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Parasitism and invasive species: effects of digenetic trematodes on mussels

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ABSTRACT: The brown mussel *Perna perna* in South Africa is threatened by the introduction of the invasive Mediterranean mussel *Mytilus galloprovincialis*. Whilst the indigenous *P. perna* has been found to be commonly infected by digenetic trematodes, the invasive *M. galloprovincialis* is free of trematodes, which may give it a competitive advantage in direct or indirect interactions between the 2 mussels. The most common parasites infecting *P. perna* are 2 species of digenetic trematodes: metacercariae of the genus *Proctoeces* and bucephalid sporocysts. The influence of these 2 parasites on the ecological fitness of their host was tested by examining their effects on survival and competitive ability of *P. perna*. The results showed significant negative effects. Both parasites significantly depressed condition, but only after spawning, when the mussels were already stressed. Neither parasite affected mortality rate or gaping behaviour of *P. perna* exposed to air. *Proctoeces* did not affect the force required to open mussels or the amount of water lost by mussels in air. In contrast, mussels infected with bucephalid sporocysts were easier to open and lost significantly more water than non-infected individuals, possibly because their valves did not seal properly. There were no significant differences in either number or size of oocytes in females infected with *Proctoeces* compared with non-infected females. However, bucephalid sporocysts had a dramatic effect on reproduction by castrating the host. *Proctoeces* reduced growth both in summer and in winter, whilst bucephalid sporocysts had no significant effect on growth. Neither parasite had a significant effect on filtration rates or oxygen consumption of the host. All these results indicate that both *Proctoeces* and the bucephalid sporocysts have detrimental effects on *P. perna*. *Proctoeces* affects primarily growth, while bucephalid sporocysts affect reproduction, adductor muscle strength and water loss. The effects of both parasites are concentrated on those size classes of mussel which channel most energy into the portion of the energy budget affected by the parasite. *Proctoeces* affects growth only in the smaller individuals, which in normal conditions would put most energy into growth; bucephalid sporocysts castrate the bigger mussels, which would expend most energy on reproduction. In energetic terms, the absence of effects on filtration and respiration indicates that there was neither re-allocation nor compensation for the energy lost from production, but that it was simply re-routed to the parasite. These negative effects, together with the high prevalence of both parasites in *P. perna* along the South African coast and their absence in *M. galloprovincialis*, suggest that lack of these parasites may contribute to the success of *M. galloprovincialis*.

KEY WORDS: Mussels · Invasive · Indigenous · Trematodes · Ecological fitness · Condition · Water loss · Survival · Adductor muscle strength · Reproduction · Growth · Filtration · Respiration

INTRODUCTION

The importance of parasites as potential regulatory agents of populations has long been controversial. Since the suggestion of Anderson & May in the late 1970s that parasites can regulate host populations (Anderson & May 1978, May & Anderson 1978), many authors have shown that macroparasites can regulate host population abundance (Anderson 1978, Anderson & Crombie 1984, Scott & Anderson 1984, Blower & Roughgarden 1987, also see Kuris 1974). Not only can parasites regulate host populations, they can also affect host behaviour (reviewed by Poulin 1994), resulting in a decrease in fitness in most cases.

Despite this many authors have noticed a lack of ecological perspective in parasitological studies (Cheng 1967, Kinne 1983, Huxham et al. 1993). Likewise, ecol-

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ogists usually ignore the effects of parasites, and Lauckner (1986) goes so far as to question the validity of many marine ecological studies since they neglect the effects of larval digeneans on the ecosystem. Nevertheless, in the last few years there has been a considerable increase in this type of study. Many examples of how parasites may alter the behaviour of their host in such a way as to leave it more vulnerable to predators are provided in a book edited by Barnard & Behnke (1990) using examples from both terrestrial and aquatic ecosystems. Two typical marine cases are those described by Granovitch (1992) and Jonsonn & Andre (1992). Granovitch showed that trematodes affect the migration patterns of the intertidal snail *Littorina saxatilis*, preventing it from making its normal tidal migrations. Those snails that do not migrate during low tides are much more susceptible to predation by birds. Jonsonn & Andre found a correlation between digenetic trematode infection and loss of burrowing ability in the cockle *Cerastoderma edule*. Again, this impaired burrowing ability increased the susceptibility of cockles to predators. Price et al. (1986) reviewed different ways in which parasitism may affect the outcome of competition, and concluded that mediation by parasites is very common in nature and must be regarded as one of the major types of interaction in ecological systems.

A second question ecologists have busied themselves with for many years is that of biological invasions (e.g. Macdonald et al. 1986, Mooney & Drake 1986, Drake et al. 1989, Hengeveld 1989, Ramakrishnan 1991). The introduction of a new organism into an ecosystem usually creates general concern about its effects on the native biota. Aliens may influence the community by changing species diversity, community structure and function and/or the ecological processes that are dependent on the interaction between organisms, e.g. competition (Breytenbach 1986, Bruton & van As 1986, Ramakrishnan & Vitousek 1989). Competition between indigenous and introduced species is central to the study of biological invasions, and it has been suggested that parasite release is important in allowing an introduced species to become invasive (Bruton 1986).

The Mediterranean mussel *Mytilus galloprovincialis* was accidentally introduced to South Africa in the late 1970s (Grant & Cherry 1985), and it has since become invasive (van Erkom Schurink & Griffiths 1990, Hockey & van Erkom Schurink 1992). Griffiths et al. (1992) estimated that *M. galloprovincialis* constituted over 70% of the intertidal mussel biomass on the west coast of South Africa, having displaced the slower-growing *Aulacomya ater*. It is now spreading rapidly onto the south and east coasts (Phillips 1994), where it has the potential to compete with the indigenous mussel *Perna perna* (van Erkom Schurink & Griffiths 1990). Comparative studies performed by van Erkom Schurink & Griffiths (1991, 1993) and Hockey & van Erkom Schurink (1992) on the 4 major species of mussels present in South Africa nowadays indicate that *M. galloprovincialis* exhibits all the characteristics of an aggressive invasive species: it has a rapid growth rate under a wide range of environmental conditions, a high level of tolerance to physiologically limiting factors, which allows it to colonize marginal areas, and a higher reproductive potential than the 3 indigenous species have. All these characteristics have been considered by Ehrlich (1989) as attributes of a successful invasive.

Parasitic infections have been recognized as one of a number of stressful factors which may lower the resistance of the host and its ability to adapt to changing environmental conditions (Williams & Jones 1994). Whether the reason for the success of *Mytilus galloprovincialis* is its competitive superiority or its lack of parasites, there is no doubt that this species has become successfully established on the west coast of South Africa and has the potential to displace the indigenous *Perna perna* on the south and east coasts.

