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Facilitation and competition between invasive and indigenous mussels over a gradient of physical stress

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Abstract

The interactions between invasive exotic and indigenous species can have profound harmful effects on the recipient community; however, not all such interactions are negative. Facilitation is increasingly recognised as important in shaping natural communities and is believed to vary under different conditions. Earlier studies have shown that the indigenous intertidal mussel *Perna perna* initially facilitates survival of the invasive *Mytilus galloprovincialis* in the low mussel zone by providing protection against waves, but later excludes *M. galloprovincialis* through interference competition for space. Here, we examined interactions between these species in the mid and upper mussel zones, moving mussels to experimental plots in different combinations of densities and species. Mussels were left on the shore for more than a year and treatment effects on mortality, shell length and condition were compared. In the high zone, treatment had no effects and *P. perna* showed greater mortality than *M. galloprovincialis*, indicating that its exclusion from the high shore is due to emersion stress. In the mid zone, treatment had no significant effects on *M. galloprovincialis*, but multiple comparisons among treatments involving *P. perna* showed that facilitation occurred. *P. perna* survived better at higher densities, but survived even better when mixed with the physiologically more tolerant *M. galloprovincialis*. Length data indicated both inter- and intraspecific competition for *P. perna* in the mid zone. Whereas facilitation occurs strongly in the low zone (*P. perna* facilitates *M. galloprovincialis*) and weakly in the mid zone (*M. galloprovincialis* facilitates *P. perna*), the lack of facilitation in the high zone suggests that the probability of facilitation is not linearly linked to increasing physical stress. Instead it is likely to be hump shaped: relatively unimportant under conditions that are benign for a particular species, significant under more severe conditions, and overridden by physical stress under very harsh conditions.

Zusammenfassung

Die Interaktionen zwischen exotischen, invasiven und einheimischen Arten können grundlegende, schädliche Auswirkungen auf die Empfängerlebensgemeinschaft haben, wenn auch nicht alle dieser Interaktionen negativ sind. In zunehmendem Maße wird die Förderung als wichtiger Faktor bei der Formung von natürlichen Lebensgemeinschaften erkannt und es wird angenommen, dass sie unter verschiedenen Bedingungen variiert. Frühere Untersuchungen haben gezeigt, dass die einheimische Muschel der Gezeitenzone *Perna perna* zunächst förderlich für das Überleben der invasiven *Mytilus galloprovincialis* in der unteren Muschelzone ist, indem sie Schutz vor den Wellen bietet, aber

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M. galloprovincialis später durch Konkurrenz um Raum verdrängt. Wir untersuchten hier die Interaktionen zwischen diesen beiden Arten in der mittleren und oberen Muschelzone, indem wir Muscheln in Probeflächen mit verschiedenen Kombinationen von Dichten und Arten setzten. Die Muscheln wurden für mehr als ein Jahr an der Küste gelassen und dann die Auswirkungen der Behandlungen auf die Mortalität, die Schalenlänge und den Zustand verglichen. In der oberen Zone hatten die Behandlungen keinen Effekt und *P. perna* zeigte eine größere Mortalität als *M. galloprovincialis*. Dies wies darauf hin, dass ihr Ausschluss aus der oberen Zone auf den Stress durch Trockenfallen zurückzuführen ist. In der mittleren Zone hatten die Behandlungen keine signifikanten Effekte auf *M. galloprovincialis*, aber multiple Vergleiche der Behandlungen, die *P. perna* beinhalteten, zeigten, dass eine Förderung auftrat. *P. perna* überlebte besser bei hohen Dichten, jedoch noch besser, wenn sie mit der physiologisch toleranteren *M. galloprovincialis* gemischt war. Die Längenmessungen wiesen sowohl auf inter- wie intraspezifische Konkurrenz für *P. perna* in der mittleren Zone hin. Während die Förderung besonders stark in der unteren Zone (*P. perna* fördert *M. galloprovincialis*) und nur schwach in der mittleren Zone auftrat (*M. galloprovincialis* fördert *P. perna*), lässt das Fehlen der Förderung in der oberen Zone vermuten, dass die Wahrscheinlichkeit für eine Förderung nicht linear mit einem zunehmenden physikalischen Stress verbunden ist. Stattdessen scheint sie einer Maximumkurve zu folgen: relativ unbedeutend unter Bedingungen, die günstig für eine bestimmte Art sind, signifikant unter schwierigeren Bedingungen, und bei sehr harten Bedingungen von physikalischem Stress überspielt.

