Interactions between parasites of the cockle *Austrovenus stutchburyi*: hitch-hikers, resident-cleaners, and habitat-facilitators

T. L. F. LEUNG* *and* R. POULIN

Department of Zoology, University of Otago, P. O. Box 56, Dunedin 9054, New Zealand

(*Received 5 July 2006; revised 15 August 2006; accepted 15 August 2006; first published online 16 October 2006*)

SUMMARY

The patterns of association between parasites within a particular host are determined by a number of factors. One of these factors is whether or not infection by one parasite influences the probability of acquiring other parasite species. This study investigates the pattern of association between various parasites of the New Zealand cockle *Austrovenus stutchburyi*. Hundreds of cockles were collected from one locality within Otago Harbour, New Zealand and examined for trematode metacercariae and other symbionts. Two interspecific associations emerged from the study. First, the presence of the myicolid copepod *Pseudomyicola spinosus* was positively associated with higher infection intensity by echinostomes. The side-effect of the copepod's activities within the cockle is suggested as the proximate mechanism that facilitates infection by echinostome cercariae, leading to a greater rate of accumulation of metacercariae in cockles harbouring the copepod. Second, a positive association was also found between infection intensity of the metacercariae of foot-encysting echinostomes and that of gymnophallid metacercariae. This supports earlier findings and suggests that the gymnophallid is a hitch-hiker parasite because, in addition to the pattern of positive association, it (a) shares the same transmission route as the echinostomes, and (b) unlike the echinostomes, it is not capable of increasing the host's susceptibility to avian predation. Thus, both active hitch-hiking and incidental facilitation lead to non-random infection patterns in this parasite community.

Key words: Bivalvia, parasite communities, interspecific interactions, echinostome, gymnophallid hitch-hiking, facilitation, copepod.

INTRODUCTION

One of the most interesting questions in ecological parasitology concerns the processes that contribute to the formation of parasite communities, and the resulting patterns of these assemblages (Esch *et al.* 1990). So what actually shapes parasite communities and how do the components of these communities interact? While some recent empirical studies have shed light upon the interactions between endoparasitic helminths within their definitive host (Byrne *et al.* 2003; Lello *et al.* 2004; Friggens and Brown, 2005), fewer studies have investigated the question of interspecific interactions inside the intermediate host. The intermediate host represents a shared habitat for the parasites it contains, many of which are at different stages of their life-cycle or have different transmission routes. Most of the studies regarding interactions between components of the parasite communities within intermediate hosts are restricted to the assemblages of digeneans in their gastropod first intermediate host (Kuris and Lafferty, 1994; Esch *et al.* 2001; Hendrickson and Curtis, 2002; but see Wang *et al.* 2002 and Fredensborg and Poulin, 2005 for exceptions).

Poulin and Valtonen (2001) found that the assemblages of larval helminth parasites occurring in fish are not random collections but are in fact structured packets determined by their transmission route. The processes that generate such patterns of association between parasites in intermediate and paratenic host organisms, as well as the consequences of these associations, are poorly known. Co-occurring parasites can have various consequences on each other's fitness and transmission success, depending on the respective goals of the different parasites that share a particular host organism (Lafferty, 1999).

The parasite community of intertidal bivalves can be quite diverse and complex (Montaudouin *et al.* 2000; Poulin *et al.* 2000), and presents an interesting model for the study of interactions between co-occurring parasites. The New Zealand cockle, *Austrovenus stutchburyi*, is commonly parasitized by metacercariae of 2 echinostome species that encyst within its foot. At high infection intensity they can impair the cockle's ability to burrow, forcing it to remain on the sediment's surface and facilitating the parasites' transmission to the definitive host by making cockles more susceptible to avian predators (Thomas and Poulin, 1998; Mouritsen, 2002; Babirat *et al.* 2004). The metacercariae that encyst in the foot of *A. stutchburyi* consist of 2 species from the Himasthlinae subfamily: *Curtuteria*

---

* Corresponding author. Tel: +64 3 4797964. E-mail: leuto618@student.otago.ac.nz

Parasitology (2007), **134**, 247–255.
doi:10.1017/S0031182006001478 Printed in the United Kingdom

australis and *Acanthoparyphium* sp. Due to similarity in their level of abundance and the identical ecological roles they play in the soft-sediment intertidal ecosystem, they are considered as ecological equivalents (Babirat *et al*. 2004), and here will be collectively referred to as 'the echinostomes'.

By impairing their hosts' ability to burrow, the echinostome metacercariae have been demonstrated to be ecosystem engineers on the intertidal mudflats, influencing the local diversity and distribution of the biotic community through their cockle hosts (Thomas *et al*. 1998; Mouritsen and Poulin, 2005*a*, *b*). How the echinostomes may influence the community of other parasites in *A. stutchburyi* is less certain. Previous studies have already found a number of associations between the two species of echinostomes and other trematodes that infect *A. stutchburyi*. These resulting associations appear to be indirect consequences of the echinostome metacercariae manipulating their host's microhabitat preference. Poulin *et al*. (1998) found that the sporocysts of *Cercaria pectinata* were more commonly found in cockles that were manipulated by echinostome metacercariae. This pattern of association with the echinostome has also been found for an undescribed species of gymnophallid (Poulin *et al*. 2000).

