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ORIGINAL PAPER

Species-specific tidal locomotion linked to a parasitic infection in sympatric sea snails

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Abstract

Parasites can play a critical role in mediating inter-species interactions. Potential effects induced by parasites can range from species-wide traits to functional alterations in host community structure. One of the most intriguing host–parasite interactions pertains to adaptative host manipulation, an evolutionary occurrence where parasites alter the phenotype of their host to increase their own fitness. This study aims to address this phenomenon in a marine setting by investigating the effect of a philophthalmid trematode, *Parorchis* sp., on the vertical upward movement and phototactic behaviour of their intermediate hosts whilst simultaneously addressing the host specificity of these effects. These behaviours could impact the odds of trematodes successfully transmitting from their intermediate snail host to their definitive shorebird host, a crucial step in the life cycle of these parasites. Most trematode species exhibit strong specificity for snail hosts, typically infecting only a single snail species. In this rare system, however, the trematode infects a pair of sympatric and congeneric littorinid sea snails found in the intertidal zone of New Zealand's rocky shores: *Austrolittorina cincta* and *A. antipodum*. Precisely, experiments were conducted in a controlled, laboratory-based setting, extending over a period of six weeks, during which vertical displacement and response to light were measured. Our results demonstrate that vertical upward movement amongst infected snails increased for *A. cincta*, but not for *A. antipodum*. No difference in response to light between infected and uninfected groups was evident across either species. Our findings highlight the complex nature of parasitic infections, where trait-specific behavioural effects are dissimilar across even congeneric host taxa.

Keywords Littorinidae · Trematode · Movement · Phototaxis · Adaptive host manipulation · Intertidal

Abbreviation
GLMM Generalized linear mixed model

Introduction

Inter-specific interactions provide the foundation for all community level processes and are thus an essential element to ecosystem functioning. Parasitism is underrepresented in ecological literature relative to its importance. Increasing evidence shows that parasitic taxa can have widespread effects across ecological scales, ranging from host population impacts to cascading effects on community structure (Curtis 1987; Minchella and Scott 1991; Mouritsen and Poulin 2009). The intertidal zone is ideal for investigating the ecological effects mediated by parasites, as it supports a rich biodiversity regulated by complex environmental heterogeneity (Grosberg 1982), in addition to being spatially constrained. Moreover, parasitic taxa are omnipresent and in high abundance in intertidal ecosystems (Mouritsen and Poulin 2002). In certain instances, they can influence density-dependent processes by directly reducing host reproductive output (Fredensborg et al. 2005). More intriguingly, parasites can also directly or indirectly influence the abundance of non-host species. For instance, the burrowing capacity in bivalves is often impaired by parasite load, thus increasing predation risk, but this also induces sediment and hydrodynamic modifications via a relaxed disturbance to the upper sediment strata, subsequently impacting the abundance of other species such as polychaetes and crustaceans (Mouritsen and Poulin 2009). Similarly, the spatial distribution of host species can be mediated by parasites, potentially remodeling ecological linkages (Curtis 1987, 1990; McCurdy et al.

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2000). Such findings demonstrate the ecological importance of parasites beyond the obvious and immediate considerations for host fitness.

Within marine intertidal ecosystems, trematodes are among the most diverse parasitic taxa (Mouritsen and Poulin 2002). Trematodes have complex, multi-host life cycles (Poulin and Cribb 2002). Generally, trematodes utilize at least one intermediate host, where the first is almost always a snail, prior to infecting a vertebrate definitive host via trophic transmission (Mouritsen and Poulin 2002; Poulin and Cribb 2002). Snails are among the most obvious and abundant invertebrates in the intertidal zone, typically densely distributed and occupying structurally diverse microhabitats (Underwood 1979). Pathological effects of trematode parasitism in snails include castration (Wilson and Denison 1980; Gorbushin 1997), inhibition of host sensitivity to predators (Belgrad and Smith 2014), reduced attachment strength (O'Dwyer et al. 2014a), and gigantism (Wilson and Denison 1980; Gorbushin 1997). In some instances, trematode-induced host behavioural alterations may be in line with adaptive host manipulation, resulting in an increase in parasite fitness (Bhattarai et al. 2021). These effects are often difficult to decipher, as behavioural modifications could represent pathological side effects or host immune responses that mitigate the effects of infection (Poulin 1995). Nevertheless, adaptive host manipulation has been suggested as the mechanism behind the differences in vertical distribution in snails infected with trematodes, as well as the increased transmission of the parasite to its definitive host (Curtis 1987). In another study, Levri and Lively (1996) found that snails infected with trematodes exhibited increased synchrony in foraging periods with their predators, thus increasing opportunities for trophic transmission.

