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## Field evidence of the impact of two acanthocephalan parasites on the mortality of three species of New Zealand shore crabs (*Brachyura*)

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**Abstract** The effects of the acanthocephalan parasites *Proflicollis antarcticus* and *P. novaezelandensis* on the fecundity and mortality of three species of shore crab (*Macrophthalmus hirtipes*, *Hemigrapsus edwardsi* and *H. crenulatus*) are examined. The number of eggs produced by female crabs was strongly correlated (all  $P < 0.05$ ) with carapace width; parasite load was not a significant determinant of female fecundity. Mortality was inferred from reduction in the mean number of parasites per crab in the largest crab size-classes, indicating that heavily infected individuals are removed from the population. Mortality attributable to the parasites was observed for all three species of crabs, although the effect of parasites varied in both time and space; significant curvilinear regressions between parasite load and crab size-classes were not found in all samples. Crab mortality appears to be influenced by more than the pathological influences exerted by the parasites. Parasite-induced behavioural alterations may cause crab hosts to be more susceptible to predation by definitive hosts. We support this suggestion with three lines of evidence: the lack of parasite effects on fecundity, the weakening of the parasite effect on mortality during the time of year when birds are absent, and previous indications of parasite-mediated alterations in crab burrowing behaviour.

dynamics and community structure (Minchella and Scott 1991; Hudson and Greenman 1998; Poulin 1999). To play such a key role, parasites must influence the number of hosts within a population, either by decreasing recruitment or increasing mortality. The immediate effects of these processes on host population dynamics are functionally equivalent: both reduce the mean rate of increase in the host population (Jaenike et al. 1995). Parasites have been shown to influence host reproductive potential in a number of ways, ranging from the complete castration of the host to reductions in fecundity as a result of altered host physiology (e.g. Minchella and Loverde 1981; Thomas et al. 1996; Dezfuli et al. 1999). While changes in host fecundity have no direct impact on parasite survival, reduced host reproduction may still be advantageous to the parasites. For example, a partial or complete reduction in host egg production could make more nutrients available for parasite development (Hurd 1990). Alternatively, reductions in host reproduction can be mere pathological effects of infection.

Host mortality attributable to the parasites can also arise in a number of ways (Price 1980). For instance, host survival can be directly reduced by the pathological consequences of parasitic infection (e.g. Goater and Ward 1992). Parasites can also increase host sensitivity to pollution (Sakanari et al. 1984; Brown and Pascoe 1989) or reduce their ability to compete with other species (Park 1948; Hudson and Greenman 1998). Furthermore, it has been well documented that parasites are able to mediate predator–prey interactions, ultimately increasing the risk of intermediate host predation by their definitive host (Lafferty 1992; Poulin 1998). Unfortunately, however, owing to the difficulty of demonstrating whether parasites influence host mortality and fecundity in nature, few quantitative studies have been performed under field conditions.

Several approaches based on statistical evidence have been used in recent years to determine whether a parasitic infection is likely to affect the host mortality rate in a natural population (Lester 1984). One frequently used

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### Introduction

Recently, ecologists have begun to recognise parasitism as an important biotic determinant of animal population

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method requires mortality to increase with the number of parasites in a host (Crofton 1971; Anderson and Gordon 1982; Gordon and Rau 1982; Adjei et al. 1986; Rousset et al. 1996). In a system in which hosts continue to accumulate parasites over time, and assuming there is no density-dependent regulation of parasite numbers, we would expect older individuals in a population to have higher parasitic infections on average than younger conspecifics. However, in many instances, older cohorts tend to have fewer parasites on average than do cohorts of intermediate age (e.g. Henricson 1977; Thomas et al. 1995; Museth 2001). This suggests that older, more heavily infected individuals are removed from the host population via some influence exerted on them by parasites.

*Proflicollis antarcticus* and *P. novaezelandensis* (Acanthocephala) are parasites known to infect shore crabs in New Zealand (Brockerhoff and Smales 2002). Along the Otago coast, South Island, three species of crabs (the stalk-eyed mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae), the common rock crab *Hemigrapsus edwardsi* (Brachyura: Grapsidae) and the hairy-handed crab *H. crenulatus* have been confirmed as intermediate hosts to one or both of these parasites (Latham and Poulin, unpublished data). These parasitic worms encyst in the crab's haemocoel after being accidentally ingested as eggs. To complete its life cycle, the larva (cystacanth) relies upon the capture and ingestion of the intermediate host by a suitable vertebrate definitive host; in *Proflicollis* a number of shorebird species fill this role (Latham and Poulin 2002). Adult worms live in the intestine of the definitive host where they reproduce sexually, releasing eggs in their host's faeces.

