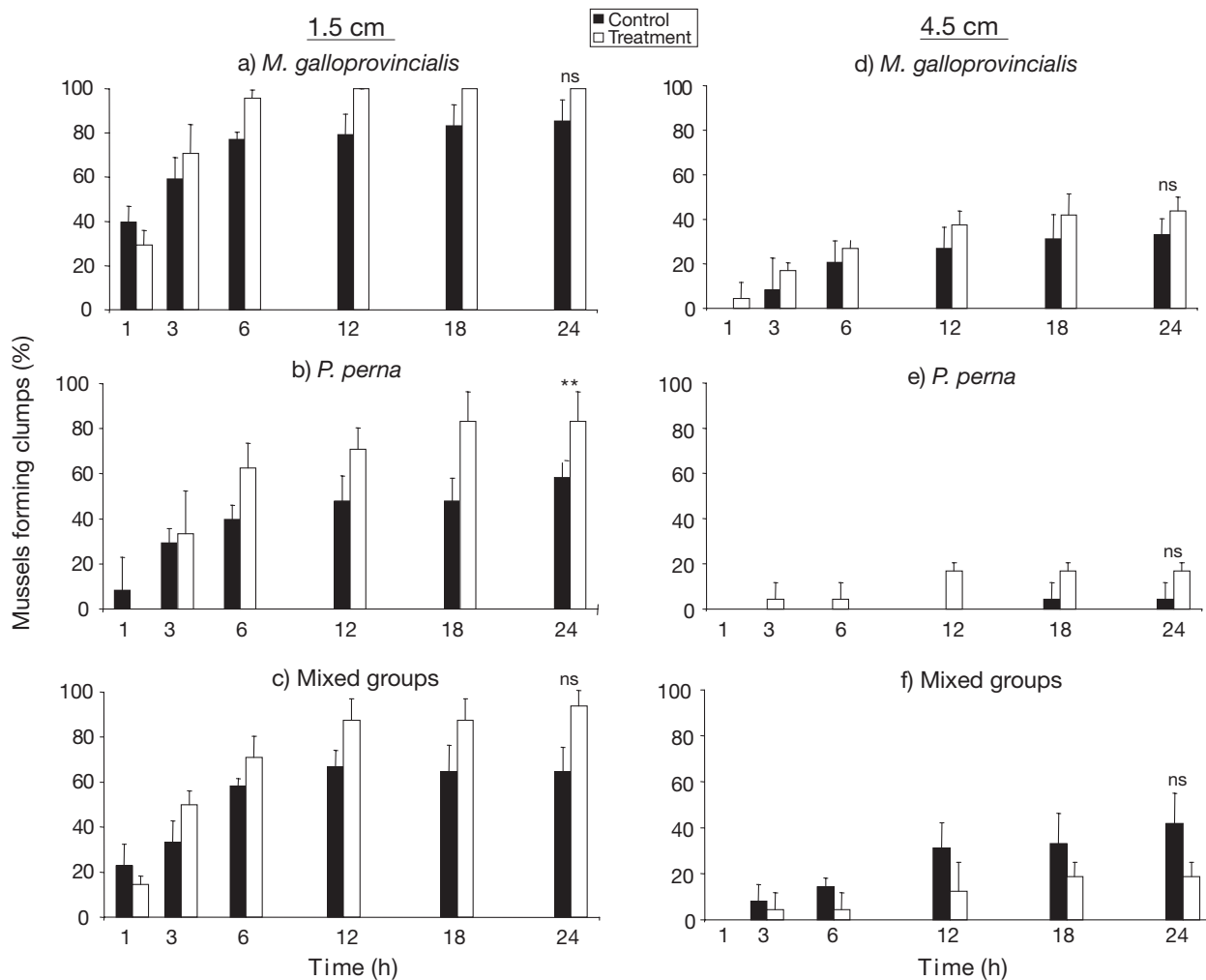


Fig. 1. *Mytilus galloprovincialis* and *Perna perna*. Percentage (+SD) of mussels forming clumps for mussels held in lobster effluent treatment and control seawater. (a,d) *M. galloprovincialis*, (b,e) *P. perna* and (c,f) mixed species groups for mussels at a distance of (a–c) 1.5 cm, and (d–f) 4.5 cm. Results of Tukey's post hoc comparisons of control vs. treatments at 24 h shown. ns: non-significant; **p < 0.001

The proportions of individuals of *Mytilus galloprovincialis* and *Perna perna* involved in mixed clumps after 24 h did not differ significantly in either experiment (data not shown).

Crawling distance

Expt 1 (lobster effluent)

Neither species showed a significant treatment effect (Kruskal-Wallis test: $p = 0.3$ and 0.4 for *Perna perna* and *Mytilus galloprovincialis*, respectively), but there was a significant difference between species when subjected to the treatment (Kruskal-Wallis test: $p > 0.01$; Fig. 3a).

