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Effect of acanthocephalan parasites on the behaviour and coloration of the mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae)

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Abstract In the field, the numbers of cystacanths of the parasitic acanthocephalan *Profilicollis* spp. harboured by crabs are relatively high and correlate with carapace width. In a field experiment, the responses of crabs to the simulated approach of a bird predator (the parasite's definitive host) was not influenced by the number of acanthocephalans they harboured. Crabs that were exposed at the surface of the sediments during receding high tide, however, tended to harbour more parasites than nearby crabs hidden in burrows. An analysis of colour patterns on the carapace of crabs showed that infection levels did not influence carapace pigmentation, and thus did not affect the conspicuousness of a crab relative to the background environment. However, the likelihood of a male crab winning a ritualized fight against a conspecific in the field was associated with its infection level, but in a way that suggests that this finding is a consequence of pathology rather than an adaptation of the parasite to increase its transmission rate. Although only weak evidence was found indicating that *Profilicollis* manipulates the behaviour or colour of its host to its own benefit, the high infection levels observed suggest that the crab population acts as a major reservoir for larval stages of this parasite that are infective to birds.

Introduction

Parasitism is now widely recognized as a factor capable of influencing the structure of natural animal communities (Minchella and Scott 1991; Hudson and Greenman 1998; Poulin 1999). Recent studies have shown that the relative abundance, or even the actual presence, of certain free-living species in natural communities is entirely dependent on the action of parasites. For instance, the outcome of intense, one-sided competition between two species can be changed when a debilitating parasite affects the dominant species, allowing the other one to coexist (Hudson and Greenman 1998). Also, the spatial distribution of infected animals may differ from that of uninfected conspecifics, because of alterations in behaviour caused by parasites; the result is that a portion of the host population may come into contact and interact with organisms that it would otherwise not encounter (Poulin 1999). The best documented effect of parasites on species interactions in animal communities, however, is the way in which they mediate predator-prey interactions. Several parasitic worms must be transmitted by predation from an intermediate host to a definitive host to complete their life cycle and reach adulthood. Many of them are known to alter the behaviour of intermediate hosts in ways that make them more susceptible to predation by definitive hosts (Lafferty 1992; Poulin 1998). For example, in littoral and intertidal ecosystems, birds often show a feeding bias in favour of invertebrate prey harbouring, and modified by, larval parasitic worms (e.g. Helluy 1984; Thomas and Poulin 1998; McCurdy et al. 1999). The influence of parasites can potentially modify the choice of prey species by predators, and consequently affect the community as a whole.

Among parasitic worms that are transmitted by predation from an intermediate host to a definitive host, members of the phylum Acanthocephala are known as master manipulators of intermediate hosts (Moore 1984). Adult acanthocephalans live in the intestine of vertebrates, from which they release eggs in their host's faeces. After an egg is accidentally ingested by a suitable arthropod intermediate host, it hatches and the juvenile worm gets into the host's hemocoel where it develops to the cystacanth stage and awaits capture by an appropriate vertebrate definitive host. Almost all

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acanthocephalan species studied to date have been found capable of altering the coloration or behaviour of their intermediate hosts, such as small crustaceans like amphipods, ostracods or isopods (e.g. Hindsbo 1972; Bethel and Holmes 1973; Bakker et al. 1997). The physiological basis of these parasite-induced alterations is unclear, but is likely to involve chemical manipulation by the parasite (Helluy and Holmes 1990). In these systems, infected crustaceans typically harbour a single cystacanth and rarely more than five; because of the small host/parasite body size ratio, one parasite is all it takes to modify the phenotype of the host. However, larger crustaceans, such as crabs, also serve as intermediate hosts for some acanthocephalan species. Their larger size may have consequences for the ability of the parasites to manipulate their behaviour and appearance. On the one hand, it means a much higher host/parasite size ratio, which suggests the host manipulation may be more difficult to achieve. On the other hand, the larger hemocoel offers more room for the accumulation of greater numbers of cystacanths, whose pooled efforts may overcome the size ratio problem and result in alterations in host coloration or behaviour.

The only system of this kind that has been studied in the context of host manipulation is the association between the acanthocephalan *Profilicollis antarcticus* and the crab *Hemigrapsus crenulatus* (Brachyura: Grapsidae) along the coast of Chile. Pulgar et al. (1995) found that experimentally inoculating two cystacanths into crabs subsequently led to a change in the coloration of their carapace, whereas Haye and Ojeda (1998) showed that naturally infected crabs had higher metabolic rates and activity levels than uninfected crabs. In these studies, infection levels were low: naturally infected crabs harboured only one or two cystacanths, whereas experimentally infected crabs were given two cystacanths. Here, we study the effects of acanthocephalan parasitism in the New Zealand mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae), which is unique among crustaceans studied thus far in harbouring large numbers of cystacanths (mean >10 cystacanths per crab). This crab harbours a mixture of cystacanths from two species of the acanthocephalan genus *Profilicollis*; one is *P. antarcticus*, as in Chile, whereas the other species is as yet undescribed (A. Brockerhoff, personal communication). Their definitive hosts at our study site no doubt include the black-backed gull *Larus dominicanus* (which is the host in Chile), and probably other bird species as well. Given that the size of *M. hirtipes* at our study site is comparable to that of the sympatric *H. crenulatus* (which gets altered by only two cystacanths), the high numbers of cystacanths harboured by *M. hirtipes* suggest that it may incur severe parasite-induced modifications. *M. hirtipes* is one of the most common inhabitants of sheltered mudflats in New Zealand (Morton and Miller 1973; Nye 1974); if acanthocephalans have serious impacts on its populations, the indirect effects on intertidal communities could be substantial.