Parasitizing surfaced cockles manipulated by the echinostomes has costly consequences for *C. pectinata*. Since *C. pectinata* utilizes *A. stutchburyi* as a first intermediate host for asexual replication (Chilton, 1904), it would be in its interest for the host to survive as long as possible. However, cockles manipulated by echinostomes experience a 7-fold increase of their risk of avian predation (Thomas and Poulin, 1998). In contrast, *A. stutchburyi* is also a second intermediate host for the metacercariae of the gymnophallid. This trematode is present in high prevalence in certain localities, shares the same transmission route and definitive host as the echinostomes, and would benefit from any increases in the probability of its cockle host being predated upon by birds. In fact Mouritsen (2004) noted that in the presence of sublethal predation on cockles by foot-cropping fish predators which can impose a cost upon the foot-encysting echinostomes (Mouristen and Poulin, 2003*a*), the gymnophallid is the only parasite to receive a clear-cut advantage from associating with cockles that are resting on the sediment surface as a result of being heavily parasitized by echinostomes.

In addition to trematodes, *A. stutchburyi* is also host to a number of other less common symbionts such as the myicolid copepod *Pseudomyicola spinosus*. The nature of the potential interactions that can occur between trematodes and this crustacean within their mutual host are unknown. The relationship between the cockle and these symbionts may not necessarily be antagonistic, as the cockle may actually benefit from housing commensals that can remove problematic materials or protect it from parasitic infections, thus forming the basis of a cleaning symbiosis relationship.

There are many known varieties of cleaning symbioses involving animals from many taxa serving as clients and cleaners (Poulin and Grutter, 1996). Among invertebrates, some studies have found situations where the host organism benefits from having commensals that can act as resident cleaners. For example, Perissinotto and Pakhomov (1997) noted that an individual tunicate *Salpa thompsoni* that has been invaded by the copepod *Rhincalanus gigas* can potentially benefit by having its filtering apparatus cleaned by the copepod when the salp experiences clogging during phytoplankton blooms. More obvious benefits to the host have been found in the relationship between branchiobdellid annelids and their freshwater crayfish host. Branchiobdellids consume material trapped in crayfish gills, and crayfish without the branchiobdellid can experience much higher mortality and slower growth rate than those with the symbiont (Brown *et al*. 2002). Some organisms associating with cockles have been found to protect it, to some extent, from parasitic infections. The mud flat anemone, *Anthopleura aureoradiata*, frequently uses cockle shells for attachment and Mouritsen and Poulin (2003*b*) found that cockles with anemones accumulated significantly less metacercariae than those without anemones. It seems that the anemones prey upon trematode cercariae, acting like a resident cleaner symbiont (Mouritsen and Poulin, 2003*b*). This is similar to the relationship between the commensal oligochaete *Chaetogaster limnaei limnaei* and its snail host *Biomphalaria glabrata*. Rodgers *et al*. (2005) found the presence of *C. limnaei limnaei* to be beneficial to its host because it protects the snail from *Schistosoma mansoni* infection by preventing the entrance of invading miracidia, thus protecting its host from being parasitized and enhancing its growth (Rodgers *et al*. 2005). It is unknown if myicolid copepods may play a similar role for their cockle host.

This study aims to explore these potential interactions between the different symbionts found within *A. stutchburyi*. Specially, the aims are (1) to investigate if there is a pattern of association between the metacercariae of the echinostomes and gymnophallids, (2) to examine the effect *Pseudomyicola spinosus* has on the number of metacercariae accumulating inside cockles, and (3) to assess if this copepod has an effect on the cockle's condition as reflected by its tissue mass.

MATERIALS AND METHODS

Cockles used for this study were collected in November 2005 in Company Bay, Otago Harbour, South Island, New Zealand. A total of 500 cockles

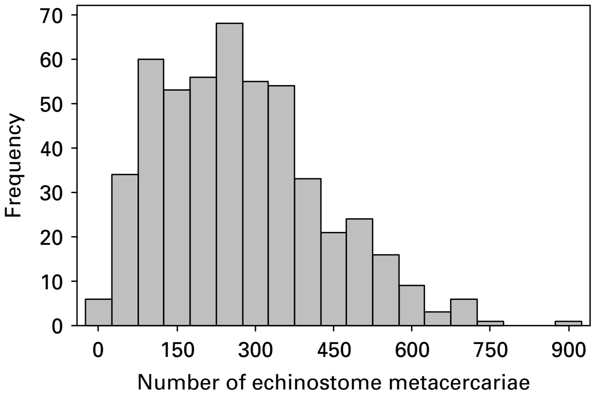

Fig. 1. Frequency distribution of the number of echinostome metacercariae per host among 500 cockles from Company Bay, Otago Harbour.

