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Altered microhabitat use and movement of littorinid gastropods: the effects of parasites

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Abstract The distribution of organisms at small spatial scales and their use of microhabitats are important determinants of species-level interactions. In many ubiquitous rocky shore invertebrates, use of intertidal microhabitats has previously been studied with relation to thermal and desiccation stress, ontogenetic changes and predation. Here, the effects of parasitism on the microhabitat use and movement of two New Zealand littorinid hosts, *Austrolittorina antipodum* and *A. cincta*, were investigated by examining the effect of infection by a philophthalmid trematode parasite. Alterations in microhabitat use and movement of infected versus uninfected individuals were found during both field mark-recapture and laboratory experiments, carried out from August 2012 to March 2013 in Otago Harbour, New Zealand (45.83°S, 170.64°E). Specifically, a trend towards increased use of rock surface habitats and a reduction in the distance moved by infected snails was observed. In addition, decreased downward movement was observed for some infected individuals. This alteration in individual distribution is likely to increase the availability of infected individuals to predators, hence aiding the successful transmission of the trematode parasite. These results highlight the importance of including parasitism as a biotic factor in studies of gastropod movement and spatial distribution.

Introduction

The intertidal zone has provided an ideal study system for investigating the interactions among species within ecological communities, or between species and the abiotic environment. For example, studies of competition among barnacles (Connell 1961), grazing by littorinid snails (Lubchenco 1978), facilitation between algae species (Dayton 1975) and predation by sea stars (Paine 1966) provide classic examples of species interactions, both direct and indirect. These examples illustrate the importance of biotic factors among the suite of mechanisms influencing species distributions. Parasitism is one such biotic factor, and it has received less attention than other factors despite the ubiquity of parasites in the intertidal environment (Mouritsen and Poulin 2002; Torchin et al. 2002; Marcogliese 2005). There is now increasing evidence that parasites have considerable community-wide impacts (Curtis 1990; Wood et al. 2007; Clausen et al. 2008).

For many organisms with a restricted distribution and reduced range, like several in the intertidal zone, small spatial scales and the availability of microhabitats can greatly influence population structure. Microhabitat use has been the focus of several recent studies of the avoidance of predation risk (Trussell et al. 2003; Orrock et al. 2013; Vaudo and Heithaus 2013). Microhabitats are a vital component of an organism's niche and can impact life history characteristics such as survival (Norton et al. 1990; Kovach and Tallmon 2010) and growth (Orrock et al. 2013). Furthermore, microhabitat use may be influenced by various biological factors, such as an organism's size, or how it is affected by predation or competition (Kemppainen et al. 2005; Perez et al. 2009). In field settings, the influence of parasites has recently been studied, in terms of alterations in phenotypic appearance (Lagrue et al. 2007;

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Minguez et al. 2012), host movement and behaviour (Dunn et al. 2011; Fredensborg and Longoria 2012), host feeding (Wood et al. 2007) and in wider ecological studies, such as in food web analyses (Lafferty et al. 2008; Britton 2013). Infection by parasites can also influence microhabitat choice and risk-taking behaviour of a variety of hosts, including crustaceans and fish (Poulin 1994; Lafferty and Shaw 2013). Although the underlying mechanisms causing such changes remain unclear, it seems likely that parasites can either directly alter microhabitat choice or indirectly affect it by modifying host size, affecting the fit of the host to its microhabitat (McCarthy et al. 2004; Chapuis 2009).