Expt 2 (damaged conspecifics)

There was a significant species \times treatment interaction, with no significant difference between species under control conditions (Tukey's test: $p = 0.8$); how-

Table 2. Results of 2-way ANOVA applied to number of mussels forming clumps after 24 h in Expt 2 (damaged conspecifics) with treatment and species as fixed factors

Source of variation	df	MS	F	p
Treatment	1	76.06	40.26	<0.0001
Species	2	7.72	4.09	0.04
Treatment \times Species	2	1.06	0.56	0.59
Error	12	1.89		

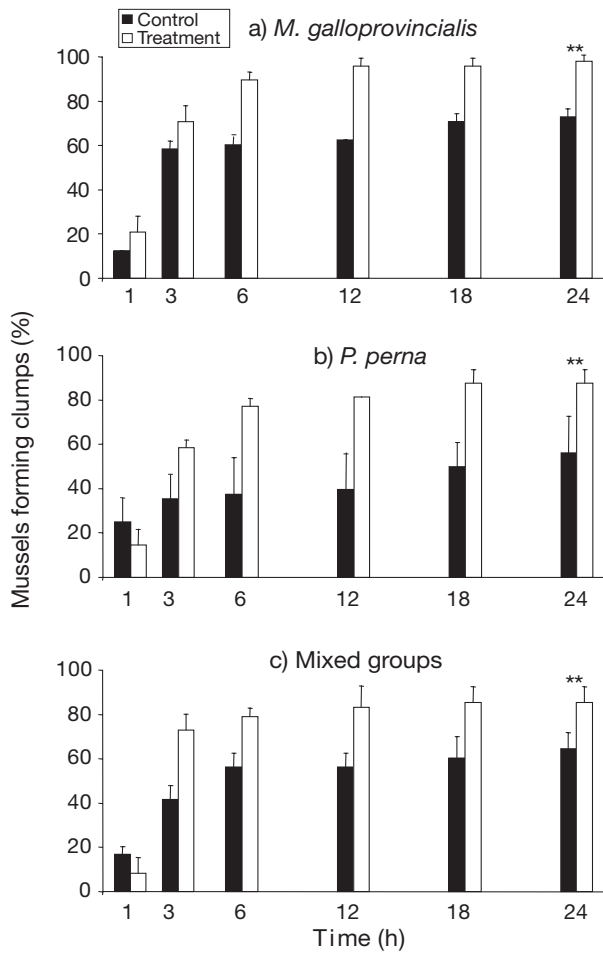


Fig. 2. *Mytilus galloprovincialis* and *Perna perna*. Percentage (+SD) of mussels forming clumps for mussels in the presence of damaged conspecifics and in control seawater. (a) *M. galloprovincialis*, (b) *P. perna* and (c) mixed species groups at a distance of 1.5 cm. Results of Tukey's post hoc comparisons of control vs. treatments at 24 h shown. ns: non-significant; **p < 0.001

ever, *Mytilus galloprovincialis* crawled farther than *Perna perna* when exposed to effluent from damaged conspecifics (2-way Model I ANOVA: p < 0.001; Fig. 3b). Again, there was no significant treatment effect for either species (p = 0.8).

Foot measurements

The slopes of regressions for shell length against foot width for the 2 species were homogenous (t = 8.86, df = 50, p < 0.001; MS = 26.38760 for shell length and MS = 4.47088 for species, error = 0.29713). The 1-way ANCOVA showed that, over the entire range of shell lengths, the foot was significantly wider in *Perna perna* than in *Mytilus galloprovincialis* (p < 0.001; Fig. 4).

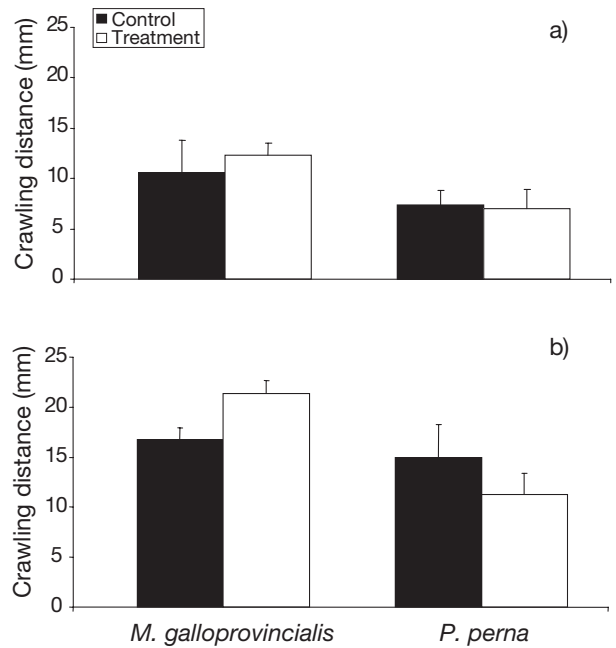


Fig. 3. *Mytilus galloprovincialis* and *Perna perna*. Crawling distance (+SD) in the first 3 h of the experiment for mussels held in (a) control seawater and lobster effluent and (b) control seawater and in the presence of damaged conspecifics

