

Non-random patterns of host use by the different parasite species exploiting a cockle population

R. POULIN*, M. J. STEEPER and A. A. MILLER

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

(Received 4 January 2000; revised 4 March 2000; accepted 4 March 2000)

SUMMARY

Different parasite species sharing the same intermediate host species may have similar or conflicting interests, depending on whether they are at the same stage in their life-cycle or whether they share the same definitive host. In the New Zealand cockle, *Austrovenus stutchburyi*, metacercariae of the digenean *Meiogymnophallus* sp. are positively associated with metacercariae of *Curtuteria australis*. This relationship is found in different cockle samples, and is independent of cockle shell size, which suggests that it is not merely the product of metacercariae accumulation over time. Both digenean species have the same definitive host, oystercatchers. Metacercariae of *C. australis* manipulate the phenotype of cockles, impairing the cockle's ability to burrow in the sediments. This makes the host more susceptible to oystercatcher predation. Thus *Meiogymnophallus* sp. can benefit by associating with *C. australis* and may hitch a ride with the manipulator parasite. This is supported by the finding that cockles impaired by *C. australis* and lying at the sediment surface harbour greater numbers of *Meiogymnophallus* than buried cockles. A third digenean species, whose sporocysts are found in cockles and which is not transmitted by predation, occurred only in surface cockles. Finally, a parasitic copepod with a direct life-cycle was found evenly distributed among buried and surface cockles, independently of their metacercarial loads. These results show that different parasite species do not use cockles in a random fashion, and that not all patterns of host use are consistent with shared or conflicting interests among parasites.

Key words: *Austrovenus stutchburyi*, *Curtuteria australis*, hitch-hiking, host manipulation, *Meiogymnophallus*, species associations.

INTRODUCTION

Typically, different parasite species sharing the same host population will not be distributed among hosts independently of one another. Patterns of host use by different species of parasites have been intensely studied in communities of helminths in their vertebrate hosts (e.g. Bush & Holmes, 1986; Moore & Simberloff, 1990; Lotz & Font, 1991; Haukisalmi & Henttonen, 1993). Often in these communities certain parasite species co-occur more or less frequently than expected by chance, suggesting that the community is not a random assemblage of species. Processes such as competition among adult helminths, heterogeneity among host individuals in susceptibility to infection, or acquisition of larval helminths in species packets can explain these associations within the vertebrate host (Moore & Simberloff, 1990; Lotz, Bush & Font, 1995; Poulin, 1998).

The patterns of host use, and the processes generating them, among parasites exploiting invertebrate hosts are not as well known and have been the subject of only few studies (e.g. Aguirre-Macedo & Kennedy, 1999). These patterns may be more

complex because invertebrates are used for two different purposes by their parasites. First, invertebrate hosts are used as a source of nutrients by many parasites. This means that competitive interactions can exist and cause some of the observed patterns of host use by parasites of invertebrates. For instance, Kuris & Lafferty (1994) surveyed the literature and found that strong competition between sporocysts and rediae of different species of digeneans in their snail hosts were the norm, and that co-occurrences of pairs of species within the same snail were much less frequent than expected. Sporocysts and rediae divert large quantities of resources from their host, and 1 snail may not be big enough for 2 species to co-exist successfully. Second, invertebrate hosts are used as vehicles to the definitive host by many helminths with complex life-cycles. The metacercariae of digeneans (or the cystacanths of acanthocephalans, or the cysticercoids of cestodes) consume few host resources and await the ingestion of their invertebrate host by their definitive host. These larval helminths are sometimes capable of altering the phenotype of their invertebrate host in ways that make it more susceptible to predation by the definitive host (Poulin, 1998). This phenomenon creates opportunities for either shared interests or conflicts between different parasite species sharing an invertebrate host (Thomas,

* Corresponding author: Tel: +64 3 479 7983. Fax: +64 3 479 7584. E-mail: robert.poulin@stonebow.otago.ac.nz

Renaud & Poulin, 1998; Lafferty, 1999; Lafferty, Thomas & Poulin, 2000). If a parasite shares its invertebrate host with another parasite species capable of modifying the phenotype of the host, and if both parasites have the same definitive host, then selection should favour active sharing of the host by the first parasite since it has the same destination as the phenotype-altering parasite. However, if the two parasites have different definitive hosts, the parasite species not capable of modifying the host should avoid the parasite that can modify host phenotype, i.e. to avoid ending up in the wrong definitive host. There are many systems in which either common interests or conflicting interests exist between parasite species sharing the same invertebrate host population, but there have been very few empirical studies of patterns of host use among such parasites (Lafferty *et al.* 2000).

