

Parasitism, movement, and distribution of the snail *Diloma subrostrata* (Trochidae) in a soft-sediment intertidal zone

Aroha A. Miller and Robert Poulin

Abstract: Despite reports of their effects on host reproduction, growth, survival, and habitat use, the role of parasites in determining community structure is still poorly understood. Trematode infections in snails are a ubiquitous feature of intertidal systems worldwide. In this study, the influence of a trematode parasite on the movement and dispersal of the trochid snail *Diloma subrostrata* on a soft-sediment shore is examined using mark–recapture experiments. The natural densities and shell widths of the snail peak between the upper and lower portions of the intertidal zone; marked snails were released within this area. Parasitized snails tended to have larger shells than nonparasitized conspecifics, and larger snails tended to move a greater linear distance than smaller snails in the 24 h following their marking and release. After shell width was corrected for, parasitized snails were found to move a significantly shorter distance than nonparasitized snails. In addition, the mean direction chosen by parasitized snails was almost parallel to the water’s edge, whereas that taken by nonparasitized snails was almost directly toward the upper portion of the intertidal zone. Although the mean directions taken by the two types of snails were statistically different, the considerable scatter in the distributions of directions taken by individual snails casts a doubt over the biological significance of the result. Without detailed knowledge of the parasite’s full life cycle it is difficult to determine whether this small bias in the direction of dispersal is an adaptive manipulation of snail behaviour by the parasitic trematode. Nevertheless, these results show that the trematode limits the range of movement, and possibly the direction of movement, of parasitized *D. subrostrata*, and can therefore contribute to the spatial structuring of the snail population.

Résumé : Bien que les effets des parasites sur la reproduction, la croissance, la survie et l’utilisation de l’habitat chez l’hôte soient connus, le rôle des parasites dans la structuration des communautés reste mal compris. Les infections de trématodes chez les gastéropodes sont un phénomène répandu dans tous les systèmes intertidaux du monde. Dans cette étude, nous examinons l’influence d’un trématode parasite sur les déplacements et la dispersion d’un gastéropode trochidé, *Diloma subrostrata*, sur les sédiments mous d’un rivage, au cours d’expériences de marquage–recapture. La densité naturelle et la largeur des coquilles du gastéropode sont maximales entre les sections supérieure et inférieure de la zone intertidale, endroit où ont été relâchés les gastéropodes marqués. La largeur des coquilles des gastéropodes parasités, avait tendance à être supérieure à celle des gastéropodes sains et les gastéropodes plus gros parcouraient en général une plus grande distance linéaire au cours des 24 h suivant leur marquage et leur relâchement. L’élimination des effets de la largeur des coquilles a permis de constater que les gastéropodes parasités font des parcours significativement plus courts que les gastéropodes non parasités. De plus, la direction moyenne choisie par les gastéropodes parasités était quasi parallèle à la rive, alors que celle suivie par les gastéropodes non parasités était orientée presque directement vers la section supérieure de la zone intertidale. Bien que les directions moyennes empruntées par les deux types de gastéropodes diffèrent statistiquement, l’éparpillement considérable des distributions des directions empruntées par les individus jette un doute sur la signification biologique des résultats. Sans une connaissance détaillée du cycle biologique complet du parasite, il est difficile de déterminer si la petite tendance directionnelle de la dispersion résulte d’une manipulation adaptative du comportement des gastéropodes par les trématodes parasites. Néanmoins, les résultats démontrent que le trématode limite les déplacements et peut-être la direction des déplacements de *D. subrostrata*, et peut, de ce fait, contribuer à la structuration spatiale de la population de gastéropodes.

[Traduit par la Rédaction]

Introduction

Although parasites are found in most of the common invertebrate species in intertidal systems, their role in determining community structure is still poorly resolved (Sousa

1991). Helminth parasites that mature in fish or shorebirds use intertidal invertebrates as intermediate hosts within their complex life cycles. To facilitate the completion of their life cycle, many helminths have evolved the ability to manipulate the physiology or behaviour of their intermediate hosts

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A.A. Miller and R. Poulin.¹ Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand.