Using this acanthocephalan–shore crab model, we investigate the existence of parasite-induced host mortality by examining the size-related changes in infection levels by cystacanths in the three intermediate host species. In this system, crabs continue to accumulate cysts over time, i.e. there is no obvious density-dependent reduction of cyst numbers. Acanthocephalan cystacanths have a long life span (Taraschewski 2000), so they can accumulate in their hosts. A rough estimate of average crab body volume (excluding limbs) suggests that it is more than 15,000 times the volume of a cystacanth. Hence, there is plenty of space in the host for cysts to accumulate; in fact as many as 204 cystacanth larvae have been found in one *H. edwardsi* (see Results). The null hypothesis that we are testing, therefore, is that in the absence of crab mortality due to the parasites the mean number of cystacanths per crab will gradually increase with crab size. Any levelling off or reduction towards the larger crab sizes would strongly suggest that heavily infected crabs are killed directly or indirectly by parasites. In addition, we searched for evidence of parasite-induced reductions in reproductive output. Acanthocephalans probably do not alter the reproduction of male crustaceans (Hynes and Nicholas 1958). In contrast, they have been found to affect the reproductive activity of females, sometimes inducing either complete

(Ward 1986; Oetinger 1987) or partial sterility (Hynes 1955; Kennedy 1985; Dezfuli et al. 1999). Hence, we investigate the effects of cystacanths on total egg production as a function of parasite load in female *M. hirtipes* and *H. edwardsi*.

## Materials and methods

The study was conducted on the intertidal mudflats of five locations on the Otago coast, South Island, New Zealand (45°52'S, 170°42'E). Two of these locations, Dowling Bay and Portobello Bay (both inside Otago Harbour), were only used for the investigation of the effects of parasite infection on female fecundity. The remaining three locations, Papanui Inlet (Otago Peninsula), Aramoana (Otago Harbour) and Blueskin Bay (north of Dunedin) were used to collect crabs for both parts of this study. All these locations experience a spring tidal range of approximately 2 m. Sediments consist of fine sand and mud; beds of sea grass *Zostera novaezelandica* cover the sediments at some of these locations, and rocks cover the upper shore at all locations.

Of the three species of crabs collected in this study, *Macrophthalmus hirtipes* and *Hemigrapsus crenulatus* are found mainly on the lower part (below mid-tide level) of estuarine habitats, whereas *H. edwardsi* is found mainly under rocks on the upper shore. All three species are very common along the Otago coast. A sample of 500 *Proflicollis* cystacanths was taken from each crab species at all locations. Examination of the 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*. Hence, both species of *Proflicollis* were pooled for the purpose of analysis in this study.

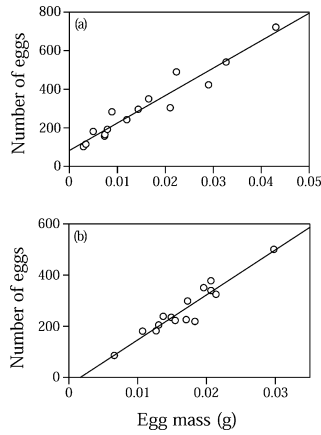
### Effects of parasitism on female fecundity

We were unable to obtain sufficient numbers of ovigerous *H. crenulatus* and therefore we investigated the effects of parasite infection on female fecundity only in *M. hirtipes* and *H. edwardsi*. Ovigerous females of both species were collected from the five locations during the winter months of May, June and July 2001, i.e. during the reproductive period of both species. All ovigerous females seen at the collection site(s) within a location were collected. Crabs were killed by freezing upon return to the laboratory. A grand total of 94 *M. hirtipes* and 115 *H. edwardsi* was examined. All crabs were measured to the nearest millimetre (carapace width, at the level of the second pair of lateral spines), dissected, and the number of cystacanths per crab recorded.

A sample of eggs (approximately 3–5% of egg mass) was taken from 15 individuals of both crab species. Samples were weighed and the number of eggs within each sample was counted. A regression analysis was performed to assess the relationship between the number of eggs within a sample and the mass of the sample. Mass proved to be an accurate predictor of egg number (*M. hirtipes*:  $R^2=0.93$ ,  $P=0.0001$ ; *H. edwardsii*:  $R^2=0.91$ ,  $P=0.0001$ ; Fig. 1), so total egg mass was used in all further analyses. Multiple-regression analyses were performed for each sample, using  $\log(x+1)$ -transformed numbers of cystacanths per crab and carapace width as predictor variables, and the total egg mass as the dependent variable. Each sample was treated independently, i.e. there was no pooling of data across locations or months, because parasite infection levels differed between locations, and the average egg mass per crab differed from month to month. Bonferroni corrections for multiple testing were applied, but are only mentioned where they affect the results.