The cockle *Austrovenus stutchburyi* is the dominant bivalve in soft-sediment, sheltered shores in New Zealand (Morton & Miller, 1973). It normally lives buried 1–2 cm below the sediment surface, with only the inhalant and exhalant siphons showing, at densities of up to a few hundred per square metre. In the Otago Harbour, South Island, New Zealand, cockles are hosts to 4 parasite species. (1) Metacercariae of the digenean *Curtuteria australis* (Echinostomatidae: Himasthlinae) are found encysted in the foot of cockles, awaiting ingestion by oystercatchers, their definitive hosts (Allison, 1979). Severe infections by this parasite impair the cockle's ability to burrow into the sediments, and result in a significantly higher rate of predation by oystercatchers (Thomas & Poulin, 1998). (2) Metacercariae of *Meiogymnophallus* sp. (Gymnophallidae) are found near the hinge of cockles, enclosed by the host's epithelium, also awaiting ingestion by their oystercatcher definitive hosts. The species has not been described from New Zealand cockles, but it looks very similar to *Meiogymnophallus minutus* from European cockles (Bowers & James, 1967). (3) Sporocysts of a digenean provisionally called *Cercaria pectinata*, only known from its larval stages (Chilton, 1905). Sporocysts can be very numerous in infected cockles, each containing several cercariae; the castration of the host is a normal consequence of the asexual reproduction of this parasite within cockles (Poulin, Hecker & Thomas, 1998). (4) Adult copepods *Pseudomyicola spinosus* (Copepoda: Poecilostomatoida) live in the mantle cavity of cockles and other bivalves (Humes, 1984), where their feeding activity may damage the host's epithelium (Dinamani & Gordon, 1974). The first 2 parasite species are very abundant and use cockles as vehicles to oystercatchers, whereas the latter 2 are rare and use cockles as sources of food. Based on their respective interests, we might expect *Meiogymnophallus* to seek cockles already harbouring several metacercariae of *C. australis*, which would

produce a positive association between their abundances. At the same time, the sporocysts of *C. pectinata* and the copepods *P. spinosus* face a higher risk of death or loss of food source by associating with cockles heavily-infected by *C. australis* and incapable of burrowing; we might expect them to avoid such cockles. We investigated the patterns of association among these 4 parasite species at 2 tidal levels in a soft-sediment intertidal zone.

MATERIALS AND METHODS

Cockles were collected on 22 November 1999, in Company Bay, Otago Harbour, South Island, New Zealand. The bay has a maximum tidal range of just under 2 m and sediments of mixed sand and mud. Two sampling sites were chosen within the bay, at 2 different tidal levels: a low site, situated at mean low water, and a high site, situated about 0.3 m above mean low water. The 2 sites were separated by a distance of approximately 50 m. At each site, surface cockles (with at least 50% of the shell exposed, usually lying on one side) were collected along a transect parallel to the water. Each time a surface cockle was picked up, a buried cockle was collected from the adjacent sediment. Thus 4 samples of cockles were obtained, from either the sediment surface or buried under them, and from 2 different tidal levels.

All cockles were returned live to the laboratory, where they were measured (maximum shell length) using vernier calipers prior to dissection. The presence or absence of *C. pectinata* sporocysts or parasitic copepods was noted for each cockle. Metacercariae of *Meiogymnophallus* sp. are easily visible lying clumped near the hinge and were counted under a dissecting microscope. Metacercariae of *C. australis* are encysted in the foot musculature of cockles. The foot of each cockle was therefore removed and placed in digestive solution (6 g pepsin and 7 ml of concentrated HCl in 1000 ml of water) for 1–2 days, to loosen the metacercariae, which were then counted under a dissecting microscope.