Trematodes generally infect a single species of first intermediate snail hosts. In New Zealand, there exists a rare system where the trematode *Parorchis* sp. exploits two sympatric and co-occurring, congeneric littorinid sea snails (Gastropoda: Littorinidae): *Austrolittorina cincta* and *A. antipodum* (O'Dwyer et al. 2014b, c). *Parorchis* sp. denotes a single species yet to be formally named, but has been subject to both morphological and genetic studies (O'Dwyer et al. 2014b). Littorinid sea snails are highly abundant in the intertidal zone and have been heavily studied in relation to physiological adaptations to living in a highly variable and desiccating environment (Chapman and Underwood 1996; Jones and Boulding 1999; Emson et al. 2002). The potential taxon-specific nature in which parasites influence their hosts may often be overlooked and this system offers a unique opportunity to investigate the host specificity of parasite-mediated effects in which meaningful comparisons can be made due to the congeneric similarities of the hosts. Both *A. cincta* and *A. antipodum* are dominant organisms of the high shore of the rocky intertidal zone (O'Dwyer et al. 2014c); for our study locality, they are found only in upper regions of the high tidal zone and thus submerged only during high tides. Once ingested, *Parorchis* sp. takes over the host gonadal and digestive tissues. *Parorchis* sp. cercariae (free-swimming stage) are periodically shed from snails; these cercariae rapidly form cysts post-emergence on nearby hard substrates (e.g., snail shell or rock) to be eventually ingested by an avian definitive host (Guilloteau et al. 2016; Weekes 1982). In laboratory experiments, they rapidly encyst on glass slides and wells in the immediate vicinity of the snail (Guilloteau et al. 2016; O'Dwyer et al. 2014b). Infected *Austrolittorina* spp. were shown to display a weaker attachment strength, likely as a pathological side effect (O'Dwyer et al. 2014a). However, the authors have also suggested the potential for adaptive host manipulation. Limited evidence suggests that infected *Austrolittorina* display reduced downwards movement and are less likely to utilize functional microhabitats such as crevices (O'Dwyer et al. 2014c). These trends, however, lack statistical support. Thus, many ecological aspects of this host–parasite system remain relatively unknown and warrant further exploration.

Here, we tested the effects of trematode infection on two ecologically relevant behaviours in *A. antipodum* and *A. cincta*: upward movement and phototactic response. Selection should increase the likelihood that infected snails move towards locations with greatest definitive host density to maximize trophic transmission. In addition, cercarial shedding is typically induced by water immersion (Mouritsen 2002; Galaktionov and Dobrovolskij 2003), in which *Parorchis* sp. is no exception (O'Dwyer and Poulin 2015), and waves are likely to impact the ability of cercariae to encyst on hard surfaces. Specifically, as *Parorchis* sp. cercariae encyst rapidly after emerging from the snail host on surrounding hard substrates, and *Austrolittorina* are found solely in the high tidal zone, upwards movement during high tidal water exposure would allow for cercariae to encyst in areas of closer proximity to their definitive hosts, whilst simultaneously increasing accessibility to birds as snails can frequently be found beneath multiple layers of rocks. During high tide, shorebirds aggregate at the unsubmerged regions, in close vicinity to *Austrolittorina*. In addition, upwards movement during tidal submersion should also reduce the chances of cercariae being washed away. Cercariae of *Parorchis* sp. can also encyst precociously in high proportions within the host snail, where instead of emerging, the cercariae remain inside the rediae and transform into metacercarial cysts (O'Dwyer and Poulin 2015). Trophic transmission to shorebirds can alternatively therefore be facilitated by direct predation on the snail. Thus, we first hypothesized that *Parorchis* sp. may increase the upwards movement of

their snail hosts when exposed to water during high tide, allowing for an increase in successful substrate encystment, substrate-bound metacercarial ingestion, and direct predation by definitive hosts.

Second, light exposure increases cercarial emergence across widespread trematode taxa (Kuntz 1947; Kaewkes et al. 2012), though this pattern is not universal (Bell et al. 1999). Shorebirds forage at the surface level with greater light exposure than underneath rocks where snails are found. Snails vary from living under a single layer of rock to multiple layers, experiencing a light intensity gradient. Thus, snails located in areas of stronger light exposure should correspond to habitats nearer to the surface level. Intertidal gastropods are generally photonegative (Brown 1977; Doering and Phillips 1983). Here, we hypothesized that *Parorchis* sp. decreases the sensitivity of snail hosts to light, thus increasing the likelihood of trophic transmission. Trophic transmission of trematodes to shorebirds via both substrate-bound metacercarial ingestion and direct predation of snails with precocious cysts likely increases if snail hosts occupy surface-level habitats. Therefore, we conducted experiments in a controlled, laboratory-based setting where vertical displacement and response to light were quantified for infected and uninfected snails of both sympatric species. Our study highlights that a single parasite species has differential impacts on sympatric, congeneric host taxa.

