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HOST PARTITIONING BY PARASITES IN AN INTERTIDAL CRUSTACEAN COMMUNITY

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ABSTRACT: Patterns of host use by parasites throughout a guild community of intermediate hosts can depend on several biological and ecological factors, including physiology, morphology, immunology, and behavior. We looked at parasite transmission in the intertidal crustacean community of Lower Portobello Bay, Dunedin, New Zealand, with the intent of: (1) mapping the flow of parasites throughout the major crustacean species, (2) identifying hosts that play the most important transmission role for each parasite, and (3) assessing the impact of parasitism on host populations. The most prevalent parasites found in 14 species of crustaceans (635 specimens) examined were the trematodes *Maritrema novaezealandensis* and *Microphallus* sp., the acanthocephalans *Profilicollis* spp., the nematode *Ascarophis* sp., and an acuariid nematode. Decapods were compatible hosts for *M. novaezealandensis*, while other crustaceans demonstrated lower host suitability as shown by high levels of melanized and immature parasite stages. Carapace thickness, gill morphology, and breathing style may contribute to the differential infection success of *M. novaezealandensis* and *Microphallus* sp. in the decapod species. Parasite-induced host mortality appears likely with *M. novaezealandensis* in the crabs *Austrohelice crassa*, *Halicarcinus varius*, *Hemigrapsus sexdentatus*, and *Macrophthalmus hirtipes*, and also with *Microphallus* sp. in *A. crassa*. Overall, the different parasite species make different use of available crustacean intermediate hosts and possibly contribute to intertidal community structure.

At any stage of their life cycle, parasites can potentially use several sympatric host species belonging to either the same taxonomic group or ecological guild (sensu Root, 1967). Thus, trophically transmitted helminths can employ, as intermediate hosts, any species used as prey by the definitive host, provided they are able to survive and develop in those species. In natural communities, several co-existing parasite species with the same definitive hosts can potentially use the same intermediate host species. Alternatively, they may flow through the community in different ways, i.e., they may differ in how they utilize the variety of intermediate hosts available. Patterns of host use can play important roles in determining the structure of host communities, since they will determine how parasites affect relative host population abundances (Minchella and Scott, 1991; Hudson and Greenman, 1998; Mouritsen and Poulin, 2002). However, except for a few studies, like those of Zander and colleagues (Zander et al., 1994; Zander, 2001) on the use of gobiid fishes by larval helminths in a locality, there have been relatively few attempts to examine the ecological partitioning of host species among sympatric parasites within a community. The benefit of exploring how parasites use available hosts within their community is that we can gain insights into ecological interactions, such as degrees of host specificity, which can be overlooked when looking only at a single host or parasite species.

Given that parasites never equally exploit all available host species, constraints imposed by host specificity appear to determine which potential transmission routes are actually used. Euzet and Combes (1980) used a series of encounter and compatibility filters to illustrate how host specificity is constrained in parasites. The encounter filter excludes hosts that would never be naturally encountered by the parasite due to either allopatric distributions or behavior. The compatibility filter excludes hosts in which the parasites are unable to survive due to host physiology, immunology, or both. The remaining hosts comprise the parasite's host range. Phylogenetic and biological/ecological factors, including physiology, morphology, immunology, behavior, and geography are thought to constrain host specificity (Adamson and Caira, 1994; Kassen, 2002; Perlman and Jaenike, 2003; Poulin, 2007). Furthermore, within this range there is variability in the susceptibility of hosts to parasites, with fully compatible hosts at one end of the spectrum and dead-end or accidental hosts at the other (Dogiel, 1964; Holmes, 1976).

In the present study, we present data on the partitioning of available host species among helminth parasites within the diverse intertidal community of crustaceans in Lower Portobello Bay (LPB) near Dunedin, South Island, New Zealand. This shallow tidal bay is covered with patches of eelgrass (*Zostera capricorni*) and sea lettuce (*Ulva* sp.) atop a muddy sand substrate bound by a rocky shoreline. It provides an ideal habitat for a wide range of burrowing, rock-dwelling, and algae-living littoral crustaceans, in addition to snails, birds, and fish that all support a rich parasite fauna.