Numbers of metacercariae (of both digenean species) per cockle were $\log(x+1)$ -transformed prior to statistical analyses. All statistical tests are standard parametric tests.

RESULTS

There were marked differences between the 4 cockle samples with respect to either shell length or infection parameters (Table 1). The overall prevalence of infection by both digenean species was very high (94.3% for *Meiogymnophallus*, 99.3% for *C. australis*), and only abundance patterns were examined. Two-way factorial ANOVAs, with sam-

Table 1. Mean shell length and infection characteristics of the 4 cockle samples

(Mean abundances (computed including uninfected cockles) of metacercariae are geometric means back-calculated from log-transformed data.)

Sample	N	Shell length (\pm S.D.), mm	Abundance of <i>Curtuteria australis</i> metacercariae (range)	Abundance of <i>Meiogymnophallus</i> sp. metacercariae (range)	Prevalence of copepods <i>Pseudomyicola</i> <i>spinus</i>	Prevalence of sporocysts <i>Cercaria</i> <i>pectinata</i>
Low site						
Surface	72	36.3 (3.1)	76.6 (2–566)	22.8 (0–122)	4/72 (5.6 %)*	0/72
Buried	73	35.9 (3.9)	73.3 (0–639)	20.1 (0–168)	4/73 (5.5 %)	0/73
High site						
Surface	74	28.4 (2.5)	402.6 (19–1673)	85.3 (0–1100)	4/74 (5.4 %)	4/74 (5.4 %)
Buried	79	27.5 (3.3)	318.2 (0–1375)	52.5 (0–706)	4/79 (5.1 %)	0/79

* One cockle in this sample harboured 2 copepods; all others harboured a single copepod.

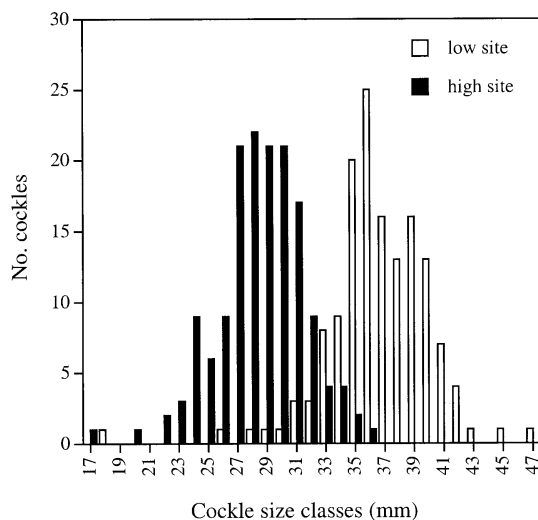


Fig. 1. Frequency distribution of shell lengths among cockles, *Austrovenus stutchburyi*, from 2 sampling sites at different tidal levels in Company Bay, Otago Harbour.

pling site (low or high) and position of cockles in relation to the substrate (surface or buried) as class variables, showed that the sampling site had a significant effect on cockle shell length and on the number of metacercariae of both digenean species per cockle (shell length: $F_{1,294} = 471.05$, $P = 0.0001$; metacercariae of *Meiogymnophallus* sp.: $F_{1,294} = 66.88$, $P = 0.0001$; metacercariae of *C. australis*: $F_{1,294} = 144.20$, $P = 0.0001$). The difference in cockle shell length between the 2 sampling sites was very pronounced, with cockles from the low site being much larger than the ones from the high site (Fig. 1). Cockles from the low site also harboured many fewer metacercariae than cockles from the high site (Table 1). The position of cockles in relation to the substrate only had a significant effect on the number of metacercariae of *Meiogymnophallus* sp., with surface cockles tending to harbour more metacercariae than buried ones (Table 1); the position of cockles had no effect on shell length or