Gastropods serve as first intermediate hosts to trematode parasites, common in marine intertidal environments (Torchin et al. 2002). Trematodes are flatworms with a complex life cycle: their juvenile stages (eggs/miracidia) infect gastropods from which they release cercariae that infect a second intermediate host, or encyst on a hard substrate, before eventually infecting either fish or bird definitive hosts, depending on the species (Galaktionov and Dobrovolskij 2003). Examples of the behavioural effects of trematodes on their intertidal gastropod hosts include reduced displacement (Williams and Ellis 1975; Miller and Poulin 2001), and greater upshore movement (Curtis 1987; McCarthy et al. 2000). Although these effects may be due to pathological side effects, they may in some cases represent manipulation by the parasite driving the host into a zone with greater probability of successful transmission to the next host (Curtis 1987; Curtis 1993; McCarthy et al. 2000; McCurdy et al. 2000). Such disrupted movement can contribute to the distribution and size structure of a species' population, for example, if infected individuals are larger (McCarthy et al. 2004) and move upshore (McCarthy et al. 2000). While many studies have focused on the effects of parasites on host behaviour, to the authors' knowledge, this is one of the rare investigations of an alteration in the use of microhabitats by the gastropod first intermediate host of a trematode parasite. The present study focused on quantifying the effect of trematode parasites on microhabitat use by their littorinid hosts on a rocky shore.

Littorinids are dominant gastropods on rocky shores worldwide (Davies and Williams 1998) and are host to many trematode species (Thieltges et al. 2009). As these gastropods are typically found in very high numbers and utilise a variety of microhabitats on the shore, such as crevices and rock pools (Saier 2000; Granovitch and Mikhailova 2004), they make for ideal study organisms. Previously, littorinids have been used as model organisms in the study of microhabitat use in relation to thermal and desiccation stress (Jones and Boulding 1999; Chapperon and Seuront 2011a), although results of such studies are equivocal (Stafford and Davies 2004). Additional factors which may influence microhabitat use of littorinids are discussed by Chapperon and Seuront (2011a) but parasitism has never been considered.

In a field mark-recapture study and a parallel laboratory study, we investigated whether infection by an undescribed castrating philophthalmid trematode would alter microhabitat use and movement by littorinid individuals, which may be due to either adaptive manipulation or underlying pathological effects. Littorinids are abundant gastropods on New Zealand rocky shores (Saies 1973). The focal philophthalmid trematode uses littorinids as first intermediate hosts. The parasite produces free-swimming stages, or cercariae, which are then released from the snails and soon encyst on rocky intertidal hard surfaces where they may be ingested by a bird definitive host (Weekes 1982; Kanev et al. 2005). This is the first study to investigate the influence of trematode parasitism on the ecology of these littorinid hosts. Specifically, we tested whether: (1) infected snails show reduced movement compared to uninfected ones, (2) infected snails occur more often in exposed microhabitats where they have increased susceptibility to predators, through reduced use of crevices, for instance and (3) infected snails have a lower recapture success than uninfected ones, due to parasite-induced mortality. Where possible, we tested these predictions in both the field and the laboratory, and conducted our study on two different littorinid species as we sought to determine the generality of the findings.

Methods

Study system and density measures

The study was carried out on a rocky shore at Portobello, Otago Harbour, Dunedin, New Zealand (45.83°S, 170.64°E), where the tidal range is approximately 1.8 m. The dominant organisms on the high rocky shore are the two species of New Zealand littorinid, *Austrolittorina antipodum* and *Austrolittorina cincta*. The 'littorinid zone' is that part of the intertidal zone which littorinids inhabit, a term developed from the global distribution of these gastropods, with those in New Zealand also defined as 'zone-forming' (Saies 1973). These two sympatric species host the same philophthalmid trematode species, which is yet to be described formally (K. O'Dwyer, unpublished data), but has been studied both morphologically and genetically. In August 2012, using a 0.25-m^2 quadrat (0.5×0.5 m) placed in grid fashion, i.e., 6 quadrats along each of three adjacent transects at the upper, mid and lower part of the littorinid zone, photographs were taken of each quadrat. Microhabitat availability was calculated using ImageJ 1.46r (Schneider et al. 2012) by determining the proportions of the surface area covered by rock surface, crevices and rock pools.