This paper is part of a broader study which attempts to bring together the topics of parasitology and marine ecology. In a previous paper (Calvo-Ugarteburu & McQuaid 1998) we have shown that the indigenous mussel *Perna perna* in South Africa is commonly infected by digenetic trematodes whilst the invasive *Mytilus galloprovincialis* is free of trematodes. The most common trematode species found in *P. perna* are metacercariae of the genus *Proctoeces* and bucephalid sporocysts, with infection rates of up to 62 and 49% respectively. Detailed information about these 2 digenean species will be given in a separate paper (Calvo-Ugarteburu & McQuaid unpubl.). The present paper attempts to assess the effects of these 2 digenetic trematodes on the survival and competitive ability of *P. perna*. A next step to be considered would be competition experiments between infected *P. perna* and non-infected *M. galloprovincialis* in an attempt to examine specific mechanisms by which parasites may affect interactions between both species of mussels as a possible example of parasite mediated competition.

The first part of this paper deals with the effects of both parasites on host survival, comparing mortality rates of infected and non-infected individuals under normal and stressful conditions. The effects of the parasites on factors that may indirectly affect survival, such as general condition, water loss and adductor mussel strength, are also considered. In the second part, the effect of the parasites on the competitive ability of their host is studied. One of the major factors shaping the composition of a mussel bed is competition

for space and food, with slower-growing mussels being at a competitive disadvantage (Kautsky 1982). In order to examine the effects of both parasites on the competitive ability of *Perna perna*, summer and winter growth rates for infected and non-infected mussels were compared. Likewise effects of parasites on the reproductive output of females were examined.

Finally, possible compensations for disruption of the energy budget by parasites were examined by testing for effects of parasitism on consumption (filtration rate) and respiration.

MATERIALS AND METHODS

Most of our tests compared the responses of infected and non-infected *Perna perna*, but infection rates of digenetic trematodes in mussels can only be determined *post hoc* by dissection of specimens. To reduce the number of mussels needed in the experiments, mussels were collected from populations on the south coast of South Africa where infection rates are high. Mussels from Kowie Point (33° 38' S, 26° 52' E) showed about 50% infection rates with *Proctoeces*, and approximately half of the mussels bigger than 70 mm from Hougham Park (33° 47' S, 25° 44' E) were infected with bucephalid sporocysts (Calvo-Ugarteburu & McQuaid 1998). Because infection was size dependent, different size classes of mussels were sometimes collected from the 2 locations. Mussels infected by each parasite were compared with non-infected individuals from the same site. Mussels seen to be infected with both parasites were discarded, but we have no doubt that in some cases heavy infection with bucephalid sporocysts masked the presence of *Proctoeces*. In the case of *Proctoeces*, the number of metacercariae was counted on some occasions, but most experiments only dealt with presence/absence of parasites and did not take different intensities of infection into account. Sporocysts undergo massive asexual reproduction within the host, and quantifying the number of sporocysts was not possible; here again we dealt with only presence/absence of parasites.

When dry weights were required, they were obtained by oven drying at 60°C for 48 h.

All data were tested for normality and homogeneity of variances prior to statistical analysis. If they did not fulfil the conditions for parametric tests, the appropriate transformations were done (Zar 1984). If after transformation the conditions were still not fulfilled, non-parametric tests were used as specified.

Condition index. Since several authors have reported a high correlation between condition index and the reproductive state of bivalves (Walne 1970, Gee et al. 1977, Pekkarinen 1991), condition index of infected and non-infected mussels was measured before (January-February) and after (April-May) the major spawning period. Mussels were collected from Kowie Point (length 60–85 mm) and Hougham Park (length 90–110 mm), and their condition was calculated as the ratio of dry weight to shell cavity volume. Total volume of each individual was measured using the water displacement method. Shell volume was measured by the same method, and the shell cavity volume was calculated as the total volume of the specimen minus the volume of the shell. Total length and weight of the mussels were also measured prior to dissection.

The soft tissues were removed, weighed (wet and dry) and examined for parasites.

The condition index was calculated as dry weight in grams divided by the shell cavity volume in millilitres multiplied by 100.

The condition indices of mussels with and without *Proctoeces* and bucephalid sporocysts were compared using *t*-tests. Separate tests were done for samples collected before and after spawning

Gaping, water loss and survival. Mussels between 60 and 90 mm long were collected from Kowie Point & Hougham Park. One hundred mussels from each locality were weighed and placed upright in the laboratory, simulating their orientation in the field, with the anterior end down. Relative humidity was kept between 10 and 30% and temperature between 20 and 30°C. Observations were made at 2 h intervals to record gaping. All individuals with valves parted were recorded as gaping, without the width of the gape being taken into account. Mussels were weighed every 6 h to measure loss of water. Under natural conditions *Perna perna* is never exposed to air for more than 12 h. Therefore, the number of infected and non-infected mussels that died in the first 12 h and the amount of water that mussels with and without parasites lost in that period were compared using a Student's *t*-test. For mussels from Kowie Point, a Spearman's correlation test was carried out to check for possible relationships between the number of times the mussels gaped in the first 12 h and the number of *Proctoeces* they contained.

In order to check whether the effects of the parasites were more marked under stressful situations, the experiment was continued until the mussels died. The experiment lasted for 84 h, by which time all the mussels had gaped and failed to react to probing and were therefore considered to be dead. The final weight of each mussel was recorded as it was declared dead. Mussels were then dissected and examined for parasites.

For each mussel, the time it took to die, the number of times it gaped and the loss of weight during that time, the presence or absence of *Proctoeces* and bucephalid sporocysts, the number of *Proctoeces*

metacercariae present and the dry weight were recorded.

Total mortality rates and the mean amount of water lost by infected and non-infected mussels were compared using *t*-tests. The relationships between the number of *Proctoeces* and the number of times the mussels gaped were studied using Spearman's correlation coefficient.

Adductor muscle strength. Mussels from Kowie Point (65–85 mm) and Hougham Park (85–105 mm) were collected in order to test for the effect of parasites on the strength of the adductor muscle.

The force needed to open mussels was measured with an Instron 4301 apparatus. Two small hooks (5–10 mm long) were inserted into the byssus opening on the anterior ventral surface of the mussels and attached to the jaws of the machine. The machine was run with a uniform speed of separation of the jaws of 100 ± 20 mm min^{-1} until the mussel stopped offering resistance. The highest force reached during this procedure was recorded. The mussels were then dissected and examined for parasites. The strength of the mussels was recorded as Newtons needed to force them open per gram of dry weight. Samples were compared using a *t*-test.