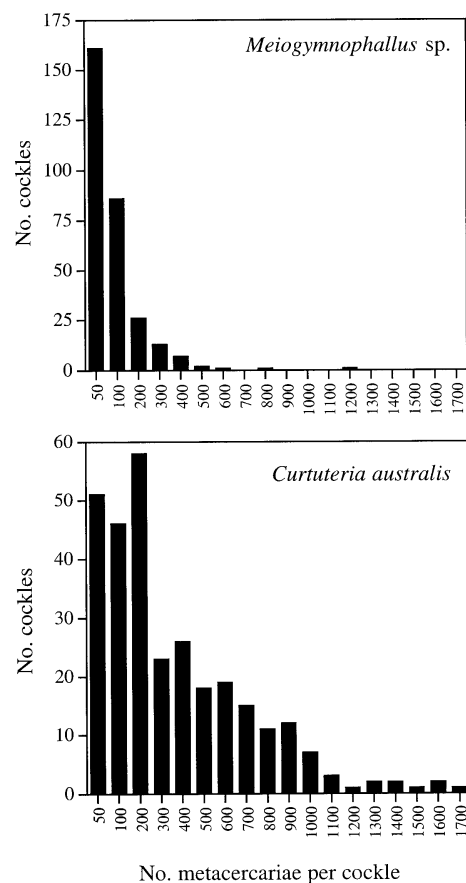


Fig. 2. Frequency distributions of numbers of metacercariae per cockle, for 2 digenean parasite species. (Note: the first 2 classes increase by steps of 50 metacercariae, the subsequent ones by steps of 100 metacercariae.)

numbers of *C. australis* metacercariae (shell length: $F_{1,294} = 3.01$, $P = 0.084$; metacercariae of *Meiogymnophallus* sp.: $F_{1,294} = 4.93$, $P = 0.027$; metacercariae of *C. australis*: $F_{1,294} = 1.16$, $P = 0.283$). All interaction terms in the ANOVAs were non-significant (shell length: $F_{1,294} = 0.57$, $P = 0.450$; metacercariae of *Meiogymnophallus* sp.:

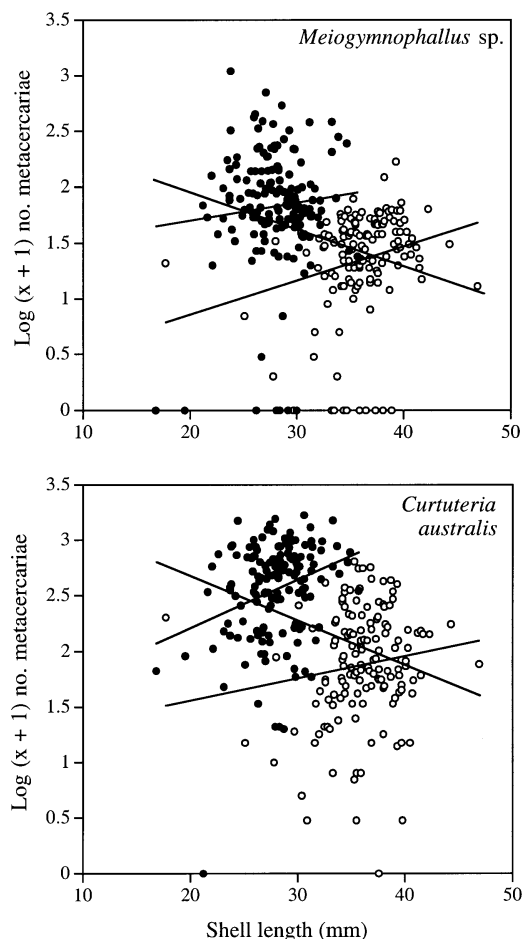


Fig. 3. Number of metacercariae per cockle as a function of shell length, for 2 digenean parasite species. Cockles sampled at the high tidal site are indicated by black circles, those sampled at the low tidal site by open circles. Positive relationships within tidal levels are indicated by lines of best fit, as is the negative relationship across all cockles.