Methods

Study system, field collection and maintenance

Austrolittorina cincta and *A. antipodum* are sympatric littorinid gastropods distributed along the high shores of the rocky intertidal zone. On April 1 2021, 195 *A. cincta* and 183 *A. antipodum* were haphazardly collected from Portobello, Dunedin, New Zealand (45.83°S, 170.64°E) at low tide (no animal ethics were required for this study). Collection was conducted at a very specific site, where sampling from previous studies have demonstrated a high prevalence of trematode infection in both species due to a high shorebird density (O'Dwyer et al. 2014a). In the laboratory, all snails were maintained in 10 L plastic containers with approximately 1 cm of seawater and rocks from the collection site. Snails were fed sea lettuce (*Ulva* sp.) ad libitum. Water was aerated with air stones and replaced every 3–4 days. For individual identification, all snails were tagged with a numbered bee tag using superglue and their shell lengths were measured to the nearest 0.02 mm using digital callipers. Snails were acclimated for 48 h without disturbance prior to infection screening.

Infection screening

To assign all snails an infection status, a common protocol involving water submersion, exposure to elevated temperatures and constant lighting was employed to induce cercarial shedding (Born-Torrijos et al. 2014). Each individual was placed into a separate well of a 12 well plate, with 3 mL of natural seawater. Plates were placed inside an incubator at 25 °C under constant lighting for six hours. Post-incubation, wells were examined under a dissecting microscope for free-swimming *Parorchis* sp. cercariae (and *Parorchis* sp. metacercarial cysts). To minimize false negatives, two additional rounds of screening were conducted on individuals initially assigned as uninfected with 48-h intervals in between. The final round of screening lasted eight hours. Based on cercarial morphology, two *A. cincta* and three *A. antipodum* were infected with a different trematode species and were thus excluded from all experiments. Another *A. cincta* and two *A. antipodum* died during screening, reducing the final number of individuals to 192 (113 infected, 79 uninfected) *A. cincta* and 178 (69 infected, 109 uninfected) *A. antipodum* for the experiments.

Vertical displacement experiment

After screening, all snails were given at least four days without disturbance prior to this experiment. Experimentation took place inside an incubator with a glass window at room temperature, under natural lighting. Little light entered the incubator, offering relatively dark conditions. Experiments were completed over four consecutive days (two days per species) and within three hours of high tide to mimic the natural temporality of tidal submersion. Daily tide times were extracted from Tideschart (https://www.tideschart.com). Snails to be used that day were relocated in clear 10 L containers inside the incubator for six hours prior to experimentation to adjust to the experimental conditions. No water was added to these tanks to mimic the low tide conditions experienced by snails prior to their submersion via the rising high tide.

Once acclimation was completed and, within the defined three-hour timeframe for high tide, 20 trials were conducted simultaneously. Trials, which lasted 5 and 8 min respectively for *A. cincta* and *A. antipodum* (due to size and speed differences between species, determined by preliminary observations), involved dropping a single snail into a 14.5 mm diameter, 25 mL glass measuring cylinder and allowing them to climb on the vertical surface. Cylinders were filled with natural seawater to the 25 mL mark to mimic tidal submersion. The vertical displacement of the snail (measured at the tip of the foot) was measured to the closest 0.5 mL at the end of the trial. If snails were attached vertically to the cylinder, but below the 3 mL mark, vertical displacement

was recorded as 0, as we defined this only as vertical attachment as opposed to vertical movement. The 20 trials were conducted simultaneously and these were defined to be in the same cohort. Containers holding snails yet to be tested that day were transferred to a similarly dark box while the previous cohort was still running, to minimize acclimation biases. Although snails in different cohorts experienced slightly different acclimation times, this was accounted for in the analyses (see below).

A total of 10 and nine cohorts were required to cycle through all individuals of *A. cincta* and *A. antipodum*, respectively. The time between dropping to recording was consistent across all snails, and cylinders were arranged to ensure an equal distribution of light across infected and uninfected trials. Between cohorts, all cylinders were thoroughly rinsed with tap water to eliminate chemical traces of previous snails before adding new seawater. Harsher chemicals were not used to minimize effects on subsequent trials.

Vertical snail displacement measurements in mL were calibrated into (1) distance in mm and (2) the number of bars crossed (each bar denoted 0.5 mL) for visualisation and analysis purposes. Snails that failed to open (i.e., the foot remained concealed within the shell) or attach were excluded from analysis. For *A. cincta*, individuals with shells larger than 14.5 mm were also excluded from analysis ($n = 26$) as their size could have obstructed movement within the cylinder. This was not an issue for *A. antipodum*, as none exceeded 12 mm in length. This cut-off length was selected as it matched the internal diameter of the measuring cylinder. Snails move with their shell tilted, thus sizes below the cut-off can move freely.