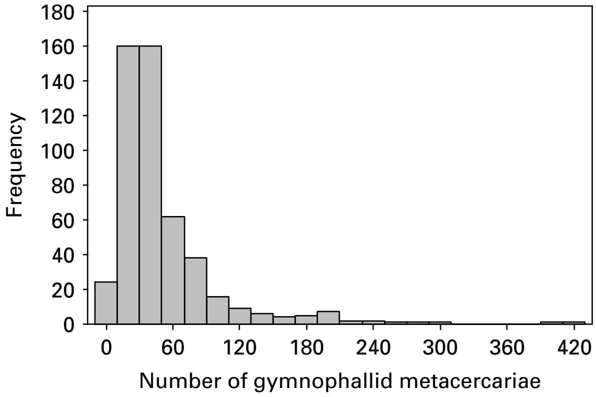

Fig. 2. Frequency distribution of the number of gymnophallid metacercariae per host among 500 cockles from Company Bay, Otago Harbour.

were collected from the site, in the lower tidal range, along a transect parallel to the waterline. Of all the cockles collected, 237 were lying on the surface of the sediment with at least 50% of their shell exposed, while the remaining 263 cockles were collected from below the sediment along the same transect.

All cockles were then returned live to the laboratory where the maximum shell length of each cockle was measured with digital callipers to the closest 0·1 mm. After the measurements were taken, the cockles were dissected and inspected for parasites under a dissecting microscope. The mantle cavity of the cockle was extensively examined for the presence of *P. spinosus*, which were collected and individually preserved in formalin. All the metacercariae of both echinostome and gymnophallid found in each cockle were counted. The gymnophallid metacercariae were easily visible and were usually found in clumps on the outer mantle epithelium of the cockle, most of them accumulating near the hinge. The echinostome metacercariae were encysted within the foot of the cockle, therefore to obtain an accurate count, each cockle's foot was removed and placed individually in a tube of pepsin digestion solution (6 g pepsin and 7 ml of 36–38% HCl in 1000 ml of water) and incubated at 40 °C for 20–30 h. The process partially dissolves most of the host tissue while leaving the metacercariae intact. After the incubation period, all the metacercariae in the tube were recovered and counted under a dissecting microscope.

After foot removal, the rest of the soft tissues of the cockles were retained and placed individually on small metal trays which were then placed in a drying oven at 110 °C for 22 h to allow dry mass measurement.

Prior to statistical analysis, the number of metacercariae of both echinostomes and gymnophallids were log-transformed. All statistical analyses conducted were parametric tests, while the Fisher's exact test was used to compare the frequency of *P. spinosus* infections in the surface and buried cockles.

RESULTS

The shell lengths of cockles collected were between 24·2 and 40·7 mm, with a mean of 30·6 (±2·4) mm. Most of the cockles harboured between 100 and 400 echinostome metacercariae (Fig. 1) and 30–60 gymnophallid metacercariae (Fig. 2). All the cockles dissected were found to be parasitized by both echinostome and gymnophallid metacercariae (overall prevalence of each trematode = 100%). The overall prevalence of *P. spinosus* in the cockles of Company Bay was found to be 4% (20 out of 500 cockles). All of the cockles found to harbour *P. spinosus* contained a single individual, except 1 cockle in the sample which had 3 copepods within its mantle cavity.

A multiple regression using cockle shell length, dry mass, and position in relation to the substrate (surfaced or buried) as predictor variables revealed the number of metacercariae correlated with the length of the cockle's shell for both echinostomes ($r=0{\cdot}178$, $P<0{\cdot}001$) and gymnophallids ($r=0{\cdot}148$, $P=0{\cdot}003$) (Figs 3 and 4), but no relationships were found between the cockle's dry mass and the number of metacercariae it harboured (echinostome: $P=0{\cdot}503$, gymnophallid: $P=0{\cdot}738$), nor was the position of the cockle in relation to the substrate found to have any effect on the intensity of infection (echinostome: $P=0{\cdot}677$, gymnophallid: $P=0{\cdot}271$). For *P. spinosus* in relation to the microhabitat of its host, 14 out of 237 surfaced cockles (5·9%) were found to be harbouring *P. spinosus* while only 6 out of 263 buried cockles (2·3%) were found to have the copepod. However, this apparent difference was not quite statistically significant (Fisher's exact test, $P=0{\cdot}0655$).

A positive association was found between numbers of echinostomes and gymnophallids ($r=0{\cdot}305$,

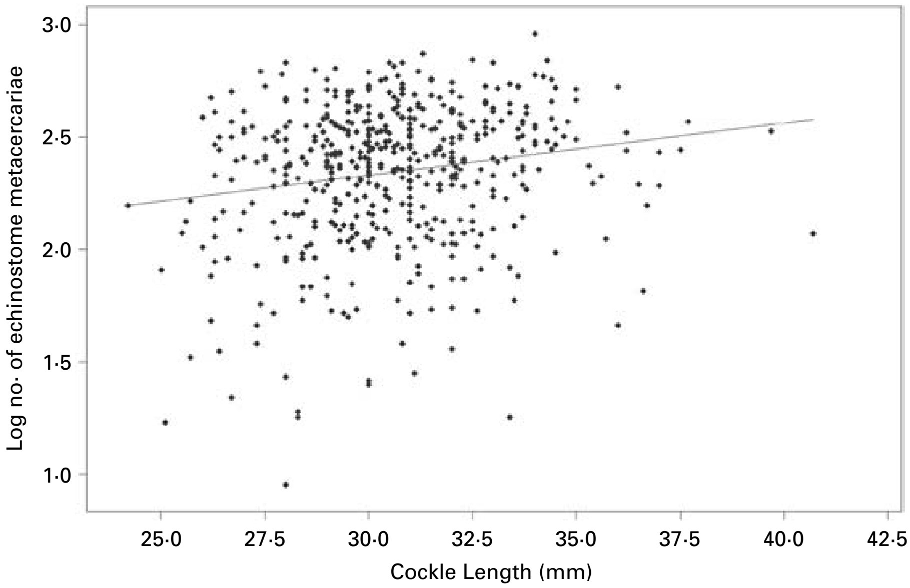

Fig. 3. Relationship between the number of echinostome metacercariae and cockle shell length (mm), for 500 cockles from Company Bay, Otago Harbour. The line is that given by a linear regression.