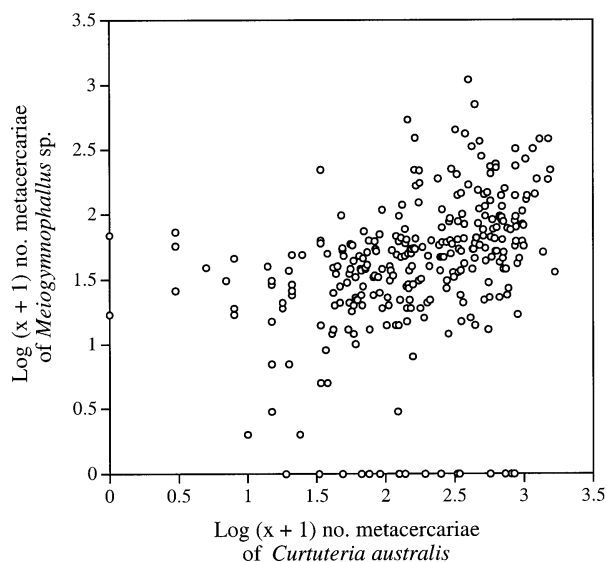


Fig. 4. Relationship between the numbers of metacercariae per cockle of 2 digenean parasite species.

$F_{1,294} = 1.76$, $P = 0.186$; metacercariae of *C. australis*: $F_{1,294} = 0.55$, $P = 0.459$).

Only 16 cockles harboured females of the parasitic copepod *P. spinosus*, many of which bore egg sacs; infected cockles were spread evenly among the 4 cockle samples (Table 1). There were no differences in shell length or numbers of metacercariae of *Meiogymnophallus* sp. and *C. australis* between the 16 cockles with copepods and the 282 without copepods (two-tailed *t*-tests, all $P > 0.40$). Only 4 cockles harboured sporocysts of *C. pectinata*, all of which were surface cockles from the high site (Table 1).

For both *Meiogymnophallus* sp. and *C. australis*, numbers of metacercariae per host were highly aggregated among cockles (variance-to-mean ratio, *Meiogymnophallus* sp.: 153.9; *C. australis*: 340.1). Most cockles harboured fewer than 100 metacercariae of *Meiogymnophallus* sp. and fewer than 200 metacercariae of *C. australis* (Fig. 2). Across all 4 cockle samples pooled, shell length correlated negatively with the numbers of metacercariae of both digenean species (*Meiogymnophallus* sp.: $r = -0.246$, $N = 298$, $P = 0.0001$; *C. australis*: $r = -0.347$, $N = 298$, $P = 0.0001$). This relationship, however, results from the pooling of samples that are not homogeneous (Fig. 3). Within samples, the relationship between shell length and numbers of metacercariae tends to be positive (*Meiogymnophallus* sp.: high site, $r = 0.087$, $N = 153$, $P = 0.283$; low site, $r = 0.226$, $N = 145$, $P = 0.006$; *C. australis*: high site, $r = 0.282$, $N = 153$, $P = 0.0004$; low site, $r = 0.135$, $N = 145$, $P = 0.105$).

Among all cockles pooled, the numbers of metacercariae of both *Meiogymnophallus* sp. and *C. australis* were positively correlated ($r = 0.337$, $N = 298$, $P = 0.0001$). There is a lot of noise in the relationship, but as a rule cockles harbouring large numbers of metacercariae of 1 species also harbour large numbers of the other species (Fig. 4). The positive relationship holds within samples, but is only statistically significant for surface cockles from the high site ($r = 0.282$, $N = 74$, $P = 0.015$) and buried cockles from the low site ($r = 0.288$, $N = 73$, $P = 0.014$).

The above positive relationship between numbers of both species of metacercariae could be the mere product of the simultaneous accumulation by cockles of the 2 larval parasites over time, rather than a true positive association between the 2 species. To correct for the effect of shell size, the residuals of regressions of numbers of metacercariae versus shell length were computed as measures of parasite load independent of shell size. Using these residuals, the relationship between numbers of metacercariae of both species was again positive across all cockles ($r = 0.277$, $N = 298$, $P = 0.0001$), as well as within samples. More importantly, for 183 of the 298 cockles, residual numbers of metacercariae of both species had the

same sign, either positive or negative; this occurred more frequently than expected by chance ($\chi^2 = 15.52$, D.F. = 1, $P < 0.001$). This means that for any shell length, if a cockle harbours more (or less) metacercariae of *C. australis* than expected based on its size, it will usually also harbour more (or less) metacercariae of *Meiogymnophallus* sp. than expected.