¹Corresponding author (e-mail: robert.poulin@stonebow.otago.ac.nz).

(Moore and Gotelli 1990; Poulin 1994, 1998). Not only will these manipulations affect the biology and population dynamics of the intermediate host, but their indirect effects may have implications for the rest of the intertidal community (Thomas et al. 1998).

Among host–parasite associations in intertidal communities, the impact of digenetic trematodes on their snail hosts is by far the best studied. Most trematodes use snails as their first intermediate host, in which they multiply asexually to produce huge numbers of larvae (cercariae) that leave the snail to encyst in a second intermediate host. The exploitation of host resources during this asexual proliferation has immediate physiological effects on the snail host. Infected snails are usually castrated by their trematode parasites, and this sometimes results in greater allocation of energy to somatic growth and thus in larger sizes for infected snails (e.g., Sousa 1983; Lafferty 1993a; Curtis 1995). Increased growth following trematode infection, however, is far from a universal outcome for snails, as this phenomenon is dependent upon the snail species' life history and the environmental conditions (Sousa 1983; Mouritsen and Jensen 1994; Mouritsen et al. 1999).

Trematodes may also have marked effects on the behaviour of their snail hosts. For the trematode to pursue its life cycle, its cercariae should ideally emerge in the vicinity of the next intermediate host. Consequently, many trematodes have seemingly evolved the ability to modify the behaviour of their snail host in ways that enhance their chances of reaching their next host (e.g., Lowenberger and Rau 1994; Levri 1999). From the very few studies performed in intertidal systems, it appears that different trematode species can have opposite effects on the same snail hosts. For instance, laboratory and field studies of periwinkles (*Littorina* spp.) show that some trematodes can induce downward movements (Lambert and Farley 1968) whereas others can induce upward migrations along the shore (McCarthy et al. 2000). These discrepancies can also occur within a single host–parasite system. The vertical distribution of the mud snail *Ilyanassa obsoleta* is known to be altered by the trematode *Gynaecotyla adunca*; detailed studies by Curtis (1987, 1990, 1993) have shown that infected snails move to the upper intertidal zone, where they shed trematode cercariae. The next hosts of *G. adunca* are semiterrestrial crustaceans, and the vertical migration induced by the parasite thus appears to increase its transmission success, with no further impact on snail fitness, as infected snails are castrated. Interestingly, a different pattern was observed in the same host–parasite system from a different locality: McCurdy et al. (2000) found that *I. obsoleta* infected with *G. adunca* were much more likely to be found in the lower intertidal zone. Differences between localities in the identity and ecology of the next intermediate host of the trematode may be responsible for the contrasting findings. Many other biotic and abiotic factors also influence the movement and spatial distribution of intertidal gastropods (e.g., Underwood 1977; Fairweather 1988; Underwood and Chapman 1989; Chapman and Underwood 1994; Byers 2000). These variables can mask, or interact with, the effects of trematode parasites on snail movements, and this may explain the discrepancies in earlier studies.

Here we investigate the effects of trematode parasitism on the movements of the mud snail *Diloma subrostrata*

(Trochidae). This species is the dominant gastropod, in terms of numbers or biomass, on soft-sediment shores of the Otago Harbour, South Island, New Zealand (Logan 1976; Mitchell 1980). It is a deposit-feeder, often relying mainly on microalgae for food (Logan 1976). *Diloma subrostrata* serves as first intermediate host for a single species of trematode parasite, practically identical with the one found in another New Zealand trochid snail, *Melagraphia aethiops*, and described in detail by Clark (1958). The parasite's life cycle is unknown; in *D. subrostrata* it occurs as sporocysts containing asexually produced cercariae. The tail-less cercariae resemble those of trematodes in the family Opecoelidae, therefore the next intermediate host (in which the cercariae must encyst) would most likely be a crustacean or, much less likely, a fish. Although the identity of this putative crustacean host is unknown, the abundance of crustaceans at the study site increases as one moves down the shore, and we thus expected the trematode, if it induces any behavioural modification in the snail host, to induce a downward movement of snails. Our objectives were (i) to obtain basic data on the spatial distribution of densities, shell widths, and infection levels in *D. subrostrata* at our study locality, and (ii) to determine how trematode infections influence the movements of the snails, using mark–recapture experiments. This experimental approach has been used to study trematode parasitism in snails before (e.g., Goater et al. 1989), but usually not in the context of trematode-induced changes in snail movement patterns. Achieving both these objectives may shed some light on the role of parasitism in determining snail distribution.

