Spatiotemporal heterogeneity in recruitment of larval parasites to shore crab intermediate hosts: the influence of shorebird definitive hosts

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Abstract: Parasitism is a major biotic determinant of animal population dynamics and community structure. Temporal and spatial heterogeneity in parasitism is commonly observed in intermediate host populations. Understanding the causes of temporal and spatial variation in the recruitment of parasites is crucial if we are to manage host populations and animal communities effectively. Here, the temporal and spatial dynamics of *Profilicollis antarcticus* and *Profilicollis novaezelandensis* (Acanthocephala) infections in three species of shore crabs (*Macrophthalmus hirtipes*, *Hemigrapsus edwardsii*, and *Hemigrapsus crenulatus*) are examined in relation to the distribution and abundance of shorebird definitive hosts. Temporal patterns of infection were observed in *M. hirtipes* but not the other two species. Spatial heterogeneity in recruitment of acanthocephalan larvae to *M. hirtipes* and *H. edwardsii* populations was found both within and between locations. Weak evidence is found that infection levels in crab populations are related to the distribution and abundance of shorebird hosts both temporally and spatially. In this system, abiotic factors seem to be at least as important in determining how infection levels vary in time and space as the input of parasite eggs from bird definitive hosts.

Résumé : Le parasitisme est un facteur déterminant biotique majeur de la dynamique de population et de la structure de communauté chez les animaux. L'hétérogénéité spatiale et temporelle du parasitisme s'observe communément chez les populations d'hôtes intermédiaires. La compréhension des causes de la variation spatiale et temporelle du recrutement des parasites est essentielle pour la gestion efficace des populations d'hôtes et des communautés animales. Nous examinons la dynamique temporelle et spatiale des infections de *Profilicollis antarcticus* et de *P. novaezelandensis* (Acanthocephala) chez trois espèces de crabes littoraux (*Macrophthalmus hirtipes*, *Hemigrapsus edwardsii* et *Hemigrapsus crenulatus*) en fonction de la répartition et de l'abondance des hôtes définitifs, des oiseaux de rivage. Il y a des patterns temporels d'infection chez *M. hirtipes*, mais pas chez les deux autres espèces. Il existe une hétérogénéité spatiale dans le recrutement des larves d'acanthocéphales chez les populations de *M. hirtipes* et *H. edwardsii*, tant entre les localités que dans chacune des localités. Il y a de faibles indications que la gravité des infections dans les populations de crabes est en relation, tant temporelle que spatiale, avec la répartition et l'abondance des oiseaux de rivage qui servent d'hôtes. Dans ce système, les facteurs abiotiques semblent avoir autant d'importance que la production d'oeufs de parasites provenant des hôtes définitifs aviaires dans la détermination de la variation dans la gravité des infections dans le temps et l'espace.

[Traduit par la Rédaction]

Introduction

In natural populations, infection levels by parasites differ between localities and between seasons. This provides strong indications that the recruitment of parasites to host populations is variable in time and space (Kuris 1990; Sousa 1990, 1993). Understanding the causes of this variation is crucial if we are to fully understand the impact that parasites have on host populations and animal communities. Epidemiological models used to assess or predict the effects of parasites and diseases on wildlife require information on what drives spatiotemporal heterogeneity in parasite recruitment (Hudson et al. 2002).

To date, most studies have focused on the temporal and spatial variation in, and population dynamics of, trematode parasites (e.g., Lafferty et al. 1994; Mouritsen et al. 1997; Marcogliese et al. 2001; Smith 2001). This variation may result from a number of factors such as host movement, density, life history, susceptibility to infection, and parasite dispersal and behaviour (Wakelin 1978; Anderson and Gordon 1982; Blower and Roughgarden 1989; Grosholz 1994; Smith 2001). It is likely, however, that the relative contribution of these factors to parasite distribution varies with spatial scale (Wiens 1989). Most parasitic helminths require the use of one or more intermediate hosts (those harbouring the larval parasite stages) and a definitive host (harbouring the adult worms) to complete their life cycle. Reproduction occurs in the definitive host, and the parasite's

Received 9 December 2002. Accepted 3 June 2003. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 26 August 2003.

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 doi: 10.1139/Z03-118

eggs are disseminated into the environment along with the host's faeces. In general, intermediate hosts tend to be relatively sessile compared with definitive hosts such as birds and fish. High mobility in definitive hosts will serve to enhance the dispersal of the parasite's eggs, infective to the intermediate host, from one location to another. Accordingly, much of the large-scale heterogeneity in the distribution of parasites observed among intermediate hosts has been attributed to the high mobility and other behavioural patterns of definitive hosts (Sousa and Grosholz 1991; Williams and Esch 1991; Marcogliese et al. 2001; Smith 2001). All else being equal, we would expect infection levels in intermediate hosts to be highest where and when definitive hosts are most abundant.

The phylum Acanthocephala consists of parasitic worms that are transmitted by predation from an intermediate host to a definitive host. Few studies (e.g., Dezfuli et al. 1999) have investigated temporal and spatial variation of acanthocephalan abundance in intermediate hosts, and to our knowledge, none attempt to correlate this variation with the abundance of definitive hosts. Adult acanthocephalans live and reproduce sexually in the intestine of vertebrates, from which they release eggs in their host's faeces. This is the only stage of the acanthocephalan life cycle that exists outside of a host, free in the environment. After an egg is accidentally ingested by a suitable arthropod intermediate host, it hatches and undergoes a series of developmental stages in the host's hemocoel where it develops to the cystacanth stage and awaits ingestion by an appropriate vertebrate definitive host (see Nickol 1985). The simple life cycle of acanthocephalans makes this system an ideal one to examine for correlations between definitive host abundance and parasite abundance in intermediate host populations.