### Effects of parasitism on crab mortality

Samples of *M. hirtipes*, *H. edwardsi* and *H. crenulatus* were collected throughout 2001. Approximately 80 *M. hirtipes* were



**Fig. 1a, b** Relationship between egg mass (g grams) and number of eggs among **a** 15 *Macrophthalmus hirtipes* ( $R^2 = 0.93$ ,  $P = 0.0001$ ), and **b** 15 *Hemigrapsus edwardsi* ( $R^2 = 0.91$ ,  $P = 0.0001$ )

collected monthly at three locations (total  $n = 2,981$ ). *H. edwardsi* was collected bimonthly from Aramoana (total  $n = 245$ ), and from two sites in Blueskin Bay: Warrington (total  $n = 120$ ) and Waitati (total  $n = 121$ ). *H. crenulatus* was collected bimonthly from one site in Blueskin Bay (total  $n = 227$ ). Individuals of all species of crabs with a carapace width of less than 17 mm were not collected, since they tend not to harbour cystacanths (Latham and Poulin, unpublished data). As described above, crabs were killed by freezing and measured and dissected for parasite counts.

Parasite infection levels in *M. hirtipes* were found to vary throughout the year at all locations. Numbers of cysts per crab tended to be highest early in the year (January to April) and then decreased gradually to their lowest levels late in the year (September to December) (Latham, unpublished data). Accordingly, *M. hirtipes* samples at all locations were split into three time periods (January–April, May–August and September–December) and analysed separately. This temporal effect was not significant in either *H. edwardsi* or *H. crenulatus*, hence monthly samples were pooled for the whole year. There was generally no difference in infection levels between sexes (all  $P \geq 0.10$ ), so sexes were pooled. However, sex differences were observed at Aramoana for *M. hirtipes* and *H. edwardsi*; sexes are treated separately for this location (for *M. hirtipes*, only results for males are presented, since female samples were too small; Latham, unpublished data).

Crabs of each species were assigned to five, six or seven size-classes (carapace width), assuming there was a close relation between age and size (see McLay 1988). The number of size-classes per species, site and location depended on crab sample sizes, particularly towards the smallest and largest sizes. Some pooling of size-classes was done at these extremes. We then estimated: (1) the

mean number of cysts per crab, including uninfected crabs, and (2) the ratio of the variance to the mean number of cysts per crab, a measure of aggregation (Margolis et al. 1982; Bush et al. 1997) which served as an index of variation in infection levels among crabs. Changes in mean parasite abundance and in the variance:mean ratio were then analysed as a function of increasing size-classes. We fitted linear and curvilinear (polynomial) regressions to mean numbers of cysts per crab as a function of size-class. A curvilinear regression that clearly provides a better fit (i.e. higher  $R^2$  value and substantially lower  $P$  value) to the data was taken as evidence of a reduction in mean parasite abundance in the larger size-classes. A few curvilinear regressions produced concave curves, but these were all non-significant and did not provide a better fit than linear regressions; all other curvilinear regressions, including all significant ones, produced convex curves. All analyses were done using  $\log_{10}(x+1)$ -transformed numbers of cysts per crab. Using raw data for the computation of variance:mean ratios would produce more pronounced, but similar, patterns to those reported here.

**Results**

**Impact of parasitism on female fecundity**

Only 12 (13%) of the 94 ovigerous *Macrophthalmus hirtipes* did not harbour *Profilicollis* cystacanths. The number of cystacanths per infected crab ranged from 1 to 108, with a mean of  $10.4 \pm 1.8$  (SE). Infection levels were positively correlated with crab carapace width across all samples, although crab size only explained about 15% of the variability in  $\log(x+1)$  numbers of cysts per crab (standardised regression coefficient:  $r = 0.39$ ,  $P = 0.0001$ ).

The total egg mass of ovigerous *M. hirtipes* was significantly and positively correlated with crab carapace width at all sites, locations and during the three months sampled with the exception of Papanui Inlet during July (Table 1). Total egg mass was not significantly correlated with infection levels at any time or at any location in *M. hirtipes* (Table 1).