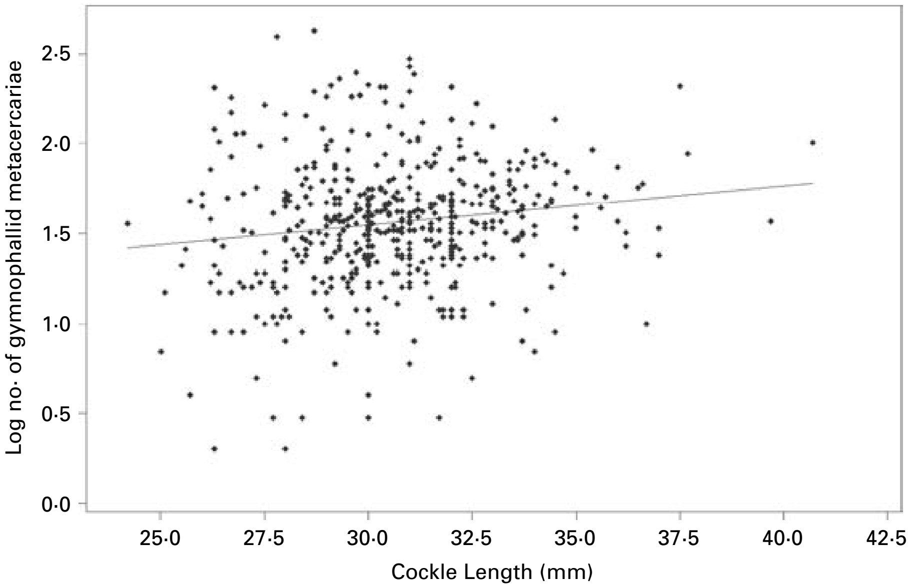

Fig. 4. Relationship between the number of gymnophallid metacercariae and cockle shell length (mm), for 500 cockles from Company Bay, Otago Harbour. The line is that given by a linear regression.

$P<0{\cdot}001$). This pattern of association remained even when it was corrected for cockle shell size by using the residuals of regressions of the number of metacercariae versus shell length ($r=0{\cdot}287$, $P<0{\cdot}001$) (Fig. 5). This shows that this pattern was not simply due to passive accumulation of the two parasites over time.

After correcting for cockle shell length using the method above, the presence of *P. spinosus* was not found to have any effect on cockle dry mass (two-sample *t*-test, $t=0{\cdot}775$, D.F. $=498$, $P=0{\cdot}439$). However, the presence of *P. spinosus* was found to be associated with a higher than expected number of echinostome metacercariae in the cockle (two-sample *t*-test, $t=2{\cdot}553$, D.F. $=498$, $P=0{\cdot}011$) but it was not found to have any significant effect on the number of gymnophallid metacercariae (two-sample *t*-test, $t=0{\cdot}807$, D.F. $=498$, $P=0{\cdot}420$). Based on back-transformed mean values (i.e. geometric means), cockles with a copepod harboured an average of 332 echinostome metacercariae, whereas those without a copepod harboured only 217.

DISCUSSION

The results of the present study show that a non-random pattern of association exists between at least 2 pairs of parasites found in *A. stutchburyi*. Firstly,

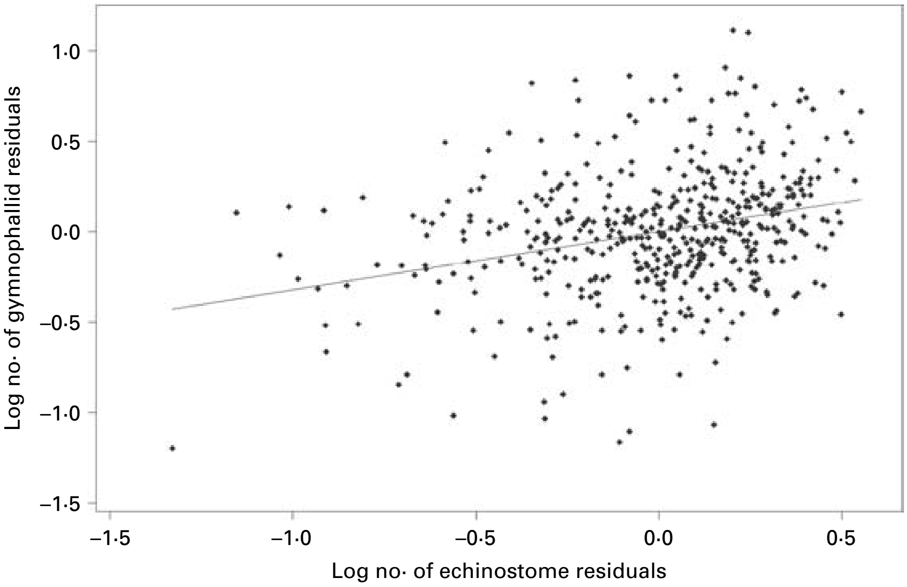

Fig. 5. Relationship between the numbers of echinostome and gymnophallid metacercariae per cockle, for 500 cockles from Company Bay, Otago Harbour. The data are residuals of separate regressions against cockle shell length, and are thus independent of cockle size.