Two species of acanthocephalans, *Profilicollis antarcticus* and *Profilicollis novaezelandensis*, use three species of shore crabs as intermediate hosts around the Otago coastline, South Island, New Zealand (Latham and Poulin 2001, 2002*a*, 2002*b*). Both species of *Profilicollis* are known from the stalk-eyed mud crab (*Macrophthalmus hirtipes*), while *P. novaezelandensis* also uses the common rock crab (*Hemigrapsus edwardsii*) and the hairy-handed crab (*Hemigrapsus crenulatus*) in the Otago region (Latham and Poulin 2002*b*). *Hemigrapsus crenulatus* is also known to be infected by *P. antarcticus* in the Canterbury region, South Island, New Zealand (Brockerhoff and Smales 2002), and in Chile (Pulgar et al. 1995). Brockerhoff and Smales (2002) also found that the tunnelling mud crab (*Helice crassa*) is an intermediate host for both *Profilicollis* species.

Both species of *Profilicollis* use various species of shorebirds as definitive hosts. *Profilicollis antarcticus* is known from the pale-faced sheathbill (*Chioniz alba*) and the southern black-backed gull (*Larus dominicanus*) in Chile (Zdzitowiecki 1985; Torres et al. 1991, 1992). In New Zealand, both *P. antarcticus* and *P. novaezelandensis* have been confirmed from the pied oystercatcher (*Haematopus ostralegus finschi*), the bar-tailed godwit (*Limosa lapponica*) (Brockerhoff and Smales 2002), and *Larus dominicanus* (Latham and Poulin 2002*a*).

These shorebirds do not use all available intertidal feeding habitats equally: their abundance varies in space and time. Thus, we would expect that *P. antarcticus* and *P. novaezelandensis* eggs would be deposited unevenly both within and among localities. Consequently, cystacanth numbers in crab populations are likely to be highest in frequently visited areas. Similarly, the abundance of shorebirds may influence temporal patterns of cystacanth numbers in crab populations. Daily, monthly, or seasonal differences in definitive host abundance could potentially create pulses of cystacanth recruitment to crab populations. These variations in definitive host abundances have been found to influence trematode recruitment to intermediate host populations (Marcogliese et al. 2001; Smith 2001); however, no data exist for acanthocephalan systems. Here, the temporal and spatial dynamics of *Profilicollis* spp. infections are examined over 12 months in three species of shore crabs from different locations and related to the abundance and distribution of a number of shorebirds that serve as definitive hosts. Specifically, we test the hypothesis that definitive hosts regulate spatial and temporal heterogeneity in infection levels in intermediate hosts. We expect that cystacanth infection levels will be highest in shore crab populations at those locations visited most frequently by shorebirds and when shorebird numbers are highest. Given the solid field evidence that *Profilicollis* spp. infections cause significant mortality in these crabs (Latham and Poulin 2002*b*), determining what factors drive the abundance of the parasites is crucial to understanding crab population dynamics.

Methods

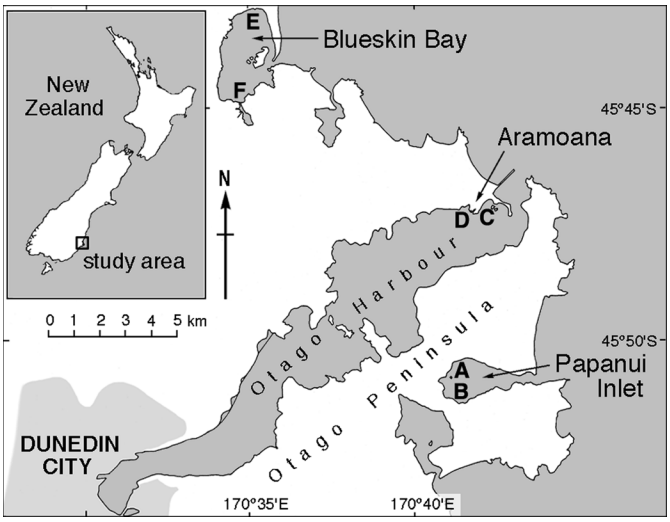
Study area

The study was conducted on the intertidal mudflats of three locations around the Otago coastline, South Island, New Zealand (Fig. 1): (*i*) Papanui Inlet, located on the eastern side of the Otago Peninsula, (*ii*) Aramoana, located within the Otago Harbour, and (*iii*) Blueskin Bay located approximately 20 km north of Dunedin. These locations were further divided into two sites per location: sites A north and B south in Papanui Inlet, C conservation area and D Waipuna Bay within Aramoana, and E Warrington and F Waitati within Blueskin Bay (Fig. 1). At each of the six sites, crabs were collected over a restricted area (approximately 50 m × 50 m) to limit the potential effects of small-scale variation in infection levels. All of the locations experience a spring tidal range of approximately 2 m. Sediments consist of fine sand and mud; beds of sea grass (*Zostera novaezelandica*) cover parts of the sediments at some of these locations, and rocks cover the upper shore at all locations.

Crab collection and parasite counts

Three species of crabs were collected in this study. Two species, *M. hirtipes* and *H. crenulatus*, are found mainly on the lower part (below midtide level) of intertidal habitats (McLay 1988). The third species, *H. edwardsii*, is found mainly under rocks around the upper shore (McLay 1988). All three species are very common around the Otago coastline. A sample of 500 *Profilicollis* spp. cystacanths was taken from each 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*. Because

Fig. 1. Map of the Otago coastline, South Island, New Zealand, showing sampling sites (upper-case letters: see Methods for site names) and locations.



of this, and the fact that both species have identical life cycles, all cystacanths are pooled for analysis in this study.