In this paper, we first quantify the infection levels by *Profilicollis* cystacanths in *M. hirtipes* and their correlates. Second, we test the hypothesis that the parasite modifies the behaviour and coloration of its crab host in ways that could make it more susceptible to bird predation. More specifically, we quantify the effects of the parasite on the responses of crabs to a predator, on their tendency to hide in burrows when the tide recedes, on the aggressive interactions among male crabs, and on the coloration of the crabs' carapace. By focussing on behaviours that determine the risk of predation and others that may be unrelated to parasite transmission, we hope to distinguish between adaptive parasite manipulation of host behaviour and general host debilitation.

Materials and methods

The study was conducted on the intertidal mudflat of Papanui Inlet, Otago Peninsula, South Island, New Zealand (45°52′S, 170°42′E). The inlet experiences a spring tidal range of approximately 2 m; sediments consist of fine sand and mud, covered in many places by beds of sea grass *Zostera novazelandica*. Apart from the very common *Macrophthalmus hirtipes*, other common crabs in the inlet are *Hemigrapsus crenulatus*, *Hemigrapsus edwardsi*, and *Helice crassa* (all three in the family Grapsidae); the latter two species are mainly confined to the upper shore.

Infection levels in the field

Crabs were collected during low tide on 9 April 2000 along two transect lines on the western side of the inlet. The transects were perpendicular to the shore but parallel to one another and separated by 500 m. Beginning 50 m from the high water mark, and at further intervals of 50 m, crabs were collected at five stations per transect. At each station, crabs were obtained from as small an area as possible (usually <1 m^2), by gently raking the sediments to collect both surface and burrowed crabs. Twenty-five crabs were caught at each station, and thus 125 per transect, for a grand total of 250 crabs. They were killed by freezing and returned to the laboratory. Later, each crab was sexed, measured to the nearest millimetre (carapace width, at the level of the second pair of lateral spines), and dissected. The number of cystacanths per crab was recorded. All cysts were superficially identical and belonged to the acanthocephalan genus *Profilicollis*. Microscopic examination of a large (>250), random sample of cysts confirmed that *P. antarcticus* is rare ($<1\%$) at our study site, and that by far the dominant species is the other undescribed *Profilicollis* species. Since the two species can only be distinguished by microscopic examination of the number and arrangement of hooks on their proboscis, we did not attempt to differentiate between them across our entire sample.

Data on numbers of cysts per crab were $\log(x+1)$ transformed to meet the assumptions of parametric tests. An analysis of covariance (ANCOVA) was then performed on these data to test for differences among heights in the intertidal zone (i.e. among collecting stations) and between transects, with crab carapace width as the covariate. The sex of the crabs was excluded from the analysis since only 37 female crabs were found in our samples and a preliminary analysis showed that a crab's sex did not significantly influence infection levels.

Responses to a predator and hiding behaviour

First, we investigated the effects of infection on a crab's response to a predator stimulus. An ethogram of eight mutually exclusive

behaviours was constructed based on field observations and on the study of Haye and Ojeda (1998), consisting of four behavioural states in which the crab is motionless and four in which it is moving: (1) at rest, partially hidden; (2) at rest, exposed; (3) semi-alert, with one or two locomotory appendages contracted; (4) alert, with all appendages contracted and the body raised above the substrate; (5) all appendages moving but no displacement; (6) slow displacement; (7) fast displacement; and (8) digging. Behaviours 4, 5, 7 and 8 are excitatory states known to be metabolically expensive (see Haye and Ojeda 1998). During daytime low tides in June 2000, 40 individual crabs in Papanui Inlet were randomly chosen and slowly approached one at a time. Their initial behavioural state was recorded, and each crab was then exposed to a simulated predator. A cardboard model (wingspan 1 m) of a black-backed gull, *Larus dominicanus*, in flight was passed over the crab. The model was fixed to a 1.5-m-long rod and was passed once approximately 20 cm above the crab, with its angle relative to the sun kept constant for all crabs. The time spent by the crab in different behavioural states was recorded for 2 min following the stimulus, and all 40 crabs exposed to the model bird were then captured, killed by freezing and returned to the laboratory. They were measured and dissected for parasite counts as described above.

All crabs initially (prior to the stimulus) displayed either behaviour 1, 2 or 4; comparisons were thus made between crabs displaying these different states with respect to their body size or the (log-transformed) number of cystacanths they harboured using an ANOVA. Subsequently, we used an ANCOVA to test the effect of initial behaviour on the percentage of time following the stimulus that crabs spent motionless (i.e. in any of behavioural states 1 through 4 above), with carapace width and number of cystacanths per crab as covariates in the analysis.