A crevice is defined as a crack in the rock in which any portion of the snail's shell could be concealed [see also Judge et al. (2009), Chapperon and Seuront (2011a) for interpretations of 'crevice']. To determine the density of littorinid snails on the shore, a 0.0625-m^2 quadrat (0.25 × 0.25 m) was haphazardly placed within each of the larger 0.25-m^2 quadrats used for the study of microhabitat availability, and individuals of the two species were counted. These data served to quantify the vertical zonation and density of each species.

Assessment of infection status

In September 2012, a total of 1545 individual littorinids of both snail species (796 *A. antipodum*, 749 *A. cincta*) were collected from the Portobello site where snail densities were measured. For the identification of infected littorinids, immersion in seawater combined with shaking has previously been shown to induce parasite shedding (McCarthy et al. 2002). Therefore, to induce parasite shedding, snails were placed individually in compartments of 12-well plates and 3 ml seawater was added to each. The plates were then put on an orbital shaker plate at 80 rpm for ~ 8 h. Due to variation in the shedding frequency of the parasites and in order to increase the likelihood of correctly identifying uninfected individuals, screening was carried out three times, with 7–10 days intervals between screenings. The prevalence of the philophthalmid parasite across all littorinids was 3.4 %. Higher prevalence was found for *A. antipodum* ($n = 35$, 4.7 % infected) than for *A. cincta* ($n = 15$, 2.0 % infected).

Mark-recapture experiment

Infected snails, along with 35 uninfected *A. antipodum* and 15 uninfected *A. cincta*, were individually labelled with bee tags (Bee Works, Orillia, Canada) applied with glue. The shell length (SL) of each snail was recorded to the nearest 0.1 mm using digital callipers. Uninfected littorinids [mean ± standard deviation (SD) SL = 8.2 ± 1.4 mm *A. antipodum*; 11.6 ± 1.7 mm *A. cincta*] were chosen of similar sizes to those infected snails (mean ± SD SL = 8.4 ± 1.5 mm *A. antipodum*; 11.7 ± 1.9 mm *A. cincta*), so that there was no significant size difference between the two groups (Welch Two Sample t test: $T = 0.489$, $P = 0.626$ for *A. antipodum*; $T = 0.225$, $P = 0.823$ for *A. cincta*). There was a clear size difference between the two littorinid species, hence they were treated separately. The littorinids were released during the evening low tide, on 23 September 2012, within a 0.0625-m^2 quadrat on a wetted rock surface in the middle of the study site. Littorinids were observed for 2 h following release to ensure they had attached to the substrate.

The position of each individual was next recorded at the evening low tide the following day. The distance moved by each snail was measured by recording its vertical and horizontal distance from the perimeter of the 0.0625-m^2 release quadrat; these values were later converted into a measure of the most direct linear route to the current position. The microhabitat in which each individual was found was also recorded as rock surface, crevice or rock pool.

The position and location of all re-sighted littorinids were recorded weekly for a total of 9 weeks and, subsequently, monthly for 2 months. At each weekly and, later, monthly shore visit, the recordings were the same as those above, i.e., distance moved and microhabitat used. In January (17 weeks after the start of the experiment), the number of marked snails on the shore dropped dramatically, prompting collection of all individuals to confirm their infection status via dissection.