Prior faunal studies from LPB and surrounding areas indicate that microphallid trematodes (Fredensborg et al., 2004, 2006; Martorelli et al., 2004, 2008; Leung et al., 2009), acanthocephalans (Latham and Poulin, 2002a, 2002b), and nematodes (Moravec et al., 2003) are the most common parasites of crustaceans in this system. Much work has been done on these parasites and hosts, yet a formal standardized survey of parasite usage of all the major crustaceans has never been undertaken.

Our specific objectives were: (1) to map the flow of major helminth species through the crustacean community of LPB; (2) to identify the crustacean species playing the most important transmission role for each species, based on parasite infection levels, development, and death from host immune responses; and (3) to assess the potential impact of parasitism on crustacean populations based on relationships between host body size and infection levels. For this last objective, the effect of each parasite on the population structure of its hosts, in the form of parasite-induced host mortality, will be inferred from the shape of the relationship between host body size and numbers of parasites per host (Anderson and May, 1978).

MATERIALS AND METHODS

Study area

In total, 635 crustaceans were sampled from a 300-m^2 section of LPB (45°49′50″S, 170°40′17″E), Otago Harbor, Dunedin, New Zealand, over a month during the summer of 2008/2009. The area sampled covered all tidal levels, from the low to the high water mark. As previously mentioned, this site was selected because of its ideal habitat for a range

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TABLE I. Prevalence (mean abundance ± SE) of helminth parasites from 14 crustacean species collected from Lower Portobello Bay, Dunedin, New Zealand.

Host	Order	N	*Maritrema*	*Microphallus* sp.	*Profilicolis* spp.	*Ascarophis* sp.
Paracalliope novizealandiae	Amphipoda	51	70.6 (4.7 ± 0.9)	0	0	0
Transorchestia chiliensis	Amphipoda	50	6.0 (0.2 ± 0.1)	0	0	0
Cyclograpsus lavauxi	Decapoda	26	27.0 (1.2 ± 0.5)	46.2 (16.3 ± 7.1)	0	30.8 (3.7 ± 3.3)
Halicarcinus varius	Decapoda	56	100 (199.1 ± 17.0)	0	5.4 (0.1*)	0
Austrohelice crassa	Decapoda	50	0	90.0 (26 ± 5.8)	0	64.0 (3.6 ± 1.0)
Hemigrapsus crenulatus	Decapoda	51	98.0 (38.3 ± 3.8)	94.1 (149.5 ± 62.5)	92.2 (8.6 ± 1.2)	15.7 (0.3 ± 0.2)
Hemigrapsus sexdentatus	Decapoda	50	98.0 (42.1 ± 5.0)	40.0 (67.8 ± 57.5)	60.0 (4.0 ± 1.0)	20.0 (0.2 ± 0.1)
Macrophthalmus hirtipes	Decapoda	50	100 (153.9 ± 12.6)	88.0 (136.5 ± 77.4)	100 (30.6 ± 5.7)	50.0 (1.0 ± 0.2)
Petrolisthes elongatus	Decapoda	20	0	0	0	0
Nyctiphanes australis	Euphausiacea	50	0	0	0	0
Isocladus armatus	Isopoda	30	0	0	0	0
Paridotea ungulata	Isopoda	50	82 (14.9 ± 4.0)	0	0	0
Chamaesipho columna	Sessilia	50	0	0	0	0
Lysiosquilla spinosa	Stomatopoda	51	43 (3.9 ± 1.5)	0	0	0

* SE was not calculated due to sample size.

of crustaceans; furthermore, it has been a site central to many previous crustacean-parasite studies and has a regionally high prevalence (89.4%) of trematode infections in the snail (first intermediate host) *Zeacumantus subcarinatus* (Fredensborg et al., 2006). This snail is sympatrically distributed with crustacean hosts throughout the upper and lower intertidal zones (65 snails per m^2) (Fredensborg and Poulin, 2006), yet much higher snail densities do occur in places.