DISCUSSION

The co-occurrence of 2 or more parasite species sharing the same intermediate and definitive hosts is common in many systems. Theoretical models (Thomas *et al.* 1998) and the few empirical studies available (reviewed by Lafferty *et al.* 2000) suggest that when one parasite species modifies the phenotype of the intermediate host and makes it more likely to be ingested by the definitive host, other species tend to associate with this manipulating parasite. Such hitch-hiking species achieve a higher transmission rate to their definitive host without having to invest in modifying the phenotype of the intermediate host. The positive association between the metacercariae of *C. australis* and *Meiogymnophallus* sp. in cockles suggests that the latter parasite is hitching a ride with the former. Several processes other than hitch-hiking can generate positive associations between parasite species, however, and these cannot be ruled out in this system (Thomas *et al.* 1998). Two aspects of our results support active hitch-hiking. First, the positive association between the 2 species is independent of cockle body size, and is thus not merely the result of the simultaneous accumulation of metacercariae of both species by cockles. Second, greater numbers of *Meiogymnophallus* sp. occurred in cockles from the surface of the sediments than in buried cockles, an observation consistent with a preference by this parasite for cockles suffering from a reduced burrowing ability induced by *C. australis*.

The benefits that *Meiogymnophallus* sp. can obtain by hitch-hiking with *C. australis* depend on the magnitude of the increase in transmission rates to oystercatchers. Norris (1999) has recently shown that oystercatchers avoid to feed on the larger, more heavily-parasitized cockles. In our study system, however, the birds preferentially feed on cockles lying at the surface as a result of the impairment caused by *C. australis*, and the hitch-hiking *Meiogymnophallus* would benefit. In fact, rather than a case of hitch-hiking, the positive association between *Meiogymnophallus* sp. and *C. australis* in their cockle hosts may be a case of cooperation, with the 2 parasites acting in synergy. Metacercariae of European species of Gymnophallidae can impair the proper closure of the 2 valves of their host's shell, or reverse the position of their host such that the valves

open upward (Bartoli, 1974, cited and discussed by Combes, 1995). These alterations, like those caused by *C. australis* (Thomas & Poulin, 1998), could also facilitate the predation of oystercatchers on infected cockles. If this is the case in the New Zealand system, then both parasite species would benefit by seeking out one another.

The copepod *P. spinosus* and sporocysts of the digenean *C. pectinata* use cockles for food and protection, and can only lose by being positively associated with *C. australis*. We would therefore expect a negative association between these 2 parasites and *C. australis* since what the latter parasite does to the host can only harm the other 2. We found that copepods are distributed at random among cockles, whereas sporocysts of *C. pectinata* are only found in surface cockles from the high site (this result confirms earlier findings by Poulin *et al.* 1998). Our results on these 2 parasite species should be viewed with caution, as very few infected cockles were found. The apparent random use of cockles by copepods may not be too disadvantageous, given that the absolute predation rate by oystercatchers, even on surface cockles, is relatively low (Thomas & Poulin, 1998). Selection may not strongly favour avoidance of surface cockles, but there is no apparent reason why it would favour a preference for surface cockles, as apparently shown by *C. pectinata*. The explanation for this result could lie in the swimming behaviour of the miracidia of *C. pectinata*. This infective stage may swim slightly above the surface of the sediments, where it would be more likely to be sucked in by the inhalant siphon of surface cockles, rather than crawl on the sediments and thus closer to the siphons of buried cockles.