Laboratory experiment

Four replicate tanks (each 45 × 42 × 37 cm) were prepared by lining the inside of each plastic tank with plaster to ensure equal substrate type within the tank. Before the plaster hardened, crevices were made using a trowel, and at the same locations for all four tanks. To ensure the removal of any powdery residue, each tank was soaked in seawater and rinsed several times before use in the experiment. The tanks were set down on a slant (~30° slope) and seawater (salinity 35) was added to create a rock pool (~3 cm maximum depth) at one end. The remaining surface area consisted of open 'rock' surface either on a slant, or more or less vertical along the four sides of the tank. A different set of snails from those of the field study was collected on 10 March 2012 and screened three times for the assessment of infection status. The 80 snails used in this experiment were also marked with numbered bee tags. Before the experiment, they were kept in 1 l tanks in the laboratory with rocks, collected at the same site, provided as a food source (encrusting algae) and natural substrate. At the start of the experiment, 20 tagged snails were added to each of the four tanks, within an 8-cm^2 quadrat, so that each tank contained 5 infected *A. antipodum*, 5 uninfected *A. antipodum*, 5 infected *A. cincta* and 5 uninfected *A. cincta*. The experiment was carried out under natural daylight conditions and at ~18 °C. Shell lengths differed between infected and uninfected snails, which could not be avoided in the sample collected, but the difference was controlled for in later statistical analysis. Following a 30-min acclimation period, recordings were made every hour, of each snail's location within the tank, in terms of the microhabitat occupied, and their distance vertically and horizontally from the release quadrat. While the experiment lasted for several hours, the littorinids virtually ceased movement after a few hours, hence only the first 3 h of data were used. Following experiments, all individuals were measured and dissected to re-assess their infection status. Of those initially classed as uninfected, 11 were infected with the philophthalmid trematode parasite under investigation and so were included in analyses as infected individuals. A further two littorinids were found to contain another parasite species and these were excluded from the study. Thus, 22 infected and 17 uninfected *A. antipodum* along with 29 infected and 10 uninfected *A. cincta* contributed to the final data set for the laboratory study.

Statistical analysis

Due to the nature of the mark-recapture data, many missing values were recorded when a snail was not observed during one of the shore visits. It is important to account for missing data in analyses to avoid losing any information and to prevent biased results (Nakagawa and Freckleton 2008, 2011). The extent of missing data points for each study is reported in Table S1 (Online Resource 1). The distribution of the missing data was random with respect to infection status [MCMCglmm: posterior mean = −0.004, credible interval (CI) = −0.34–0.33].

All statistical analyses were carried out in R version 3.0.0 (R Core Team 2013) using Bayesian generalised linear mixed models in the *MCMCglmm* function from the package *MCMCglmm*, which allows the inclusion of missing data (Hadfield 2010). Using this package, generalised linear mixed models are fitted using a Markov chain Monte Carlo (MCMC) algorithm with inverse Wishart priors (Hadfield 2010). This method samples from a posterior distribution and provides the mean and CIs of that distribution. In any case where the CI does not cross zero, the difference is considered significant.

Separate models were run for each species of littorinid, and the number of iterations, thinning interval and burnin were specified in order to ensure that >1,000 samples were obtained from the posterior distribution (Tables S2, S3, S4). The default inverse Wishart prior was used for the movement data and a modified prior assuming variance of 1 was used for the binomial microhabitat and recovery data, followed by c2 correction (Hadfield 2010).

For the microhabitat choice models in the laboratory study, the data were one-sided (i.e. larger sample size in one group), and therefore a prior utilising the *Gelman prior* function was specified (Gelman et al. 2008). We observed that almost every chain had mixed thoroughly as autocorrelation between subsequent lags was consistently low (<0.1) (Tables S2, S3, S4). Data for the overall distance moved by individual littorinids, as well as for the distance moved vertically, were square-root transformed. Microhabitat use data were analysed by comparing the use of rock surface and crevice only, because too few snails were found in rock pools to allow analysis of these data. For all models, the fixed-effect predictor variables were infection status and snail SL while the random-effect variables changed according to the specific model; see Tables S2, S3 and S4 for more details.