Samples of *M. hirtipes*, *H. edwardsii*, and *H. crenulatus* were collected from January to December 2001. Crabs were collected by hand by an observer picking up both buried and exposed crabs while walking in the collection area (or found under randomly chosen rocks in the case of *H. edwardsii*). Approximately 40 *M. hirtipes* were collected monthly at all six sites (total n = 2981). *Hemigrapsus edwardsii* was collected bimonthly from site C in Aramoana (total n = 245) and from both sites (20 per month) within Blueskin Bay, E Warrington (total n = 120), and F Waitati (total n = 121). *Hemigrapsus crenulatus* was collected bimonthly from site F within Bluskin Bay (total n = 227). Individuals of all species of crabs with a carapace width of less than 17 mm were not collected, as they tend not to harbour cystacanths (A.D.M. Latham and R. Poulin, unpublished data). Crabs were killed by feezing upon return to the laboratory. 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 was recorded.

Shorebirds

Bird observations were done at least five times per month at all six sites within the three locations throughout 2001 (except January). The abundance of confirmed and suspected definitive host shorebirds was recorded on each occasion. Because shorebirds are mobile and the spatial scale of the crab collection site (i.e., 50 m × 50 m) may be too small to adequately account for the shorebird community, we counted all shorebirds within the greater study area (i.e., the entire exposed mudflat) encompassing a crab collection site. As some areas were larger than others, bird numbers were corrected for study area size, and bird abundance is presented as $\log(x + 1)$, where x is the number of birds per square kilometre. Confirmed definitive hosts of *Profilicollis* species in New Zealand include *Larus dominicanus*, *Haematopus ostralegus finschi*, and *Limosa lapponica* (Brockerhoff and Smales 2002; Latham and Poulin 2002*a*). Because of ethical or logistical constraints, many species of shorebirds that are suspected definitive hosts have not been confirmed as such via dissections but have been included in this study. These birds are suspected to act as definitive hosts for *Profilicollis* species based on their diet and the fact that related species elsewhere harbour acanthocephalans. These include the white-faced heron (*Ardea novaehollandiae*), royal spoonbill (*Platalea regia*), variable oystercatcher (*Haematopus unicolor*), masked plover (*Vanellus miles*), pied stilt (*Himantopus himantopus*), banded dotterel (*Charadrius bicinctus*), red-billed gull (*Larus novaehollandiae*), and sacred kingfisher (*Halcyon sancta*).

Data analysis

Because prevalence of infection was 100% or close to 100% in almost all crab samples, we used the numbers of cysts per crabs as a measure of infection level. To determine if any temporal or spatial variation exists in cystacanth infection levels in crab populations, the three species of shore crabs were analysed separately. The first analyses were also performed separately for each location to assess whether there were between-site differences within locations. 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 in infection levels in crabs among months, between sexes, and between sites within a location with crab carapace width as the covariate. Where no significant difference ($P > 0.30$) was found between two sites within a location for a species of crab, data were pooled for the subsequent analysis. An ANCOVA was then performed to test for differences in infection levels in crabs between locations (sites that differed significantly within one location were treated as distinct locations in this analysis) with crab carapace width as the covariate. In cases where numbers of cystacanths per crab correlated significantly with crab carapace width (see Results), we used residuals of this relationship, which are measures of infection level corrected for host size, to derive population mean values that could then be related to shorebird abundances. If infection levels did not correlate with carapace width, we used the (log-transformed) numbers of cystacanths per crab instead. This rule was also applied for illustrative purposes in the figures. An additional sample of *M. hirtipes* was collected from all three locations in January 2002, 6 weeks after the December 2001 sample, to ascertain whether cystacanth infection levels followed the trend observed during the month of January 2001. Data from this month were used for illustrative purposes in the figures only.

An analysis of variance (ANOVA) was performed to examine for differences in the abundance of confirmed definitive bird hosts among the six sites and over the 11 months during which bird numbers were recorded; we also examined for a possible site × month interaction effect. This analysis was repeated for suspected definitive bird hosts (here, "suspected" includes confirmed hosts as well as bird species likely to serve as hosts). A series of simple regressions were then performed, separately for each site, correlating monthly confirmed or suspected definitive bird host abundances with monthly cystacanth infection levels in *M. hirtipes* (as this was the only species of crab in which significant seasonal

Table 1. ANCOVA results for the effect of month, site, location, sex, and the covariate crab body size on *Profilicollis* spp. cystacanth infection levels in *Macrophthalmus hirtipes* populations at three intertidal mudflats around the Otago coastline, South Island, New Zealand.

Location	Source	df	*F*	*P*
Papanui Inlet	Carapace width	1,976	413.50	0.0001
	Month	11,976	2.77	0.001
	Site	1,976	3.51	0.061
	Sex	1,976	0.05	0.817
Aramoana	Carapace width	1,954	102.71	0.0001
	Month	11,954	4.28	0.0001
	Site	1,954	339.37	0.0001
	Sex	1,954	0.35	0.552
Blueskin Bay	Carapace width	1,1005	161.96	0.0001
	Month	11,1005	2.19	0.013
	Site	1,1005	1.85	0.175
	Sex	1,1005	1.61	0.205
Among locations	Carapace width	1,2963	707.64	0.0001
	Month	11,2963	7.85	0.0001
	Location	3,2963	210.55	0.0001
	Sex	1,2963	5.33	0.021

differences in cystacanth infection levels were observed); these analyses were based on monthly average values for both parameters. These regressions were performed (*i*) without a time lag and (*ii*) with a time lag of 1 month, i.e., infection levels in crabs were paired with the previous month's bird numbers. A 1-month time lag was chosen based on the expected time for an ingested egg to develop into a cystacanth inside a crab. Finally, mean annual residual numbers of cysts per crab (i.e., measures of infection corrected for crab size) were correlated with mean annual numbers of bird hosts per square kilometre across all six sites. *Hemigrapsus edwardsii* and *H. crenulatus* were not included in this analysis, as there were insufficient data for these two species.

