

Sitka periwinkle grazing behaviour related to trematode infection: a multi-site study

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ABSTRACT: Parasites are known to affect several aspects of the ecology, physiology and behaviour of their hosts. The intertidal periwinkle *Littorina sitkana* (Gastropoda: Mollusca) is host to a diverse assemblage of parasites, the best studied of which are within the Class Trematoda. Following sampling of *L. sitkana* from 4 sites in Barkley Sound, British Columbia, Canada we show that trematode prevalence and species richness differ among sites. We assessed the effects of trematode infection on grazing behaviour in periwinkles, behaviour commonly affected by the presence of trematodes. We observed decreased grazing activity in parasite-infected *L. sitkana* and the strength of this effect varied among collection sites. This has important implications because most experimental studies consider snails from a single location.

KEY WORDS: Sitka periwinkle · *Littorina sitkana* · Snail ecology · Parasites · Trematode community · Barkley Sound

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1. INTRODUCTION

Parasites influence several aspects of the ecology of their host (Freeland 1983). Parasites can affect host population dynamics (Granovitch & Maximovich 2013) by, for example, reducing host survival (Huxham et al. 1993, Lafferty 1993, Fredensborg et al. 2005) and reproductive success (Zohar & Holmes 1998), and altering host fecundity (Cheng et al. 1973, Baudoin 1975, Granovitch et al. 2009). Some parasites alter aspects of host behaviour, such as dispersal (Curtis 1987, 2007, Sánchez et al. 2007), phototaxis (Bethel & Holmes 1973), avoidance of predators (Bethel & Holmes 1974, Santiago Bass & Weis 2009) and feeding rates (Levri & Lively 1996, Morton 2018). The mechanisms for these alterations remain unclear as they are difficult to study, but examples of host altered behaviour due to parasitism are still being discovered (Belgrad & Smith 2014, Soghigian et al. 2017).

Trematode parasites in marine snails can affect the energy requirements of their host, thus altering the

grazing rate of herbivore snails. In some species, infected snails tend to decrease their grazing rate by 40 to 80 % in comparison to uninfected individuals (Wood et al. 2007, Clausen et al. 2008, Morton 2018). If trematode infection in a key grazing species is reduced, the ecosystem composition may be affected, increasing the amount of vegetation and thus altering the abundance of other grazing organisms and specific predators (Mouritsen 2017, Morton 2018).

The periwinkle *Littorina sitkana* Philippi, 1846 is a caenogastropod present in high densities along the rocky intertidal zone on the east coast of the Pacific Ocean. It feeds mainly on macro- and microalgae by scraping it from substrate (Vollstoll & Sacchi 1990). Due to their high densities, *L. sitkana* can be an important grazer species of intertidal communities, potentially driving algal community structure by feeding preferentially on some algae over others (Van Alstyne et al. 2009). *L. sitkana* is a potential intermediate host for several trematode species. Alteration of grazing behaviour in *L. sitkana* due to trematode parasites therefore has the potential to

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affect intertidal community structure (Wood et al. 2007).

Here, we used laboratory experiments to test the hypothesis that grazing behaviour of trematode-infected periwinkles *L. sitkana* differs from that of uninfected individuals. We assessed the influence of trematode species on periwinkle grazing rate by quantifying species prevalence and species richness of trematodes inhabiting *L. sitkana*, and related each of these measures to individual periwinkle algal consumption. The majority of research on how trematodes affect their intermediate host's ecology and behaviour are focused on a particular population of intermediate hosts (Curtis 1987, 1990, McCarthy et al. 2000, Miller & Poulin 2001, Miura et al. 2006), and comparisons among different populations that can reveal more general patterns are lacking. We tested for a general pattern by comparing trematode infection and its effects on *L. sitkana* grazing behaviour at 4 sites that are geographically close to each other but have different biotic and abiotic components.