Only 9 (8%) of the 115 ovigerous *Hemigrapsus edwardsi* did not harbour *Profilicollis* cystacanths. The number of cystacanths per infected crab ranged from 1 to 204, with a mean of  $11.5 \pm 2.6$  (SE). Infection levels were not significantly correlated with crab carapace

**Table 1** Summary data on the effects of crab size (carapace width) and parasitism on total egg mass in two species of shore crabs (*Macrophthalmus hirtipes* and *Hemigrapsus edwardsi*) at various locations along the Otago coast, South Island, New Zealand. Values are standardised partial regression coefficients from multiple regressions; therefore they can exceed 1

Crab species	Location	Site	Month	Carapace width	Log number of parasites	<i>n</i>
<i>M. hirtipes</i>	Papanui		May	0.70*	0.27	10
			July	0.78**	0.11	13
			July	0.92	-0.44	10
	Aramoana	Aramoana	May	0.80***	-0.24	17
			June	0.69***	0.05	24
		Waipuna	May	0.88**	-0.13	10
		July	0.85**	0.14	10	
<i>H. edwardsi</i>	Aramoana		May	0.81***	0.08	26
			June	0.94***	-0.09	20
			July	0.83***	0.01	28
	Dowling Bay		July	0.79***	0.03	15
		Portobello	July	0.63*	-0.16	15
	Blueskin Bay	Waitati	July	1.07***	-0.24*	11

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

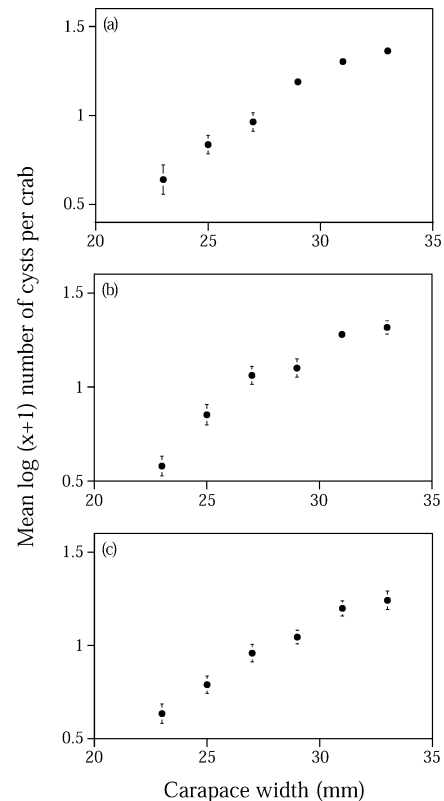
width in *H. edwardsi* across all samples (standardised regression coefficient:  $r=0.14$ ,  $P=0.133$ ).

The total egg mass of ovigerous *H. edwardsi* was positively correlated with crab carapace width at all locations, and during all three months sampled (Table 1). This relationship was highly significant at all locations except Portobello. Total egg mass was not significantly correlated with infection levels at Aramoana, Dowling Bay or Portobello. There was, however, an apparent negative relationship at Waitati, Blueskin Bay (standardised partial regression coefficient:  $r=-0.24$ ,  $P=0.027$ ; Table 1). Using an  $\alpha$ -value corrected by the Bonferroni procedure, this relationship was not significant.

### Impact of parasitism on crab mortality

The relationships between *Proflicollis* cystacanth numbers in *M. hirtipes* and crab size-classes are summarised in Table 2. At Papanui Inlet, linear-regression analysis showed a significant positive increase in infection levels with *M. hirtipes* body size during all three sampling periods; curvilinear regressions did not achieve a better fit (Fig. 2). In general, high mean numbers of cysts per crab were associated with low variance:mean ratio values, and vice-versa, for all three species of crabs (see Figs. 3 and 4 for examples).

In contrast to Papanui Inlet, Waipuna Bay clearly shows a more curvilinear relationship between parasite infection levels and *M. hirtipes* size-classes for the January to April and May to August periods (Table 2; Fig. 5a, b). There is, however, a linear increase in infection levels with increasing size-classes during September to December at Waipuna Bay (Table 2; Fig. 5c). The other two locations at which infection levels in *M. hirtipes* were examined, Aramoana and Blueskin Bay, showed patterns intermediate between the Papanui Inlet and Waipuna Bay extremes (Table 2). During the January to April and May to August periods at these two