Results

Cystacanth infections in crab populations

Cystacanth infection levels (performed on grand totals for each species) were highest in *M. hirtipes* (mean = 11.8, range = 1–145), intermediate in *H. edwardsii* (mean = 5.7, range = 1–86), and lowest in *H. crenulatus* (mean = 2.4, range = 1–31).

Populations of *M. hirtipes* at all three locations showed a strong positive correlation between *Profilicollis* spp. cystacanth infection levels and crab carapace width (Table 1). In other words, larger crabs tended to harbour more cysts, on average, than smaller conspecifics. After correcting for crab body size, infection levels within *M. hirtipes* populations were found to differ significantly among months at all three locations (Fig. 2; Table 1). Conversely, differences between sites within a location were only observed at the Aramoana location (Table 1). When the sites at this location were treated separately, crab carapace width and month of collection still had a significant effect on the infection levels of crabs (Fig. 3). Infection levels in *M. hirtipes* tended to be highest during January and February (summer months) at all three locations, with a general decrease in infection levels over the winter months. A return to high infection levels during the summer is seen in the crab samples collected in January 2002 (Figs. 2 and 3). Cystacanth infection levels at the three locations were not significantly related to crab sex (Table 1). However, when the Aramoana sites were treated separately, cystacanth infection levels were found to differ significantly between sexes at the conservation area (site C), although not at Waipuna Bay (site D). The results of the interlocation ANCOVA (Papanui Inlet, Aramoana conservation area, Waipuna Bay, and Blueskin Bay) show that there is a significant difference in cystacanth infection levels among the four locations (Table 1). This analysis on all crabs sampled also revealed a weak but significant sex difference in infection levels (Table 1), with females showing generally higher infection levels than males.

Cystacanth infection levels in *H. edwardsii* were significantly correlated with crab carapace width at the Aramoana location (Table 2). However, crab body size was not significantly correlated with infection levels for either *H. edwardsii* or *H. crenulatus* at Blueskin Bay (Table 2). Similarly, infection levels within *H. edwardsii* and *H. crenulatus* populations were not significantly influenced by the month in which they were collected (Figs. 4 and 5). Infection levels between the Blueskin Bay sites differed significantly (Fig. 4*b*; Table 2) and hence were analysed separately: crab carapace width and month of collection still had no significant effect on the infection levels of crabs at either site. However, a significant sex effect was found when the two Blueskin Bay sites were analysed separately. At Warrington (site E), male *H. edwardsii* tended to have more cysts than females (log-transformed values: 0.96 ± 0.041 (±SE) and 0.82 ± 0.062, respectively). Conversely, at Waitati (site F), males tended to have fewer cysts than females (log-transformed values: 0.34 ± 0.056 (±SE) and 0.52 ± 0.083, respectively). Cystacanth infection levels also differed significantly between male and female *H. edwardsii* at Aramoana (Table 2). Infection levels in *H. crenulatus* (Blueskin Bay) did not differ significantly between sexes. The results of the interlocation ANCOVA (Aramoana,

Fig. 2. Mean (±SE) residual numbers of cystacanth larvae per *Macrophthalmus hirtipes* for all 12 months of 2001 plus January 2002. (*a*) Papanui Inlet sites. (*b*) Aramoana sites. (*c*) Blueskin Bay sites.

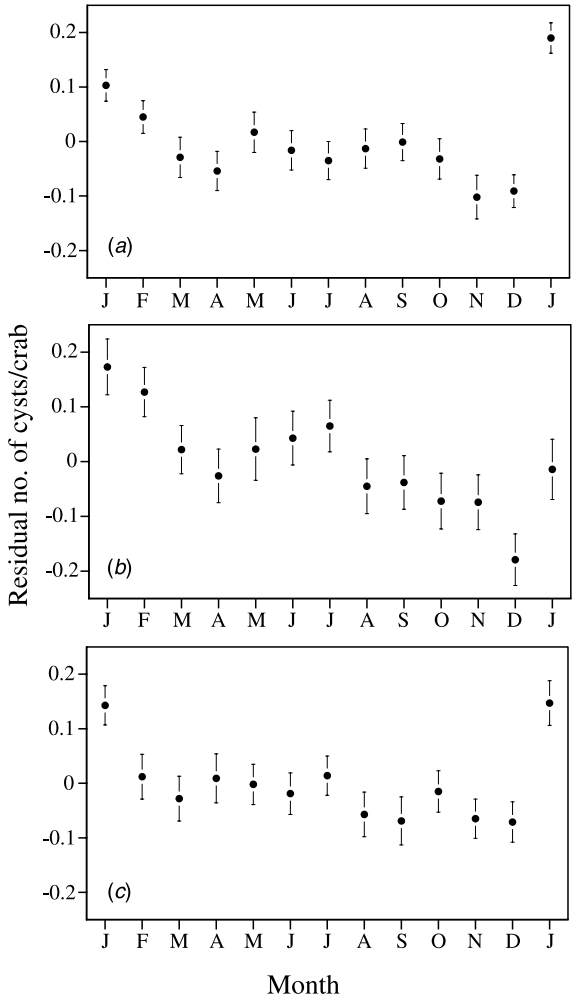
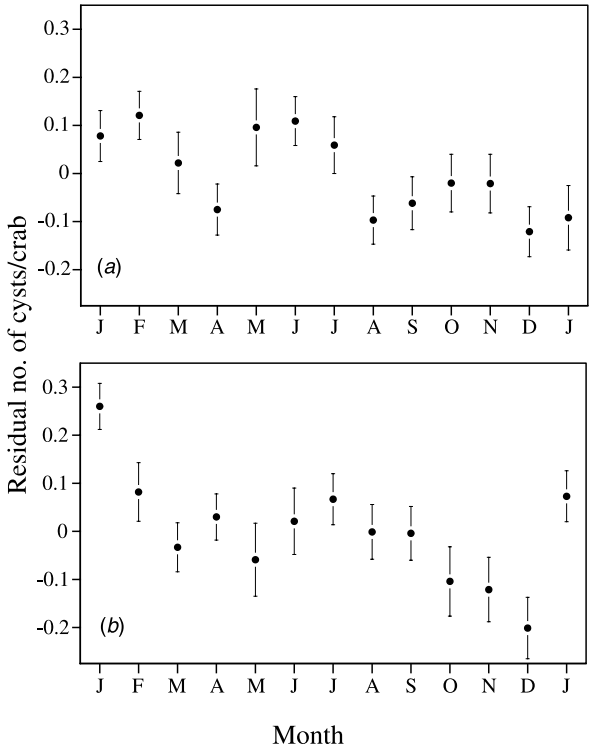