2. MATERIALS AND METHODS

2.1. Sample and data collection

We collected 381 *Littorina sitkana* (shell height = 13.27 ± 1.47 mm; mean \pm SD) by searching the rocky intertidal zone of 4 sites located on the West Coast of Vancouver Island, BC, Canada (Fig. 1). Periwinkles used for trematode community assessment presented in this study are a subset of the data set of Ayala-Díaz et al. (2017), and were also used for laboratory dispersal trials in another study by the same authors (unpubl. data). From the 4 sites, 87 to 116 periwinkles (mean = 95.25 ± 13.89) were collected from March to June of 2012 (see Table 1). After collection, periwinkles were transported alive within an hour to our laboratory at the Bamfield Marine Sciences Centre (BMSC). Periwinkles were kept in constant sea water flow (at approximately 10°C) and provided *Ulva intestinalis* Linnaeus, 1753 ad libitum as food. Protocol and procedures for this study were reviewed and approved by the Animal Care Committee at BMSC.

All behavioural data were collected prior to knowledge of periwinkle infection status. Grazing rate of snails may vary with size, gender and reproductive condition (Levri & Lively 1996). Thus, shell height, gender and collection locality were recorded for each periwinkle.

2.2. Grazing behaviour

Grazing behaviour was quantified for all 381 periwinkles (shell height = 13.27 ± 1.47 mm) collected at the 4 sites in 2012. Periwinkles were divided into 13 groups of $n = 29 \pm 1$ snails for each trial. Samples of periwinkles were tested interspersed with respect to collection location. During trials, each periwinkle was housed individually in a 100 mm diameter \times 15 mm high polypropylene Petri dish. A 35 mm diameter opening made in both the bottom and lid of the Petri dish and covered with 0.5 mm plastic screening allowed sea water flow while preventing periwinkles from escaping. Petri dish lids were secured to bottoms with rubber bands.

Each periwinkle was provided with pieces of *U. intestinalis* (algae weight = 250.07 ± 0.32 mg after blotting dry) following the procedure described by Van Alstyne et al. (2009). Modified Petri dishes containing periwinkles and algae were placed in a wet sea table (all Petri dishes were placed together so they had the most similar environmental conditions possible) with a constant flow of seawater at approximately 10°C for 5 d. For each trial, 4 Petri dishes

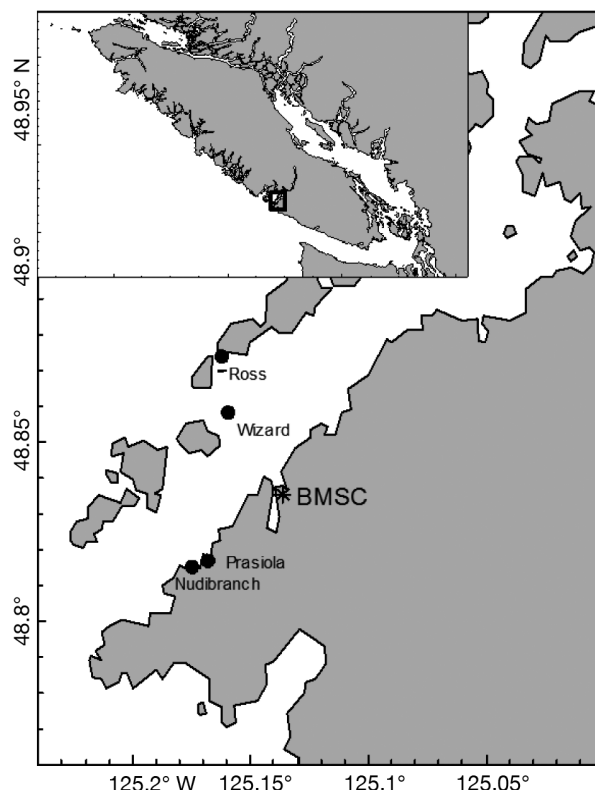


Fig. 1. The 4 collection sites located in Barkley Sound (British Columbia, Canada) and the Bamfield Marine Sciences Centre (BMSC), where samples were processed

with algae only were also placed in the sea table as controls. At the end of 5 d, the remaining *U. intestinalis* from each dish was blotted dry and weighed to estimate the amount of algae consumed by the periwinkles (initial algae mass – final algae mass), correcting for the gain or loss of algae mass obtained from the controls of each trial.