Crustacean collections

A preliminary survey of LPB identified the predominant crustacean species greater than 2 mm in length to be included in the survey; meiofauna or interstitial crustaceans (including copepods, ostracods, and cumacea) were excluded. The targeted species were haphazardly collected using the following species-dependent methods: burrow digging, rock turning, and netting. In total, 14 species of crustaceans were collected, including 7 decapods, 2 isopods, 2 amphipods, 1 euphausiid, 1 stomatopod, and 1 barnacle (Table I). Crustaceans were kept in the laboratory and killed within a week of collection. Upon necropsy, animals were sexed and measured (carapace width for crabs, diameter for barnacles, body length for others), using either vernier calipers or a calibrated ocular micrometer.

Prevalence, mean intensity, and mean abundance were recorded for each of the common parasites found. When feasible, the stage of microphallid trematode development was recorded in accordance with the classification used by Keeney et al. (2007), where: stage 1 are early immature unencysted metacercariae; stage 2 are late immature unencysted metacercariae; stage 3 are early single-walled cysts and; stage 4 are mature double-walled cysts. Crustaceans can sometimes encapsulate and melanize metacercariae through an immune response, resulting in the parasite's death (see Bryan-Walker et al., 2007). Therefore, melanized metacercariae were also recorded for species where melanization was evident. For 1 nematode species, only parasite presence/absence was noted due to their small size and high intensity.

Data analysis

Data were tested for normality using the Shapiro Wilk test and log (x+1) transformed to meet assumptions of normality when necessary. If transformations did not result in normally distributed data, nonparametric tests were used. All statistical tests were performed using JMP 7.0 (SAS Inst., 2007, Cary, North Carolina).

To determine whether parasites have an impact on host mortality, the relationship between intensity of infection and host body size was computed across all infected host individuals, separately for each host-parasite species combination for which there were sufficient data. Host-induced parasite mortality could also account for the decrease in infections; however, metacercariae generally remain in their hosts (even when melanized) throughout their host's lifespan, which makes them suitable for detecting parasite-induced host mortality (Anderson and Gordon, 1982). If parasites passively accumulate over time as hosts grow, then a linear relationship is expected between host size and intensity of infection. If heavy infections result in higher mortality, however, the relationship will be different, i.e., intensity of infection should increase with increasing host size, but only up to a certain point, after which it levels off or even starts decreasing since heavily infected hosts are removed from the population (Anderson and May, 1978; Gordon and Rau, 1982; Latham and Poulin, 2002a). We determined which of a linear regression or a second order polynomial regression provided the best fit to the data, based on R^2 values.

RESULTS

General survey statistics

In total, 45,182 parasites were recorded from 635 crustaceans including 2 trematode, 2 nematode, 2 acanthocephalan, and 1 parasitic isopod species. Double-walled, ovoid metacercariae cysts (~300 μm in length) found in the gills, hepatopancreas, appendages, or free floating within the body cavity of several crustaceans were identified as *Maritrema novaezealandensis*. We obtained molecular confirmation of this identification based on cytochrome oxidase I (COI) sequences from several specimens (Leung et al., 2009). Other trematode metacercariae, found in the gonads and hepatopancreas, showed 2 stages of development. One stage was a smaller, spherical, thin-walled cyst (~300 μm); the other was a larger (~425 μm) double-walled cyst. Sequences of COI confirmed that these cysts were 2 developmental stages of *Microphallus* sp. (Leung et al., 2009). Cercariae of *M. novaezealandensis* and *Microphallus* sp. are released from the snail *Z. subcarinatus* and enter a crustacean intermediate host to await predation by an avian definitive host. The nematodes correspond to those found in a previous study of nematodes from the crab *Macrophthalmus hirtipes*, i.e., *Ascarophis* sp. and an unidentified species of acuariid (Moravec et al., 2003). The former has fish definitive hosts, and the latter avian definitive hosts. Acanthocephalan cystacanths found in this survey will be referred to as *Profilicollis* spp. An earlier study of acanthocephalans recovered from the body cavity of the crab *M. hirtipes* demonstrated that 1% were *Profilicollis antarcticus*, while the rest were *P. novaezealandensis* (Latham and Poulin, 2002a). The definitive