Keywords: Facilitation; Competition; *Mytilus galloprovincialis*; *Perna perna*; Mussels; Intertidal

Introduction

Invasive species can have profound deleterious effects on native ecosystems through changes to community functioning and biodiversity (Crooks & Khim 1999; Grosholz 2002; Vermeij 1996). Although most studies studying the interactions among invasive and native species have focused on competition (Bando 2006; Corbin & D'Antonio 2004; Piazzi & Ceccherelli 2002; Rius, Turon, & Marshall 2009), there is increasing recognition that facilitation can be important in such interactions (Bruno, Stachowicz, & Bertness 2003; Rodriguez 2006). This is believed to be particularly likely in situations where abiotic stresses are high (Stephens & Bertness 1991) and there are examples of facilitation from marine systems that include situations in which interactions between exotic and indigenous species may entail facilitation (Crooks 2002; Rodriguez 2006). This can be a simple effect of enhancing habitat complexity and providing habitats for associated species, as in the case of byssal mats formed by the exotic mussel *Musculista senhousia* (Crooks 1998; Crooks & Khim 1999) or facilitation of bivalve settlement by exotic macroalgae in both the Adriatic Sea and Australia (Bulleri, Airoldi, Branca, & Abbiati 2006; Gribben & Wright 2006).

The Mediterranean mussel *Mytilus galloprovincialis* is one of the most widespread marine invasive species worldwide (Branch & Steffani 2004; Carlton 1996) and is believed to have been introduced to South Africa around the 1960/1970s (Grant & Cherry 1985). It has subsequently spread along the entire west coast of the country, extending into Namibia and has more recently spread onto the south coast (Robinson, Griffiths, McQuaid, & Rius 2005). This has resulted in dramatic effects on the lower intertidal zone on both coastlines (Bownes & McQuaid 2006; Griffiths, Hockey, van Erkom Schurink, & Le Roux 1992; Steffani & Branch 2005). On the west coast, limpets and native mussels have been negatively affected (Branch & Steffani, 2004; Steffani & Branch 2003b). On the south coast, *M. galloprovincialis* has occupied the high mussel zone, and the indigenous brown mussel *Perna perna*, which is an important resource for small-scale fisheries (Dye, Schleyer, Lambert, & Lasiak 1994; Lasiak & Dye 1989), is limited to the mid and low mussel zones (Bownes & McQuaid 2006). There are, however, differences in the ecology of *M. galloprovincialis* on the two coasts. On the west coast, *M. galloprovincialis* extends to the sublittoral fringe and shows optimum performance on moderately exposed shores, where it has been an especially aggressive invader (Steffani & Branch 2003b, 2005). On the south coast, wave action, particularly during storms, is one of the leading factors determining mussel distribution (Erlandsson, Pal, & McQuaid 2006; Zardi, Nicastro, McQuaid, Rius, & Porri 2006); *M. galloprovincialis* is most abundant under moderately sheltered conditions and occurs on the low intertidal only at extremely low densities (Bownes & McQuaid 2006; Erlandsson et al. 2006). Within the zones occupied by mussels, *M. galloprovincialis* now numerically dominates the high shore, while *P. perna* dominates the low shore and the two mussels co-exist in mixed beds on the mid shore (Robinson et al. 2005). In addition, patterns of recruitment in these three mussel zones differ between the two species (Bownes & McQuaid 2006). Thus, the distributions of the two species within the zone occupied by mussels result from a combination of biotic and physical conditions along a gradient of multiple stresses: while wave action decreases upshore, aerial temperature and desiccation stress increase.