2.3. Trematode infection status

After grazing (and other behavioural experiments described elsewhere), all 381 periwinkles used in grazing experiments were dissected for identification of trematode infection. To assess trematode community composition of *L. sitkana* accurately and ensure all trematodes present were detected, we crushed the shell of each periwinkle and thoroughly examined the entire contents of the periwinkle's digestive and reproductive glands using an inverted microscope. All trematodes were identified morphologically to the lowest taxonomic level possible using identification keys developed by Ching (1962, 1963, 1991), Gorbushin & Shaposhnikova (2002), James (1968), Saville et al. (1997) and Yamaguti (1975). Two species (*Himasthla* sp. and *Microphallus* sp.) could be identified only to genus and 1 species (Unidentified 1) with >5 individuals could not be identified due to lack of internal structures, but resembled microphallid cercariae previously described by Ching (1991) in *Littorina scutulata*. Infection status, maturity of infection and trematode species present were noted for each individual and used as explanatory categorical variables in analyses.

2.4. Statistical analysis

All analyses were run using the statistical software R (R Development Core Team 2019). We used data from all 371 infected periwinkles (we excluded periwinkles that were co-infected) to analyse overall trematode community patterns. Because site by species abundance data were highly non-normal with unequal variance, we used a randomization analysis to test the hypothesis that trematode species prevalence differs among sites (Manly 2001). We randomly reassigned individual trematodes to sites, while holding the number of trematodes in each site constant (iterations = 10 000). For each permutation, the chi-square statistic was calculated and the p-value of the observed chi-square statistic was tested against this distribution. We further calculated the abundance of

each species in each site at each permutation and used the 95 % CI of site by species abundance values from the permutations to assess where observed values were higher or lower than expected under the null hypothesis of species being randomly distributed among sites.

We tested for potential periwinkle size differences among the 4 sites with a 1-way ANOVA, using the `aov` function included in the `stats` package of R. We then tested the hypothesis that larger periwinkles are more likely to be infected with any kind of trematode by applying exact 2-sample permutation *t*-tests using the function '`oneway_test`' included in the `coin` package (Hothorn et al. 2008). Data were analysed separately for each study site as trematode presence varies among sites. We included both size and sex in all subsequent analyses to control for any potential effects they might have on periwinkle behaviour.

Grazing behaviour of *L. sitkana* was analysed with general linear models using the `lm` function included in the `stats` package of R. We used the amount of algae consumed over the 5 d trial as the response variable. Site, infection status, periwinkle size and sex were used as explanatory variables, and model assumptions checked with residuals vs. fitted values and normal Q-Q plots. Interactions among variables with no significant effect (i.e. interaction terms showing *p*-values > 0.05) were removed from the fully parameterized linear model. Removing non-significant interactions from the models improved their Akaike's information criterion (AIC) score, and results were interpreted after interactions were removed (see Table 2). The subset of periwinkles used in laboratory trials that were found to be infected with trematodes were then used to further assess the effect of trematode species, maturity of trematode infection, periwinkle size, and sex on algae consumed.

3. RESULTS

3.1. Trematode infection status

Five morphological trematode species were identified in periwinkles from all 4 sites. One of those species was seen only in 1 periwinkle (prevalence < 0.01 %) and was excluded from statistical analyses. Prasiola Point and Ross and Wizard Islets had 3 of the 4 most prevalent trematode species, whereas Nudi-branch Point had 2 of the most prevalent trematode species (Table 1). At our study sites, *Microphallus* sp., unlike other trematode species found, did not produce cercariae; sporocysts of this species only

Table 1. Prevalence of 4 most prevalent trematode species found in *Littorina sitkana* is not random ($\chi^2 = 101.39$, randomization $p < 0.0001$)

Site	No. of samples	Uninfected (%)	Infected (single species) (%)	Infected with >1 species (%)	Number infected ^a	<i>Himasthla</i> sp. (%) [n]	<i>Maritrema loricola</i> Ching, 1962 (%) [n]	<i>Microphallus</i> sp. (%) [n]	Unidentified 1 (U1) (%) [n]
Nudibranch	87	56.32	43.68	2.30	38	19.54 [17]	0.00 [0]	24.13 [21]	0.00 [0]
Prasiola	116	70.69	29.31	1.72	34	12.93 [15]	5.17 [6]	11.20 [13]	0.00 [6]
Ross	88	86.36	13.64	0.00	12	0.00 [0]	5.68 [5]	4.55 [4]	3.41 [3]
Wizard	90	40.00	60.00	5.56	54	36.67 [33]	16.67 [15]	0.00 [0]	6.67 [6]

^aOnly single species infections included

produced metacercariae; inside periwinkle hosts.