Methods

The study was performed in Company Bay, a sheltered mud flat in the Otago Harbour, with a tidal range of just under 2 m. The sediment consists mainly of fine silt and sand, pebbles, and shells, with microalgae growing on all substrata. Only two gastropods are found on the sediments in large numbers, *D. subrostrata* and the whelk *Cominella glandiformis*.

Spatial distribution of *D. subrostrata* densities and shell widths

We quantified the spatial distribution of *D. subrostrata* densities and shell widths from the lower to the upper intertidal zone. Our only goal was to identify general patterns that may indicate preferences by the snails for certain locations. During daytime low tide on one occasion in February 2000, three transect lines were laid out perpendicular to the low-water mark, with 15 m separating adjacent transect lines. Beginning at the low-water mark and then every 10 m along each transect, a quadrat (surface area 2 m²) was placed on the sediments. All *D. subrostrata* in each quadrat were counted and individually measured (maximum shell width) to the nearest millimetre with vernier calipers before being released on site.

Movement of marked *D. subrostrata*

We quantified the effect of trematode infections on movement of *D. subrostrata* using mark–recapture experiments. Two replicate experiments were performed, one on 20–22 December 1999 and the other on 18–20 January 2000. Snails were collected from three zones (10 × 10 m): a low zone close to the low water mark, a middle zone 15 m higher up, and a high zone a further 15 m from the low-water mark. These three zones covered the same range as the

transects described above, and provide individuals from the full spectrum of habitats of *D. subrostrata* at Company Bay. On the first day of each experiment, 75 randomly chosen *D. subrostrata* from each zone were collected and returned to the laboratory in seawater. A part of the shell of each snail was gently and quickly dried, and a small numbered label was then glued to the shell. The numbering began with snails from the low zone (1–75) followed by those from the middle zone (76–150), and ended with those from the high zone (151–225). All snails were maintained overnight in seawater and returned to Company Bay during low tide on the second day. They were released along a measuring tape placed parallel to the water line and approximately 60 m above the low-water mark. Snails were positioned along the tape at 10-cm intervals, in a sequence matching their numbered labels and with all shells aligned similarly with respect to the water (i.e., with the shell opening facing the water), then the tape was removed. The snails were then left undisturbed for 24 h (two tidal cycles) until low tide the next day. This period is sufficient to assess the short-term movement patterns of intertidal snails (e.g., Underwood 1977). On the third day of each experiment, the measuring tape was placed in its original position and the location of each marked snail was noted with respect to its exact point of release the day before. We measured both the linear distance moved by each snail and the direction in which it had moved. This was recorded as an angle, with the 0–180° line running along the measuring tape; angles less than 180° represented movement toward the upper intertidal area, whereas angles greater than 180° indicated movement toward the low-water mark. Live snails were returned to the laboratory in seawater and processed within 48 h. They were individually measured (maximum shell width to the nearest millimetre) prior to dissection. The shell of each snail was crushed and the soft tissues were searched for the presence or absence of trematode sporocysts.