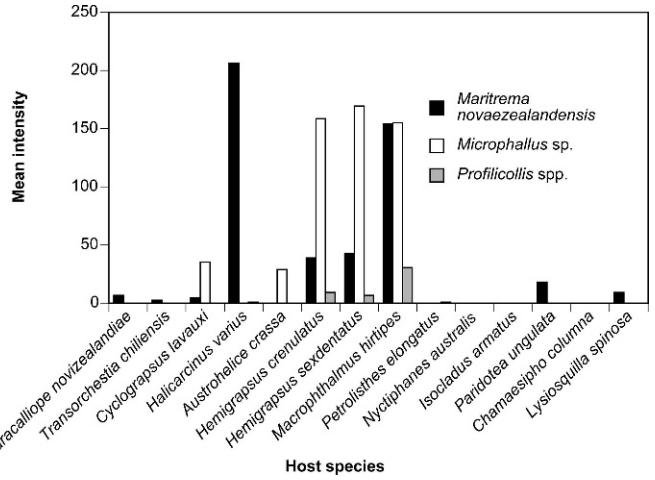

FIGURE 1. Mean intensity of *Maritrema novaezealandensis*, *Microphallus* sp., and *Profilicollis* spp. in 14 crustacean host species.

hosts of *Profilicollis* spp. are birds. Finally, the parasitic isopod in the body cavity of some decapods was identified as *Portunion* sp. (Brockerhoff, 2004).

Parasite prevalence and mean abundance were relatively high in infected host species (Table I; Fig. 1). Trematodes accounted for 95% of the total abundance, acanthocephalans 5%, and nematodes and parasitic isopods <1%. *Maritrema novaezealandensis* was the most common parasite (found in 64% [9 of 14] of the crustacean species sampled) and exhibited high prevalence in many of the hosts (Table I). The trematode *Microphallus* sp., acanthocephalans, and the nematode *Ascarophis* sp. were only found in decapods, with the exception of *Ascarophis* sp., which additionally occurred in the amphipod *Transorchestia chiliensis*. Acuariid nematodes were present in half of the crustacean species.

Decapods harbored the vast majority of *M. novaezealandensis* metacercariae (24,126 recovered), with the majority being found in *Halicarcinus varius* (46%) and *M. hirtipes* (32%). *Microphallus* sp. occurred only in decapods and, of the 19,562 metacercariae recovered, 39% were found in *Hemigrapsus crenulatus*, 35% in *M. hirtipes*, and 17% in *Hemigrapsus sexdentatus*. Of the 2,174 acanthocephalans *Profilicollis* spp. found, *M. hirtipes* had the highest prevalence at 71%, followed by *H. crenulatus* (20%) and *H. sexdentatus* (9%). The nematode *Ascarophis* sp. was predominantly found in *Austrohelice crassa* (50%) and *Cyclograpsus lavauxi* (28%) (n = 349). The acuariid nematode was present in 50% of the species examined and 86% of the decapod species. The parasitic isopod *Portunion* sp. was the rarest parasite, occurring on only 4 occasions in the decapods *M. hirtipes*, *H. crenulatus*, *A. crassa*, and *C. lavauxi*. No parasites were found in *Nyctiphanes australis*, *Isocladus armatus*, or *Chamaesipho columna*.

Developmental stages of *M. novaezealandensis* and melanizations were not distributed equally among the crustaceans (Table II). Some crustaceans, such as the amphipods *Paracalliope novizealandiae* and *T. chiliensis*, had high abundance of the uninfective stage 2 and 3 forms. Developmental stage was approximated for most decapods; most possessed infective, mature, stage 4 cysts, while 25% of *H. varius*'s cysts were immature stage 3. Melanization was rare in the majority of the decapods and was not recorded, except for *C. lavauxi*, for which nearly all cysts were melanized.