Results

Littorinid densities and microhabitat availability

There was a difference in the mean overall density of each species, with *A. antipodum* averaging 694 m^{-2} and *A. cincta* 572 m^{-2}. The two species differed in their patterns of density on the shore, with substantially more *A. antipodum* found in the lower part of the littorinid zone (Fig. S1). For the upper zone, and among microhabitats, there were smaller differences in density between littorinid species, except that *A. antipodum* was found at higher density in pools than *A. cincta* (Fig. S1). For both species, more individuals were found in crevices than on the rock surface or in rock pools (Fig. S1). Microhabitat availability was measured as surface area across the shore at each of the upper, mid and lower parts of the littorinid zone. The only differences found were for rock pools which were more abundant towards the lower shore (0.181) compared to the upper and mid parts of the littorinid zone (0.005 and 0.029, respectively). The proportional surface area for each microhabitat was: rock surface = 0.880, crevice = 0.048, rock pool: 0.072.

Microhabitat use

In all studies, few littorinids were observed in pools (e.g. 30/630, 4/270 number of records for pools in the weekly data of *A. antipodum* and *A. cincta*, respectively). Due to their scarcity, these data could not be analysed, instead all analyses of microhabitat use compare the occupancy of crevices versus rock surface only. Overall, infected littorinids were found more on the rock surface than in crevices relative to uninfected snails, although the CI crossed zero in all comparisons, except in the weekly study for *A. antipodum* where it did not cross zero, indicating a significant difference (Fig. 1, Fig. S2; Table S2). Larger individuals were also found more on the rock surface in comparison with crevices (Table S2). The results differed between species with typically stronger effects of infection for *A. antipodum* than for *A. cincta*, although there was a considerable difference in sample size between the two species (Fig. 1, Fig. S2; Table S2). In the laboratory study, the mean estimate for both littorinid species indicated greater use of the rock surface microhabitat by infected than uninfected snails,

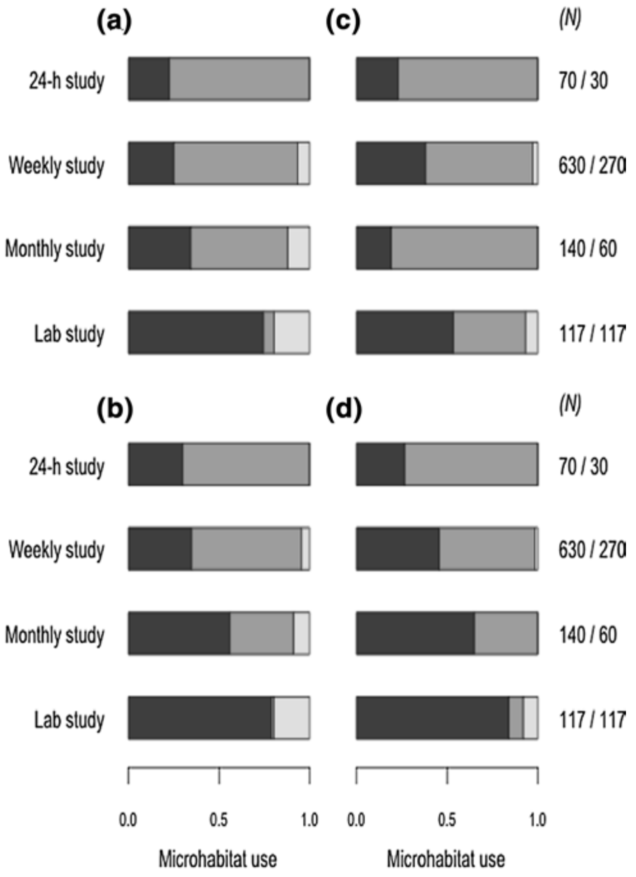

Fig. 1 Proportional use of each microhabitat by **a** uninfected *Austrolittorina antipodum*, **b** infected *A. antipodum*, **c** uninfected *Austrolittorina cincta*, **d** infected *A. cincta*. *Dark grey* represents rock surface, *light grey* crevices and *white* rock pools. For the 24-h study, results indicate relative number of snails microhabitat^{-1}, while for all other studies, results indicate mean microhabitat use by an average infected or uninfected snail. Sample sizes (*N*) shown are total number of possible data points for *A. antipodum* and *A. cincta*, respectively

however the CIs crossed zero so these differences were not significant (Fig. 1, Fig. S2; Table S2).