Second, we searched for an association between infection levels and the likelihood that a crab was exposed on the sediment as opposed to hidden in a burrow, when the high tide recedes and bird predation increases. On 28 January 2001, exposed and hidden crabs were collected just after high tide, in the receding water. An observer walking slowly looked for individual crabs exposed on the sediments, away from the entrance to a burrow. Forty exposed crabs were collected in water 5–10 cm deep. Each time an exposed crab was collected, a paired hidden crab of similar size was collected from a burrow as close as possible to the position of the exposed crab, usually no farther than 3 m away (occasionally, when the exposed crab was found in an area without burrows, the paired hidden crab had to be captured from up to 10 m away). Only male crabs were used in this comparison, to avoid the confounding influence of sexual differences in behaviour, if any. All 40 pairs of crabs were then captured, killed by freezing and returned to the laboratory, where they were measured and dissected for parasite counts. Paired *t*-tests were used to compare carapace width and number of cystacanths per crab (corrected for crab size using the residuals of a regression against carapace width) between exposed and hidden crabs.

Male-male aggressive interactions

Ritualized fights between male crabs are a common occurrence in the dense populations of *M. hirtipes*, mainly at the entrance of burrows and peaking during the mating period (Beer 1959). The mating season of *M. hirtipes* occurs during the austral autumn and is over by the beginning of winter (Beer 1959; Simons and Jones 1981). Fights between male crabs were observed on two occasions, once during the mating season (28 April 2000) and once after the mating season (27 June 2000). On each occasion, observations were made during high tide, when the crabs are most active, in water ≤ 50 cm deep. Once spotted, a pair of fighting crabs was gently approached to within 1.5 m. A fight consists of posing and pushing by both crabs with their chelipeds extended outwards. At the completion of a fight, the crab standing its ground was deemed the winner and the one retreating was considered to be the loser. Both were captured and placed in labelled containers. If they were later found to differ by 1 mm or more in carapace width, they were excluded from the analysis and released. Crabs that were retained were killed by freezing, measured (carapace width) and dissected for parasite counts as before. In addition, the length of both the left and right chelae was measured, and right and left values were averaged to obtain a mean chelae length for each crab.

Pairs of crabs collected during and after the mating season were analysed separately as well as together, where appropriate. Paired *t*-tests were used to compare carapace width, chelae length, and number of cystacanths per crab (corrected for crab size using the residuals of a regression against carapace width) between winners and losers.

Carapace coloration

Forty male crabs were selected from the 250 that had been collected in the inlet on 9 April 2000 (see above). These crabs were selected to encompass the complete range of carapace coloration found at the site. The background colour of the *M. hirtipes* carapace is predominantly light olive-green, and most carapaces also have spots or patches of various shades of purple. Most variation in coloration among individual crabs is due to this purple, which ranges from a few small spots on some crabs to large patches covering most of the carapace on other crabs. Patches of purple colour make crabs more visible to a human observer against the natural background. Killing the crabs by freezing had no effect on the actual pattern of colours. Crabs were photographed under the same conditions, on Kodak Ektachrome EPN-100 135 mm reversal film. The photographs were then scanned and digitized at 400 dpi, using standard settings. The proportion of purple on the carapace of each crab was analysed with the geographic imaging software package Erdas Imagine (Erdas, Atlanta, Ga.; www.erdas.com). Details regarding the use of this software can be found in its users' guide. In brief, the software can compute the number of pixels of given colours in a specified area. We selected a rectangular area that covered most of the carapace, and gave precisely the same proportional coverage of all 40 carapaces examined, despite small differences in carapace width. The number of pixels corresponding to purple was counted on each selected area; no distinction was made among the slightly different shades of purple that occurred on the same or different carapaces. The proportion of purple in the selected area was obtained by dividing the purple pixel count by the total number of pixels in the selected area.

All crabs were measured (carapace width) and dissected for parasite counts. This was done independently of the colour analysis, such that colour measurements were taken in complete ignorance of numbers of cystacanths per crab, and vice versa. A multiple regression analysis was the performed, using log-transformed numbers of cystacanths per crab and carapace width as predictor variables, and the proportion of purple on the carapace as the dependent variable.

Results

Infection levels in the field

Only 15 (6%) of the 250 crabs did not harbour *Profilicollis* cystacanths. The number of cystacanths per infected crab ranged from 1 to 86, with a mean of 11.8 ± 0.7 (SE). Crab carapace width came out as a strong covariate of infection levels in the ANCOVA ($F_{1,239} = 175.55$, $P < 0.001$), with the two variables being positively correlated and crab size explaining about 40% of the variability in numbers of cysts per crab (Fig. 1).

