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Effect of acanthocephalan parasites on hiding behaviour in two species of shore crabs

A.D.M. Latham* and R. Poulin

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

Abstract

The effect of acanthocephalan parasites (*Profilicollis* spp.) on the hiding behaviour during low tide of two species of shore crabs (intermediate hosts), *Macrophthalmus hirtipes* (Brachyura: Ocypodidae) and *Hemigrapsus crenulatus* (Brachyura: Grapsidae), was examined at Blueskin Bay, South Island, New Zealand. Exposed *M. hirtipes* were found to have significantly higher infection levels than did hidden conspecifics. This pattern was not observed for *H. crenulatus*. Mean cystacanth numbers were found to be considerably higher in *M. hirtipes* than *H. crenulatus*. Crabs exposed at low tide are at a greater risk of predation by definitive shorebird hosts than are hidden conspecifics. Preferential manipulation of one intermediate host species over another could influence diversity within ecosystems.

Introduction

Recent theoretical, experimental and field studies indicate that parasitism is an important biotic determinant of animal community structure (Minchella & Scott, 1991; Hudson & Greenman, 1998; Poulin, 1999). For example, parasites that preferentially infect a competitively dominant host species can lead to increased diversity within ecosystems (Ayling, 1981; Thomas *et al.*, 1995). However, the most widely documented effect of parasitism on animal population dynamics and community structure 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 these parasites are known to alter the behaviour or physiology of their 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, shorebirds often show a feeding bias in favour of invertebrate prey harbouring, and modified by, larval parasitic worms (e.g. Helluy, 1984; Thomas & Poulin, 1998; McCurdy *et al.*, 1999). The influence of parasites can potentially modify predator prey choice, consequently affecting the community as a whole.

The phylum Acanthocephala consists of parasitic worms that are transmitted by predation from an intermediate host to a definitive host: these worms are arguably the master manipulators of intermediate host phenotype (Moore, 1984). Adult acanthocephalans live and reproduce sexually in the intestine of vertebrates, from which they release eggs in their host's faeces. The egg is the only stage of the acanthocephalan life cycle that exists outside the host, free in the environment. After an egg is accidentally ingested by a suitable arthropod intermediate host, it hatches and develops in the haemocoel of the host to the cystacanth stage, and awaits ingestion by an appropriate vertebrate definitive host (see Nickol, 1985). Most acanthocephalans studied to date have been found capable of altering the coloration or behaviour of their crustacean intermediate hosts (e.g. Hindsbo, 1972; Bethel & Holmes, 1973; Bakker *et al.*, 1997). The physiological basis of these parasite-induced alterations is unclear, but may involve chemical manipulation by the parasite (Helluy & Holmes, 1990).

Most acanthocephalan–crustacean systems studied to date have focused on relatively small crustaceans, such as

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*Fax: +64 3 479 7584
e-mail: valhalla_sf@yahoo.co.nz

amphipods, ostracods or isopods (Hindsbo, 1972; Bethel & Holmes, 1973; Bakker *et al.*, 1997). Typically, these crustaceans 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 act as intermediate hosts for some acanthocephalan species. The larger body size of crabs may dampen the ability of the parasites to manipulate intermediate host behaviour and coloration: a rough estimate of average crab body volume (excluding limbs) in our system suggests that it is more than 15,000 times the volume of a cystacanth larvae (Latham & Poulin, in press a). Comparatively few studies have looked at the potential effects of acanthocephalans on large crustaceans such as crabs. Pulgar *et al.* (1995) and Haye & Ojeda (1998) studied 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 crabs that were experimentally inoculated with two cystacanths differed significantly in carapace coloration when compared with uninfected conspecifics. Similarly, Haye & Ojeda (1998) found that naturally infected crabs had higher metabolic rates and activity levels than uninfected crabs. In contrast, Latham & Poulin (2001) found only weak evidence that *P. antarcticus* and *P. novaezelandensis* are able to alter the behaviour and coloration of the mud crab, *Macrophthalmus hirtipes* (Brachyura: Ocypodidae) in New Zealand.

In this study we compare the effects of two species of acanthocephalan parasites (*P. antarcticus* and *P. novaezelandensis*) on the low tide hiding behaviour of two species of intertidal shore crabs, the stalk-eyed mud crab (*M. hirtipes*) and the hairy-handed crab (*H. crenulatus*) in New Zealand. Both species of crabs are common inhabitants of the lower part (below mid-tide level) of sheltered mudflats in New Zealand, and are frequently found coexisting (Nye, 1974; McLay, 1988). *Macrophthalmus hirtipes* is most active at high tide, generally hiding in water-logged burrows at low tide (Williams *et al.*, 1985). Whilst little is known about the behaviour of *H. crenulatus* in New Zealand, it typically appears to hide under stones, shells or in burrows at low tide (McLay, 1988). Although it is typical for these two species of crabs to hide at low tide, many individuals (of both species) are to be found totally exposed even when the tide is at its lowest (A.D.M. Latham, personal observation).