Some of the patterns reported here also have implications for the biology of cockles. There was a marked decrease in cockle shell sizes in an upshore direction at our study site. Other studies have found that growth rates of most molluscs decline with increasing height in intertidal zones (see Vermeij, 1980). This is often attributed to the effect of longer exposure to air and greater heat stress at higher tidal levels. Greater exposure to digenean metacercariae, however, may contribute to the smaller size of the cockles from the high site. Despite infection levels by metacercariae usually increasing with bivalve age or size (Bowers & James, 1967; Lim & Green, 1991; Goater, 1993), cockles from the high site harboured much higher numbers of metacercariae of both species than their much larger conspecifics from the low site. Greater risks of infection at higher tidal levels have been reported elsewhere. For instance, Lim & Green (1991) found higher numbers of metacercariae of 3 species of gymnophallid digeneans in clams from high tidal levels than in clams from low tidal levels. The cause of this difference is unclear. It may have to do with the spatial distribution of the first intermediate host of both

digeneans (the whelk *Cominella glandiformis* for the parasite *C. australis*, unknown for *Meiogymnophallus* sp.), or the preferred foraging site of oystercatchers, from which eggs are released in faeces. Whatever the explanation, high-tide cockles experience a greater risk of infection from both parasite species, which may or may not contribute to their lower growth rates and smaller shell sizes.

There was no difference in the number of *C. australis* metacercariae between surface and buried cockles, a result that may appear surprising given the effect of this parasite on the foot development and burrowing ability of cockles. This is consistent with what Thomas & Poulin (1998) found, however. Cockles from our study site, Company Bay, are more heavily parasitized by *C. australis* than cockles from other sites within the Otago Harbour (by 1 order of magnitude; Thomas & Poulin, 1998). Presumably all cockles burrow when young and start accumulating metacercariae. As they grow, their foot is stunted and their ability to burrow properly diminishes gradually. Which cockles end up lying at the surface may be determined by various biotic (e.g. the digging activity of flatfishes) and abiotic (e.g. wave action) processes that shift the sediments and uncover some cockles. Once exposed, cockles are unable to burrow again, although they are not necessarily more heavily parasitized than buried ones.

Our evidence is correlational only and comes from a single sample; it does not allow us to conclude to active hitch-hiking. If *Meiogymnophallus* sp. actively seeks to associate with either cockles lying at the surface or cockles already harbouring large numbers of *C. australis* metacercariae, how do its cercariae discriminate among cockles? In the only experimental study of the parasite hitch-hiking phenomenon, cercarial host-finding behaviour appeared to be a key mechanism leading to a positive association between a hitch-hiking parasite and a manipulative parasite (Thomas *et al.* 1997). Stronger evidence would be welcome, though. Once the first intermediate host of *Meiogymnophallus* sp. is identified in our system, the next step will be to investigate the mechanisms of host location and host acceptance by its cercariae. In particular, a field experiment examining whether the cercariae of *Meiogymnophallus* prefer cockles lying at the surface over buried ones would be informative.

We thank S. Rate and D. Wilson for assistance in the field and laboratory, and the University of Otago for funding the study.