Reproduction. Prevalence of *Proctoeces* is much higher in females that in males (Calvo-Ugarteburu & McQuaid 1998) and only females were used to study the effects of parasites on reproduction. Four females infected with *Proctoeces* and 4 non-infected females were dissected. A small portion of the gonad was weighed and placed in Davidson's fixative for histological examination. Five 7 µm sections 70 µm apart were cut from each gonad and stained with haematoxylin-eosin to study the reproductive state of the mussel. The number of oocytes present in 3 random microscope fields per section was counted, and 20 oocytes that had been cut through the nucleus were measured in each section using a graduated ocular. The number of oocytes and mean oocyte size in infected and non-infected females were tested using a nested ANOVA (Zar 1984).

In mussels infected with bucephalid sporocysts the gonad is almost obliterated and it is often not possible to determine the sex of the host. Ten animals with parasites, and 10 non-infected females were dissected and processed as above.

Growth. A size range of mussels (20 to 90 mm) was collected in October 1992 from Kowie Point (n = 1300) and Hougham Park (n = 260). The shell of each mussel was cleaned and measured and individuals were marked by glueing a small plastic tag to the shell. The mussels were then placed in mesh cages and hung in the sea at approximately 2 m depth in a mussel farm at Port Elizabeth (33° 58' S, 25° 38' E). Mesh size was 1 cm, which is large enough to ensure a continuous flow of water through the cages and small enough to retain the smaller mussels. In order to check whether the mussels acquired new infections during the experiment, a random subsample (n = 10 to 20) was taken every month and rates of infection were checked. The size of each individual was recorded monthly during summer (October 1992 to March 1993). At the end of this period the mussels were dissected and examined for parasites.

Growth rates for infected and non-infected mussels were compared using analysis of covariance, with the initial size of the mussels as a covariate, since growth rates decrease with increasing size (du Plessis 1977, Kautsky 1982, Crawford & Bower 1983, Cheung 1991). The presence or absence of parasites and, in the case of *Proctoeces*, host sex were the main effects. Subsequently, mussels were divided into six 10 mm size classes (Kowie Point: smallest size class <30 mm, largest class >70 mm; Hougham Park: <60 mm to >100 mm) to study size dependent effects of the parasites. The results were analyzed separately for each size class using the Mann-Whitney *U*-test. In order to assess whether the effects of the parasites differed between seasons, the experiment was repeated during winter (May 1993 to November 1993). During the winter experiment, initial sample sizes were 700 for each population. Size dependant effects were examined by dividing samples from each locality into seven 10 mm size classes (21 to 30 mm ... up to >80 mm), with 100 mussels in each size class for each locality. The results were again analyzed using ANCOVA and Mann-Whitney *U*-tests as above.

Filtration and respiration. *Perna perna* were collected from Kowie Point (60 to 85 mm length) and Hougham Park (70 to 95 mm length). The mussels were then transferred to the laboratory, cleaned of fouling organisms and maintained in a re-circulating seawater system at a temperature of 17 to 20°C and a salinity of 35‰. Mussels were fed twice a day with a suspension of the unicellular alga *Dunaliella salina* until used in experiments. A flow-through system was used to determine oxygen consumption and filtration rates simultaneously. From a header tank, water was distributed to sixteen 500 ml flasks. Fourteen of the flasks were occupied by 1 mussel each; the remaining two acted as controls and had no mussels. Each flask had an outgoing pipe which siphoned water from the immediate vicinity of the mussel. Outgoing water was collected in a bottom tank, from which it was pumped back to the header tank. Mussels were introduced into the system, with great care taken not to leave any air bubbles which would interfere with the oxygen readings, and left for 1 h to acclimate before readings were taken. The flow rate through

each of the flasks was kept between 2 and 20 ml min^{-1}.

Oxygen consumption was measured using an automatic multi-channel respirometer. Each of the outgoing pipes was connected to an oxygen electrode which was calibrated using the 2 control flasks. After allowing a couple of seconds for stabilization, the oxygen concentration from the water in the vicinity of the mussels was measured for 4 min. The difference in oxygen concentration between the control and the experimental flasks was considered to be the oxygen consumed by the mussels. For each mussel, oxygen consumption was noted after 1, 3 and 5 h.

Filtration rates were calculated from the difference in algal concentration between the control and experimental flasks. Sinking of algae was insignificant and the decrease in algal concentration was assumed to be due solely to the feeding activity of the mussels. After respiration was measured, 10 ml of water was collected from the outgoing pipe of each flask and diluted with 10 ml of electrolyte, and the number of algal cells was counted using a Coulter counter model ZM with an aperture of 5 µm.

Filtration and respiration rates were calculated according to the following equations:

$$F = \text{flow rate} \times (1 - \text{initial cell concentration}/\text{final cell concentration}) \quad (1)$$

$$R = \delta PO_2 \times \text{flow rate} \times 12.487 \quad (2)$$

where F is filtration rate, R is respiration and δPO_2 is the partial pressure of oxygen.

After all the measurements were taken the mussels were examined for parasites. Filtration rates and oxygen consumption were normalised to dry weight for each individual, and the data were then tested for normality and homogeneity of variances. Raw filtration rates deviated significantly from the assumption of homoscedasticity and were logarithmically transformed. Filtration rates and oxygen consumption were compared using a 2-way ANOVA, with the presence or absence of parasites and time as the main effects.

RESULTS

Condition index

The results of the t-tests showed that mussels infected with either parasite had a significantly lower condition index than non-infected mussels, but only in the samples taken after spawning (Table 1, $p < 0.05$ for both parasites). Neither parasite had a significant effect on the condition of the host before spawning (Table 1, $p > 0.05$ for both parasites).

Table 1 *Perna perna*. Condition indices of mussels with and without parasites (*Proctoeces* and bucephalid sporocysts) before and after spawning. p-values significant at $p < 0.05$

	Proctoeces		Bucephalid sporocysts	
	With	Without	With	Without
Before spawning				
Sample size	37	43	15	22
Mean	6.19	6.09	5.11	5.67
SD	1.12	1.13	1.00	1.22
	$p > 0.05$		$p > 0.05$	
After spawning				
Sample size	52	22	7	35
Mean	4.77	5.57	5.11	6.39
SD	1.18	1.35	1.43	1.53
	$p < 0.05$		$p < 0.05$	

Table 2. *Perna perna*. Amount of water lost (g water g^{-1} dry wt) by mussels with and without parasites after 12 h and at the end (after 84 h) of the gaping experiment. p-values significant at $p < 0.05$

	Proctoeces		Bucephalid sporocysts	
	With	Without	With	Without
12 hours				
Sample size	51	41	18	80
Mean	2.72	2.09	2.43	2.52
SD	2.92	1.27	1.57	2.09
	$p > 0.05$		$p > 0.05$	
84 hours				
Sample size	51	41	18	80
Mean	13.79	12.98	13.44	7.63
SD	7.23	5.61	5.55	2.64
	$p > 0.05$		$p < 0.01$	

Gaping, water loss and survival

The variances of the amount of water lost by mussels from Kowie Point after 12 h were not homogeneous, even after logarithmic transformation, therefore Mann-Whitney U-tests were used to compare water loss by infected and non-infected specimens. The results showed no significant differences for either parasite after 12 h ($p > 0.05$) nor for *Proctoeces* by the end of the experiment (Table 2). However, mussels infected with bucephalid sporocysts lost significantly more water than non-infected individuals by the time the experiment ended ($p < 0.01$; Table 2).