Fig. 3. Mean (±SE) residual numbers of cystacanth larvae per *M. hirtipes* for all 12 months of 2001 plus January 2002 for both Aramoana sites. (*a*) Conservation area. (*b*) Waipuna Bay.



Warrington, and Waitati) show that there is a significant difference in cystacanth infection levels in *H. edwardsii* among the three locations (Table 2).

Shorebird hosts

Both confirmed and suspected shorebird host abundances differed significantly between sites and among months; a significant site × month interaction effect was also observed for the suspected shorebird hosts (Table 3). Monthly averages in confirmed and suspected shorebird host numbers correlated positively with cystacanth infection levels in *M. hirtipes* in 11 out of 12 regressions (from each of the six sites, with confirmed and suspected hosts analysed separately) when no time lag was incorporated into the analyses and in 8 out of 12 when a time lag was used in the analyses. However, none of these regression analyses were statistically significant (although four came close, with $P < 0.10$). There is thus weak evidence suggesting a link between bird abundance and seasonal fluctuations in infection levels in crabs.

The mean (log (x + 1)) monthly shorebird numbers for all six sites are shown in Fig. 6. In general, there tends to be a decrease in bird numbers from approximately July to October before they once again tend to increase. There are also, however, comparatively low bird numbers during February at four of the six locations (Fig. 6). Of these six sites, the two Blueskin Bay sites show the most variability in shorebird abundance over the year, while Aramoana shows the least. Despite the correlation between the mean annual numbers of confirmed or suspected shorebird hosts and the mean cystacanth infection levels in *M. hirtipes* across the six sites being positive (Fig. 7*a*), it was not statistically significant ($r^2 = 0.307$, $P = 0.2543$ and $r^2 = 0.472$, $P = 0.1315$ for confirmed and suspected hosts, respectively). It is clear, however, that the three sites with the most birds had the highest infection levels in crabs. Similarly, within a location, sites with the most birds tended to have the highest cystacanth infection levels in crab populations (Fig. 7). Figure 7*b* shows that the relationship between the mean annual numbers of suspected shorebird hosts and cystacanth infection levels in *H. edwardsii* was also positive, although we lacked sufficient data to test this statistically.

Discussion

The results of our study support previous findings that temporal and spatial heterogeneity in parasitism is commonly observed in intermediate-host populations (Robson and Williams 1970; Sousa 1993; Kuris and Lafferty 1994; Lafferty et al. 1994; Mouritsen et al. 1997; Latham and Poulin 2001; Marcogliese et al. 2001; Smith 2001). Our results show that cystacanth infection levels in *M. hirtipes* populations differed significantly throughout the year, with

Table 2. ANCOVA results for the effect of month, site, location, sex, and the covariate crab body size on *Profilicollis* spp. cystacanth infection levels in *Hemigrapsus edwardsii* and *Hemigrapsus crenulatus* populations at two intertidal mudflats around the Otago coastline, South Island, New Zealand.

Location	Source	df	*F*	*P*
Hemigrapsus edwardsii				
Aramoana	Carapace width	1,237	9.02	0.003
	Month	5,237	0.43	0.828
	Sex	1,237	9.64	0.002
Blueskin Bay	Carapace width	1,232	0.01	0.913
	Month	5,232	0.61	0.691
	Site	1,232	70.04	0.0001
	Sex	1,232	0.02	0.876
Among locations	Carapace width	1,476	1.10	0.295
	Month	5,476	0.36	0.875
	Location	2,476	60.75	0.0001
	Sex	1,476	0.58	0.446
Hemigrapsus crenulatus				
Blueskin Bay	Carapace width	1,219	0.48	0.490
	Month	5,219	1.59	0.165
	Sex	1,219	2.05	0.153

Fig. 4. (*a*) Mean (±SE) residual numbers of cystacanth larvae per *Hemigrapsus edwardsii* for the 6 months sampled (bimonthly) during 2001 for Aramoana. (*b*) Mean (±SE) log((numbers of cystacanth larvae per crab) + 1) for the 6 months sampled (bimonthly) during 2001 for the Blueskin Bay sites. ●, Warrington; ○, Waitati.

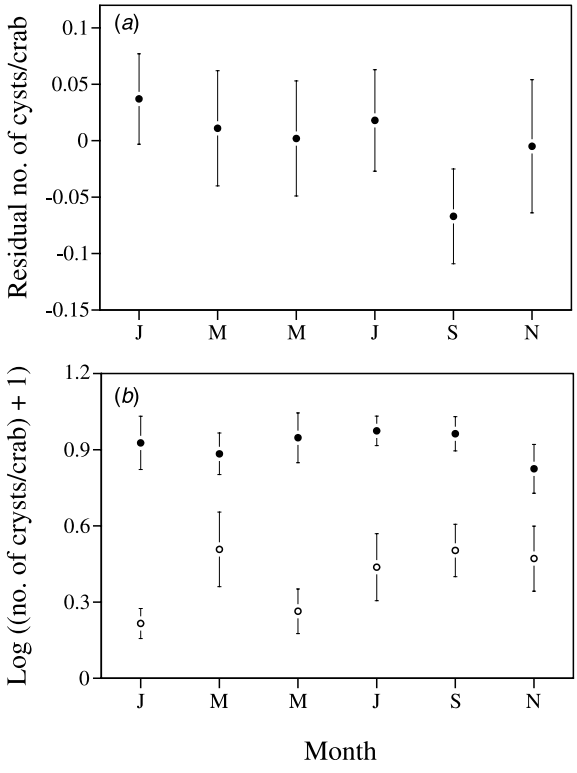


Fig. 5. Mean (±SE) log((numbers of cystacanth larvae per *Hemigrapsus crenulatus*) + 1) for the 6 months sampled (bimonthly) during 2001 at Waitati, Blueskin Bay.