there is a positive association between the infection intensity of echinostome and gymnophallid metacercariae. Secondly, the presence of a parasitic copepod appears to be associated with a higher abundance of echinostome metacercariae, but not of the gymnophallid. What could be the basis behind these patterns of association?

The myicolid copepod *Pseudomyicola spinosus* has been recorded in about 50 species of bivalves worldwide (Ho, 2001). Its presence within the mantle (branchial) cavity causes varying degrees of pathology in its bivalve hosts, the severity of which depends upon the intensity of infection (Dinamani and Gordon, 1974; Olivas-Valdez and Cáceres-Martínez, 2002). The damage caused usually involves erosion or alteration of the epithelium wall within the mantle cavity (Dinamani and Gordon, 1974; Cáceres-Martinez and Vásquez-Yeomans, 1997; Olivas-Valdez and Cáceres-Martínez, 2002; Cáceres-Martínez *et al.* 2005), although at low infection intensity the damage caused by the copepod is generally considered to be innocuous (Cáceres-Martínez *et al.* 2005). While *P. spinosus* can feed upon host tissue (host gill tissue has been used as food for rearing *P. spinosus* in the laboratory: Kajihara and Nakamura (1985)), myicolid copepods feed mainly upon host mucus (Ho and Zheng, 1994) and any mechanical injuries are most likely caused by the copepod's attachment appendages as it moves within its host (Cáceres-Martinez and Vásquez-Yeomans, 1997). Unlike many other parasitic copepods, the body of *P. spinosus* is comparatively unmodified and it is highly mobile inside its host.

The modification of the host epithelium within the mantle cavity by *P. spinosus* may have consequences for the infectivity of echinostome cercariae that enter the cockle. Wegeberg *et al.* (1999) noted that once within the mantle cavity of a cockle, the toughness of the host epidermis was one of the factors affecting infection efficiency for cercariae of the 3 *Himasthla* species they studied. Once a cercaria has entered the cockle through its inhalant siphon, it needs to adhere to host tissue with its ventral sucker, move to the appropriate infection site, and penetrate the epidermis in order to deny the host the opportunity to expel it from its mantle cavity (Wegeberg *et al.* 1999). By modifying the epithelium walls within the cockle's mantle cavity, *P. spinosus* may in fact enhance the infection efficiency of the echinostome cercariae.

The process of accumulation of metacercariae in a cockle bears some similarities to the recruitment of sessile intertidal organisms on rocky shores. Both involve free-living larval stages that must find the appropriate substrate to settle upon. In the case of a cercaria, the 'appropriate substrate' is the second intermediate host. For the free-living larvae of intertidal organisms (such as barnacle cyprids), the presence of other organisms (such as gastropods) that inhabit the rocky shore ecosystem can have indirect influences on settlement success. Holmes *et al.* (2005) found that the presence of the limpet *Patella vulgata* has a positive effect on the settlement success of *Semibalanus balanoides* cyprids on rocky shores. Earlier, Holmes (2002) found that through adhesive enmeshment, the pedal mucus produced by *P. vulgata* enhances cyprid settlement by a factor of about 6 in laboratory studies and by a factor of about 4 in field experiments. Thus, the presence of *P. vulgata* effectively modifies the nature of the substrate in a manner that facilitates the settlement success of *S. balanoides* (Holmes *et al.* 2005). This is an example of 'niche construction', where an organism's activities alter the selection pressure of the environment on itself and/or other organisms (Odling-Smee *et al.* 2003). In the case of *P. spinosus* and its cockle host, the copepod is also, in effect, modifying its 'substrate' (the epithelium wall of the cockle's mantle cavity) in a way that can enhance the settlement success of another organism (the echinostomes) that uses the same 'habitat' (the cockle). While the modified epithelium of the cockle is a mere 'by-product' of the copepod's presence and activities, it can still be considered as a form of habitat facilitation or niche construction if other organisms can take advantage of it (Laland *et al.* 2005).