There is evidence of interference competition between *P. perna* and *M. galloprovincialis* on the low shore, but the relationship is not simple. *M. galloprovincialis* is negatively affected by wave action and monospecific plots of *M. galloprovincialis* translocated from higher on the shore show 100% mortality due to waves. When experimentally mixed with *P. perna*, *M. galloprovincialis* initially shows much higher survival though it is later eliminated by competition (Rius & McQuaid 2006). As it has been suggested that the strength of both facilitation and competition can vary along gradients of stress (Bruno et al. 2003; Menge & Branch 2001; Steffani & Branch 2003b), we examined facilitation and competition between these two mussels in the mid and high mussel zones, recognising that wave action decreases upshore (Zardi et al. 2006), while desiccation and thermal stress intensify (Petes, Menge, & Murphy 2007). Our prediction was that on the mid shore, where wave action is stronger, *M. galloprovincialis* survival would be facilitated by *P. perna*, while in the high zone thermal stress or competition with *M. galloprovincialis* would exclude *P. perna*.

Materials and methods

The study was undertaken on a sandstone platform at Old Woman's River (33°30′S, 27°10′E), in the mid (Mean Low Water Neap-Mean High Water Neap) and high (Mean High Water Neap) mussel zones, following the methodology in Rius and McQuaid (2006), with some modifications (see below).

The experimental design, derived from Underwood (1986), involved treatments with combinations of species at different densities that allowed simultaneous examination of inter- and intraspecific competition. Densities of 25 and 50 mussels per 100 cm^2 in 5 treatments (see Table 1 for details) were used with 6 replicates on the high mussel zone, and 4 replicates on the mid zone. A total of 1000 individuals of each species (shell length 25–30 mm) were collected in situ and immediately placed within metal quadrats ($10 \times 10 \times 0.5$ cm) that had been positioned randomly within each mussel zone and attached to the substratum by screws. The surface where the quadrats were placed was scraped using a chisel to avoid any effects of the original community. Quadrats were covered with mesh (2 mm mesh size) that held the mussels firmly in place for the first 4 weeks. The mesh was then replaced with a framed lid to which a coarser mesh (4 mm) was loosely attached, offering some protection against wave action, but allowing both lateral and vertical growth. The experiments started on 15 May 2005 on the mid zone and on 27 May 2005 on the high zone, and both ended on 26 July 2006. This date was selected based on the fact that July is when both mussel species have shown lower condition (i.e. are not subject to gonadic fluctuations) in a nearby location (Zardi, McQuaid, & Nicastro 2007). The total initial number of quadrats was 50, of which 7 were lost by the end of the experiment due to wave action. These were, for the high zone one quadrat with 25 *M. galloprovincialis*, two with 25 *P. perna*, two mixed plots, and for the mid zone, one with 25 *M. galloprovincialis* and one mixed plot. At the end of the experiment, all surviving mussels were collected from the quadrats and taken to the laboratory for measurement of maximum shell length using Vernier callipers (precision 1 mm). Mussel condition was also measured following Calvo-Ugarteburu and McQuaid (1998), by calculating dry weight divided by the shell cavity volume. Because the mussels were not individually marked, we could not correlate individual shell measurements at the start and end of the experiment. New recruits appeared in some samples and were identifiable as being smaller than the original starting sizes. As transplanted mussels would have grown at least 5 mm during the experiment (Rius & McQuaid 2006), any mussels of <30 mm were considered to be recruits and were discarded from the analysis. These formed $<5\%$ of all mussels in each zone. We identified competition whenever a treatment showed a significant negative effect on mortality, shell length or condition, while facilitation was identified whenever a positive effect was detected.

Table 1. Design of the experiment used to investigate intra- and interspecific competition between *M. galloprovincialis* and *P. perna*.

Treatment	1	2	3	4	5
M. galloprovincialis	25	50	25	–	–
P. perna	–	–	25	25	50

Values in cells are numbers of mussels per quadrat. Note that the comparisons 2 versus 3 for *M. galloprovincialis* and 5 versus 3 for *P. perna* compare 25 individuals growing with 25 conspecifics against 25 individuals growing with 25 members of the other species. Thus, the effects of interspecific competition are confounded with the effects of intraspecific competition (i.e. there is a change in intraspecific density).