Light experiment

A four-day period without disturbance was allowed prior to this experiment for all snails. This experiment took place inside the same incubator used in the previous experiment. Snails were acclimated for six hours at 20 °C without lighting. While one cohort was tested, other cohorts were moved to a similarly dark box. Within the incubator, each experimental unit consisted of a $20 \times 13.3 \times 3.5$ cm (L × W × H) black plastic container with a clear lid. Black cloth tape was lined on one side of the exterior surface of the lid up to its midline, casting shadow over half the area of the container. All containers had 1 cm of natural seawater added prior to the initiation of a trial to promote movement.

During trials, the incubator was set to 20 °C with constant lighting. This temperature was chosen to ensure constant temperatures across both illuminated and dark sides of the container, making light independent from temperature. Partitioning light from temperature is important as parasites may affect the thermal biology of their hosts (Bates et al. 2011). To ensure that temperature was equal across light and dark sides of the containers, four HOBO loggers (Onset, Massachusetts, United States of America) were deployed in two empty containers before the trials, one in the illuminated and dark sides of each container to log the light intensity and temperature. Logging was performed every minute for three hours. This took place under the same conditions as during the trials.

For this experiment, a cohort comprised of four simultaneous trials, with two of each infected and uninfected snails. Incubator sides were alternated between cohorts to control for incubator position. Additionally, the illuminated side was randomized to control for container orientation and light distribution within the incubator. A trial involved placing an individual snail into a black container, followed by immediate lid attachment. Conspecifics can influence movement and behaviour in snails (Townsend 1974; Chapman 1998), therefore each container had only one snail for independence and to eliminate confounding factors. Snails were positioned in the centre of the container. Snails were placed with the shell tip facing the back wall of the incubator to eliminate any orientation bias.

Trials lasted 20 min, including two minutes acclimation whereafter snail position was scored as dark side (0) or illuminated side (1) every minute. Snail position could usually be assessed through the incubator window, although it was occasionally necessary to briefly open the incubator door. Snails that did not open and attach within the acclimation period, or did not move from the initial position, were excluded from analyses. For each trial, the sum of scores was considered the light score.

Because conspecific mucus trails may influence snail behaviour (Townsend, 1974; Chapman, 1998), containers were scrubbed with soap between cohorts, rinsed and dried, then fresh seawater was added. A total of 45 cohorts were required to cycle through all snails. Acclimation time varied but was accounted for in the statistical analysis (see below).

Statistical analysis

Statistical analyses were completed in R version 3.6.2 (R Core Team 2019). Data from both experiments were analyzed separately for each species. To assess the relationship between size and infection status, we fit simple linear models where shell length was the response variable and infection status was included as a fixed factor. For vertical upward movement, the vertical displacement measured in mL was transformed into the number of bars crossed, where each bar represented 0.5 mL; the response thus became a count variable. This was done to allow the responses to be modelled as a discrete distribution and thus optimise our analyses. This was analysed as a generalised linear mixed model (GLMM). First, we fit the GLMM implementing the Poisson distribution with a log link using the package *lme4*

(Bates et al. 2015). We tested for overdispersion using the package performance (Ludecke et al. 2021); the estimated dispersion parameter far exceeded 1 for all models (Chi-squared test for overdispersion: $p < 0.05$ for all models). To account for overdispersion and an overabundance of zeros (> 40% for all response variables), the zero-inflated negative binomial distribution was implemented in the models with the package *glmmTMB* (Brooks et al. 2017). Infection status (reference level = uninfected) was the fixed factor and shell length was included as an adjustment covariate to minimize systematic bias. Additionally, cohort was included as a random factor to account for any cohort-dependent stochastic effects (i.e., internal clock and acclimation time). Similarly, GLMMs with zero-inflated negative binomial distributions were fitted with the same model parameters to analyse light score. Any percentage estimates provided (see results) were calculated via the inverse of the log link function. All tests were two-tailed and model estimates were provided with their 95% confidence intervals (95% C.I.).

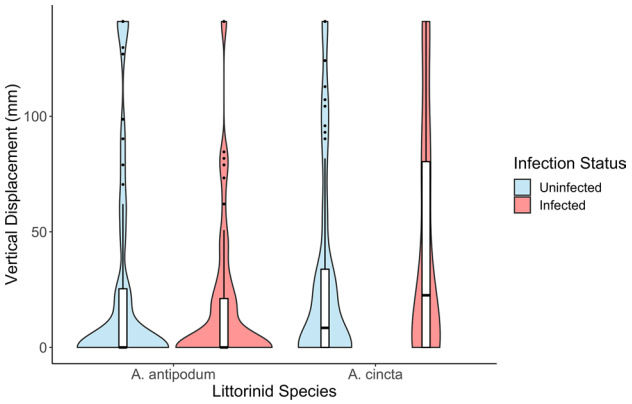

Fig. 1 Distributions of the vertical displacement (mm) over an eight-minute period in *Austrolittorina antipodum* ($n = 97$ uninfected, $n = 62$ infected) and a five-minute period in *A. cincta* ($n = 73$ uninfected, $n = 90$ infected), either uninfected or infected with *Parorchis* sp. (Trematoda: Philophthalmidae). Boxes nested within violin density plots represent box plots