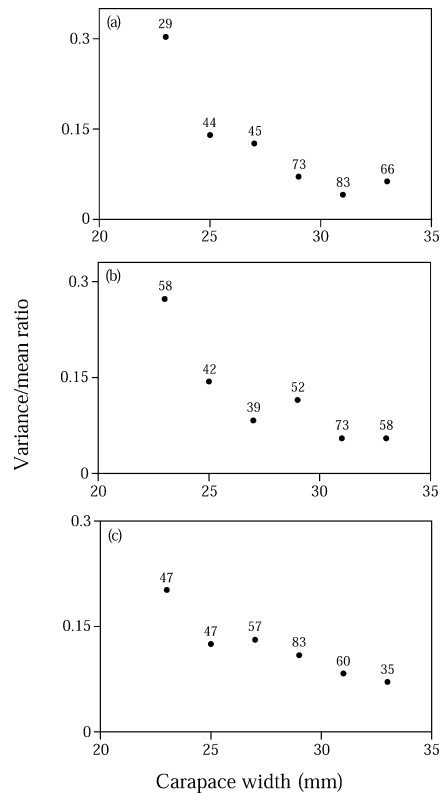


**Fig. 2a–c** Mean numbers, expressed as  $\log(x+1)$  ( $\pm$  SE vertical bars), of *Proflicollis* spp. cysts per crab in relation to host size-class (carapace width in millimetres) in *Macrophthalmus hirtipes* at Papanui Inlet, **a** January to April, **b** May to August and **c** September to December. See Fig. 3 for sample sizes

locations the curvilinear regression provided a better fit to the data than the linear one, between parasite infection levels and crab size-classes. In other words, mean number of cysts per crab tended to decrease in the larger size-classes. However, as in Waipuna Bay, infection levels tended to increase linearly with size-class in the September to December period.

**Table 2** Summary of the results of the regression analyses performed on the mean numbers of cystacanth larvae per crab as a function of crab size-class in *Macrophthalmus hirtipes*. Monthly time periods reflect seasonal differences in parasite loads

Sample	<i>n</i>	Linear		Curvilinear	
		$R^2$	<i>P</i>	$R^2$	<i>P</i>
Papanui Inlet					
January–April	340	0.98	0.0002	0.99	0.0009
May–August	322	0.93	0.0019	0.98	0.0023
September–December	329	0.98	0.0002	0.99	0.0005
Aramoana (males)					
January–April	134	0.71	0.0362	0.99	0.0013
May–August	103	0.79	0.0178	0.96	0.0084
September–December	120	0.92	0.0024	0.93	0.0192
Waipuna Bay					
January–April	160	0.15	0.4416	0.85	0.0565
May–August	165	0.003	0.9143	0.93	0.0182
September–December	162	0.94	0.0012	0.94	0.0131
Blueskin Bay					
January–April	324	0.86	0.0082	0.97	0.0055
May–August	358	0.90	0.0037	0.96	0.0082
September–December	338	0.95	0.0010	0.95	0.0107



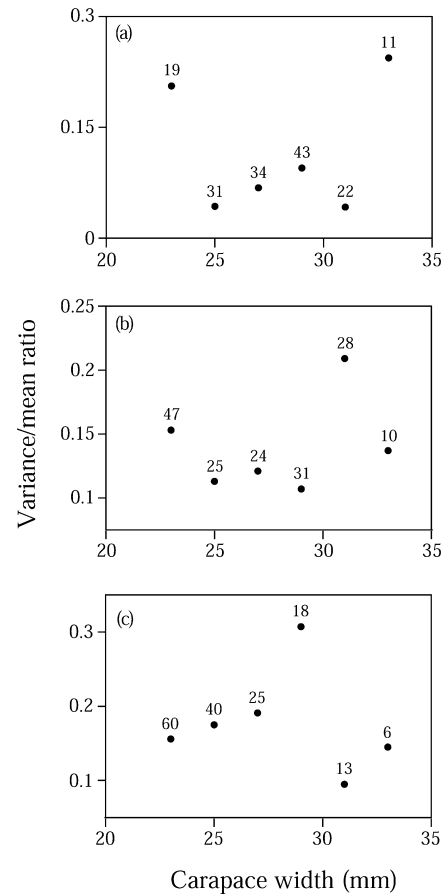
**Fig. 3a-c** Variance to mean ratio in numbers [expressed as  $\log(x + 1)$ ] of *Profilicollis* spp. in relation to host size-class (carapace width in millimetres) in *Macrophthalmus hirtipes* at Papanui Inlet, **a** January to April, **b** May to August, and **c** September to December. The number of hosts in each size-class is indicated above each point

Parasite infection levels in *H. edwardsi* tend to increase linearly with crab size at Aramoana, but only among males; neither the linear nor the curvilinear regressions provided a good fit to the data on female crabs (Table 3, Fig. 6). At the Blueskin Bay sites, there were no relationships between crab size-classes and mean number of parasites per host, with neither linear nor curvilinear regressions proving significant (Table 3). However, Figure 7 shows that the highest infection levels are in intermediate size-classes, and not in the largest size-classes.