Relationships with host size

Sufficient host and parasite data were available to conduct 21 regressions between host size and intensity of infection of which 8 were significant. Infection intensity decreased with host size for the crab *H. sexdentatus* infected with *M. novaezealandensis* (R^2 = 0.146, P = 0.0061) (Fig. 2A). For some species, there was a concave curvilinear relationship between host size and intensity of infection. For the following crab hosts, parasite infection intensity increased at first then decreased in *H. varius* infected with *M. novaezealandensis* (R^2 = 0.304, P = 0.0001) (Fig. 2B), *A. crassa* infected with *Microphallus* sp. (R^2 = 0.126, P = 0.0417), and *M. hirtipes* infected with *M. novaezealandensis* (R^2 = 0.136, P = 0.0323). An increase in intensity of infection was significantly correlated with an increase in host size for several crustaceans: *H. crenulatus* infected with *Microphallus* sp. (R^2 = 0.253, P = 0.0002), *M. hirtipes* infected with *Microphallus* sp. (R^2 = 0.517, P < 0.0001) (Fig. 2C), *M. hirtipes* infected with *Profilicollis* spp. (Spearman's rho = 0.41, P = 0.0027), and the amphipod *P. novizealandiae* infected with *M. novaezealandensis* (Spearman's rho = 0.43, P = 0.0017).

DISCUSSION

General commentary

The community-wide approach of this survey of crustacean parasites identified some of the more crucial members involved in the life cycles of intertidal parasites. Our results indicate that the available crustacean species are not used evenly by the parasites. Some crustaceans play no, or a very small, role in parasite transmission, whereas others harbor most of the larval parasite populations. Different parasite species show different patterns of host use, but a small number of crustaceans are important for

TABLE II. Prevalence (mean intensity ± SE) of *Maritrema novaezealandensis* sorted by developmental stage and melanization in selected crustacean hosts collected from LPB.

Host	Order	N	Stage 2 (unencysted)	Stage 3 (uninfective cyst)	Stage 4 (infective cyst)	Melanized
Paracalliope novizealandiae	Amphipoda	50	83.0 (5.9 ± 1.0)	12.0 (1.7 ± 0.3)	0.4 (1.0*)	4.6 (1.8 ± 0.7)
Transorchestia chiliensis	Amphipoda	50	100 (2.7 ± 1.2)	0	0	0
Cyclograpsus lavauxi	Decapoda	26	0	0	6.3 (2.0*)	93.8 (4.3 ± 1.1)
Paridotea ungulata	Isopoda	50	24.1 (36.0 ± 11.7)	34.0 (8.5 ± 2.6)	9.5 (23.7 ± 22.7)	32.4 (9.7 ± 3.9)
Lysiosquilla spinosa	Stomatopoda	51	10.4 (7.0 ± 3.6)	23.9 (24.0 ± 11.0)	32.8 (4.7 ± 2.6)	32.8 (4.7 ± 2.0)

* SE was not calculated due to sample size.