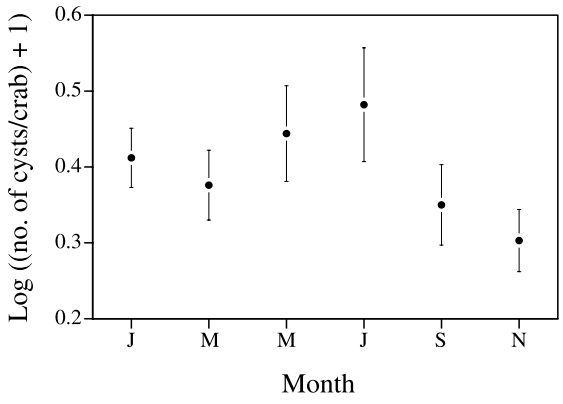
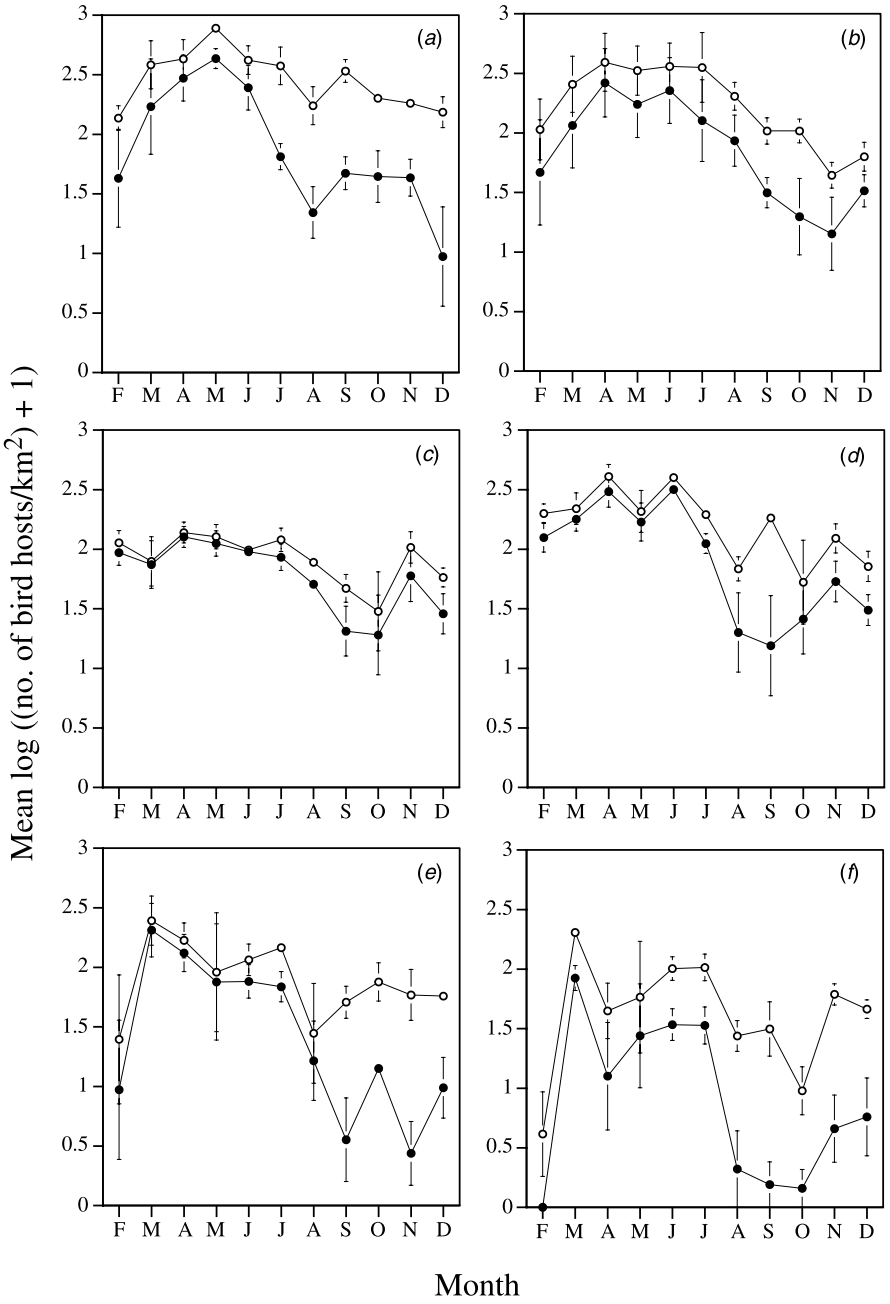


Table 3. ANOVA results for the effect of site and month on the abundance of confirmed and suspected definitive shorebird hosts at six sites within three intertidal mudflats around the Otago coastline, South Island, New Zealand.