Spearman's correlation test for data on all mussels showed a significant positive correlation between the amount of water lost during the first 12 h and the number of times that the mussels gaped (Table 3, $p < 0.01$). However, there was no significant relationship between the presence or number of parasites and either the amount of water lost or the number of times the

mussels gaped during the first 12 h (Table 3). This situation had changed by the end of the experiment, at which stage there was no significant relationship between the water lost and the gaping behaviour of the mussels (Table 3). At the end of the experiment, again, there was no significant correlation between the number of *Proctoeces* and either the amount of water lost by the mussels or the number of times they gaped (Table 3). However, the presence of bucephalid sporocysts was associated with a significant increase in the amount of water lost by the mussels (Table 3).

Fig. 1 represents the survival of mussels with and without parasites when exposed to air. No mussels died during the first 12 h. The *t*-tests comparing the mean time that infected and non-infected mussels took to die showed no significant differences for either *Proctoeces* or bucephalid sporocysts ($p = 0.68$ and $p = 0.23$ respectively).

Table 3. *Perna perna*. Values of r generated by Spearman's correlation tests on the relationships among parasitism, frequency of gaping and water loss of mussels after 12 h and at the end (after 84 h) of the gaping experiment. p-values significant at $p < 0.05$

	12 hours		84 hours	
	Gaping	Water lost	Gaping	Water lost
Proctoeces				
Presence	0.19 ($p > 0.05$)	0.08 ($p > 0.05$)	0.15 ($p > 0.05$)	0.01 ($p > 0.05$)
Number	0.14 ($p = 0.05$)	0.07 ($p > 0.05$)	0.13 ($p > 0.05$)	0.01 ($p > 0.05$)
Water lost (all mussels)	0.34 ($p < 0.01$)		0.04 ($p > 0.05$)	
Bucephalid sporocysts				
Presence	0.04 ($p > 0.05$)	0.001 ($p > 0.05$)	0.15 ($p > 0.05$)	0.48 ($p < 0.01$)
Water lost (all mussels)	0.34 ($p < 0.01$)		0.15 ($p > 0.05$)	

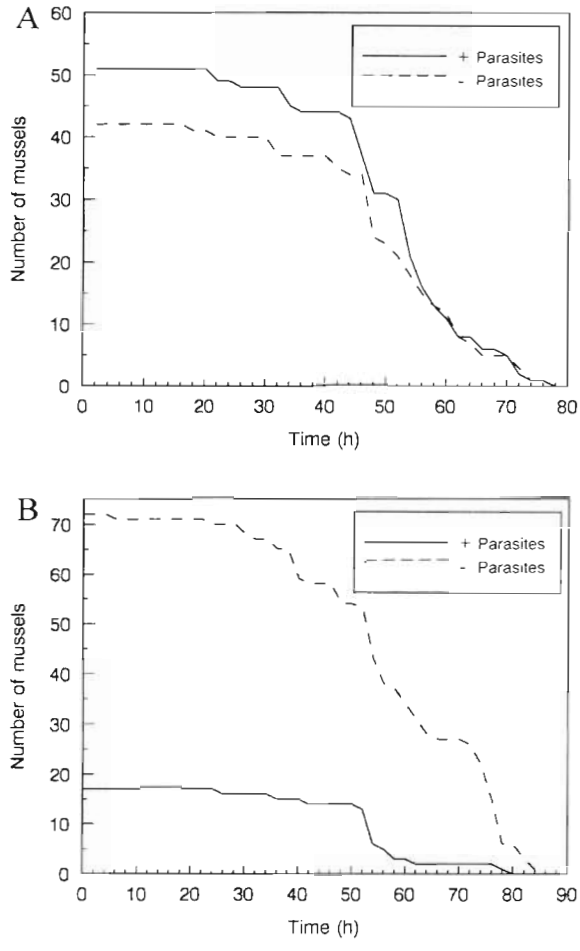

Fig. 1. *Perna perna*. Survival of mussels with (+) and without (–) *Proctoeces* (A) or bucephalid sporocysts (B) when exposed to air

Adductor muscle strength

To allow for differences in size, the force required to open mussels was standardized to dry body weight. In the case of mussels infected with *Proctoeces*, the variances were not homogeneous; therefore, the data were logarithmically transformed and compared using a *t*-test. There was no significant difference in the force required to open *Proctoeces*-infected and parasite-free mussels (Table 4, $p > 0.05$). In the case of the sporocysts, a significantly greater force was needed to open non-infected mussels than infected ones ($p < 0.05$). More force was needed to open mussels from Kowie Point than mussels from Hougham Park, even though they were smaller.

Table 4. *Perna perna*. Newtons per gram dry body weight needed to force open infected and non-infected mussels. p-values significant at $p < 0.05$

	Proctoeces		Bucephalid sporocysts	
	With	Without	With	Without
Sample size	41	21	18	47
Mean	85.84	76.29	51.43	59.70
SD	22.38	14.16	14.81	13.40
	$p > 0.05$		$p < 0.05$	

Reproduction

Histologically and morphologically, the ovaries of mussels infected with *Proctoeces* are identical to those of non-infected individuals. The nested ANOVA com-

paring the number of oocytes in infected and non-infected females showed no significant differences in oocyte number owing to *Proctoeces* (5% of the variation); most of the variation observed (84%) was due to the microscope field examined.

Likewise, nested ANOVA indicated that mean oocyte diameter did not vary significantly between individual mussels (0.3% of the variation), nor was it affected by the presence of *Proctoeces* (1.3%). Histological examination of individuals infected with bucephalid sporocysts revealed that all of them were completely castrated, with no trace of sex products left, so that it was not possible to count or measure oocytes.

Growth

Data on infection rates in the subsamples of 10 to 20 mussels taken every month showed that infection rates stayed constant during the whole experiment (Chi-squared test, $p > 0.05$).

Growth rates of mussels with and without *Proctoeces* or bucephalid sporocysts are shown separately for summer and winter months in Fig. 2. Analysis of covariance using initial size as a co-variate showed that sex had no significant effect on growth. However, mussels infected with *Proctoeces* grew significantly less than non-infected mussels both in summer and in winter (Table 5).