There was a significant difference in infection levels between the two transects ($F_{1,239} = 5.76$, $P = 0.017$): crabs collected along one transect tended to harbour

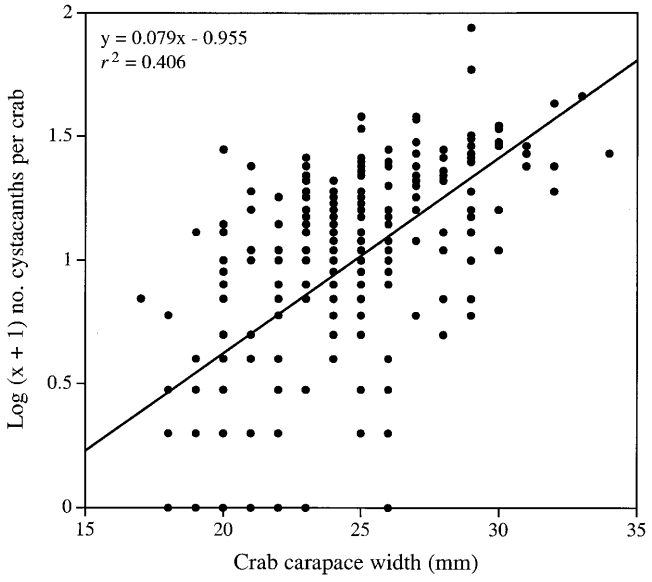

Fig. 1 Relationship between the number of *Profilicollis* spp. cystacanths per crab and crab carapace width among 250 *Macrophthalmus hirtipes*. The equation and fitted line of a linear regression are also shown

more cystacanths than expected based on their body size, whereas crabs from the other transect tended to harbour fewer cystacanths than expected (Fig. 2). There was, however, no significant variation in infection levels as a function of distance from the high water mark ($F_{4,239} = 1.91$, $P = 0.109$; Fig. 2), and no significant interaction between transect and distance from the high water mark ($F_{4,239} = 1.47$, $P = 0.213$).

Responses to a predator and hiding behaviour

There was no difference among crabs initially displaying behaviours 1, 2 or 4 (i.e. hidden at rest, exposed at rest, and alert and contracted) in either carapace width (ANOVA: $F_{2,37} = 1.20$, $P = 0.313$) or in number of cystacanths per crab ($F_{2,37} = 0.35$, $P = 0.709$). Initial behaviour had a significant influence on the percentage of time following the stimulus that crabs spent motionless (ANCOVA: $F_{2,35} = 5.25$, $P = 0.011$). Crabs that were initially hidden tended to remain hidden, whereas the behaviour of other crabs was more likely to change following the stimulus (Fig. 3). Neither of the two covariates in the ANCOVA, carapace width and the number of cystacanths per crab, had a significant effect on how much time was spent motionless by crabs following exposure to the simulated predator (both $P \geq 0.18$).

Among the 40 pairs of male crabs caught in receding water, hidden crabs were slightly larger in carapace width than the exposed crab with which they were paired (paired test: $t = 2.564$, $df = 39$, $P = 0.014$), despite our effort to match both crabs in a pair with respect to size. Again, carapace width was a significant predictor of log-transformed number of cysts per crab ($r^2 = 0.20$, $P < 0.001$). However, after correcting for crab size, there was a slight difference between exposed and hidden

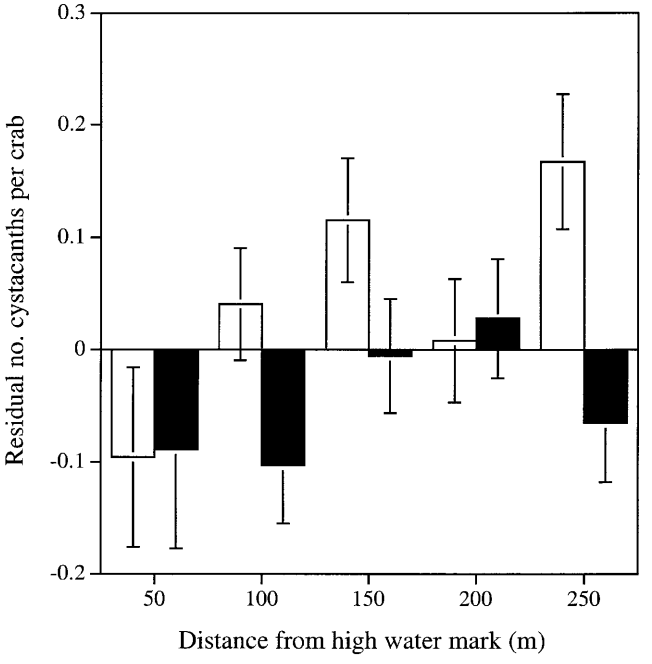

Fig. 2 Mean (±SE) number of *Profilicollis* spp. cystacanths per crab, corrected for crab carapace width, as a function of distance from the high water mark. Results from two transects (*black* and *white bars*) are shown separately. The data are residuals from the regression in Fig. 1, with 25 crabs examined at each distance and for each transect