Results

Infection prevalence

Infection prevalence of *Parorchis* sp. was found to be 69 of 178 (38.8%) for *A. antipodum* and 113 of 192 (58.9%) for *A. cincta*. For both species, infected individuals were significantly larger than uninfected conspecifics (*A. cincta*: *estimate* = 1.887, 95% C.I. = 1.169 to 2.604, $t = 5.187$, $df = 190$, $p < 0.001$; *A. antipodum*: *estimate* = 3.518, 95% C.I. = 2.958 to 4.079, $t = 12.39$, $df = 176$, $p < 0.001$).

Vertical displacement experiment

Infected *A. cincta* climbed greater distances than uninfected counterparts, crossing 74% more bars in the measuring cylinders (Fig. 1, 2; estimate = 0.556, 95% C.I. = 0.064 to 1.049, $z = 2.213$, $p = 0.027$). No such difference was evident in *A. antipodum* (Fig. 1, 2; estimate = 0.030, 95% C.I. = − 0.984 to 1.044, $z = 0.058$, $p = 0.953$). Shell length was inversely correlated with vertical displacement in both snail species, though significant only in *A. cincta* (Fig. 2; *A. cincta*: estimate = − 0.143, 95% C.I. = − 0.268 to − 0.018, $z = -2.237$, $p = 0.0253$; *A. antipodum*: estimate = − 0.185, 95% C.I. = − 0.380 to 0.009, $z = -1.867$, $p = 0.062$).

Light experiment

The illuminated side of the container measured 288.7 ± 5.4 lx (mean ± standard error) and the dark side 41.0 ± 1.8 lx, and temperature varied within 1.0 C between the sides according to the data loggers. No difference in light score was evident between infected and uninfected snails for either species (Fig. 3, 4; *A. cincta*: estimate = 0.188, 95% C.I. = − 0.186 to 0.562, $z = 0.983$, $p = 0.325$; *A. antipodum*: estimate = − 0.473, 95% C.I. = − 1.295 to 0.348, $z = -1.130$, $p = 0.259$). Snail shell length was inversely correlated with light score in *A. cincta*, though this effect only approaches the significance level (Fig. 4; estimate = − 0.076, 95% C.I. = − 0.154 to 0.001, $z = -1.924$, $p = 0.054$). No clear trend was detected in *A. antipodum* (Fig. 4; estimate = 0.078, 95% C.I. = − 0.103 to 0.259, $z = 0.844$, $p = 0.399$).

Discussion

Our study provides evidence that parasites can induce differential behavioural responses in congeneric, sympatric host taxa. *A. cincta* infected with *Parorchis* sp. displayed greater vertical upwards displacement upon submersion than their uninfected counterparts, whereas no difference was apparent for *A. antipodum*. *Parorchis* sp. infection seemingly had no observable effect on their host's response to light in either species, though the disparity between laboratory and natural conditions may play a role. Additionally, an inverse trend between vertical displacement and shell length was consistent, though statistically significant in only *A. cincta*. Evidence from our findings highlights the role of parasites in impacting tide-dependent movement of host organisms, which may in turn regulate predator–prey interactions and potentially enhance substrate encystment success of trematode cercariae.

Infected snails were larger. There are three possible, though non-conclusive explanations for this. First, the cumulative risk of parasite infection can vary as a positive

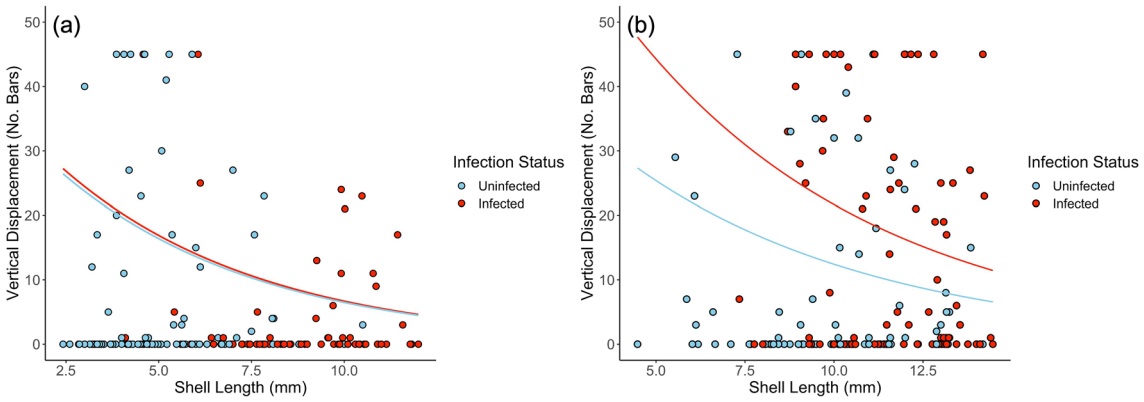

Fig. 2 The association between shell length and vertical displacement (number of bars crossed; one bar = 2.82 mm) in (**a**) *Austrolittorina antipodum* ($n = 97$ uninfected, $n = 62$ infected) and (**b**) *A. cincta* ($n = 73$ uninfected, $n = 90$ infected) partitioned by infection status by *Parorchis* sp. (Trematoda: Philophthalmidae). Fitted lines represent the linear predictor of the model transformed via the inverse of the log link function. Note that the scale of the response is in number of bars crossed to match the model response