Mann-Whitney *U*-tests comparing growth rates of mussels with and without parasites in each of the 6 size classes showed that *Proctoeces* had a detrimental effect on the growth of only the smallest individuals ($p < 0.05$ for mussels <30 mm during both summer and winter). Although infected mussels grew less than non-infected individuals in most of the other size classes, the differences were not statistically significant ($p > 0.05$ for all size classes >30 mm; Fig. 3).

In the case of mussels infected with bucephalid sporocysts, it was not possible to determine the sex of infected animals in most cases, therefore the ANCOVA used only parasitism as a main effect. The presence of parasites had no significant effect on the

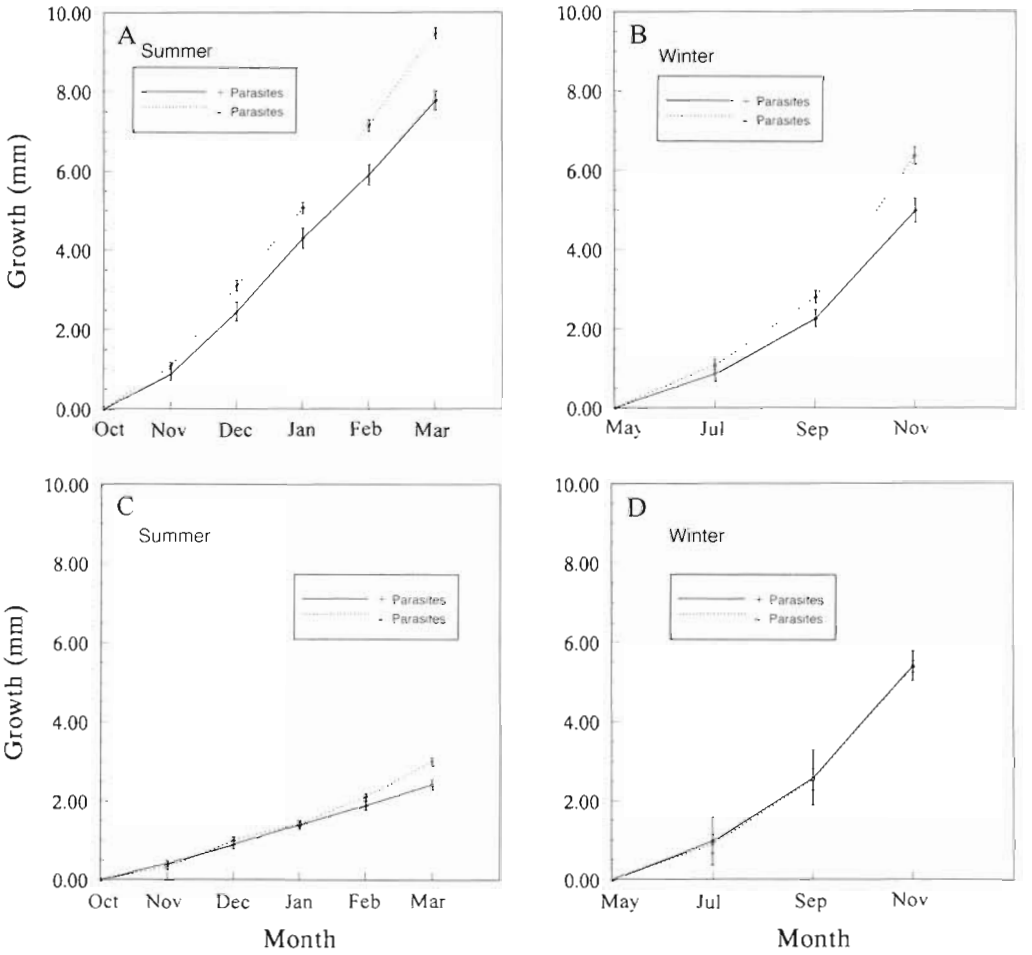

Fig. 2. *Perna perna*. Growth rates of mussels with (+) and without (–) *Proctoeces* (A, B) or bucephalid sporocysts (C, D) in summer and winter. Means ± SD

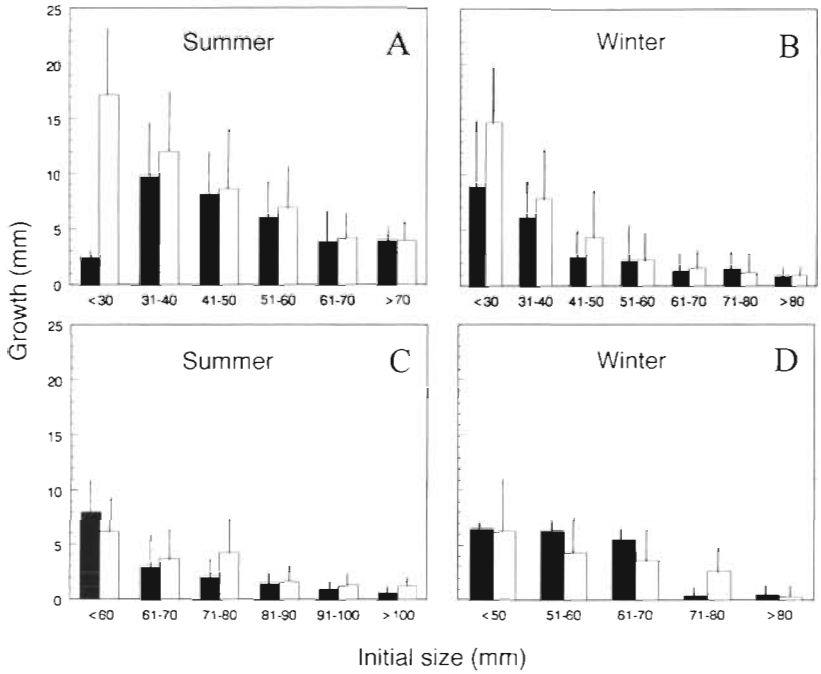

Fig. 3. *Perna perna*. Growth rates of different size classes of mussels with (solid bars) and without (open bars) *Proctoeces* (A, B) or bucephalid sporocysts (C, D) during summer and winter. Means + SD

growth of the host either in summer or in winter (Table 6). However, the Mann-Whitney *U*-tests showed that mussels of 71 to 80 mm with sporocysts did grow significantly less than non-infected individuals of the same size ($p < 0.05$ both in summer and in winter, Fig. 3).