The relationship between *H. crenulatus* size-class and mean infection levels was not explained by either a linear or a curvilinear regression ( $R^2=0.001$ ,  $P=0.94$ , and  $R^2=0.001$ ,  $P=0.9972$ , respectively). Despite no clear relationship existing between infection levels and crab size-class in this species, it can be seen (Fig. 8) that, on average, larger crab size-classes do not tend to have higher mean numbers of cysts per crab than do smaller size-classes.

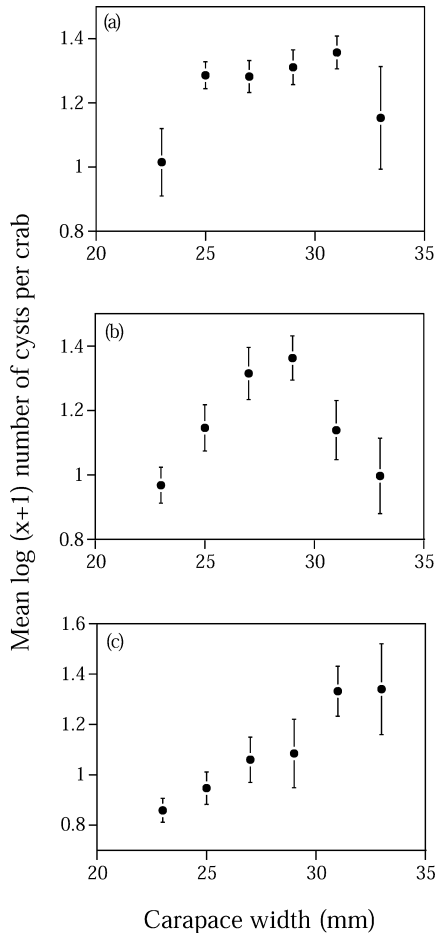
## Discussion

Our data suggest that *Profilicollis antarcticus* and *P. novaezelandensis* cystacanths do not have a major



**Fig. 4a-c** Variance to mean ratio in numbers [expressed as  $\log(x + 1)$ ] of *Profilicollis* spp. in relation to host size-class (carapace width in millimetres) in *Macrophthalmus hirtipes* at Waipuna Bay, **a** January to April, **b** May to August and **c** September to December. The number of hosts in each size-class is indicated above each point

influence on the fecundity of female *Macrophthalmus hirtipes* or *Hemigrapsus edwardsi*. There was no significant relationship between egg production and infection level in either *M. hirtipes* or *H. edwardsi* at any of the locations, nor during any of the three months sampled (Table 1). Rather, female fecundity in the two species of shore crabs was largely influenced by crab size, i.e. large females produce more eggs than smaller ones. This relationship between female fecundity and body size has been well documented among crustaceans in general (Rhodes and Holdich 1982; Sastry 1983; Ward 1988; Thomas et al. 1996), including New Zealand shore crabs (McLay 1988). Parasites such as rhizocephalans (Cirripedia) have huge negative effects on crab fecundity (Høeg 1995); however, to our knowledge no other studies have examined the effects of acanthocephalans on crab reproduction. Because there is evidence that heavily parasitised crabs are removed from the populations (see below), our test for the effect of acanthocephalans on crab fecundity may have been restricted to survivors. Still, if parasites could depress crab fecundity, we should have expected an effect among these crabs too.

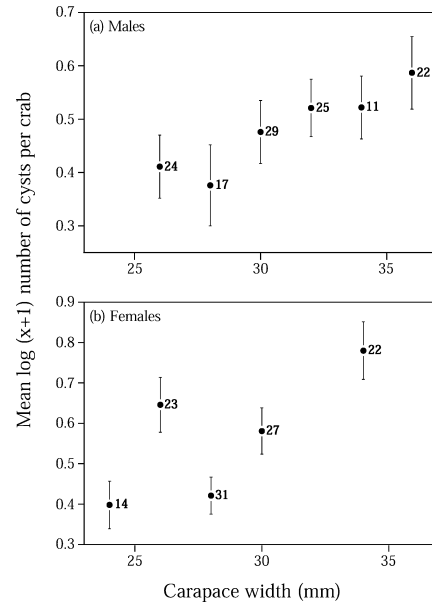


**Fig. 5a–c** Mean numbers, expressed as  $\log(x+1)$  ( $\pm$  SE vertical bars), of *Proflicollis* spp. cysts per crab in relation to host size-class (carapace width in millimetres) in *Macrophthalmus hirtipes* at Waipuna Bay, **a** January to April, **b** May to August and **c** September to December. See Fig. 4 for sample sizes