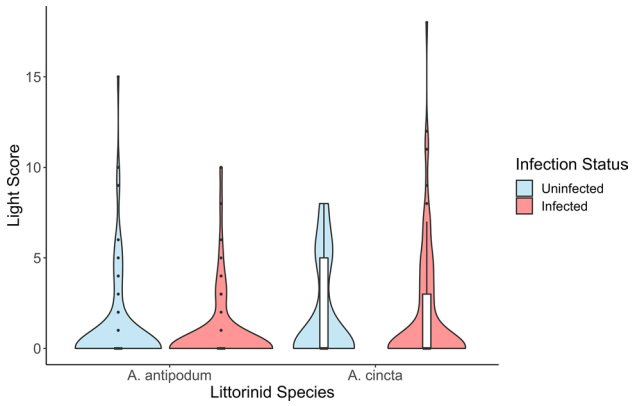

Fig. 3 Distributions of the total count spent in the illuminated compartment (light score) over a 20-min period by *Austrolittorina antipodum* ($n = 102$ uninfected, $n = 64$ infected) and *A. cincta* ($n = 75$ uninfected, $n = 98$ infected), either uninfected or infected with *Parorchis* sp. (Trematoda: Philophthalmidae). Counts were recorded every minute starting from the third minute (scores ranged from 0–18). Boxes nested within violin density plots represent box plots

function of age (Brown et al. 1988). Second, smaller individuals are distributed at lower vertical zones in the high shore, due to their weaker tolerance to physical stressors (Vermeij 1972). This means that size-dependent vertical migration could bring larger snails into closer vicinity with shorebird faeces harbouring trematode eggs, further amplifying their risk of infection. Finally, snail gigantism has been linked to trematode-induced castration, stemming from alterations in energetic allocation between growth and reproduction upon infection (Wilson and Denison 1980; Gorbushin 1997). This phenomenon is, however, unknown in this system. Here, *A. antipodum* had a much lower density than *A. cincta* at the collection site (personal observation). Thus, we had to collect a higher number of relatively small individuals to achieve an equally robust sample size. This would inevitably lead to an underestimation of infection prevalence for *A. antipodum*, whereas the same statistic would be unbiased in *A. cincta*. Regardless, this should not impact on the hypotheses tested here.

A limitation of this study is that we did not dissect the snails to screen for infection status and the non-invasive method we employed may underestimate prevalence. Nevertheless, *Parorchis sp.* multiplies asexually within its snail host (Guilloteau et al. 2016), and any precocious encystment would be simultaneous and co-occurring to actively shedding cercariae (O'Dwer and Poulin 2015), thus missing precociously encysted infections should not be an issue. O'Dywer and Poulin (2015) found a small underestimation from non-invasive screening via cercarial shedding in *A. cincta* and *A. antipodum* upon dissection in a study explicitly investigating precocious encystment. Also, extra cases of infection detected by dissection, but not by non-invasive screening, may represent early infections. These cases may be somewhat ambiguous in their effects on hosts anyhow. For the purpose of this study, a snail was defined as infected if cercariae were shed. Given the multi-phase screening conducted here, we are confident that an extensive coverage of mature infections was provided.

Our findings suggest adaptive host manipulation of *A. cincta* by *Parorchis* sp. To qualify, *Parorchis* sp. must induce a change in behaviour of *A. cincta* that confers a fitness benefit. Our study demonstrated increased vertical movement when infected *A. cincta* were exposed to water. Increased vertical movement may confer increased fitness to *Parorchis* sp. in multiple intuitive ways: better chances of encystment, and better chances of cysts being consumed by appropriate definitive hosts. Cercariae emerge upon water exposure (Mouritsen 2002; Galaktionov and Dobrovolskij 2003; O'Dwyer and Poulin 2015), and once