Table 5. Results of analysis of covariance (using initial size as a covariate) comparing growth rates of *Perna perna* with and without *Proctoeces* during summer and winter months. p-values significant at $p < 0.05$

Source of variation	S	df	*F*-ratio	p
SUMMER				
Covariate:				
Size	4320.66	1	180.01	< 0.01
Effects:				
Sex	45.36	1	1.89	> 0.05
Parasite	124.66	1	5.19	< 0.05
Interactions	30.23	1	1.26	> 0.05
Residual	10681.28	445		
WINTER				
Covariate:				
Size	4071.87	1	219.36	< 0.01
Effects:				
Sex	4.37	1	0.23	> 0.05
Parasite	76.93	1	4.14	< 0.05
Interactions	128.15	1	6.90	< 0.01
Residual	6719.52	362		

Filtration and respiration

Fig. 4 shows filtration rates (l h^{-1} g^{-1} dry wt) of *Perna perna* with and without metacercariae of *Proctoeces* and bucephalid sporocysts. Neither *Proctoeces* nor the sporocysts had a significant effect on the filtration rates of the mussels ($p = 0.5$ and 0.9 respectively). In both cases filtration was highly dependent on time ($p < 0.01$ for both parasites), with lower filtration rates as time increased.

A 2-way ANOVA showed that respiration was not significantly influenced by either time ($p > 0.05$ for both parasites) or the presence of parasites ($p = 0.09$ for *Proctoeces* and $p = 0.41$ for bucephalid sporocysts) (Fig. 5). There were no significant interactions between the effects of the parasite and time for either parasite.

DISCUSSION

The first set of tests examined the effects of the 2 parasites on the general health and survival of *Perna perna*. Condition indices are considered to be good indicators of the health status of bivalves, although they may be affected by many factors. Fluctuations of

Table 6. Results of the analysis of covariance (using the initial size as a covariate) comparing growth rates of *Perna perna* with and without bucephalid sporocysts during summer and winter months. p-values significant at $p < 0.05$

Source of variation	S	df	*F*-ratio	p
SUMMER				
Covariate:				
Size	326.67	1	75.17	< 0.01
Effects:				
Parasite	12.02	1	2.77	> 0.05
Residual	604.01	139		
WINTER				
Covariate:				
Size	5659.82	1	301.08	< 0.01
Effects:				
Parasite	0.02	1	0.001	> 0.05
Residual	6109.56	325		

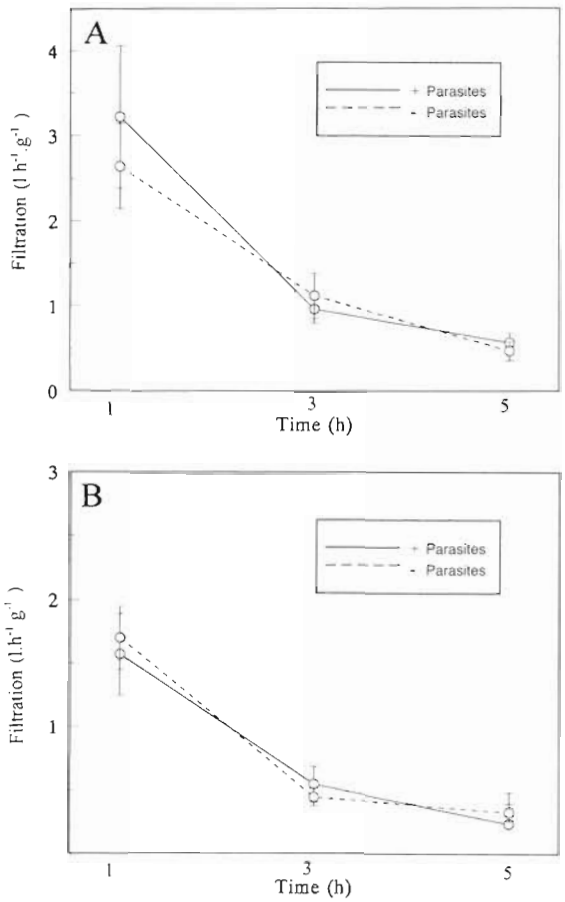

Fig. 4. *Perna perna*. Filtration rates of mussels with (+) and without (–) *Proctoeces* (A) or bucephalid sporocysts (B). Means ± SD

condition have been reported to result from environmental stressors, such as thermal stress and starvation (Gee et al. 1977) and exposure to parasites (Kent 1979, Pregenzer 1981, Theisen 1987, Gauthier et al. 1990). Several authors have noticed seasonal changes in the condition of bivalve molluscs, and have related them to the gametogenic cycle (Baird 1966, Walne 1970, Gee et al. 1977, Kent 1979, Pekkarinen 1991).

Previous studies on the effects of bucephalids on the condition of the host have shown contradictory results. Whilst Gauthier et al. (1990) found that oysters infected with *Bucephalus* tend to have low values of condition index, Pekkarinen (1993) concluded that unionid mussels infected with bucephalid sporocysts did not always have a lower condition than non-infected individuals. This could be the result of seasonal differences in the timing of the 2 studies. It could also be due to experimental error. Since the bucephalid sporocysts infiltrate the gonad of the host, eventually replacing it, distinction between gonad tissue and parasite tissue is not always possible. Thus this method is not very accurate for this parasite and the results are not always completely reliable.

The results of our study show that there was no apparent effect of either *Proctoeces* or bucephalid sporocysts on the condition index of *Perna perna* before spawning, but that both parasites had a negative effect on condition after spawning (Table 1). This would agree with the results of those authors who have found a deleterious effect of parasites only under stressful situations (Hepper 1955, Bayne et al. 1978). Spawning can be considered a natural stressor since it can cause a reduction in filtration rate and post-spawning individuals are frequently depleted of energy reserves (Newell & Barber 1988). Our results also raise the question of why the bucephalid sporocysts have a negative effect on condition after spawning if they castrate the host. A possible answer may be related to the degree of infection and castration, since only the presence/absence of sporocysts was considered and not the intensity of infection.

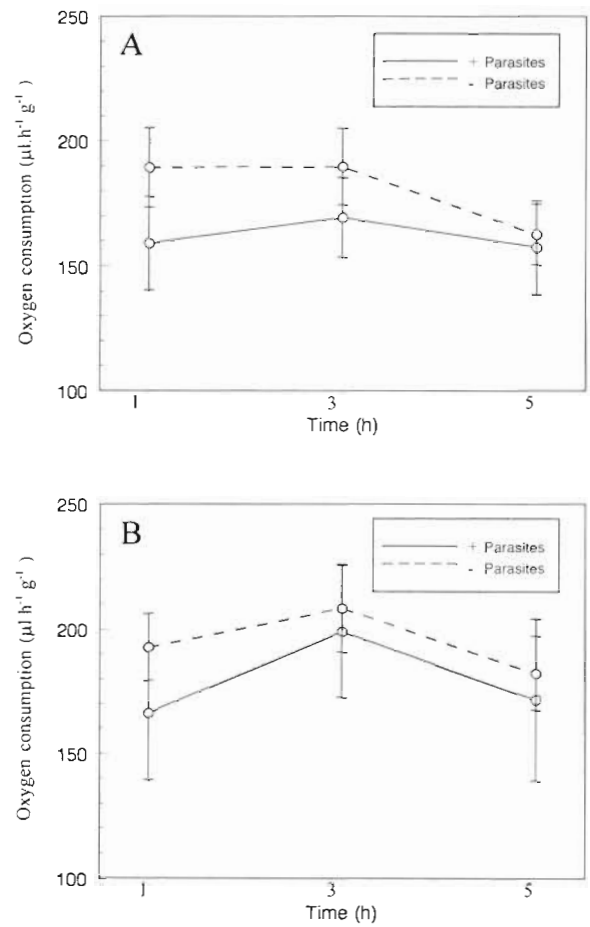

Fig. 5. *Perna perna*. Oxygen consumption of mussels with (+) and without (–) *Proctoeces* (A) or bucephalid sporocysts (B). Means ± SD

Even if parasites affect the host only when it is already under some sort of environmental stress, the importance of these effects must not be underestimated. As Zuk (1987) pointed out, parasites which exert detrimental effects only when environmental conditions are stressful may have a profound effect on host biology.