Because the experiment was started on different dates in the two zones, the data were analysed separately for each species and zone using 1-way analysis of variance (ANOVA), testing treatment as a fixed factor. Post-hoc multiple comparisons were done using Tukey's test. All tests were analysed using the SPSS computer program (SPSS Inc., version 15.0.1, 2006) and a critical probability of 5%.

Results

The mortality results showed that *M. galloprovincialis* performance was similar in all treatments in both zones

(Fig. 1A) and comparisons among treatments showed non-significant differences in mortality (both zones ANOVA, $P > 0.05$). Thus, an analysis of mortality provided no evidence for competition or facilitation for this species. For *P. perna*, mortality was higher in the high zone than in the mid zone (Fig. 1A). No significant effect of treatment was found in the high zone (ANOVA, $F_{2,13} = 0.047$, $P = 0.954$), while a marginally significant effect of treatment was found in the mid zone (ANOVA, $F_{2,8} = 4.279$, $P = 0.054$). Post-hoc comparisons showed that mortality in the mixed treatment was significantly (Tukey test, $P < 0.05$) lower than for the treatment with 25 *P. perna*. This indicates facilitation of *P. perna* survival by *M. galloprovincialis*.

P. perna had a greater mean final shell length than *M. galloprovincialis* in both mussel zones (Fig. 1B). No significant effects of treatment on shell length were found for *M. galloprovincialis* (both zones, $P > 0.05$). The effect of treatment for *P. perna* in the high zone was not significant (ANOVA, $F_{2,185} = 1.473$, $P = 0.232$) while in the mid zone the test showed significant effects (ANOVA, $F_{2,266} = 456.3$, $P < 0.001$). Shell length in the 25 *P. perna* treatment was significantly higher than in the mixed and 50 *P. perna* treatments (Tukey test, $P < 0.05$). This reduction in growth of mussels in higher density quadrats indicates both inter- and intraspecific competition.

Both species showed similar mean condition index values among zones (Fig. 1C). For *P. perna,* condition index values were similar among treatments, while *M. galloprovincialis* had a higher mean condition index in monospecific quadrats than in the presence of *P. perna* (Fig. 1C). However, no significant effects of treatment were found in either species (ANOVA, $P > 0.05$ in both cases).

Our results can be summarised by zone.