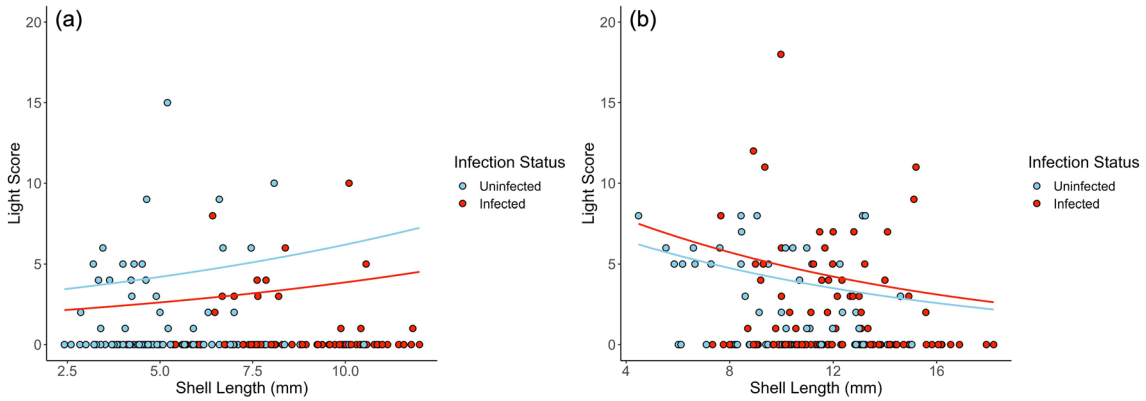

Fig. 4 The association between shell length and total count spent in the illuminated compartment (light score) over a 20-min period in (**a**) *Austrolittorina antipodum* ($n=102$ uninfected, $n=64$ infected) and (**b**) *A. cincta* ($n=75$ uninfected, $n=98$ infected) partitioned by infection status by *Parorchis* sp. (Trematoda: Philophthalmidae). Counts were recorded every minute starting from the third minute (scores ranged from 0–18). Fitted lines represent the linear predictor of the model transformed via the inverse of the log link function

emerged, *Parorchis* sp. rapidly encyst on hard substrates (Guilloteau et al. 2016; O'Dwyer et al. 2014b, c). But, cercariae shed while the snail is heavily submerged under are likely to be washed away and unable to encyst, thus encystment is likely more frequently achieved if the host migrates upwards away from the tide. Shorebirds cluster on unsubmerged areas at high tide (personal observation), thus upwards migration of the snail brings infected hosts in closer proximity to the definitive hosts, likely improving chances of transmission both via direct predation (made possible by precocious encystment) and substrate-bound ingestion of metacercariae. Though *Parorchis* sp. encyst on hard substrates and lack a second intermediate host, and experiments have demonstrated their rapid encystment on surfaces in the immediate vicinity of snail hosts (Guilloteau et al. 2016), the chances of an isolated metacercariae on a rock being ingested by a bird is likely low.

Very little is known regarding substrate preferences in *Parorchis* sp., but other philopthalmid species have demonstrated a preference for encystment on molluscan shells (Neal and Poulin 2012). Though we did not explicitly examine for any metacercariae bound to *Austrolittorina* shells, encystment on the shell of the same host snail species and individual seems likely given their rapid and local encystment. Trophic transmission in such a case follows the same route of predation as those that are precociously encysted inside the snail, where snails moving closer to their definitive hosts would result in greater trematode transmission. Determining whether *Parorchis* sp. directly causes this change in *A. cincta* is beyond the scope of this study, however, it seems unlikely that the compulsion to climb when submerged could be an incidental consequence of infection, nor a response of *A. cincta* to mitigate the impact of infection. Furthermore, similar correlations have been reported previously and were attributed to adaptive host manipulation in other snail-trematode associations (Curtis 1987).

O'Dwyer et al. (2014c) showed limited evidence of infected *A. antipodum* displaying reduced total movement, whereas no difference was found for *A. cincta*, in a series of field observations. This was observed in addition to trends of reduced downward vertical movement in infected snails from both taxa, though evidence is limited statistically. A reduction in downwards movement may similarly increase trophic transmission, where snails located higher up are more likely to be eaten. Such effects contrast to O'Dwyer et al. (2014a), in which infected snails exhibiting diminished attachment strength was interpreted as a pathological side effect, as opposed to possible manipulation. Both species of snail generally only move when exposed to water (though full submersion is not a requirement) and are distributed only along the upper reaches of the high tidal zone. Hence, these parasite-mediated effects on movement and distribution should only manifest principally during tidal water exposure.