Source	df	*F*	*P*
Confirmed shorebird hosts			
Site	5,268	27.679	0.0001
Month	10,268	18.506	0.0001
Site × month interaction	50,268	1.324	0.084
Suspected shorebird hosts			
Site	5,268	27.028	0.0001
Month	10,268	9.779	0.0001
Site × month interaction	50,268	1.422	0.042

an obvious peak in cyst numbers during the warmer summer months: there was no significant temporal variation in cystacanth infection levels in *H. edwardsii* or *H. crenulatus* populations. Our results also show a significant spatial difference in cystacanth infection levels among *M. hirtipes* and *H. edwardsii* populations. These spatial differences in infection levels in crab populations were observed both within and among intertidal marine mudflats. Our results do not,

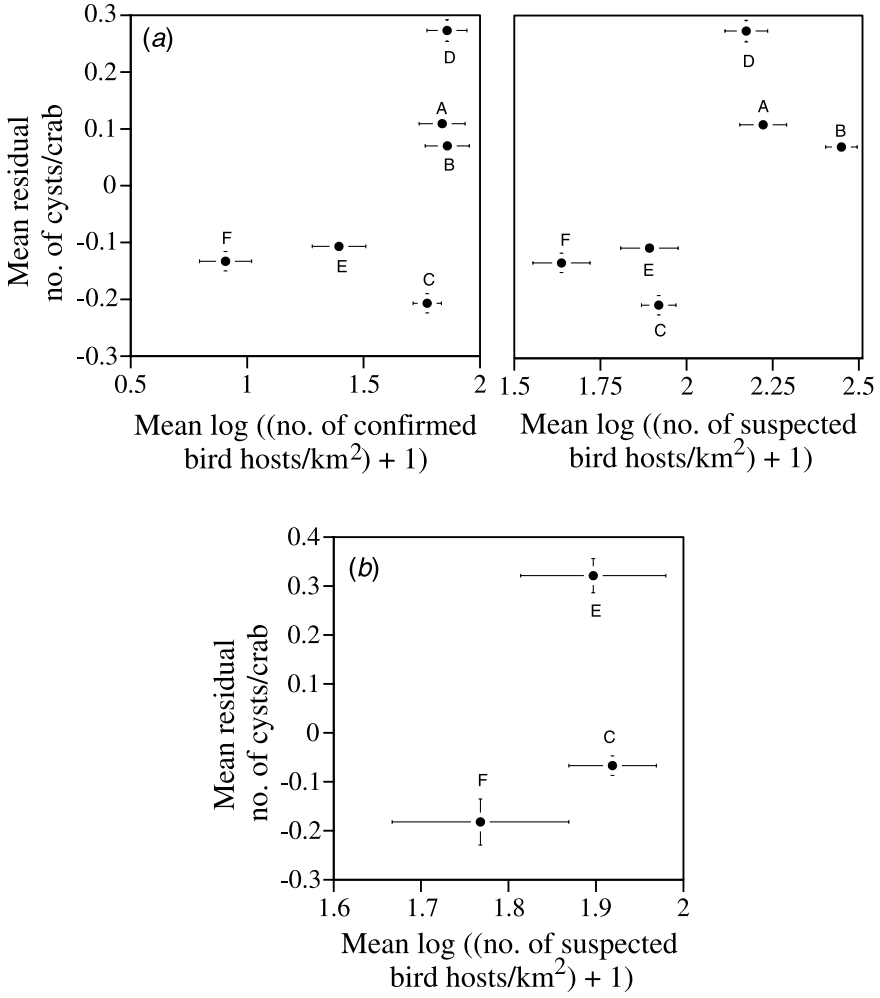
Fig. 6. Mean (±SE) log((monthly shorebird numbers per square kilometre) + 1) for all six sites during 2001 (January 2001 numbers were not recorded). (*a*) North Papanui Inlet. (*b*) South Papanui Inlet. (*c*) Conservation area, Aramoana. (*d*) Waipuna Bay, Aramoana. (*e*) Warrington, Blueskin Bay. (*f*) Waitati, Blueskin Bay. ●, confirmed definitive hosts; ○, suspected definitive hosts.



however, provide strong support of previous findings that heterogeneity in parasitism in intermediate hosts is strongly influenced by the distribution and abundance of definitive hosts (Robson and Williams 1970; Marcogliese et al. 2001; Smith 2001). Cystacanth infection levels in crab populations were in general positively correlated with definitive shorebird host abundances both temporally and spatially, but in no case was this correlation statistically significant. However, the modest number of sites included in the analysis and the low power of these correlations mean that we must be careful not to incorrectly accept the null hypothesis just yet. To our knowledge, this is the first study that has attempted to correlate acanthocephalan infection levels in their intermediate hosts with definitive host distribution and abundance. Differences between acanthocephalan–crustacean systems and previously studied systems may explain why our results show a weaker link between definitive host abundance and infection levels in crabs.

The mortality induced by the acanthocephalan *Profilicollis* species in our crabs only affects the most heavily infected crab hosts (Latham and Poulin 2002*b*), but it may still obscure any spatial or temporal changes in mean infection levels. There is, however, no evidence of density dependence in the recruitment of cystacanths in crabs or of intensity-

Fig. 7. Relationship between the annual mean (±SE) residual numbers of cystacanth larvae per *M. hirtipes* (*a*) and *H. edwardsii* (*b*) and the annual mean (±SE) log((numbers of confirmed or suspected shorebird hosts per square kilometre) + 1) (upper-case letters represent study sites; see Methods and Fig. 1).



dependent immunity (Latham and Poulin 2002*b*). Additional cystacanths accumulate at the same rate whether the crab is lightly or heavily infected. This should facilitate the detection of spatial or temporal differences in infection levels.