**Table 3** Summary of regression analyses performed on the mean numbers of cystacanth larvae per crab as a function of crab size-class in *Hemigrapsus edwardsi*. Note that differences in parasite loads between sexes were only observed at Aramoana

Sample	n	Linear		Curvilinear	
		R <sup>2</sup>	P	R <sup>2</sup>	P
Aramoana					
Males	128	0.87	0.0065	0.88	0.0439
Females	117	0.48	0.1943	0.54	0.4615
Blueskin Bay					
Warrington	120	0.31	0.3348	0.54	0.4568
Waitati	121	0.09	0.5716	0.77	0.1074

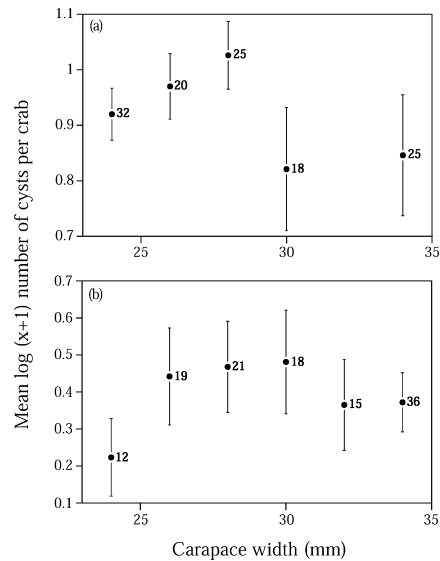
In contrast to the lack of effect of cystacanths on female crab fecundity, there is an apparent effect on crab mortality, i.e. there is generally a levelling off or a reduction in the mean number of cystacanths per crab towards the larger size-classes (e.g. Figs. 5, 7 and 8). Given the long life span of cystacanths, and the available space in the haemocoel of crabs, the most parsimonious



**Fig. 6a, b** Mean numbers, expressed as  $\log(x+1)$  ( $\pm$  SE vertical bars), of *Proflicollis* spp. cysts per crab in relation to host size-class (carapace width in millimetres) in *Hemigrapsus edwardsi* at Aramoana, for **a** males and **b** females. The number of hosts in each size-class is indicated to the right of each point

explanation for the drop in mean infection levels among larger size-classes is that heavily infected crabs are removed from the population at higher rates than lightly infected crabs (see Lester 1984; Rousset et al. 1996). This would also explain why variability in infection levels, measured by the variance:mean ratio, does not automatically increase with crab size-classes (Figs. 3 and 4). The gradual accumulation of parasites as an animal ages is the simplest pattern one might expect in the absence of, for example, mortality attributable to the parasites. This is because individual differences between crabs in the rate at which they accumulate parasites should create increasing variability in infection levels with increasing host age or size. We did not observe this consistently, again suggesting that heavily infected crabs disappeared from the population.

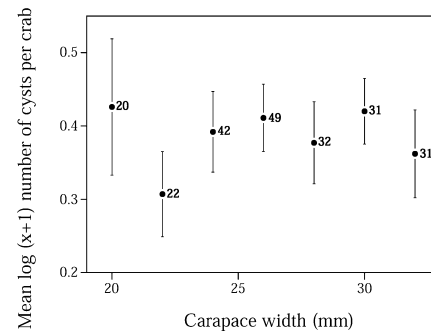
The impact of parasites on crab mortality was more obvious at some locations than others. For example, the larger *M. hirtipes* size-classes at Waipuna Bay showed a significant reduction in parasite load from January to August, whereas this effect was not observed in *M. hirtipes* at Papanui Inlet (contrast Figs. 2 and 5). Similarly, a reduction in mean parasite loads in the larger size-classes was more obvious at some times of the year than others. This effect was observed in *M. hirtipes* at Aramoana, Waipuna Bay and Blueskin Bay, where the mean numbers of cystacanths per crab increased with increasing size-class during the September to December period. This increase in parasite load in the larger crab size-classes coincided with a reduction in the number of shorebirds that feed on crabs in the Otago area in the last months of the year (Latham, unpublished data).