This is not merely a case of the copepod's presence and activities within the host inducing a general stress reaction making it more susceptible to other parasitic infections. That is the case for another myicolid copepod, *Ostrincola koe*, in the hard clam *Meretrix meretrix*, which suffer mass mortality due to acute enteritis caused by the bacterium *Vibrio alginolyticus* (Ho and Zheng, 1994). While *V. alginolyticus* is a common coastal marine microbe, *O. koe* can induce considerable stress in *M. meretrix*, brought about by the irritation caused by the copepod's attachment appendages, thus compromising the clam's defence system and resulting in heightened susceptibility to vibrio infections (Ho and Zheng, 1994). However, unlike *O. koe*, which can occupy the mantle cavity of *M. meretrix* in large numbers (up to 30 copepods in a single host: Ho and Zheng, 1994) during peak periods of reproduction, *P. spinosus* were only found in small numbers (usually 1 per cockle host) in *A. stutchburyi*. No significant differences were found between the dry mass of cockles with and without the copepod, showing that it is not causing its host any significant physiological stress reflected in lower tissue mass. In addition, numbers of gymnophallid metacercariae were not affected by the presence of *P. spinosus* in the cockle as would be expected if the pattern observed was merely due to a process of passive accumulation of metacercariae aided by a general stress reaction suppressing the cockle's defensive system. As explained earlier, the effect that a small number of *P. spinosus* have on their cockle hosts appears to be more subtle. A potential reason behind this phenomenon could be the different migration routes taken by the two trematodes through their cockle host before reaching their final settlement site. Unlike echinostome cercariae, which encyst in the foot by entering through the cockle's siphon to reach the mantle cavity (Wegeberg *et al.* 1999) where *P. spinosus* resides, gymnophallid cercariae migrate through the extrapapillial space before settling between the outer mantle epithelium and inner shell surface (Cremonte and Ituarte, 2003). Thus, they do not encounter the copepod or its immediate environment. Therefore, any modification of the epithelium wall *within* the mantle cavity caused by the presence of *P. spinosus* would not alter the infectivity of gymnophallid cercariae. Ultimately, this kind of habitat modification may actually be detrimental to *P. spinosus*, because the accumulation of echinostome metacercariae modifies the behaviour of the cockle, making it more vulnerable to predation.

It is unknown just how important the 'habitat facilitation' provided by *P. spinosus* contributes to the overall ecology of the echinostomes; it may just be a minor effect of relatively little ecological relevance. While the copepod's effect on the settlement of echinostomes may not be major, it still results in an effect that is statistically detectable, making it a potential factor to consider in the transmission ecology of the echinostomes. It may be worthwhile to follow-up those findings with histopathological studies to verify that *P. spinosus* causes the kind of pathology in *A. stutchburyi* that has been reported for the copepod's other hosts. It would establish whether cockles harbouring the copepod have altered epithelium walls within the mantle cavity that may facilitate the establishment of echinostome metacercariae. Experimental infection of cockles by *P. spinosus* is not possible at present, and therefore the apparent positive effect of the copepod on echinostome infection cannot yet be confirmed experimentally.

The pattern of association found between the gymnophallid and echinostomes is interesting to consider in the context of the roles played by these two parasites in trophic transmission and host manipulation of the cockle. While it is possible that certain individuals may simply be more susceptible to a range of infections due to variability in parasite resistance, a more intriguing possibility is that intermediate hosts that already harbour manipulative parasite(s) may be actively exploited by other parasites that adopt the 'hitch-hiking' life-history strategy (Thomas *et al.* 1998). However, there are few empirical studies of the occurrence or proximate mechanism of this strategy in nature. One exception is the system involving the amphipod *Gammarus insensibilis* and the two trematodes *Microphallus papillorobustus* and *Maritrema subdolum*. Thomas *et al.* (1997) found that while *M. subdolum* cannot manipulate the behaviour of *G. insensibilis*, it is positively associated with the manipulative *M. papillorobustus*. Amphipods parasitized by *M. papillorobustus* exhibit modified behaviours in the form of positive phototaxis and the tendency to swim near the water's surface, which changes their spatial distribution (Helluy, 1983). It was found that *M. subdolum* achieves positive association with *M. papillorobustus* through cercariae that exhibit swimming behaviours which increase their likelihood of encountering amphipods that are distributed closer to the water's surface due to behavioural manipulation by *M. papillorobustus* (Thomas *et al.* 1997).

Thus a possible mechanism behind the hitch-hiking life-history strategy relates to the spatial distribution and altered microhabitat of hosts that are being manipulated. Previous studies show how altered microhabitat can lead to higher risk of infection by parasites. For instance, Poulin and Fitzgerald (1989) found that juvenile fish that swim closer to the bottom and/or vegetation are at greater risk of becoming parasitized by the ectoparasitic branchiuran *Argulus canadensis*. Fish actually modified their spatial distribution in the presence of *A. canadensis* to avoid becoming parasitized. On a larger spatial scale, Lysne *et al.* (1998) conducted an experiment showing that caged fish kept at shallower depths accumulated significantly more cercariae of the trematode *Cryptocotyle lingua* than those kept deeper. Lysne *et al.* (1998) suggested that the observed pattern of parasite accumulation may be due to the swimming behaviour of *C. lingua* cercariae, which tend to swim closer to the water surface.