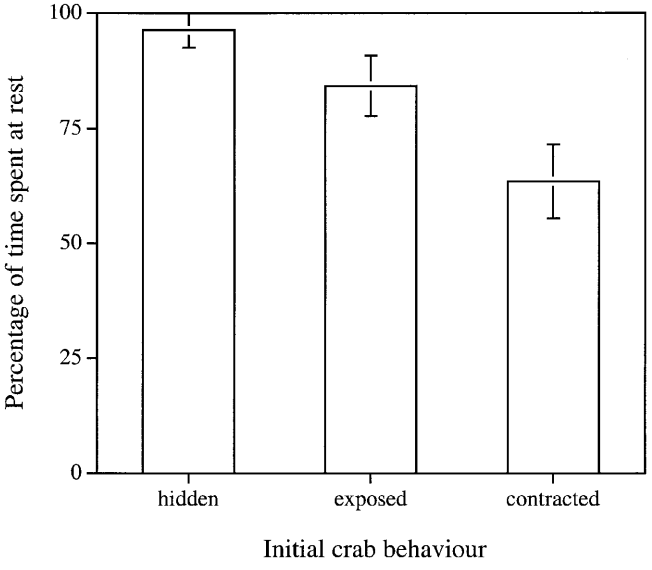

Fig. 3 Mean (±SE) percentage of time spent at rest, i.e. motionless (any behavioural state 1–4; see text) by crabs in the 2 min following a predator stimulus. The data are presented separately for crabs initially hidden and resting ($n = 12$), exposed and resting ($n = 14$), and alert with appendages contracted ($n = 14$)

crabs with respect to infection levels ($t = 1.868$, $df = 39$, $P = 0.069$): exposed crabs tended to harbour more cystacanths than expected based on their carapace width (mean residual value ± SE: 0.06 ± 0.037), whereas hidden crabs tended to harbour fewer than expected (–0.06 ± 0.046).

Male-male aggressive interactions

After pairs of crabs with widely different carapace sizes were excluded, a total of 13 male-male fights were observed during the mating season, and ten fights after the mating season. Male crabs that won fights had on average wider carapaces (paired test: $t = 2.19$, $df = 22$, $P = 0.039$) and longer chelae ($t = 3.45$, $df = 22$, $P = 0.002$) than losing crabs; this result holds also when fights observed during and after the mating season are analysed separately. After correcting for crab size by using the residuals from a regression, we found opposite associations between infection levels and the chance of winning a fight depending on when it took place (Fig. 4). During the mating season, fight winners had more cystacanths than expected based on their size, whereas losers had fewer cystacanths than expected ($t = 2.196$, $df = 12$, $P = 0.048$). After the mating season, fight winners tended to have fewer cystacanths than expected based on their size, whereas losers tended to have more cystacanths than expected ($t = 2.101$, $df = 9$, $P = 0.065$).

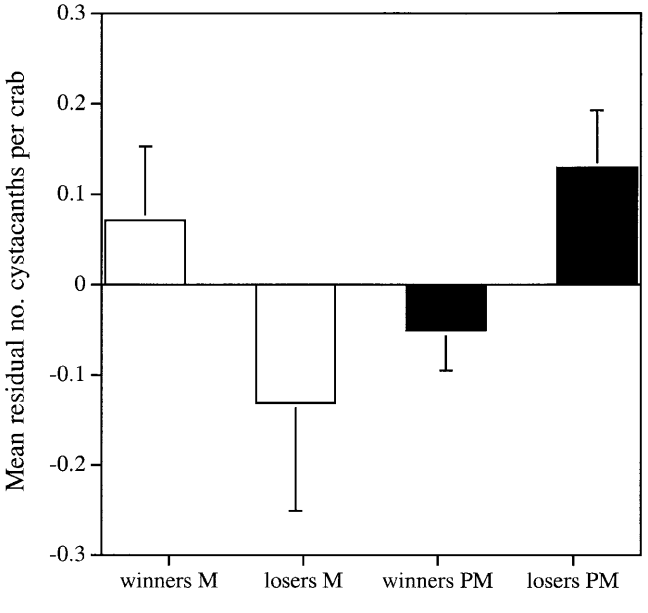

Fig. 4 Mean (± SE) number of *Profilicollis* cystacanths per crab in winners and losers of male-male ritualistic fights. The values shown are based on residuals from a regression of log-transformed number of cysts versus carapace width ($r^2 = 0.35$, $P = 0.019$), and are thus corrected for host size. Results are presented separately for fights observed during the mating season (*M*; *open bars*, $n = 13$) and post-mating (*PM*; *black bars*, $n = 10$)

Carapace coloration

The mean (± SE) number of cystacanths per crab among the 40 crabs selected for the colour analysis was 21.9 ± 2.4 cystacanths (range 0–77). The multiple regression indicated that carapace width did not correlate with the proportion of purple on the carapace (standardized regression coefficient: $r = 0.117$, $P = 0.487$). Similarly, there was no significant correlation between the number of cystacanths per crab and the extent of purple on the carapace ($r = 0.241$, $P = 0.156$). Thus even after correcting for carapace width, infection levels did not influence the coloration of the host carapace (Fig. 5).