With respect to mortality, even when exposed to air for abnormally long periods, there were no significant differences in the time that infected and non-infected mussels took to die. Indeed, not one mussel died in the first 12 h of the gaping experiment (Fig. 1), which is longer than they would be exposed to air in the field. However, while parasites did not affect mortality in relation to air exposure, there was an effect on water loss.

Mussels are facultative anaerobes, and when exposed to air they have 2 alternatives: they may close their valves and switch to anaerobic metabolism, minimizing the risk of desiccation, but using energy reserves less efficiently, or they may carry on with aerobic metabolism. Marshall & McQuaid (1993) suggested that *Perna perna* relies on aerobic metabolism during air exposure, which implies a certain degree of shell gaping. Under natural conditions, mussels do not gape all the time, but open and close the valves according to their oxygen demands, losing some water every time they gape. The results of this experiment showed that there was a correlation between the number of times the mussels gaped and the amount of water they lost during the first 12 h (Table 3).

By the end of the experiment there was no significant relationship between water loss and the number of times that the mussels gaped. In the case of individuals from Kowie Point (non-infected and those infected with *Proctoeces*), the amount of water lost at the end of the experiment was not related to the time that the mussels spent out of water either. Nor did the presence of *Proctoeces* affect water loss. Mussels from Hougham Park showed different behaviour. For them, there was again no significant relationship between the amount of water that the mussels lost and the number of times they gaped, but the longer the mussels were exposed to air the more water they lost. Also, specimens infected with bucephalid sporocysts lost significantly more water than non-infected specimens (Table 2). This increase in water loss was not the result of parasite-induced abnormal gaping behaviour as there was no relationship between presence of parasites and the number of times the mussels gaped. An alternative explanation is that the mussels, when not gaping, did not seal the valves properly and continuous evaporation of water took place. This conforms with the observed weakening of the adductor muscle by bucephalid sporocysts (Table 4).

Weakening of infected hosts has been noticed before (Howell 1967, Canzonier 1972) and, apart from the effect on the amount of water lost, it has obvious ecological implications by rendering the host more susceptible to certain predators. This debilitation of the mussels would not affect predation by all predators. For example, octopuses which fail to pull a mussel open instead drill a hole in it, inject saliva, which paralyses the adductor muscles, and then pull it open (McQuaid 1994); in this case the strength of the mussel affects how it is killed, not whether it is killed. But weakening of the adductor muscles may facilitate predation by other animals such as starfish. Norberg & Tedengren (1995) measured the force applied by *Asteria rubens* trying to open mussels and found that the starfish applied a maximum force between 7.6 and 70 Newtons (cf. Table 5). Jonsson & Andre (1992) noticed that cockles *Cerastoderma edule* heavily infected with *Cercaria cerastodermae* were slow to close their valves and on several occasions they found the whelk *Nassarius reticulatus* attacking gaping cockles that were not yet dead. Similarly, Howell (1967) observed shrimps probing between the valves of gaping oysters which were heavily infected with *Bucephalus longicornutus*. Although bucephalid sporocysts do not directly affect mortality of the mussels, it is possible that, through the weakening of the adductor muscle, this parasite may make *Perna perna* more susceptible to some predators.

The second aspect we considered was the effect of parasites on the competitive abilities of *Perna perna*. One of the main effects of trematode infection in molluscs is parasitic castration. This may lead to an increase in growth rate and/or gigantism as energy formerly allocated by the host to reproduction is put into somatic growth (e.g. Wright 1971, Wilson & Denison 1980, Sluiters 1981). However, the effect on growth rate may depend on the timing of infection. If destruction of the gonad occurs before the host is reproductively active it will not free energy since the host was not using energy for reproduction. In this case, if there is any effect on growth it will be a reduction, since not only is no energy re-routed from reproduction, but the host also has to deal with damage caused by the parasite (Sousa 1983).

Our results indicate that there is no fixed relationship between the effects of parasites on growth and reproduction; the effect depends on the parasite-host system studied. In our case, 2 parasites affected different components of the host energy budget. *Proctoeces* affected growth but not reproduction, and bucephalid sporocysts affected reproduction but (except for the largest mussels) not growth.

These results are in agreement with most of the literature referring to these 2 parasites. In general most infections by bucephalid sporocysts and cercariae in

bivalve molluscs have been reported to start in the gonad, with the sporocysts eventually replacing all the gonadal tissue and spreading onto other organs (see Howell 1967 and Lauckner 1983 for references). One exception was found by Cheng & Burton (1965), who noted that *Bucephalus* sp. infests mainly the digestive gland of the oyster *Crassostrea virginica* (Gmelin).

The fact that the bucephalid sporocysts castrate *Perna perna* will have an obvious effect on the mussel population, especially in places with a high prevalence of this parasite. We must also take into account the fact that the prevalence of this parasite increases with the size of the individual, with mussels bigger than 70 mm having up to 70% infection rates in some locations (Calvo-Ugarteburu & McQuaid 1998). Partitioning of energy in mussels varies with size, with small mussels spending more energy on growth and large mussels putting most energy (sometimes over 90%) into reproduction (reviewed by Seed & Suchanek 1992). The effect on growth is less important, as bucephalid sporocysts decrease growth of only large mussels (71 to 80 mm). These individuals channel most of their energy into reproduction and exhibit low growth rates anyway.

Lasiak (1989) found prevalences of *Proctoeces* metacercariae in *Perna perna* at several places along the South African coast similar to ours. She concluded that, being an active growth phase in the life-cycle, the metacercariae probably ingest material from the host's tissues, disturbing its growth and reproduction. This study shows that *Proctoeces* has a harmful effect on the growth of the mussels, especially of those smaller mussels which, under normal conditions, would expend most of their energy on growth (see Seed & Suchanek 1992 for references). Within a mussel bed, mussels compete for space and food, with slower-growing mussels having a competitive disadvantage (Kautsky 1982). Therefore, any depression of growth rate is likely to reduce the competitive ability of the mussels. Furthermore, although *Proctoeces* has no direct effect on mussel reproduction, it may have an indirect effect by reducing growth rates, since fecundity is size related and smaller mussels spend less energy on reproduction than larger ones (Seed & Suchanek 1992).