For snails infected by a single trematode species, the site by species abundance was significantly different from random ($\chi^2 = 101.39$, randomization $p < 0.0001$). *Himasthla* sp. was found more frequently than expected by chance at Wizard Islet ($n = 33$, randomization 95% CI: 20–31), but less often than expected at Ross Islet ($n = 0$, 95% CI: 2–9). *Maritrema loricola* was found less often than expected at Nudibranch Point ($n = 0$, 95% CI: 3–11). *Microphallus* sp. was more abundant at Nudibranch Point ($n = 21$, 95% CI: 6–15) and less abundant at Wizard Islet ($n = 0$, 95% CI: 10–20) than expected (Table 1).

Periwinkle size differed significantly among the 4 sites ($F_{3,377} = 78.75$, $p < 0.001$). Snails at Prasiola Point were the largest (14.24 ± 1.12 mm; mean \pm SE), followed by snails at Nudibranch Point (13.88 ± 1.02 mm), Wizard Islet (12.65 ± 1.42 mm) and Ross Islet (12.01 ± 1.02 mm). Permutation *t*-tests suggested that *Littorina sitkana* infected with trematodes are significantly larger than uninfected periwinkles at Wizard

Islet ($F = 20.44$, $p < 0.0001$), but not at the other study sites (Prasiola Point: $F = 0.02$, $p = 0.90$; Nudibranch Point: $F = 0.49$, $p = 0.48$; Ross Islet: $F = 0.18$, $p = 0.13$).

3.2. Grazing behaviour

The best model for algae consumption included all 4 main variables (snail site, infection status, sex, and size) as well as the interaction effects of site by sex and site by size (Tables 2 & 3). Larger periwinkles consumed more algae than smaller periwinkles at Prasiola and Nudibranch Points, but not at Ross and Wizard Islets (2-way interaction: $F_{3,368} = 5.98$, $p < 0.001$; Fig. 2). Female periwinkles from Wizard Islet ate more than males, whereas females from Prasiola Point ate less algae than males (2-way interaction: $F_{3,368} = 5.92$, $p < 0.001$). Periwinkles infected with trematodes had a tendency toward decreased algae consumption, except for individuals from Wizard Islet ($F_{1,368} = 4.04$, $p = 0.046$; Figs. 3 & 4).

Among only infected periwinkles, trematode species had no detectable effect on the amount of algae consumed by *L. sitkana* (Prasiola Point: $F_{2,28} = 0.41$,

Table 2. Comparison of AIC values for general linear models using Δ dry algae weight as response variable and site, infection status, periwinkle size and sex as explanatory variables

Model	Δ AIC	df	Weight
Full model:			
algae.consumed ~ site \times infected \times sex \times size	20.6	33	<0.001
Remove 3-way interactions:			
algae.consumed ~ site + size + site:infected + site:sex + site:size + infected:sex + infected:size + sex:size	0.3	20	0.35
Remove non-significant 2-way interactions:			
algae.consumed ~ site + infected + sex + size + site:sex + site:size + infected:size	1.2	15	0.23
Final model:			
algae.consumed ~ site + infected + sex + size + site:sex + site:size	0.0	14	0.42