Discussion

The ability of acanthocephalan parasites to alter the physiology, coloration and behaviour of their crustacean hosts is almost universal (see Hindsbo 1972; Bethel and Holmes 1973; Moore 1984; Helluy and Holmes 1990; Bakker et al. 1997). Often these changes, especially changes in coloration, are so conspicuous as to be unmistakable signs of infection for any human observer. These changes have repercussions on host spatial distribution, interspecific interactions, and, more importantly, their risk of predation. After all, the changes induced by acanthocephalans are believed to be an ancestral trait possessed by all members of the phylum and serving to increase the probability of completing the life cycle (Moore 1984). Here, however, we found only weak evidence that acanthocephalans modify the vulnerability

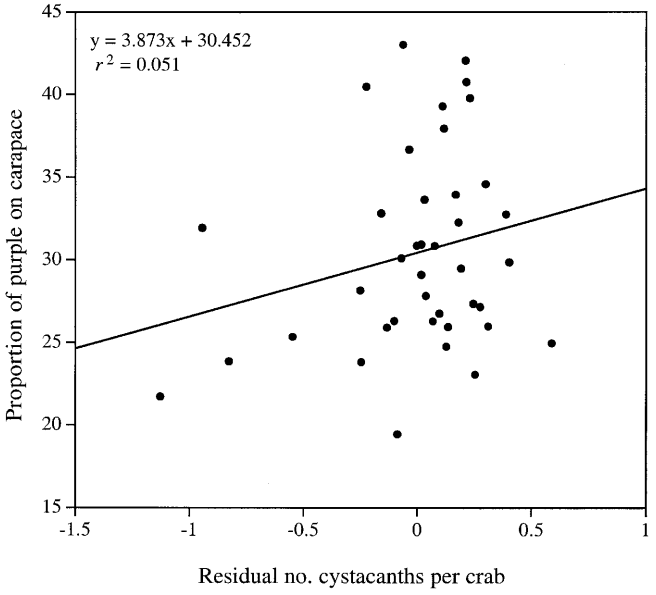

Fig. 5 Relationship between the proportion of purple colour on the carapace and the number of *Profilicollis* cystacanths per crab, corrected for carapace width, among 40 *Macrophthalmus hirtipes*. The equation and fitted line of a linear regression are also shown

of their intermediate host to a passing predator, in their crab host, *Macrophthalmus hirtipes*. The only apparent effects we observed were: (1) a slight tendency for exposed crabs to harbour more cystacanths than nearby crabs hidden in burrows, and (2) a relatively weak association between infection levels and the likelihood that a male crab wins a ritualized fight with a conspecific, with the direction of this association depending on whether fights were observed during or after the mating season.

Why are *Profilicollis* spp. cystacanths not causing clear-cut changes in crab coloration or in responses associated with anti-predator behaviour? There are several possible explanations. Discrepancies between our results and those of the Chilean studies may be due to methodological differences. For instance, Pulgar et al. (1995) experimentally inoculated crabs with two cystacanths by lifting part of the carapace and placing the cystacanths in the hemocoel; no sham-inoculated crabs were used as controls. Surely, this invasive procedure is stressful to the host and may explain why inoculated crabs showed changes in their carapace coloration within days. Also, Pulgar et al. (1995) used a subjective assessment of carapace coloration based on visual inspection. Our more objective and quantitative methods for measuring colour variation among crabs should have been more sensitive to small parasite-induced changes. Therefore, the changes in carapace pigmentation reported by Pulgar et al. (1995) may have been the product of their method of infection rather than of parasite manipulation. The crabs in our sample with large patches of purple on their carapace may indeed be more visible to bird predators against a background of mud and sea grass, but there is no evidence that acanthocephalan infections are responsible. Many other factors influence carapace coloration of crabs in the field (e.g. McKnight et al. 2000), and more detailed laboratory studies will be necessary to isolate the potential effects of acanthocephalans.

With respect to behaviour, our study was performed in the field whereas that of Haye and Ojeda (1998) was done in the laboratory. The immediate response of crabs to a bird passing overhead had appeared as an important determinant of risk of predation in earlier field observation. It was chosen for this reason, and our observations were made at low tide, a time when the crabs are accessible to potential avian definitive hosts of the parasite (though *M. hirtipes* is most active just before and after high tide: Williams et al. 1985). Our finding that exposed crabs tend to harbour more cystacanths than nearby crabs hidden in burrows supports the hypothesis that the acanthocephalans make their intermediate crab hosts more susceptible to bird predation. The trend was relatively weak, though. It remains possible, also, that the acanthocephalans modify other behavioural responses not explored here.

There may be biological reasons as well to explain why we observed only weak effects of the acanthocephalans on their crab hosts. The mean number of cystacanths per host (11.8) found in our field survey is much higher than the one or two cysts commonly found to induce behavioural or colour changes in small crustaceans. However, even when combining all cystacanths found in a crab, the host/parasite size ratio is still much higher than in studies on isopods or amphipods. If the manipulation is achieved via chemical secretions (see Helluy and Holmes 1990), the parasite products may simply become diluted within the large crab hemocoel. Yet, Haye and Ojeda (1998) found that merely a couple of cystacanths were enough to increase the metabolic rate and activity levels of *Hemigrapsus crenulatus*, a crab very similar in size to the *M. hirtipes* in our study. At our field site, the two grapsid crabs *H. crenulatus* and *H. edwardsi* occur in sympatry with *M. hirtipes*, and both are also infected by *Profilicollis* cystacanths (A. D. M. Latham and R. Poulin, unpublished data). In fact, the highest number of cystacanths we found in a crab at Papanui inlet was 135 from a female *H. edwardsi*. It is possible that *M. hirtipes* is a suitable intermediate host for *Profilicollis* spp., allowing their development to the cystacanth stage, but that for some reason it is not easily amenable to manipulation. Perhaps the parasite evolved using mainly grapsid crabs and fine-tuned its chemical weaponry to the physiology of these crabs; now, it may also use *M. hirtipes* but may not have evolved the ability to manipulate them as efficiently.