REFERENCES

- AGUIRRE-MACEDO, M. L. & KENNEDY, C. R. (1999). Patterns in metazoan parasite communities of some oyster species. *Journal of Helminthology* **73**, 283–288.
- ALLISON, F. R. (1979). Life cycle of *Curtuteria australis* n. sp. (Digenea: Echinostomatidae: Himasthinae), intestinal parasite of the South Island pied oystercatcher. *New Zealand Journal of Zoology* **6**, 13–20.
- BOWERS, E. A. & JAMES, B. L. (1967). Studies on the morphology, ecology and life-cycle of *Meiogymnophallus minutus* (Cobbold, 1859) comb. nov. (Trematoda: Gymnophallidae). *Parasitology* **57**, 281–300.
- BUSH, A. O. & HOLMES, J. C. (1986). Intestinal helminths of lesser scaup ducks: patterns of association. *Canadian Journal of Zoology* **64**, 132–141.
- CHILTON, C. (1905). On the occurrence of a species of cercaria in the cockle *Chione stutchburyi*. *Transactions and Proceedings of the New Zealand Institute* **37**, 322–325.
- COMBES, C. (1995). *Interactions Durables: Ecologie et Evolution du Parasitisme*. Paris, Masson.
- DINAMANI, P. & GORDON, D. B. (1974). On the habits and nature of association of the copepod *Pseudomyicola spinosus* with the rock oyster *Crassostrea glomerata* in New Zealand. *Journal of Invertebrate Pathology* **24**, 305–310.
- GOATER, C. P. (1993). Population biology of *Meiogymnophallus minutus* (Trematoda: Gymnophallidae) in cockles from the Exe Estuary. *Journal of the Marine Biological Association of the UK* **73**, 163–177.
- HAUKISALMI, V. & HENTTONEN, H. (1993). Coexistence in helminths of the bank vole *Clethrionomys glareolus*. I. Patterns of co-occurrence. *Journal of Animal Ecology* **62**, 221–229.
- HUMES, A. G. (1984). *Ostrincola* and *Pseudomyicola* (Crustacea: Copepoda: Poecilostomatoida) associated with marine bivalve mollusks on the Pacific coast of Panama. *Proceedings of the Biological Society of Washington* **97**, 589–600.
- KURIS, A. M. & LAFFERTY, K. D. (1994). Community structure: larval trematodes in snail hosts. *Annual Review of Ecology and Systematics* **25**, 189–217.
- LAFFERTY, K. D. (1999). The evolution of trophic transmission. *Parasitology Today* **15**, 111–115.
- LAFFERTY, K. D., THOMAS, F. & POULIN, R. (2000). Evolution of host phenotype manipulation by parasites and its consequences. In *Evolutionary Biology of Host-Parasite Relationships: Theory Meets Reality* (ed. Poulin, R., Morand, S. & Skorping, A.). Amsterdam: Elsevier Science Publishers (in the Press).
- LIM, S. S. L. & GREEN, R. H. (1991). The relationship between parasite load, crawling behaviour, and growth rate of *Macoma balthica* (L.) (Mollusca, Pelecypoda) from Hudson Bay, Canada. *Canadian Journal of Zoology* **69**, 2202–2208.
- LOTZ, J. M., BUSH, A. O. & FONT, W. F. (1995). Recruitment-driven, spatially discontinuous communities: a null model for transferred patterns in target communities of intestinal helminths. *Journal of Parasitology* **81**, 12–24.
- LOTZ, J. M. & FONT, W. F. (1991). The role of positive and negative interspecific associations in the organization of communities of intestinal helminths of bats. *Parasitology* **103**, 127–138.

- MOORE, J. & SIMBERLOFF, D. (1990). Gastrointestinal helminth communities of bobwhite quail. *Ecology* **71**, 344–359.
- MORTON, J. & MILLER, M. (1973). *The New Zealand Sea Shore*, 2nd Edn.. Collins, London.
- NORRIS, K. (1999). A trade-off between energy intake and exposure to parasites in oystercatchers feeding on a bivalve mollusc. *Proceedings of the Royal Society of London, B* **266**, 1703–1709.
- POULIN, R. (1998). *Evolutionary Ecology of Parasites: From Individuals to Communities*. Chapman and Hall, London.
- POULIN, R., HECKER, K. & THOMAS, F. (1998). Hosts manipulated by one parasite incur additional costs from infection by another parasite. *Journal of Parasitology* **84**, 1050–1052.
- THOMAS, F., METE, K., HELLUY, S., SANTALLA, F., VERNEAU, O., DEMEEUS, T., CEZILLY, F. & RENAUD, F. (1997). Hitch-hiker parasites or how to benefit from the strategy of another parasite. *Evolution* **51**, 1316–1318.
- THOMAS, F. & POULIN, R. (1998). Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? *Parasitology* **116**, 431–436.
- THOMAS, F., RENAUD, F. & POULIN, R. (1998). Exploitation of manipulators: ‘hitch-hiking’ as a parasite transmission strategy. *Animal Behaviour* **56**, 199–206.
- VERMEIJ, G. J. (1980). Gastropod shell growth, geometry and adult size: environmental implications. In *Skeletal Growth of Aquatic Organisms* (ed. Rhoads, D. C. & Lutz, R. A.), pp. 379–394. Plenum Publishing, New York.