Movement

During the weekly and monthly field studies, infected *A. antipodum* moved a shorter distance from their previous position, on average, than their uninfected conspecifics, with a CI not including zero, while for *A. cincta* no difference in movement between infected and uninfected individuals was observed (Fig. 2, Fig. S3; Table S3). Larger individuals in both species, on average, moved further than smaller individuals (Table S3).

In terms of vertical movement, infected individuals moved downwards less than uninfected individuals during the 24-h study for *A. cincta*. This trend was also observed in the weekly study for *A. antipodum* but the CI just included zero (Fig. 3, Fig. S4 Table S4). In the laboratory, no clear differences were found between infected and uninfected littorinids with respect to either total distance moved or vertical movement (Figs. 2, 3, Figs. S3 and S4; Tables S3 and S4), with the CI for both analyses overlapping zero. It is noteworthy that the general trend was similar in terms of reduced overall movement by infected snails, at least for *A. antipodum* (Fig. 2, Fig. S3; Table S3), while in the laboratory infected individuals of both species tended to move downward more (Fig. 3, Fig. S4; Table S4).

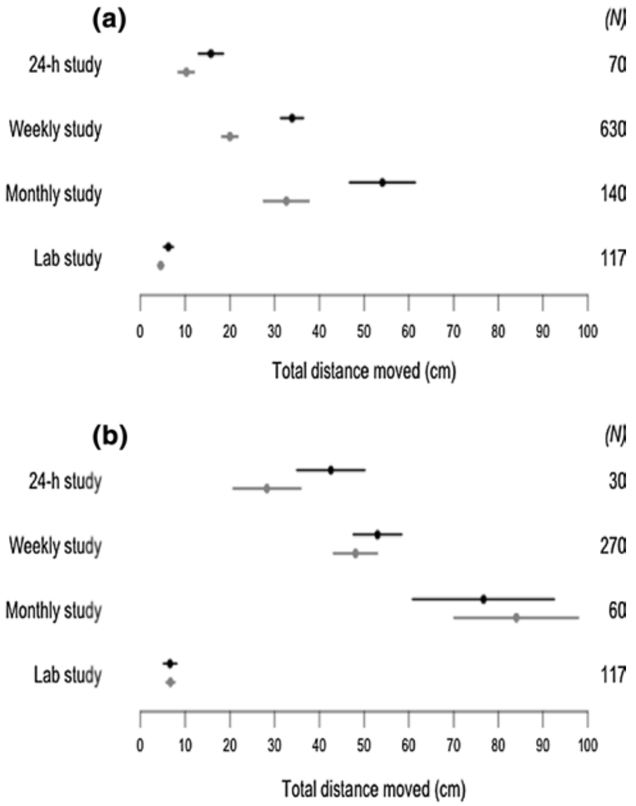

Fig. 2 Mean total distance moved during each study period, with 95 % confidence intervals (CIs), for **a** *Austrolittorina antipodum* and **b** *Austrolittorina cincta*. *Black* and *grey lines* represent uninfected and infected snails, respectively. Sample sizes (*N*) shown are total number of possible data points for infected and uninfected combined

Littorinid recovery success

Overall, on collection of the snails at the final shore visit, 57 % of the combined littorinid species were recovered after 5 months of the field mark-recapture study. For *A. antipodum*, 62.9 % of the uninfected and 48.6 % of the infected individuals were recovered, while these numbers were, respectively, 66.7 and 53.3 % for *A. cincta*. Although proportionally fewer infected snails were recovered in both littorinid species, the differences were not significant, with a CI overlapping zero (MCMCglmm:

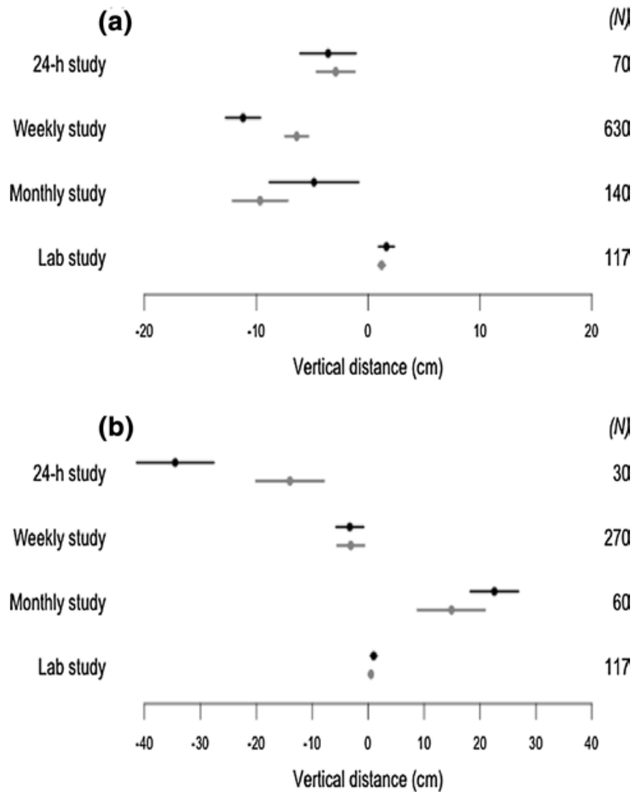

Fig. 3 Mean vertical distance moved during each study period, with 95 % confidence intervals (CIs), for **a** *Austrolittorina antipodum* and **b** *Austrolittorina cincta*. *Black* and *grey lines* represent uninfected and infected snails, respectively. *Negative values* indicate downshore movement and *positive values* upshore movement. Sample sizes (*N*) shown are total number of possible data points for infected and uninfected combined

A. antipodum posterior mean = −0.65, CI = −1.72 to 0.41, *A. cincta* posterior mean = −0.81, CI = −2.59 to 0.91).

Discussion

Evidence from our study suggests that philophthalmid trematode parasites affect the ecology of their hosts in a number of ways, by altering their use of microhabitat, typically increasing occupancy of rock surfaces, by reducing their overall movement in terms of distance travelled and in some instances by decreasing their downward movement on the rocky shore, while having no apparent effect on snail survival. We observed some discrepancy between our field and laboratory experimental results, which may in part be due to the somewhat unnatural environment provided in the laboratory and the other biotic and abiotic processes acting on the littorinids in the field but not in the laboratory. Overall, the implications of these results are numerous, with possible influences on the distribution of littorinid populations on the shore, their use of algal food sources, and their interactions with predators and various sympatric organisms.

Microhabitat use has been studied in terms of predation risk for many organisms and a meta-analysis on the topic has found that the selection of microhabitats to avoid predation can result in an increase in non-consumptive effects, at least in aquatic habitats (Orrock et al. 2013). The influence of microhabitats on the thermal biology of intertidal organisms is also well documented (Jones and Boulding 1999; Chapperon and Seuront 2011b). In this context, the influence of parasitism on host microhabitat use is worthy of further investigation, since parasites are known to affect the thermal biology (McDaniel 1969; Bates et al. 2011) and predation risk of hosts (Lafferty and Shaw 2013). Furthermore, the fine-scale distribution of gastropods has been investigated using observations of trail following behaviour (Chapman 1998), though this too is affected by parasitism (Davies and Knowles 2001). To our knowledge, the effect of parasitism on microhabitat use by gastropod first intermediate hosts on the rocky shore has not previously been examined, and in previous meta-analyses of behavioural alteration by parasites there were no data from gastropod-trematode systems (Poulin 1994; Lafferty and Shaw 2013).