To date, the majority of systems studied have focused on temporal and spatial variation in, and population dynamics of, trematode parasites (e.g., Robson and Williams 1970; Brassard et al. 1982; Lafferty et al. 1994; Mouritsen et al. 1997; Marcogliese et al. 2001; Smith 2001). For example, Marcogliese et al. (2001) studied infection levels of eyeflukes (*Diplostomum* species) in minnows and young perch from different types of habitat in the St. Lawrence River in eastern Canada in relation to the distribution of the bird definitive host the ring-billed gull (*Larus delawarensis*). They found that a closer proximity to gull colonies tended to enhance the abundance of *Diplostomum* species in the lens of fish hosts. However, that system differs from the present one in that it requires two intermediate hosts: lymnaeid snails (first intermediate hosts) and various fish species (second intermediate hosts). Furthermore, Marcogliese et al. (2001) examined the cercarial stage of the trematode life cycle, whereas our acanthocephalan system examines the infective egg stage of that life cycle. Trematode cercariae survive a few hours to a few days in the water (Kearn 1998), whereas acanthocephalan eggs may survive as long as a few months (Taraschewski 2000). The use of a second intermediate host by a parasite should theoretically complicate temporal and spatial heterogeneity in parasitism. This is because the second intermediate host is not infected directly by the definitive host, but via the first intermediate host, thus making any effect of definitive host distribution and abundance on infection levels in second intermediate host populations more difficult to detect. Accordingly, we were expecting the effects of definitive host distribution and abundance on infection levels in intermediate hosts to be more obvious in the acanthocephalan–crustacean system.

In a similar vein, Smith (2001) studied the spatial heterogeneity of larval trematode infections in snail (*Cerithidea scalariformis*) intermediate hosts in a mangrove marsh in Florida. She found that avian definitive hosts initiate spatial patterns of parasitism in snails through their perching behaviours. In that system, snails are generally infected by the accidental ingestion of trematode eggs in a way similar to the present acanthocephalan study: trematode eggs are viable for

a much longer time than cercariae (Kearn 1998). However, Smith (2001) studied spatial heterogeneity of parasite infections in intermediate host populations on a very small scale (approximately 5000 m^2) in comparison with the present study (three locations separated by many kilometres; see Fig. 1). Here, we found weak evidence that within a location, shorebird distribution and abundance tend to influence the infection levels of crab populations over both time and space. Thus, it is likely that the effects of definitive host distribution and abundance on parasitism in intermediate host populations are more easily detected at smaller spatial scales (e.g., between sites within one system rather than among sites in a number of systems). This may be due to a number of factors, both biotic and abiotic.

A number of studies have examined the role of abiotic factors in the transmission efficiency of parasites, for example, oxygen concentration, water currents, humidity, levels of precipitation, temperature, and light (Stables and Chappell 1986; Sousa and Grosholz 1991; Lyholt and Buchmann 1996; Mouritsen and Poulin 2002). Abiotic factors undoubtedly have an effect on the transmission efficiency of *Profilicollis* spp. to intermediate shore crab hosts at the locations examined in this study. It is possible, for example, that the differences in cystacanth infection levels in *H. edwardsii* observed between the Warrington and Waitati sites in Blueskin Bay are influenced by sediment particle size. The sediment at the Warrington site is composed predominantly of sand, whereas it is predominantly fine mud at the Waitati site (A.D.M. Latham, personal observation): *Profilicollis* spp. eggs deposited on the Bay may be more likely to be covered at areas composed of fine mud. Similarly, it is possible that temperature plays an important role in the transmission efficiency of *Profilicollis* spp. to crab hosts. For example, *M. hirtipes* appears to be most active (peak periods of fighting and sexual behaviour) when temperatures are highest (McLay 1988); thus, crab metabolism and feeding should also be greatest. As acanthocephalan eggs are accidentally ingested while feeding, an increase in feeding behaviour should result in an increase in the number of eggs accidentally ingested by the crabs. If temperature is an important factor in the dynamics of this system, then this may explain the peak in cystacanth infection levels that we found in *M. hirtipes* during the warmer months (January and February).

Tidal movements and water currents also play a possible role in the transmission efficiency of *Profilicollis* spp. For example, the Aramoana conservation site is exposed to lateral tidal currents that may move many of the *Profilicollis* spp. eggs deposited at that site to the neighbouring site of Waipuna Bay: Waipuna Bay is not exposed to as much lateral movement, as it is sheltered by two rocky points. This may explain why the Aramoana conservation site has relatively high shorebird numbers, yet crabs there have low cystacanth infection levels. There may also be differences among sites in rates of predation on acanthocephalan eggs by organisms other than crabs. Although these and many other physical and biological factors undoubtedly play a significant role in this system, they are difficult to quantify, and further research is needed to establish what role, if any, they play.

In summary, the dynamics of *Profilicollis* spp. infections in this study vary among hosts, between habitats, and over seasons. Cystacanth infections tended to be highest in *M. hirtipes*, and it is in this species that temporal patterns of infection were observed. Spatial heterogeneity in recruitment of cystacanth larvae to crab intermediate hosts (*M. hirtipes* and *H. edwardsii*) was found both within and between locations. As shorebird definitive hosts release *Profilicollis* spp. eggs (the source of infection) along with their faeces onto the intertidal marine environment, their distribution and abundance must in some way be related to the infection levels observed in crab populations. This study provides evidence (albeit weak) that infection levels in intermediate host populations are related to the distribution and abundance of shorebird hosts, both temporally and spatially. However, the dynamics of *Profilicollis* spp. infections are undoubtedly influenced by a number of biotic and abiotic factors. Parasitism is now recognized as an important biotic determinant of animal population dynamics and community structure (Minchella and Scott 1991; Sousa 1991; Combes 1996; Hudson and Greenman 1998; Poulin 1999). Accordingly, understanding the causes of temporal and spatial variation in the recruitment of parasites is crucial if we are to manage host populations and animal communities effectively.

Acknowledgements

The research described in this paper follows the guidelines of the University of Otago's Animal Ethics Committee and was partially funded by a grant from the Marsden Fund. We thank P. Latham, J. Leiendecker, and M. Salmon for field assistance, and B. Fredensborg and K. Mouritsen for commenting on an earlier draft of the manuscript.

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