Table 3. Coefficients for factor levels in final model of Table 2

Coefficient	Estimate (\pm SE)	<i>t</i>	<i>p</i>
(Intercept)	-165.93 (\pm 44.03)	-3.77	<0.001
sitePrasiola	140.79 (\pm 56.50)	2.49	0.013
siteRoss	210.29 (\pm 57.78)	3.64	<0.001
siteWizard	207.96 (\pm 52.45)	3.97	<0.001
infectedYes	-7.75 (\pm 3.46)	-2.24	0.026
sexMale	6.27 (\pm 6.39)	0.98	0.327
size	17.99 (\pm 3.14)	5.73	<0.001
sitePrasiola:sexMale	11.49 (\pm 9.48)	1.21	0.226
siteRoss:sexMale	-14.03 (\pm 11.22)	-1.25	0.212
siteWizard:sexMale	-26.54 (\pm 9.82)	-2.70	0.007
sitePrasiola:size	-11.44 (\pm 3.99)	-2.86	0.004
siteRoss:size	-16.73 (\pm 4.41)	-3.79	<0.001
siteWizard:size	-15.43 (\pm 3.87)	-3.99	<0.001

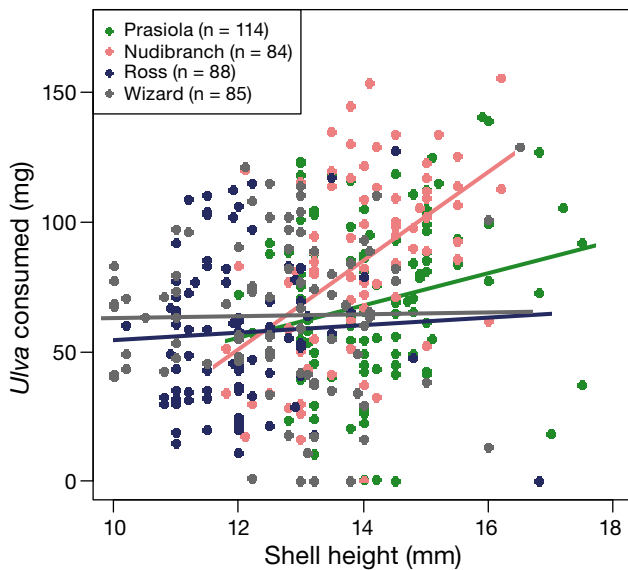


Fig. 2. Correlation between *Ulva intestinalis* consumed and shell height of *Littorina sitkana*. Data from 4 sites showing the significant 2-way interaction between periwinkle size and collection site on algae consumed. Data from laboratory experiments in 2012

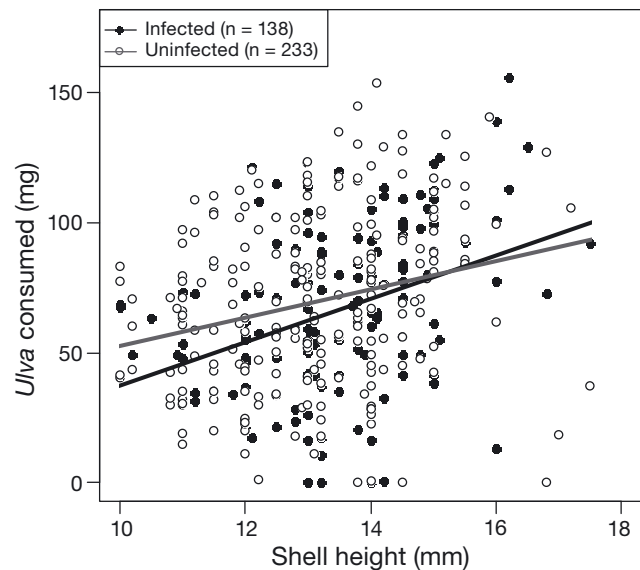


Fig. 3. Correlation between *Ulva intestinalis* consumed and infection status of *Littorina sitkana*. Data from 4 sites combined show the main effect of infection on algae consumed; the interaction term was not statistically significant (Tables 2 & 3). Data from laboratory experiments in 2012

$p = 0.671$; Nudibranch Point: $F_{1,33} = 0.03$, $p = 0.875$; Ross Islet: $F_{2,6} = 3.10$, $p = 0.119$; Wizard Islet: $F_{2,48} = 0.01$, $p = 0.993$). Maturity of infection also had no detectable effect on grazing activity of periwinkles at any site (Prasiola Point: $F_{1,28} = 0.43$, $p = 0.518$; Nudibranch Point: $F_{1,33} = 1.13$, $p = 0.296$; Ross Islet: $F_{1,6} = 1.28$, $p = 0.301$; Wizard Islet: $F_{1,48} = 0.47$, $p = 0.498$).