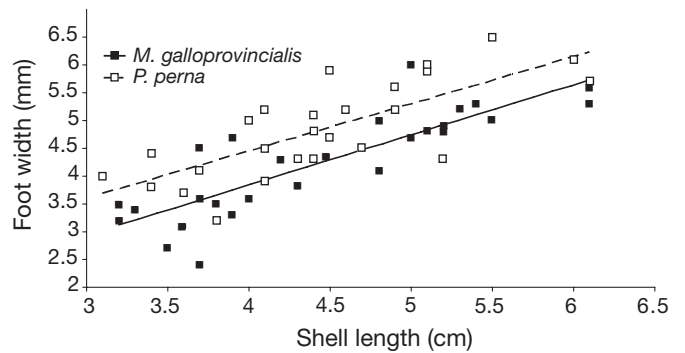


Fig. 4. *Mytilus galloprovincialis* and *Perna perna*. Relationship between shell length and maximum foot width. *M. galloprovincialis*: $y = 0.9012x + 0.2387$, $R^2 = 0.7034$, n = 30; *P. perna*: $y = 0.8502x + 1.0525$, $R^2 = 0.5724$, n = 30

DISCUSSION

In contrast to previous investigations of *Mytilus edulis* (Côté & Jelnikar 1999), our results show that initial distance has a significant effect on clumping behaviour; here, both mussel species clumped significantly more when the distance among individuals could be covered by the extended foot. This suggests that the detection of another mussel or of a solid object encourages clumping. Some studies have suggested

that mussel clumps are a result of random movement (e.g. Urya et al. 1996). However, other studies indicated chemotaxis as a promoter of aggregation, and recently it has been shown that tripeptides are the molecules involved in specific mussel communication (de Voys 2003). We suggest that mussels respond not only to chemical stimuli but also to tactile cues.

Mytilus galloprovincialis tended to crawl farther than *Perna perna* under treatment conditions and generally aggregated more in all experiments, underlining the greater mobility of the invasive species. Mussels move by extending the muscular foot between the valves attaching it and then contracting it, pulling themselves forward. Measurements of the fully contracted foot exclude the possibility that morphological differences are responsible for behavioural differences. *Perna perna* has a longer foot, but *M. galloprovincialis* exhibited a stronger effect of treatment on crawling distance (significant species \times treatment interaction). This suggests that responses to chemical cues, induced by the presence of nearby conspecifics, may be enhanced in the invasive species. *Perna perna* has higher byssal attachment strength than *M. galloprovincialis*, and is consequently more tolerant to hydrodynamic stress (Zardi et al. 2006), but this is balanced by a lower reproductive output than that of *M. galloprovincialis* (van Erkom Schurink & Griffiths 1991). Together with our results, this points to an evolutionary strategy in *P. perna* that emphasises safety against wave action. The indigenous species invests more in byssal production, whereas the invasive species adopts a more dynamic strategy, seeking aggregation or a safer arrangement.

In the mixed groups there was no species-specific attraction. The proportion of individuals involved in a clump was the same for the 2 species. The threat of predation did not enhance the speed of mussel locomotion. We thus exclude the possibility that the higher number of clumped mussels under treatment conditions is a consequence of enhanced crawling and random movement, and conclude that chemical attraction between mussels is involved.

Intraspecific behavioural and morphological comparisons have been made between individuals living in predator free environments and individuals living in areas where predation pressure is high. For example, Geller (1982) showed that gastropods from areas with high predation pressure from crabs responded strongly to chemical cues released by the crabs, whereas gastropods from sites where crabs were absent did not react. Similarly, crab and starfish effluent induced a weaker response in predator-free Baltic Sea mussels than in individuals from the North Sea (Reimer & Harms-Ringdahl 2001). Caro & Castilla (2004) proposed that the distribution and abundance of

predators in the field explain inter-population shell thickness differences in the mussel *Semimytilus algosus*. Because *Mytilus galloprovincialis* only invaded South Africa in the late 1970s, we initially hypothesised that its response to the local risk of predation would be relatively limited. Our results confirmed this hypothesis. Clumping behaviour of the invasive *M. galloprovincialis* was not influenced by the risk of rock lobster predation, whereas rock lobster effluent had a significant effect on the indigenous species. Given that the invasion of the European mussel is recent (Robinson et al. 2005), it is possible that the invasive species does not perceive the rock lobster as a predator. However, both species reacted to damaged conspecifics and the difference between the species was less pronounced when exposed to this general risk of predation, again supporting our initial hypothesis.

The European mussel has several properties that favour its spread on the South African coast, including resistance to parasites, desiccation and sand stress (van Erkom Schurink & Griffiths 1993, Calvo-Ugarteburu & McQuaid 1998, Zardi et al. 2006). Local predators can play a crucial role in regulating the interaction between invasive and indigenous prey, but given the generally low levels of predation pressure in South Africa (Bustamante & Branch 1996), the selective effect of predation probably does not drastically affect competition between these species on this coast.

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