The most intriguing finding here is the species-specific effect on host movement mediated by *Parorchis* sp. This is notable and surprising due to their shared phylogenetic history where molecular data indicate *A. cincta* and *A. antipodum* are sister taxa (Williams et al. 2003; Waters et al. 2006). Despite occupying the same habitat, patterns of density across the littorinid zone (high tidal zone here) differ between the pair, where little difference is present in the upper reaches but a substantially higher density of *A. antipodum* occurs in the lower reaches (O'Dwyer et al. 2014c). This disparity in density may result in stronger selection for *Parorchis* sp. to manipulate *A. cincta*, as the benefits of snail movement may be greater at the high shore due to greater bird density at the height of high tide. Furthermore, if *A. cincta* experiences a higher predation risk than

A. antipodum, perhaps resulting from their larger size as shorebirds are known to exhibit size-selectivity in foraging (Hilton et al. 2002), selection could also be stronger for *Parorchis sp*. to manipulate *A. cincta*. Nevertheless, no difference in size-zonal distributional gradients or field-based movement patterns are evident between *A. cincta* and *A. antipodum* (Vander Veur 2011). Microhabitat preferences are also similar between both species, in which crevices are preferred over bare surfaces or rock pools (O'Dwyer et al. 2014c). This species-specific response may not contribute to the disparities observed in movement or microhabitat preference. Similar occurrences regarding species-specific host manipulation have been shown in a fungal parasite infecting ants, where despite being infective to all experimental ant taxa, behavioural manipulation only exists in a select few, due to the production of highly specific compounds within the host's brain (Bekker et al. 2014). Such species-specific dynamics are not only limited to the interactions between hosts and their parasites. Sympatric host species may behave differently toward their mutualist or commensal partners, which may impact the success of the latter. For example, Farrell et al. (2014) found that, for two sympatric crayfish species both in mutualistic cleaning symbioses with branchiobdellidan worms, the crayfish species exhibited differential worm-directed grooming behaviours to avoid overexploitation by the worms. Likewise, the intensities of behaviours linked to rejecting seemingly commensal flatworm symbionts were dissimilar across sympatric intertidal snail species, which was reflected in the flatworm symbiont's host preference (Lee et al. 2021).

Whether the correlation between vertical displacement and shell length is specific to upwards movement cannot be deduced from this experiment. This trend should not be a simple by-product of a heavier weight-impairing movement, as the time of the trials was enough to allow for all snails regardless of size to move the full cylinder distance based on preliminary trials. It is possible that the tendency of smaller individuals to move more may reduce the extent of intraspecific competition with larger conspecifics by promoting movement into regions where competition is more relaxed, in addition to combating the pressures exerted by physical stressors (Vermeij 1973), though this is speculative. It is worth noting that this trend was significant in *A. cincta*, but just above the significance level for *A. antipodum*, despite a clear trend.

Our light sensitivity hypothesis was formulated on the basis that if the light sensitivity of the snail hosts is reduced, cercariae can encyst closer to the surface and snails nearer to the surface are more likely to be predated upon. However, no apparent difference in the snails' response to light was evident across infection groups for either species, suggesting here, phototactic behaviour is not linked to *Parorchis* sp. infection. Nevertheless, the responses of both species were unsurprisingly photonegative, spending the vast majority of the trial times in the dark compartment. Photonegativity is common among marine gastropods (Brown 1977; Doering and Phillips 1983). In amphipods, trematode-induced changes in phototactic behaviour are linked to differences in serotonin levels, suggesting serotonergic system interference (Tain et al. 2007). Regarding molecular mechanisms in snails, upregulation of the *npy* gene expression in neural tissues apparently alters egg-laying behaviour in infected freshwater snails (Hoek et al. 1997). However, the level of gene regulation in which this molecular interference takes place is unknown. Additionally, in *A. cincta*, the non-significant negative trend between light score and shell length suggests that smaller snails are repelled by light to a lesser extent. Such is also evident in past studies involving other intertidal snail species, thereby contributing to the formation of vertical size gradients (Doering and Phillips 1983). Though here, this trend may be confounded differences in movement across sizes, where smaller snails move more systematically, resulting in higher scores in the lighted side of the container.

In summary, we show that the trematode *Parorchis* sp. induced differential effects on vertical upward movement during submersion in two sympatric species of littorinid sea snails. Specifically, *Parorchis* sp. exerted no effect on *A. antipodum*, whereas infected *A. cincta* exhibited increased upward movement; the effect on the latter appeared to be in line with adaptive host manipulation. In contrast, *Parorchis* sp. did not influence the phototactic response of either species. This study highlights the complexity of host–parasite relationships and the dissimilar behavioural outcomes that can be unveiled even between closely related host taxa.

Glossary

Abundance	Average number of parasites per individual in a sample or population.
Cercariae	Free-living immature stage of trematodes after emerging from the first intermediate host.
Metacercariae	Cyst formed from cercariae post-emergence.
Precocious encystment	Direct transition of the trematode rediae into metacercariae (cyst) within the intermediate host.
Prevalence	Proportion of individuals infected with a parasite in a sample or population.
Redia	Larval trematode stage found within the snail host, which produces more rediae and forms cercariae.

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Author contributions SN and J-FD: designed the study. SN: collected and analysed the data and led the writing of the manuscript, with critical input from J-FD throughout.

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Data availability Data available from corresponding author upon reasonable request.

Declarations

Conflict of interest Both authors declare no conflict of interest.

Ethics approval No ethical approval was required for this study.

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