4. DISCUSSION

In this study, we show that trematode species prevalence and richness in the periwinkle *Littorina sitkana* vary among sites that are geographically close to each other. Further, we show that the effect of infection status on grazing behaviour depends on site. Our methods did not allow us to distinguish between different life history strategies of snails at different study sites independent of trematode infection (but see Hechinger 2010 for an example of disentangling causation from life history strategies of hosts). Nevertheless, as we compared infected snails to uninfected snails within each study site, we feel confident our results are not affected by potential pre-infection differences in host behaviour among study sites. Our result that trematode communities differ among sites is in keeping with previous suggestions that separated localities in a small geographical area might differ in trematode community composition

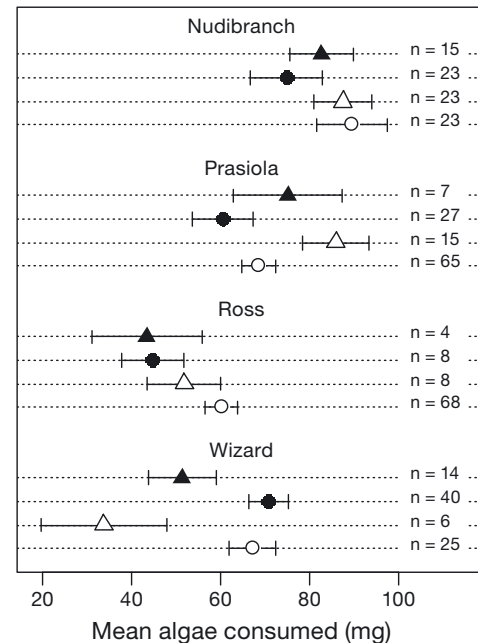


Fig. 4. Algae *Ulva intestinalis* consumed (mean \pm SE) by *Littorina sitkana*. Data from 4 sites is displayed by periwinkle infection status and sex (males: triangles; females: circles). Inf.: infected (black); Uninf.: uninfected (white). A significant 2-way interaction between collection site and periwinkle sex was present. Data from laboratory experiments in 2012

(Kube et al. 2002). Such differences among localities arise, among other factors, because trematode prevalence, intensity and species richness vary according

to the species richness of second intermediate and definitive hosts within the same habitat (Hechinger & Lafferty 2005). Different trematode communities might have differential effects on snail ecology depending on both biotic (e.g. invertebrate and vertebrate species richness and abundance) and abiotic components (e.g. wave exposure, substrate composition, temperature) present in their environment; hereafter we refer to these combined components as habitat composition.

Snail grazing behaviour is a phenotypic trait often affected by trematode infection (Levri & Lively 1996, Wood et al. 2007, Clausen et al. 2008, Morton 2018). In this study, infected periwinkles consumed less algae than uninfected periwinkles for 3 of the 4 sites studied. Decreased feeding of trematode-infected individuals has been observed for other species of *Littorina* (Wood et al. 2007, Clausen et al. 2008). The decrease in algae consumption has been hypothesized to be a product of host castration, slow or stunted growth or damage to digestive tissue. It is not possible to distinguish among these possibilities with the data from this study, but all the identified species of trematodes found here are related to known parasitic castrators of their snail host (Levri 1999, Sorensen & Minchella 2001, Hechinger et al. 2009), and may be host castrators themselves. As all trematodes found in this study were found within the reproductive and digestive glands of their periwinkle host, direct damage to the tissue of the periwinkle is also a plausible explanation for decreased feeding rates in infected individuals. Wizard Islet is the only site where grazing rate of infected periwinkles did not differ when compared to uninfected periwinkles. Interestingly, Wizard Islet showed the highest trematode prevalence among the 4 sites and a larger size of infected periwinkles. This suggests that Wizard Islet is the most different of the 4 sites studied, although the reason(s) for these differences remain unclear.