In this study while the availability of rock surfaces as a microhabitat was greatest, higher snail density, in general, was found in crevices. However, on closer inspection, we found relatively more infected littorinids occupying the rock surface rather than the safety of crevices which suggests they may be more vulnerable to predation than uninfected conspecifics. Gulls, including the New Zealand southern black-backed gull, *Larus dominicanus* (Fordham and Cormack 1970), are known to prey on molluscs (Bertellotti and Yorio 1999; Forero et al. 2004), Furthermore, philophthalmid parasites use birds, including gulls, as definitive hosts (Weekes 1982), usually following encystment on hard substrata (Kanev et al. 2005). A previous New Zealand study examining the encystment of another philophthalmid species found preferential encystment on gastropod shells, including the first intermediate host (Neal and Poulin 2012). Hence, trematode parasites may alter host microhabitat choice, and thereby increase the chance of successful transmission to the avian host. Interestingly, ‘precocious encystment’, within the two *Austrolittorina* species in this study, has been observed (K. O’Dwyer, pers. obs.). Briefly, this involves the trematode sometimes developing into its next life cycle stage within the littorinid, thus, littorinid snails may serve as both first and second intermediate host. This may be an additional adaptation for transmission in a zone where littorinids are the dominant invertebrates. In light of this unusual life cycle, any alteration in host microhabitat use might increase parasite transmission to birds.

Low rates of predation on littorinids have previously been reported (Chapman and Johnson 1990), although many trematode species infect these gastropods (Thieltges et al. 2009). Nevertheless, a sufficient level of predation must exist to allow the maintenance of the parasite population; a high local abundance of gulls (Fredensborg et al. 2006) may compensate for low predation rates, and allow the persistence of the parasite population in the littorinids (Bustnes and Galaktionov 1999; Byers et al. 2008; Herrmann and Sorensen 2009).

In addition to increasing exposure of their host to predation (Lafferty and Shaw 2013), parasites of invertebrates, including those of gastropods, often alter the activity level of hosts (Lambert and Farley 1968; Poulin 1994; Miller and Poulin 2001). In this study, the reduced movement of infected hosts is likely a result of pathological side effects and/or energetic drain from infection. In the case of this philophthalmid parasite, perhaps reduced host movement combined with its position on the rock surface together increase transmission to gulls via predation. As a result of pathological side effects of infection and increased predation, it is not surprising that mortality of infected hosts, including littorinids, is generally higher than for uninfected individuals (Huxham et al. 1993; Tétreault et al. 2000; Herrmann and Sorensen 2009). In this study, while no direct measure of mortality was obtained, the recovery success of individuals did suggest a slightly higher loss of infected individuals. However, the causal mechanisms are unknown, and could include both higher predation and greater susceptibility to physical stress such as wave exposure.

Finally, parasites can have significant indirect effects through trait-mediated indirect interactions (Hatcher et al. 2006; Raffel et al. 2010). For instance, in marine systems, parasitism can cause reduced anti-predator responses in gastropods (Kamiya and Poulin 2012) and parasites in littorinids impact community structure via increased algal growth as a result of reduced grazing by infected hosts (Wood et al. 2007; Clausen et al. 2008). Parasites also mediate interspecific competition in mussels (Calvo-Ugarteburu and McQuaid 1998). From these few examples, it is clear that parasitism likely generates confounding effects on various processes relating to the structure of rocky shore communities. Along with the nature of context dependency of species interactions in the intertidal [e.g. developmental stages (Kordas and Dudgeon 2011), habitat structure (Wilson and Weissburg 2013) and wave exposure (Zardi et al. 2006) alter facilitation, predation and competition, respectively], parasitism adds yet another noteworthy layer towards a holistic understanding of such interactions. Overall, due to the multitude of demonstrated effects of parasites on their hosts and the diversity of parasites in the marine environment, we extend Sousa's (1991) call for the inclusion of parasites in studies of soft-sediment community structure to the investigations of community structure on rocky shores.

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