**Fig. 7a, b** Mean numbers, expressed as  $\log(x+1) (\pm \text{SE vertical bars})$ , of *Profilicollis* spp. cysts per crab in relation to host size-class (carapace width in millimetres) in *Hemigrapsus edwardsi* at **a** Warrington, and **b** Waitati, Blueskin Bay. The number of hosts in each size-class is indicated to the right of each point

The obvious difference between the effects of cyst-acanth on fecundity and mortality suggests that increased mortality of the large, heavily infected crabs was not merely a result of pathology. Rather, the parasites seemed to be actively manipulating their intermediate hosts to increase their susceptibility to bird predators. Three lines of evidence support this conclusion. Firstly, if mortality increased among large heavily infected crabs due to a parasite-induced nutrient depletion or some other form of debilitation, this should also be mirrored in a reduction in the number of eggs a female crab is able to produce. However, our results showed that crabs with heavier infections are not generally handicapped in egg production. Alternatively, infected crabs might compensate by allocating more resources to egg production than body maintenance in an effort to make up for the effects of parasites. Secondly, we should not observe a temporal difference in mortality rates of the more heavily infected crabs if mortality was due only to the intensity-dependent pathological effects of infection; rather large, heavily infected individuals should be removed from the system at a constant rate throughout the year. The fact that this only happens when shore-birds were abundant at our study sites is telling; it suggests that cysts can only accumulate without effects on the crabs when bird predators are absent.

The third line of evidence that suggests that increased mortality in the larger, heavily infected crabs is due to more than pathology, is that acanthocephalans are known to actively manipulate their intermediate hosts, making them more susceptible to predation by their definitive hosts (Moore 1984; Lafferty 1992; Poulin 1998). Latham and Poulin (2001) found evidence, albeit weak, that *Profilicollis* cystacanths are able to manipu-



**Fig. 8** Mean numbers, expressed as  $\log(x+1) (\pm \text{SE vertical bars})$ , of *Profilicollis* spp. cysts per crab in relation to host size-class (carapace width in millimetres) in *Hemigrapsus crenulatus* at Blueskin Bay. The number of hosts in each size-class is indicated to the right of each point

late the behaviour and colour of their intermediate host, *M. hirtipes*. Other studies have found that *P. antarcticus* is able to manipulate both the carapace colouration (Pulgar et al. 1995) and the behaviour (Haye and Ojeda 1998) of the shore crab *H. crenulatus*.

The majority of studies that have examined the effects of acanthocephalans on their intermediate hosts have concentrated on relatively small crustaceans like amphipods, ostracods or isopods (e.g. Hindsbo 1972; Bethel and Holmes 1973; Moore 1984; Bakker et al. 1997). The results of those studies show that the mere presence of one or two cystacanths in small crustaceans can be sufficient to induce marked behavioural or colour changes. In *M. hirtipes* and *H. edwardsi* the mean number of cystacanths per host is about ten, and it is lower in *H. crenulatus*. Even when combining all cystacanths found in a crab, the host:parasite size ratio is still much higher than that found in isopods or amphipods. Hence, it is possible that if manipulation is achieved via chemical secretions (Helluy and Holmes 1990), the parasite products may become too diluted in the large crab haemocoel. Consequently, the effects of parasites on their crab hosts, at the individual level, may be subtle compared with small crustaceans. At the level of host populations, however, we found relatively clear-cut effects.

The effects of parasitism on crab mortality found in the present study did not appear to differ significantly between crab species (levelling off or reductions in parasite numbers with crab size were observed in all three species of crabs). Instead, we observed both temporal and spatial variability within crab species. This differs from the study by Thomas et al. (1995) on mortality in two species of congeneric and sympatric amphipods (*Gammarus aequicauda* and *G. insensibilis*) infected by the same trematode parasite (*Microphallus papillorobustus*). Using an approach similar to ours, the authors found that *M. papillorobustus* has no significant effect on the survival of *G. aequicauda* compared with *G. insensibilis*. Thus in our system, the presence of *Profilicollis* spp. may have similar regulatory effects on all these crab species,

rather than causing reductions in the abundance of one species and indirectly benefiting the other species (see Park 1948; Hudson and Greenman 1998).

In summary, numbers of cystacanths per crab did not influence the number of eggs a female was able to produce. Conversely, parasitism affected the survival of all three species of shore crabs studied. However, temporal and spatial differences in mortality rates were observed. These results suggest that mortality among the larger, heavily infected crabs is not merely due to pathology. Instead, the parasites are apparently actively manipulating their intermediate hosts to increase the likelihood of predation by definitive hosts (i.e. shorebirds). This is one of the first demonstrations that host manipulation by parasites, evolved to facilitate the completion of their life cycle, can have measurable impacts on host populations.

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