Accordingly, if the gymnophallid is indeed a hitch-hiker parasite, then its cercariae should exhibit swimming behaviour leading to higher probability of encountering a cockle resting on the sediment surface than buried cockles, because cockles on the surface are usually heavily infected by echinostomes. While the preferred microhabitat of *A. stutchburyi* is a few centimetres below the sediment surface, when manipulated by the echinostomes, the cockle is forced to remain above the sediment (Thomas and Poulin, 1998). Preferential infection of surfaced cockles may be the mechanism through which the gymnophallid associates with the echinostomes. While this study did not find surface cockles to harbour significantly more gymnophallid metacercariae than buried cockles, this had been found before (Poulin *et al.* 2000). The absence of difference in this study may simply be due to the fact that individuals heavily parasitized by the echinostomes are not necessarily always found on the surface of the sediment. Cockles are haphazardly brought up to the surface by currents or other form of disturbances and due to the mechanism of the host manipulation, some heavily parasitized individuals may remain buried in the sediment. Conversely, manipulated cockles that were previously stranded on the surface may also be reburied by sediment carried by tidal movements. These abiotic factors can obscure the pattern of association that exists between the echinostomes and the gymnophallid.

The pattern of positive association between the gymnophallid and echinostomes found here confirms the findings of a previous study (Poulin *et al.* 2000). As the correlation between numbers of gymnophallids and echinostomes is independent of cockle shell length, it is not simply the outcome of the simultaneous accumulation of metacercariae as cockles grow older. A field experiment involving non-parasitized cockles forced to remain above or below the sediment would confirm whether the gymnophallid displays a preference for parasitizing cockles lying on the sediment's surface.

The authors would like to thank the Ecological Parasitology Group of University of Otago for useful comments on an earlier version of the manuscript.

REFERENCES

Babirat, C., Mouritsen, K. N. and Poulin, R. (2004). Equal partnership: two trematode species, not one, manipulate the burrowing behaviour of the New Zealand cockle, *Austrovenus stutchburyi*. *Journal of Helminthology* **78**, 195–199.

Brown, B. L., Creed, R. P. Jr and Dobson, W. E. (2002). Branchiobdellid annelids and their crayfish hosts: are they engaged in a cleaning symbiosis? *Oecologia* **132**, 250–255.

Byrne, C. J., Holland, C. V., Kennedy, C. R. and Poole, W. R. (2003). Interspecific interactions between Acanthocephala in the intestine of brown trout: are they more frequent in Ireland? *Parasitology* **127**, 399–409.

Cáceres-Martínez, C., Chávez-Villalba, J. and Garduño-Méndez, L. (2005). First record of *Pseudomyicola spinosus* in *Argopecten ventricosus* in Baja California, Mexico. *Journal of Invertebrate Pathology* **89**, 95–100.

Cáceres-Martínez, J. and Vásquez-Yeomans, R. (1997). Presence and histopathological effects of the copepod *Pseudomyicola spinosus* in *Mytilus galloprovincialis* and *Mytilus californianus*. *Journal of Invertebrate Pathology* **70**, 150–155.

Chilton, C. (1904). On the occurrence of a species of cercariae in the cockle *Chione stutchburyi*. *Transactions and Proceedings of the New Zealand Institute* **37**, 322–325.

Cremonte, F. and Ituarte, C. (2003). Pathologies elicited by the gymnophallid metacercariae of *Bartolius* in the clam *Darina solenoides*. *Journal of the Marine Biological Association of the United Kingdom* **83**, 311–318.

Dinamani, P. and Gordon, D. B. (1974). On the habits and nature of association of the copepod *Pseudomyicola spinosus* with the rock oyster *Crassostrea glomerate* in New Zealand. *Journal of Invertebrate Pathology* **24**, 305–310.

Esch, G. W., Bush, A. O. and Aho, J. M. (1990). *Parasite Communities: Patterns and Processes*. Chapman and Hall, New York.

Esch, G. W., Curtis, L. A. and Barger, M. A. (2001). A perspective on the ecology of trematode communities in snails. *Parasitology* **123** (Suppl.), S57–S75.

Fredensborg, B. L. and Poulin, R. (2005). Larval helminths in intermediate hosts: does competition early in life determine the fitness of adult parasites? *International Journal for Parasitology* **35**, 1061–1070.

Friggens, M. M. and Brown, J. H. (2005). Niche partitioning in the cestode communities of two elasmobranchs. *Oikos* **108**, 76–84.

Helluy, S. (1983). Relations hôtes-parasites du trématode *Microphallus papillorobutus* (Rankin, 1940). II Modifications du comportement des *Gammarus* hôtes intermédiaires et localisation des métacercaires. *Annales de Parasitologie Humaine et Comparée* **58**, 1–17.

Hendrickson, M. A. and Curtis, L. A. (2002). Infrapopulation sizes of co-occurring trematodes in the snail *Ilyanassa obsoleta*. *Journal of Parasitology* **88**, 884–889.

Ho, J.-S. (2001). Why do symbiotic copepods matter? *Hydrobiologia* **453/454**, 1–7.

Ho, J.-S. and Zheng, G.-X. (1994). *Ostrincola koe* (Copepoda, Myicolidae) and mass mortality of cultured hard clam (*Meretrix meretrix*) in China. *Hydrobiologia* **284**, 169–173.

Holmes, S. P. (2002). The effect of pedal mucus on barnacle cyprid settlement: a source for indirect interactions in the rocky intertidal? *Journal of the Marine Biological Association of the United Kingdom* **82**, 117–129.

Holmes, S. P., Walker, G. and van der Meer, J. (2005). Barnacles, limpets and periwinkles: the effects of direct and indirect interactions on cyprid settlement success. *Journal of Sea Research* **53**, 181–204.