Previous research suggests that snails infected with trematodes lower their grazing activity by up to 80 % (Morton 2018). Nevertheless, our results show a grazing reduction of between 12.8 and 20.85 % in Prasiola, Nudibranch and Ross Islet. Taking into account that trematode prevalence ranged from 14 to 47 % at these 3 sites, we calculate a potential increase in algal coverage for the 3 different populations of between 2.92 and 6.04 % due to lower periwinkle grazing activity alone. These results suggest that trematode infection might not have an important impact on the community structure at any of the 3 sites where lower grazing activity is a product of trematode infec-

tion. However, at Wizard Islet, infected periwinkles grazed 35 % more than uninfected periwinkles. Trematode prevalence at this site reached 66 %, suggesting that the existence of trematodes at this site has the potential to reduce algal cover in the community by 23.1 %. Thus, trematode infection could potentially have an important impact on the community structure at Wizard Islet.

Contrary to our results, previous studies on snail grazing activity have shown that smaller (i.e. younger) snails graze more than larger (i.e. older) snails due to higher metabolic demands on younger, growing snails (Levri & Lively 1996, Carlsson & Bronmark 2006). However, studies that suggested smaller snails graze more than larger snails compared juvenile to adult snails. In our study, we used periwinkles with very similar shell height ($SE = \pm 0.08$ mm in shell height) to ensure they were from similar cohorts and all were adults. Snail growth and reproductive output has been shown to differ among sites as a result of life history trade-offs when mortality rates differ among sites (Hechinger, 2010). In our study system, periwinkles from Ross and Wizard Islets have higher mortality rates than periwinkles from mainland sites (Ayala-Díaz et al. 2017). This suggests that periwinkles from the islets might decrease resource allocation to growth, and thus reach sexual maturity at a smaller size. This increases the probability of all periwinkles used in this study being adults. Thus, we propose that larger periwinkles from our study grazed more simply because they have more mass and thus greater energy requirements directly related to cell energy consumption.

Infected periwinkles were bigger than uninfected periwinkles at Wizard Islet. This result is in accordance with previous findings in marine snails (Mouritsen & Jensen 1994, Miller & Poulin 2001, McCarthy et al. 2004). Different hypotheses have been proposed to explain larger shell sizes of infected snails. Freshwater snails infected with trematodes can grow faster and get to larger sizes than uninfected individuals (a process known as gigantism) (Rothschild 1936), but this explanation lacks convincing support in the marine system (but see Miura et al. 2006). Thus, here we adopt the explanation proposed by Miller & Poulin (2001) that larger snails are simply older than smaller snails, have therefore been exposed to trematodes for longer, and are thus more likely to have contracted parasites.

Wizard Islet was also the only site where infected periwinkles showed no tendency for lower grazing rates. A potential explanation could be that the general tendency for larger snails to have higher grazing

rates obscured any effect of trematode infection on consumption rate in *L. sitkana* at this site, such that larger infected snails and smaller uninfected snails converged on similar algae consumption rates. Nevertheless, size was controlled for in our models and the increase in algal consumption was observed afterwards. This suggests that the trend for infected snails to increase algal consumption is likely caused by trematode infection, but more specific studies are necessary in order to confirm our results. Calculating the size-specific energetic costs of locomotion and trematode infection in *L. sitkana* are necessary, and further research involving trematode/snail physiology and energetic flows are in order.

5. CONCLUSIONS

The results from our study reveal that trematode infection in *Littorina sitkana* varies depending on the habitat composition of the locality studied; habitat composition also modulates the effect of trematode infection on the periwinkle intermediate host. We suggest that a decreased rate of grazing behaviour depends on environmental factors other than trematode infection that vary among sites. This variation stands even when sites are geographically close and in the presence of similar trematode communities inhabiting the same snail host species. We suggest that in some cases, trematode infection can have an important impact on algal community structure, as our calculations suggest at Wizard Islet. It would be interesting to transplant post-trematode infection snail hosts among sites to test the hypothesis that snail grazing behaviour depends on habitat composition, and ascertain whether trematodes affect snail behaviour differently depending on host habitat. Including information from algal community structure in future analyses of trematode infection effects on snail grazing behaviour are necessary to test the real relevance of trematode infection at a community level.

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