Both *M. hirtipes* and *H. crenulatus* are confirmed intermediate hosts of *Profilicollis* spp. (Brockerhoff & Smales, 2002): both crabs are also similar in size (*H. crenulatus* is slightly larger) (McLay, 1988). Several species of shorebirds are known to prey on *M. hirtipes* and *H. crenulatus* (McLay, 1988), although only three species have been confirmed as definitive hosts of *Profilicollis* spp. in New Zealand. These include the pied oystercatcher (*Haematopus ostralegus finchi*), the bar-tailed godwit (*Limosa lapponica*) (Brockerhoff & Smales, 2002), and the southern black-backed gull (*Larus dominicanus*) (Latham & Poulin, in press b). It is likely that a number of other shorebirds that prey on crabs also serve as definitive hosts of *Profilicollis* spp. in New Zealand (A.D.M. Latham & R. Poulin, unpublished data). As most shorebirds feed on exposed areas of mudflat or in adjacent areas of shallow water, *M. hirtipes* and *Hemigrapsus crenulatus* are at greatest risk of predation from shorebirds at low tide. Thus, we test the hypothesis that *M. hirtipes* and *H. crenulatus* individuals exposed at low tide will, on average, have higher cystacanth infection levels than conspecifics that are hidden at low tide. This would provide evidence of host behavioural manipulation by the parasites. Further, because the acanthocephalans appear to have a greater impact on populations of *M. hirtipes* than on those of *H. crenulatus*, we expected the behavioural manipulation to be more pronounced in *M. hirtipes* (Latham & Poulin, in press a; A.D.M. Latham & S. Poulin, unpublished data).

Materials and methods

The study was conducted on the intertidal mudflats of Blueskin Bay, located approximately 20 km north of Dunedin (Otago), South Island, New Zealand (45°43′S, 170°35′E). Blueskin Bay experiences a spring tidal range of approximately 2 m. Sediments consist of fine sand and mud; rocks cover the upper shore. Apart from *M. hirtipes* and *H. crenulatus*, other common crabs in the bay include, the common rock crab (*H. edwardsi*) and the tunnelling mud crab (*Helice crassa*). *Hemigrapsus edwardsi* is found mainly under rocks around the upper shore, and is a confirmed intermediate host of *P. novaezelandensis* in the Otago region (Latham & Poulin, in press b). *Helice crassa* is found in burrows around the upper shore; cystacanth larvae have been found in this species around the Canterbury coastline (Brockerhoff & Smales, 2002), but not around the Otago coastline (A.D.M. Latham, unpublished data).

A total of 74 (50 hidden and 24 exposed) *M. hirtipes* were collected on 15 July 2001, from one site located near the township of Warrington at the northern end of the bay (all *M. hirtipes* collected were male). *Macrophthalmus hirtipes* were collected at low tide by hand by an observer picking up individuals that were: (i) either completely exposed or that were only partially buried into the sediment (i.e. the carapace was still clearly visible); and (ii) individuals that were completely hidden from view buried beneath the sediment surface. A total of 68 (37 hidden and 31 exposed) *Hemigrapsus crenulatus* were collected on two occasions, 14 (n = 30) and 17 (n = 38) February 2002, from one site located near the township of Waitati at the southern end of the bay. *Hemigrapsus crenulatus* were also collected at low tide by hand by an observer, however, only individuals that were (i) completely exposed or (ii) completely hidden (i.e. under stones, shells, seaweed, wood or buried) were taken. Individuals of both species with a carapace width of less than 17 mm were not collected, as they tend not to harbour cystacanths at this location (A.D.M. Latham & R. Poulin, unpublished data). Crabs were killed upon return to the laboratory by freezing. All crabs were measured to the nearest mm (carapace width, at the second pair of lateral spines), dissected, and the number of cystacanths per crab was recorded. Examination of a sample of 500 *Profilicollis* cystacanths under a stereomicroscope, and their identification based on the number of rows of hooks on their proboscis, showed that less than

1% were *P. antarcticus* (A.D.M. Latham & R. Poulin, unpublished data). Due to this, and the fact that both species have identical life cycles, all cystacanths are pooled for analysis in this study.

To test for differences in infection levels between exposed and hidden *M. hirtipes* and *H. crenulatus*, 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 for each crab species to test for differences in infection levels between exposed and hidden crabs, and between sexes and collection dates for *H. crenulatus*, with crab carapace width as the covariate.

Results

Cystacanth infection levels were generally higher in *M. hirtipes* (mean = 10.6 ± 1.2 (SE), range = 1–60) than in *H. crenulatus* (mean = 2.2 ± 0.3 (SE), range = 1–11).