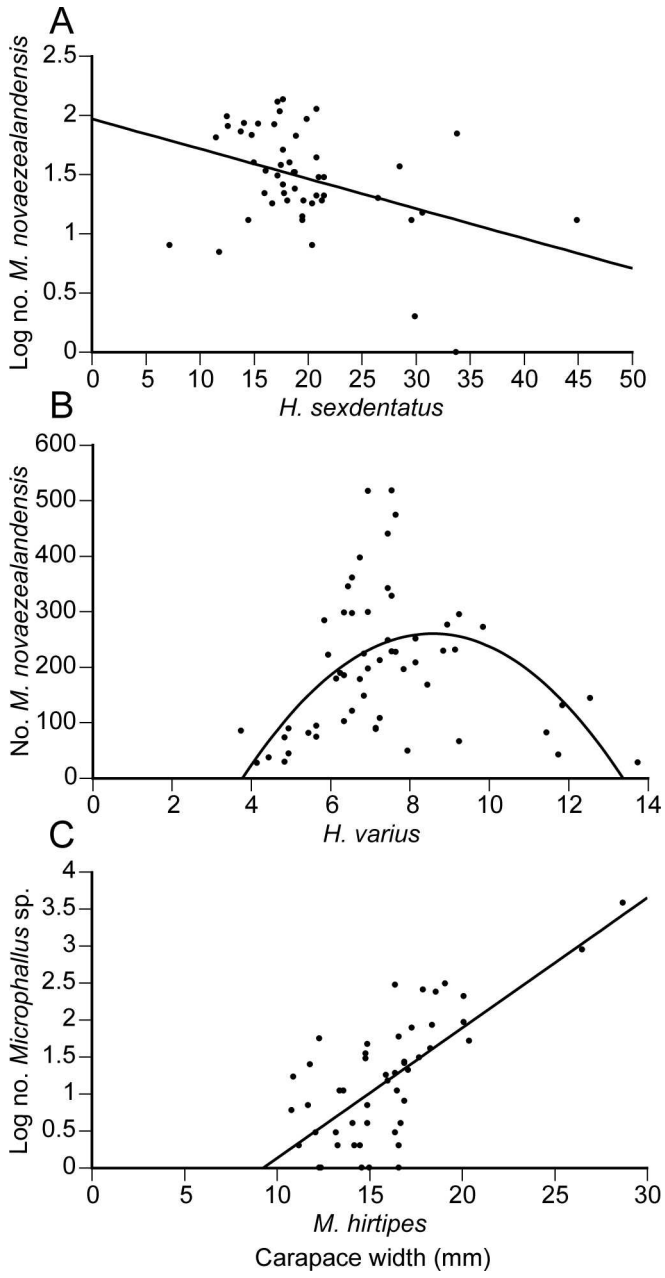

FIGURE 2. Examples of relationships between total number of parasites (or log of total number) and size of crab host (measured by carapace width) for (**A**) *Maritrema novaezealandensis* infecting *Hemigrapsus sexdentatus* (R^2 = 0.146, P = 0.0061); (**B**) *M. novaezealandensis* infecting *Halicarcinus varius* (R^2 = 0.304, P = 0.0001); and (**C**) *Microphallus* sp. infecting *Macrophthalmus hirtipes* (R^2 = 0.517, P = <0.0001).

most parasites. Each parasite showed a different flow through this crustacean community and toward their definitive hosts. No parasites were found to be entirely host specific in this system, although there were some interesting host incompatibilities. Based on parasite abundance, decapods were the most significant intermediate hosts for *M. novaezealandensis*, *Microphallus* sp., *Profilicollis* spp., and the nematodes, with *M. novaezealandensis* being the numerically dominant parasite species. Although all hosts in this survey were sympatric with first intermediate hosts like *Z. subcarinatus*, several were completely free of parasites or had low prevalences, possibly due to morphology, immunology, microhabitat, temporal effects, or phylogeny. We acknowledge that data on intermediate host density and definitive host prey preference (not feasible in this survey) would provide a deeper understanding of the true importance of these hosts for parasite transmission.

Host partitioning

Morphology: Certain aspects of host morphology such as carapace thickness and gill structure, play important roles in the partitioning of parasites within this community. The isopod *I. armatus* may escape parasitism due to its heavily armored body and lack of gills (isopods use pleopods for respiration instead of gills). For most decapods surveyed, the carapace is thick enough to prevent penetration by microphallid cercariae; however, the crab *H. varius* has a comparatively thin carapace, which may account for it having the highest mean abundance of *M. novaezealandensis*. The small size and thin carapace of the amphipod *P. novizealandiae* makes it particularly vulnerable to *M. novaezealandensis.* Most of the trematodes recovered in this amphipod were immature developmental stages, or melanized (Table II). Several factors account for low prevalence of mature infective stage 4 cysts in this host: (1) approximately 4–5 wk are needed for *M. novaezealandensis* to mature to stage 4 (Martorelli et al., 2004); (2) the volume of a cercaria increases 200-fold as it matures into a metacercaria which, if there were multiple infections, could lead to mortality for these relatively small amphipods (Fredensborg et al., 2004); and (3) large numbers of penetrating cercariae can cause loss of hemolymph, resulting in mortality (Fredensborg et al., 2004).