Why then would the likelihood of male *M. hirtipes* winning fights against other males be influenced by how many cystacanths they harbour? Parasites are known to affect male-male interactions in other systems for a variety of reasons (Howard and Minchella 1990). The trend we observed is most likely a side-effect of infection rather than a product of parasite manipulation. A pair of fighting crabs may be more visible to avian predators than resting crabs, but there would be no benefit for the parasite in affecting the outcome of the fight if all it wants is to attract birds. Two cystacanths are enough to cause an increase in metabolic rates in the crab *H. crenulatus*, an effect that is most likely a pathological consequence of infection (Haye and Ojeda 1998). It is possible that acanthocephalan infections deplete the energy reserves of male *M. hirtipes* to the extent that the most heavily infected male, relative to body size, is likely to be forced to back down first during a fight. This would explain what we observed after the mating season (see Fig. 4). During the mating season, male crabs may be making strategic decisions about how much to invest in a fight. Ritualized fights between *M. hirtipes* males are common only in dense populations such as the one at Papanui inlet, and serve mainly to defend access to burrows, which may serve as strategic locations from which to intercept passing females (Beer 1959; Jennings et al. 2000). Therefore investing in fighting may enhance male reproductive success. There is considerable evidence suggesting that males in general, when infected by parasites that can reduce their remaining lifespan and thus their future reproductive success, increase their current investment in reproduction (e.g. Minchella 1985;

Forbes 1993). During the mating season, then, the most heavily infected male crabs may invest more in fighting since their long-term prospects are not as good as those of more lightly infected conspecifics. In any event, our results on the effects of acanthocephalan parasitism on male fighting ability suggest that, although the parasites do not appear to benefit from their influence on male-male interactions, they still can affect their biology in other ways.

Within the inlet, infection levels did not vary as a function of distance from the high water mark. The spatial variation we observed between the two transects may result from currents within the inlet, or the patchy use of the habitat by avian definitive hosts. The high prevalence and mean number of cystacanths per host, however, indicate that the two species of *Profilicollis* are cycling well at that site. The only other relevant host-parasite system available for comparisons is the one involving the acanthocephalan *Profilicollis botulus*, which uses the crab *Carcinus maenas* as intermediate host and the eider duck, *Somateria mollissima*, as the definitive host in northern Scotland. Host manipulation has not been investigated in this system, but its ecology has been thoroughly studied (Liat and Pike 1980; Thompson 1985a, b, c). Even though *M. hirtipes* is clearly smaller than *C. maenas* in carapace width, the mean number of cystacanths per crab in *C. maenas* samples were always lower (less than five cystacanths per crab; Liat and Pike 1980; Thompson 1985a) than what we observed in *M. hirtipes*. Based on the numbers and sizes of crabs eaten by birds, and on the relationship between infection levels and crab size, Thompson (1985b) calculated that eider ducks were ingesting between zero and almost nine cystacanths per duck per day, depending on the season. Prevalence of infection in the ducks was always high, though it showed an annual cycle reflecting seasonal peaks in crab consumption and the longevity of the adult acanthocephalans (Liat and Pike 1980; Thompson 1985c). Numbers of adult worms per bird host were in the hundreds for juvenile ducks, but usually < 100 for adult birds. Taking these results into account, it seems safe to speculate that the *Profilicollis* spp. in our system must also be abundant in their bird hosts, given the high infection levels in *M. hirtipes* (as well as in *H. crenulatus* and *H. edwardsi*) in Papanui Inlet. The crab populations at our study site must represent a major reservoir of infective parasites for the birds in the area.

In summary, our results indicate that acanthocephalan parasites occur at high abundance within the *M. hirtipes* population of Papanui inlet, and that they may influence male decisions regarding investments in current reproduction. We obtained suggestive evidence that the parasites may also induce their hosts to spend more time exposed outside their burrows at a time when birds arrive at the inlet to search for prey. We found no evidence, however, that the parasites manipulate other aspects of the crabs' biology, i.e. the coloration or antipredator behaviour of their crab hosts, in order to facilitate their transmission via predation to avian definitive hosts. There may be a size threshold beyond which a crustacean host gains some protection from the actions of relatively small acanthocephalan cystacanths. Alternatively, although we focused our study on the most common crab in the inlet, we may have neglected the crab species to which this parasite species is better adapted. It is therefore not clear whether parasite-mediated increases in susceptibility to bird predation influence the population dynamics of *M. hirtipes* or the relative abundances of the various crab species occurring in the inlet. In any case, this system represents an exception to the long list of examples of acanthocephalan parasites capable of modifying the phenotype of their crustacean intermediate hosts, because the effects observed here are weak.