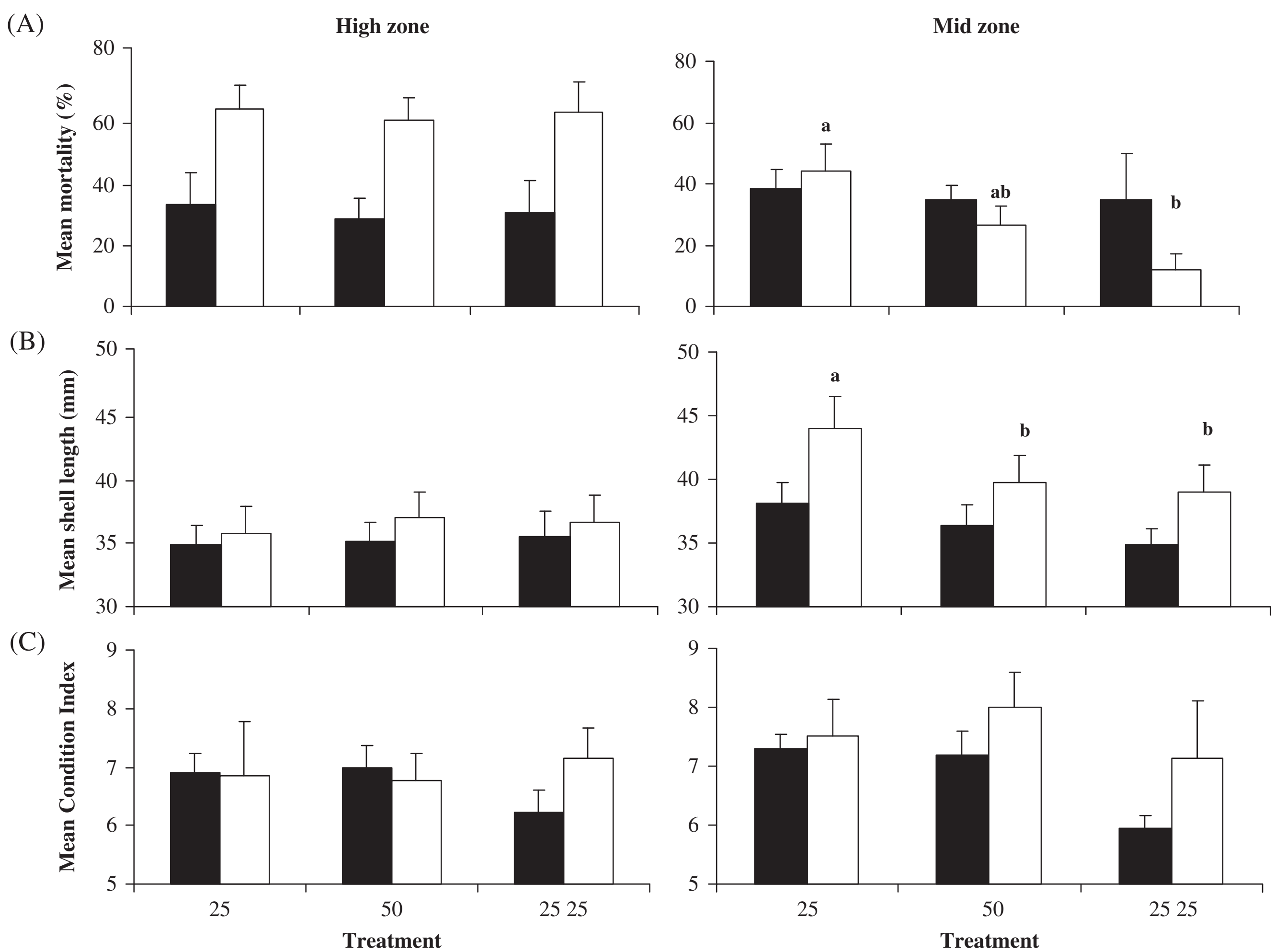

Fig. 1. Mean mortality (A), final mean shell length (B) and mean condition index (C) of *Mytilus galloprovincialis* (black bars) and *Perna perna* (white bars) among zones and treatments. Vertical bars denote standard errors, while identical letters above the bars indicate which treatments were not significantly different. Treatments are monospecific at densities of 25 or 50 and mixed (i.e. 25 25) at density of 25 per species.

High zone: mortality and final shell length were higher for *P. perna* than *M. galloprovincialis*, with no difference in condition and no evidence of either competition or facilitation.

Mid zone: final shell length was greater for *P. perna* than *M. galloprovincialis*, evidence of facilitation of *P. perna* survival by *M. galloprovincialis*, and of inter- and intraspecific competition effects on *P. perna*. Condition data suggested interspecific competition (*P. perna* affects *M. galloprovincialis*).

Discussion

In an earlier study, we described interspecific facilitation between two mussel species, which share the same broad niche requirements in terms of space and food. Survival of *M. galloprovincialis* on the lower shore was enhanced in the short term by *P. perna*, which has stronger byssal attachment (Zardi et al. 2006) and so protected *M. galloprovincialis* against wave action. However, *P. perna* eventually eliminated *M. galloprovincialis* through interspecific competition (Rius & McQuaid 2006). Thus, the interaction between these two species is bidirectional on the low shore (see also Kawai & Tokeshi 2006) and shifts from initial facilitation to later competition. In the present study, we did not find any harmful effects of *M. galloprovincialis* on *P. perna* or vice versa on the high zone, while in the mid zone, both facilitation (*M. galloprovincialis* reduced mortality of *P. perna*) and interspecific competition (*P. perna* negatively affected *M. galloprovincialis*) occurred.