Parasites that cannot gain entry via the exoskeleton must use an alternative path, most likely through the gills (Cable and Hunninen, 1940; Sarkisian, 1957; Saville and Irwin, 2005) or joints. Some crabs, such as the anomuran decapod *P. elongatus*, are able to prevent infection with a unique gill-cleaning structure (Ritchie and Høeg, 1981) consisting of a specially developed fifth pereiopod (Bauer, 1981; Förster and Baeza, 2001). Brachyurans (all other decapods in this survey) rely on a different method of gill cleaning (Bauer, 1981), which may be ineffectual in preventing the establishment of cercariae (Brokerhoff, 2004).

The absence of *M. novaezealandensis* in *A. crassa* may be explained by this crab's unique gill structure and respiratory method. A comparative study of the gills of *A. crassa* and *M. hirtipes* (Hawkins and Jones, 1982) concluded that *A. crassa* is capable of prolonged exposure to air due to its smaller gill surface area and ability to survive on recirculated branchial fluids. Perhaps this recirculation of branchial fluid prevents the establishment of *M. novaezealandensis*, which generally remains on the host's gills during its development, whereas *Microphallus* sp. is associated with the gonads and hepatopancreas. Similarly, the crab *C. lavauxi* spends its time exposed to air higher up in the littoral fringe (Innes et al., 1986) and may be exposed to relatively low numbers of *M. novaezealandensis*, compared to *Microphallus* sp. Finally, the acanthocephalans *Profilicollis* spp. were absent from both *C. lavauxi* and *A. crassa*. Crabs become infected with *Profilicollis* spp. when they accidentally ingest eggs, which develop into larval cystacanths within the body cavity. These

larval stages may not survive in hosts that are subject to high levels of body water loss, e.g., *C. lavauxi* or *A. crassa*.

Immunology: Some hosts are able to prevent parasitic infections through the immunological reaction known as melanization. When an invading organism such as a cercaria penetrates a crustacean, which lacks the benefits of an adaptive immune system as found in vertebrates, an immune response is triggered via the hemolymph, inducing the pro-phenoloxidase (pro-PO) cascade, resulting in melanization and death of the cercaria (Söderhäll and Cerenius, 1998). It has been shown that bimodally breathing crustaceans (like *C. lavauxi*) (Morris and Bridges, 1994) experience changes in hemolymph chemistry associated with hemocyanin (Innes et al., 1986; Tanner et al., 2006), which is involved in the melanization response in crustaceans (Terwilliger, 2007; Cerenius et al., 2008). This could account for the high levels of melanization found in *C. lavauxi* (Table II). Alternatively, desiccation of the gills and overall body water loss is routine in *C. lavauxi* (Innes et al., 1986) and could lead to inhospitable conditions for the cysts. Other unsuitable hosts, which are located at the accidental or dead-end of the host spectrum for *M. novaezealandensis*, include those with high rates of melanization such as the isopod *Paridotea ungulata* and stomatopod *Lysiosquilla spinosa*. Melanization patterns in these hosts suggest a differential immune response (Thomas et al., 2000), since some metacercariae were melanized and others were not in the same individuals.