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References

Bakker TCM, Mazzi D, Zala S (1997) Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation. Ecology 78:1098–1104

Beer CG (1959) Notes on the behaviour of two estuarine crab species. Trans R Soc NZ 86:197–203

Bethel WM, Holmes JC (1973) Altered evasive behavior and responses to light in amphipods harboring acanthocephalan cystacanths. J Parasitol 59:945–956

Forbes MRL (1993) Parasitism and host reproductive effort. Oikos 67:444–450

Haye PA, Ojeda FP (1998) Metabolic and behavioral alterations in the crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) induced by its acanthocephalan parasite *Profilicollis antarcticus* (Zdzitowiecki 1985). J Exp Mar Biol Ecol 228:73–82

Helluy S (1984) Relations hôtes-parasites du trématode *Microphallus papillorobustus* (Rankin 1940). III. Facteurs impliqués dans les modifications du comportement des *Gammarus* hôtes intermédiaires et tests de prédation. Ann Parasitol Hum Comp 59:41–56

Helluy S, Holmes JC (1990) Serotonin, octopamine, and the clinging behaviour induced by the parasite *Polymorphus paradoxus* (Acanthocephala) in *Gammarus lacustris* (Crustacea). Can J Zool 1214–1220

Hindsbo O (1972) Effects of *Polymorphus* (Acanthocephala) on colour and behaviour of *Gammarus lacustris*. Nature 238:333

Howard RD, Minchella DJ (1990) Parasitism and mate competition. Oikos 58:120–122

Hudson PJ, Greenman J (1998) Competition mediated by parasites: biological and theoretical progress. Trends Ecol Evol 13:387–390

Jennings AC, McLay CL, Brockerhoff AM (2000) Mating behaviour of *Macrophthalmus hirtipes* (Brachyura: Ocypodidae). Mar Biol 137:267–278

Lafferty KD (1992) Foraging on prey that are modified by parasites. Am Nat 140:854–867

Liat LB, Pike AW (1980) The incidence and distribution of *Profilicollis botulus* (Acanthocephala), in the eider duck, *Somateria mollissima*, and in its intermediate host the shore crab, *Carcinus maenas*, in north east Scotland. J Zool (Lond) 190:39–51

McCurdy DG, Forbes MR, Boates JS (1999) Evidence that the parasitic nematode *Skrjabinoclava* manipulates host *Corophium*

behaviour to increase transmission to the sandpiper, *Calidris pusilla*. Behav Ecol 10:351–357
McKnight A, Mathews LM, Avery R, Lee KT (2000) Distribution is correlated with color phase in green crabs, *Carcinus maenas* (Linnaeus, 1758) in southern New England. Crustaceana 73:763–768
Minchella DJ (1985) Host life-history variation in response to parasitism. Parasitology 90:205–216
Minchella DJ, Scott ME (1991) Parasitism: a cryptic determinant of animal community structure. Trends Ecol Evol 6:250–254
Moore J (1984) Altered behavioral responses in intermediate hosts: an acanthocephalan parasite strategy. Am Nat 123:572–577
Morton JE, Miller MC (1973) The New Zealand sea shore, 2nd edn. Collins, London
Nye PA (1974) Burrowing and burying by the crab *Macrophthalmus hirtipes*. N Z J Mar Freshw Res 8:243–254
Poulin R (1998) Evolutionary ecology of parasites: from individuals to communities. Chapman and Hall, London
Poulin R (1999) The functional importance of parasites in animal communities: many roles at many levels? Int J Parasitol 29:903–914
Pulgar J, Aldana M, Vergara E, George-Nascimento M (1995) La conducta de la jaiba estuarina *Hemigrapsus crenulatus* (Milne-Edwards 1837) en relación al parasitismo por el acantocefalo *Profilicollis antarcticus* (Zdzitowiecki 1985) en el sur de Chile. Rev Chil Hist Nat 68:439–450
Simons MJ, Jones MB (1981) Population and reproductive biology of the mud crab, *Macrophthalmus hirtipes* (Jacquinot, 1853) (Ocypodidae), from marine and estuarine habitats. J Nat Hist 15:981–994
Thomas F, Poulin R (1998) Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? Parasitology 116:431–436
Thompson AB (1985a) Analysis of *Profilicollis botulus* (Acanthocephala: Echinorhynchidae) burdens in the shore crab, *Carcinus maenas*. J Anim Ecol 54:595–604
Thompson AB (1985b) Transmission dynamics of *Profilicollis botulus* (Acanthocephala) from crabs (*Carcinus maenas*) to eider ducks (*Somateria mollissima*) on the Ythan estuary, N.E. Scotland. J Anim Ecol 54:605–616
Thompson AB (1985c) *Profilicollis botulus* (Acanthocephala) abundance in the eider duck (*Somateria mollissima*) on the Ythan estuary, Aberdeenshire. Parasitology 91:563–575
Williams BG, Naylor E, Chatterton TD (1985) The activity patterns of New Zealand mud crabs under field and laboratory conditions. J Exp Mar Biol Ecol 89:269–282