P. perna in the high zone showed poorer survival than in the mid zone and than *M. galloprovincialis* in either zone. *P. perna* is normally rare or absent in the high zone (Bownes & McQuaid 2006). Because mortality was very similar among treatments for both species, with no signs of either intra- or interspecific competition, it is clear that survival of *P. perna* on the high shore is limited by abiotic conditions (van Erkom Schurink & Griffiths 1993). On the other hand, good survival of *M. galloprovincialis* in the high zone is due to its better tolerance to desiccation (Petes et al. 2007). In the mid zone, treatment had no effect on *M. galloprovincialis* survival. For *P. perna*, comparisons between the mixed treatment and 25 *P. perna* were significantly different, with lower mortality in the mixed quadrat, indicating that the presence of *M. galloprovincialis* enhanced the survival of *P. perna*. Thus, *M. galloprovincialis* in the mid zone can facilitate *P. perna* survival by providing a physical matrix within which *P. perna* is partially protected from desiccation and shows better survival.

Shell length data gave an indirect measure of growth rates and showed that both species had larger final sizes in the mid than the high zone. *P. perna* had longer shell lengths than *M. galloprovincialis* in both zones, reflecting its higher growth rate, but the difference was especially strong in the mid zone. Comparing treatments for each species, significant differences were found only in the mid zone for *P. perna* and indicated the negative effects of intraspecific competition on shell lengths in the plots with higher mussel densities. In mussel beds, intraspecific competition is an important factor determining mussel survival as mussels grow and space limitation produces an increase in adult mortality (Griffiths & Hockey 1987). In our study, *P. perna* in quadrats with high numbers of mussels (treatments with 50 mussels) in the mid zone showed (non-significantly) lower mortality than quadrats with 25 mussels, while mussel growth tended to be lower. This suggests that mussel growth is depressed at higher densities, while survival is enhanced, regardless of species composition.

In summary, *P. perna* shows intraspecific competition in the mid zone (this study) and the low zone (Rius & McQuaid 2006), and is eliminated from the high zone by both adult mortality due to abiotic stress (this study) and recruitment limitation caused by low settlement and high post-settlement mortality (Bownes & McQuaid 2006). *M. galloprovincialis* survives well in the high zone, while in the low zone *P. perna* directly affects the mortality of *M. galloprovincialis* through initial facilitation, followed by later exclusion (Rius & McQuaid 2006). In the mid zone, *P. perna* suppressed *M. galloprovincialis* growth and condition (sublethal effects), although these effects were not significant, whereas *M. galloprovincialis* significantly facilitated *P. perna* survival. Kawai and Tokeshi (2006) found that the facilitative effect of goose barnacles on mussel survival increased with increasing abiotic stress and it has been suggested that this is a general phenomenon (Bruno et al. 2003). However, Norkko, Hewitt, Thrush, and Funnell (2006) describe a case in which increased stress in the form of high suspended sediment loads reduced the facilitative effect of the soft-substratum bivalve *Atrina* on nearby fauna. This is closer to our finding that higher up the shore the effects of abiotic stress were so great as to override any advantages to *P. perna* of protection provided by *M. galloprovincialis*. It seems likely that the relationship between the effectiveness of facilitation and gradients of environmental stress is shaped like a camel's hump, with weak effects when conditions are either so benign that facilitation is relatively unimportant, or so extreme as to overwhelm the positive effects of facilitation. However, it is important to identify the relevant stress. For *P. perna*, the critical stressor seems to be desiccation, which increases upshore, the low shore being a benign environment where no facilitation was recorded. In contrast, the high shore imposes such severe stress that facilitation is not effective and again was not detected. *M. galloprovincialis* has greater tolerance of desiccation than *P. perna*, but is less tolerant of wave action, which appears to be the critical stressor for this species. This accords with the finding of Steffani and Branch (2003a) on the west coast of South Africa that *M. galloprovincialis* thrives under conditions of moderate rather than strong wave exposure. On the south coast, the results from the present study and previous studies (Bownes & McQuaid 2006; Rius & McQuaid 2006; Zardi et al. 2006) indicate that *M. galloprovincialis* succeeds only under conditions of moderate wave stress. Overall, these results suggest that *M. galloprovincialis* will not be as successful on the south coast as it has been on the west coast, partly because it is outcompeted by *P. perna* on the low shore, and partly because it can facilitate survival of *P. perna* on the mid shore.

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