Microhabitat: The particular microhabitat occupied by a potential host may factor into its susceptibility to parasitism. For example, the amphipod *T. chiliensis* lives amongst the decaying seaweed in the wrack line of the bay, which may not provide enough water for the snails to shed cercariae to infect these hosts. Additionally, observing the absence of certain parasites from some hosts and their presence in other hosts with nearly identical microhabitats highlights susceptibility issues facing some hosts and parasites. One example is the absence of *Microphallus* sp. and presence of *M. novaezealandensis* in the crab *H. varius*. Both *Microphallus* sp. and *M. novaezealandensis* share the snail *Z. subcarinatus* as their first intermediate host. The morphological descriptions of the cercariae of *M. novaezealandensis* (Martorelli et al., 2004) and *Microphallus* sp. (Martorelli et al., 2008) are nearly identical (*Microphallus* sp. is slightly smaller), suggesting that cercaria morphology should not create an obstacle preventing establishment in the same intermediate hosts. Another example of differential host susceptibility is found with the crabs *A. crassa* and *M. hirtipes*, which live sympatrically and share a high prevalence of *Microphallus* sp. The prevalence of *M. novaezealandensis* in *M. hirtipes* is high, yet the parasite is absent from *A. crassa*. It is not known whether snails infected with *Microphallus* sp. are distributed differently from those infected with *M. novaezealandensis* or whether cercariae behavior differs between the 2 trematode species.

Temporal: Some parasites might not be in contact with potential hosts for long enough periods of time. The euphasiid's, e.g., *N. australis*, lack of parasites may be attributed to the nature of its ephemeral visits to the bay. Over the course of the survey, millions of *N. australis* saturated the bay, but, as the temperatures warmed, they died and were either eaten, decomposed, or washed back out into the harbor. The sudden influx of *N. australis* and other species, like the squat lobster *Munida gregaria*, could act as a sink for cercariae shed during their brief presence.

Phylogeny: Finally, even though other barnacles are known to host microphallid trematodes (Sari and Malek, 2000), the barnacle *C. columna* may be too phylogenetically distant from other host species in our system to support these parasites. Having said that, it does not appear that phylogeny plays a major role in the flow of *M. novaezealandensis* amongst the decapods, since infection levels vary hugely among species within the same family, i.e., Grapsidae (*Hemigrapsus* and *Austrohelice* spp.).

Host mortality induced by infection

Parasite-induced host mortality, inferred from a decrease in intensity of infection in older hosts, has been regularly reported in the parasite literature (Anderson and May, 1978; Gordon and Rau, 1982; Rousset et al., 1996). For instance, using an acanthocephalan/crab system, Latham and Poulin (2002a) suggest that reduced numbers of parasites in larger (older) hosts can be attributed to the loss of heavily infected hosts from the population. Alternatively, if a parasite does not induce mortality of the host, then a positive linear relationship between host size and parasite abundance is expected, as the parasites simply accumulate in the host over time (Hudson and Dobson, 1995). The present survey detected both scenarios. Parasite-induced mortality was found for several parasite-host associations, as inferred from either a linear decrease of parasite intensities with host size (Fig. 2A) or a curvilinear relationship between intensity and host size, i.e., intensity increases with increasing host size but then decreases beyond a certain size (Fig. 2B). Interestingly, these results suggest that *M. novaezealandensis* directly impacts the populations in 3 of its many second intermediate hosts and potentially contributes to the structure of the crustacean community at LPB. Additionally, a linear accumulation of parasites with host size was seen with several host/parasite relationships (Fig. 2C), indicating that for several host-parasite species combinations, parasitism has no measurable impact on host populations. It is possible that the presence of a curvilinear relationship in some hosts and not others could be attributed to host-induced parasite mortality in older hosts, or to other unknown species-specific physiological and behavioral reasons.

Concluding remarks

The present survey represents only a snapshot of parasite transmission through the crustacean community of the study locality, and its findings are yet to be validated with data from other localities. Although there are no migratory birds causing temporal changes in the input of parasite eggs in our system, it remains to be determined whether this snapshot would be affected by abiotic factors and whether it applies to other seasons. Overall, our results suggest that different parasite species use different subsets of the crustacean community during their transmission to definitive hosts, although some crustacean species incur much more severe infections than others. The results also indicate that some of these parasites can impact the relative abundance, and thus the community structure, of these crustaceans. It remains to be determined, at a proximate level, why certain crustaceans escape from infections by 1 or more species, while others accumulate large numbers of parasites. Both intermediate host densities and prey preferences by definitive hosts, although not included in this survey, should also be considered when evaluating the relative importance of parasite community structure.

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