Mytilids are widely reported to have different seasonal growth rates (Andreu 1965, Dare & Edwards 1976, du Plessis 1977, Berry 1978, Crawford & Bower 1983, Rodhouse et al. 1984, Page & Hubbard 1987, Anwar et al. 1990, Richardson et al. 1990, Cheung 1991, 1993, Sukhotin & Kulakowski 1992, van Erkom Schurink & Griffiths 1993). We did not set out to study seasonal growth rates, and the faster growth in winter at Hougham Park was probably due to the larger initial size of the mussels used in the summer trial. In both cases the effects of the parasites were consistent between seasons; the bucephalid sporocysts had no significant effect on growth in either summer or winter whilst *Proctoeces* significantly depressed growth of mussels both in summer and in winter, even though the Mann-Whitney *U*-test showed that it only affected the smallest individuals (21 to 30 mm; Fig. 3). This presumably reflects the fact that small mussels put more energy into growth.

Finally we considered possible re-allocation or compensation within the energy budget. Many studies have been done on the physiological responses of mussels to different environmental conditions (e.g. Winter 1973, Andreu 1976, Bayne et al. 1978, Cabanas et al. 1979, Kiorboe et al. 1980, Navarro & Winter 1982, Hawkins et al. 1985, Meyhofer 1985, Clarke & Griffiths 1990, Grant & Thorpe 1991, Navarro et al. 1991, van Erkom Schurink & Griffiths 1992, Widdows & Page 1993). Most of these works found filtration rates between 0.1 and 5.3 $l\ h^{-1}$, depending on the size of the mussel and the conditions of temperature, particle concentration and flow rate (Winter 1973, Andreu 1976, Cabanas et al. 1979, Kiorboe et al. 1980, Meyhofer 1985, Clarke & Griffiths 1990, Navarro et al. 1991, van Erkom Schurink & Griffiths 1992, Widdows & Page 1993). Filtration rates found in this study were very low (Fig 4), possibly because of low flow rates (Walne 1972), but within the range of values previously reported.

In comparison, very little is known about the effects of parasites on molluscan host physiological processes, and results from different studies are often contradictory. Ishak et al. (1970) found that schistosome-infected *Biomphalaria alexandrina* showed a consistently lower rate of oxygen consumption than uninfected individuals, whilst Meakins (1980) concluded that larval *Schistosoma mansoni* elevated the oxygen consumption of *Biomphalaria glabrata*. Several authors have used changes in filtration or respiration to explain changes in other parameters of the energy budget. For example, Wesenberg-Lund (1934) explained gigantism as a result of an increase in the amount of food eaten, and Williams & Gilbertson (1983) found that *B. glabrata* infected with *S. mansoni* for 33 d fed more often than uninfected snails. On the other hand, this has been contradicted in several studies. For example, Meuleman (1972) found that infected snails consumed less food than controls from the third week after infection onwards.

With respect to bivalves, the effects of parasites seem to be more uniform. Bayne et al. (1978) found lowered filtration rates in *Mytilus edulis* infected with *Mytilicola intestinalis*, although only under extreme conditions of temperature and/or food availability. Ward & Langdon (1986) demonstrated that parasitism by natu-

rally occurring densities of *Boonea impressa* deleteriously affects the oyster *Crassostrea virginica* by significantly reducing filtration rates, and Bierbaum & Shumway (1988) found lower respiration and filtration rates in *Mytilus edulis* infected with *Pinnotheres maculatus* than in non-infected individuals, though they failed to find any differences in assimilation efficiency.

The results from this study show that neither infection with *Proctoeces* nor infection with bucephalid sporocysts had a significant effect on filtration rates or oxygen consumption of *Perna perna*, even though the parasites affected either reproduction or growth. Thus there was no compensation for the energy lost within the production fraction (growth and reproduction) of the energy budget via either decreased respiration or increased consumption. The fact that the effects of the parasites are directed at the fraction of the energy budget allocated to production rather than maintenance could be considered a parasitic adaptation. Host survival is necessary for parasite survival, therefore the parasite should influence the metabolism of the host as little as possible (Davis & Farley 1973, Jokela et al. 1993, J. Taskinen pers. comm.).

Even though there is no apparent direct effect of either *Proctoeces* or the bucephalid sporocysts on survival of their host, infection seems to be associated with a substantial reduction in fitness. The 2 parasites studied affect the host in different but complementary ways. The effects of both parasites are concentrated on those size classes of mussel which channel most energy into the portion of the energy budget affected by the parasite. *Proctoeces* affects growth only in the smaller individuals, which normally put most energy into growth; and the bucephalid sporocysts castrate the larger mussels, which expend most energy on reproduction. By reducing growth rates of small mussels or castrating large mussels, these parasites effectively remove them from the breeding population and reduce their competitive abilities. These effects on growth and reproduction are 2 of the mechanisms by which parasites may influence interactions between competing hosts species. *Perna perna* does not show any compensation for these negative effects. The energy lost for growth or reproduction is not replaced by an increase in filtration or compensated for by a reduction in respiration, rather it is simply lost to the parasite.

In this study we have seen how parasites affect the indigenous mussel *Perna perna* and hence are likely to affect its interactions with the invasive *Mytilus galloprovincialis*. Since for a parasite community the resource base is the host population, this situation raises the question of the fate of the parasite community if *P. perna* is competitively displaced by *M. galloprovincialis*. Will the parasites in turn also become extinct or will they develop in *M. galloprovincialis*?

Survival of the parasite implies new adaptations for infecting new hosts. Combes (1991) outlined 3 possible outcomes for a case like this: (1) The parasite may develop in the new host incidentally, without dynamic or genetic consequences for the parasite. (2) The parasite may develop in both hosts, which means an increase in host spectrum with possible dynamic consequences for the parasite. (3) The parasite may develop in the new host, but its lineage may diverge genetically and undergo speciation.

In conclusion, the absence of digenetic trematodes in *Mytilus galloprovincialis*, together with their high prevalences and negative effects on *Perna perna*, may help to explain the success of *M. galloprovincialis* in South Africa. Not only is *M. galloprovincialis* competitively superior to *P. perna*, but it is also free of parasites. It remains to be seen whether either parasite will develop in *M. galloprovincialis*, in which case this mussel may lose some of its competitive advantage; or whether *M. galloprovincialis* will drive both *P. perna* and its parasites to extinction.

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