The results of the ANCOVA performed on *M. hirtipes* shows a significant difference in infection levels between crabs that were exposed or partially exposed at the sediment surface compared with conspecifics that were totally buried beneath the sediment surface (table 1). The mean number of cysts per exposed crab was 15.7 (±2.5 SE, range 1–60), whilst the mean number of cysts per hidden crab was 8.1 (±1.2 SE, range 1–36). Crab carapace width did not have a significant effect on infection levels in *M. hirtipes* (table 1).

The results of the ANCOVA performed on *H. crenulatus* shows a significant correlation between *Profilicollis* cystacanth infection levels and crab carapace width (table 1). In other words, larger crabs tended to harbour more cysts on average than smaller conspecifics. There was, however, no effect of date of collection or sex on cystacanth infection levels in *H. crenulatus*. Likewise, there was no significant difference in infection levels between exposed and hidden *H. crenulatus* (table 1).

Discussion

The ability of acanthocephalan parasites to alter the physiology, carapace coloration and behaviour of their crustacean hosts has been well documented (see Hindsbo, 1972; Bethel & Holmes, 1973; Moore, 1984; Helluy & Holmes, 1990; Bakker *et al.*, 1997). In some instances, these changes may alter host spatial distribution or activity, thus enhancing the intermediate host's risk of predation by the definitive host. Alterations of intermediate host phenotype by acanthocephalans are believed to be an ancestral trait possessed by all members of the phylum, and serve to increase the probability of the parasites completing their life cycle (Moore, 1984). Here we find strong evidence that *Profilicollis* cystacanths are able to increase the vulnerability of their intermediate host, *M. hirtipes*, to predation: exposed *M. hirtipes* harboured significantly more cysts than did hidden conspecifics. Interestingly, however, cystacanth infection levels in *H. crenulatus* did not differ significantly between exposed and hidden individuals.

Infection levels in *M. hirtipes* were much higher than in *H. crenulatus*. These results support previous studies that found that *Profilicollis* infections tend to have a greater impact on *M. hirtipes* survival than on the other crab species studied (Latham & Poulin, in press a). Since crabs are relatively large intermediate hosts, host manipulation by a small number of cysts may be more difficult to achieve due to the much higher crab/parasite size ratio. However, where the accumulation of cysts in crabs is highest, the pooled efforts of the parasites may be enough to induce alterations in host behaviour. If so, it would explain why we observed a significant difference between exposed and hidden *M. hirtipes*, yet not between exposed and hidden *H. crenulatus*. It is also possible that *Profilicollis* cystacanths affect their intermediate hosts differentially. Instances of this phenomenon have been found in other systems, for example Thomas *et al.* (1995) found differential mortality in two closely related amphipod host species induced by the same species of trematode parasite. Interestingly, in contrast with the present study, they found that infection levels were highest in the host that was not significantly influenced by the parasite. *Macrophthalmus hirtipes* is an extremely common crab around the Otago coastline, for example reaching a density of 88 crabs per m^2 (Nye, 1974). Although *H. crenulatus* is abundant around the Otago coastline, it is found at much lower densities than *M. hirtipes* (A.D.M. Latham, unpublished data). Thus, if (i) *M. hirtipes* is the competitively dominant crab species at the mid to low water mark, and (ii) *Profilicollis* spp. preferentially manipulate *M. hirtipes* over other intermediate host species, it is possible that these parasites increase

Table 1. ANCOVA results for the effect of date of collection, sex, state (hidden versus exposed), and the covariate crab carapace width on *Profilicollis* cystacanth infection levels in *Macrophthalmus hirtipes* and *Hemigrapsus crenulatus* during low tide at Blueskin Bay.

Species	Source	DF	F	P
Macrophthalmus hirtipes	State	1, 71	9.04	0.004
	Carapace width	1, 71	0.65	0.423
Hemigrapsus crenulatus	Date	1, 63	0.05	0.825
	Sex	1, 63	2.64	0.109
	State	1, 63	0.01	0.930
	Carapace width	1, 63	6.78	0.011

Note: all *M. hirtipes* were male.

diversity within Blueskin Bay and similar ecosystems, by depressing the abundance of the dominant crab species.

In summary, our results indicate that the likelihood of *M. hirtipes* being exposed during low tide at Blueskin Bay appears to be correlated with high intensities of cystacanths: this relationship was not found in *H. crenulatus*. As cystacanth larvae appear to influence the two crab species differentially, it would appear likely that parasite-mediated increases in susceptibility to bird predation in *M. hirtipes* influences not only the population dynamics of that species, but also the relative abundances of various other crab species occurring in the bay. Thus, understanding parasite-mediated intermediate host manipulation is of great importance if we are to manage host populations and animal communities effectively.

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