Kajihara, T. and Nakamura, K. (1985). Lifespan and oviposition of the parasitic copepod *Pseudomyicola spinosus* under rearing conditions. *Marine Biology* **87**, 55–60.

Kuris, A. M. and 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.

Laland, K. N., Odling-Smee, J. and Feldman, M. W. (2005). On the breadth and significance of niche construction: a reply to Griffiths, Okasha and Sterelny. *Biology and Philosophy* **20**, 37–55.

Lello, J., Boag, B., Fenton, A., Stevenson, I. R. and Hudson, P. J. (2004). Competition and mutualism among the gut helminths of a mammalian host. *Nature, London* **428**, 840–844.

Lysne, D. A., Skorping, A. and Hemmingsen, W. (1998). Transmission of *Cryptocotyle lingua* cercariae in natural environments: a field experiment. *Journal of Fish Biology* **53**, 879–885.

Montaudouin, X. de., Kisielewski, I., Bachelet, G. and Desclaux, C. (2000). A census of macroparasites in the intertidal bivalve community, Arcachon Bay, France. *Oceanologica Acta* **23**, 453–468.

Mouritsen, K. N. (2002). The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. *Parasitology* **124**, 521–528.

Mouritsen, K. N. (2004). Intertidal facilitation and indirect effects: cause and consequences of crawling in the New Zealand cockle. *Marine Ecology Progress Series* **271**, 207–220.

Mouritsen, K. N. and Poulin, R. (2003*a*). Parasite-induced trophic facilitation exploited by non-host predator: a manipulator's nightmare. *International Journal for Parasitology* **33**, 1043–1050.

Mouritsen, K. N. and Poulin, R. (2003*b*). The mud flat anemone-cockle association: mutualism in the intertidal zone? *Oecologia* **135**, 131–137.

Mouritsen, K. N. and Poulin, R. (2005*a*). Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos* **108**, 344–350.

Mouritsen, K. N. and Poulin, R. (2005*b*). Parasitism can influence the intertidal zonation of non-host organisms. *Marine Biology* **148**, 1–11.

Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. (2003). *Niche Construction: the Neglected Process in Evolution*. Princeton University Press, New Jersey.

Olivas-Valdez, J. A. and Cáceres-Martínez, J. (2002). Infestation of the blue mussel *Mytilus galloprovincialis* by the copepod *Pseudomyicola spinosus* and its relation to size, density, and condition index of the host. *Journal of Invertebrate Pathology* **79**, 65–71.

Perissinotto, R. and Pakhomov, E. A. (1997). Feeding association of the copepod *Rhincalanus gigas* with the tunicate salp *Salpa thompsoni* in the southern ocean. *Marine Biology* **127**, 479–483.

Poulin, R. and Fitzgerald, G. J. (1989). Risk of parasitism and microhabitat selection in juvenile sticklebacks. *Canadian Journal of Zoology* **67**, 14–18.

Poulin, R. and Grutter, A. S. (1996). Cleaning symbioses: proximate and adaptive explanations. *BioScience* **46**, 512–517.

Poulin, R. and Valtonen, E. T. (2001). Interspecific associations among larval helminths in fish. *International Journal for Parasitology* **31**, 1589–1596.

Poulin, R., Hecker, K. and Thomas, F. (1998). Host manipulated by one parasite incur additional costs from infection by another parasite. *Journal of Parasitology* **84**, 1050–1052.

Poulin, R., Steeper, M. J. and Miller, A. A. (2000). Non-random patterns of host use by the different parasite species exploiting a cockle population. *Parasitology* **121**, 289–295.

Rodgers, J. K., Sandland, G. J., Joyce, S. R. and Minchella, D. J. (2005). Multi-species interactions among a commensal (*Chaetogaster limnaei limnaei*), a parasite (*Schistosoma mansoni*), and an aquatic snail host (*Biomphalaria glabrata*). *Journal of Parasitology* **91**, 709–712.

Thomas, F., Mete, K., Helluy, S., Santalla, F., Verneau, O., de Meeüs, T., Cézilly, F. and Renaud, F. (1997). Hitch-hiker parasites or how to benefit from the strategy of another parasite. *Evolution* **51**, 1316–1318.

Thomas, F. and 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., de Meeüs, T. and Poulin, R. (1998). Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone? *Proceedings of the Royal Society of London, B* **265**, 1091–1096.

Thomas, F., Renaud, F. and Poulin, R. (1998). Exploitation of manipulators: 'hitch-hiking' as a parasite transmission strategy. *Animal Behaviour* **56**, 199–206.

Wang, C. L., Renaud, F. and Thomas, F. (2002). Negative influence of *Gammarinema gammari* (Nematoda) on the fecundity of *Microphallus papillorobustus* (Trematoda): field and experimental evidence. *Journal of Parasitology* **88**, 425–427.

Wegeberg, A. M., Montaudouin, X. de. and Jensen, K. T. (1999). Effect of intermediate host size (*Cerastoderma edule*) on infectivity of cercariae of three *Himasthla* species (Echinostomatoidae, Trematoda). *Journal of Experimental Marine Biology and Ecology* **238**, 259–269.