All statistical procedures involved standard parametric tests, with distance moved requiring logarithmic transformation. Angular data on the direction taken by snails were analysed using the circular statistics methods described in Zar (1996). For any group of angles, a mean angle, A , and a mean vector, r , were computed as follows:

$$\sin A = \frac{\left(\sum_{i=1}^n \sin a_i / n \right)}{r}$$

and

$$r = \sqrt{\left(\frac{\sum_{i=1}^n \cos a_i}{n} \right)^2 + \left(\frac{\sum_{i=1}^n \sin a_i}{n} \right)^2}$$

where a_i is one angle in a group of n angles. The mean angle represents the average direction in which snails moved, whereas the mean vector is a measure of the concentration of the individual angles (i.e., the inverse of their variability). The mean vector has no units and its value ranges from 0 (when there is so much dispersion that a mean angle cannot be computed) to 1 (when all the data are concentrated at the same direction, i.e., at the mean angle). The directions of movement of different groups of snails (i.e., infected or uninfected) were compared using the Watson–Williams test, which is based on the mean angle and mean vector of both groups (Zar 1996).

Results

Spatial distribution of *D. subrostrata* densities and shell widths

In total, 648 snails were collected from the three transects. The variation in the density of snails over the intertidal zone showed a clear pattern, reaching its highest value between 30 and 60 m from the low-water mark (Fig. 1). There was no difference in densities of *D. subrostrata* among the three transects (ANOVA, $F_{[2,21]} = 0.516$, $P = 0.604$). Shells ranged between 8 and 23 mm in width. Mean shell widths varied considerably among quadrats from the same transect as well as among transects (Fig. 1). A two-way ANOVA showed that shell widths varied significantly from the lower to the upper parts of the intertidal zone, i.e., among quadrats ($F_{[7,634]} = 16.139$, $P = 0.0001$), but did not differ significantly between transects ($F_{[2,634]} = 1.183$, $P = 0.2771$). Shells were generally larger between 10 and 30 m from the low-water mark (Fig. 1). The interaction between transects and the position of the quadrats was significant ($F_{[14,634]} = 4.455$, $P = 0.0001$), as reflected by the weaker pattern of variation in transect 1.

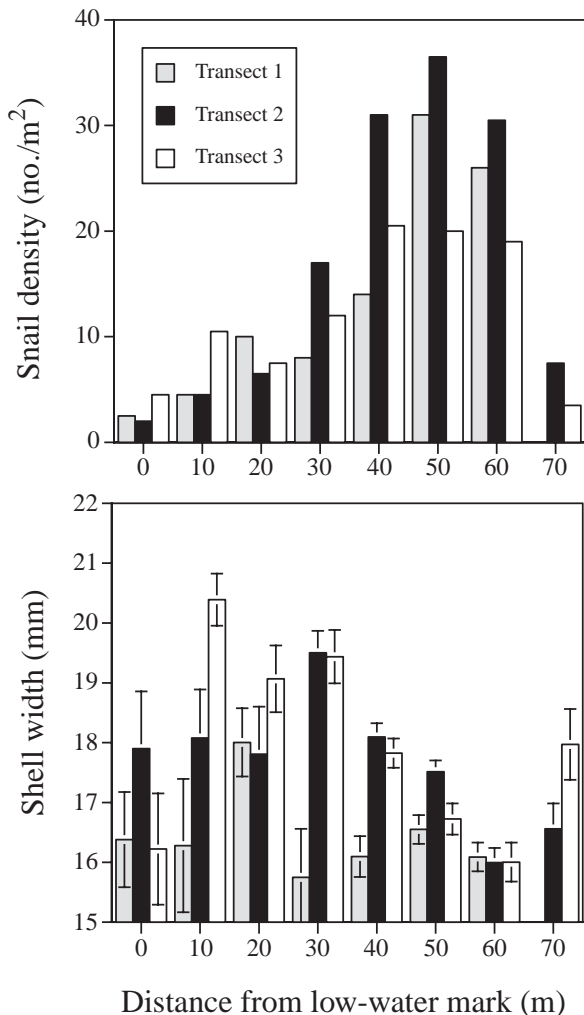
Movement of marked *D. subrostrata*

Not all snails were recovered in the two mark–recapture experiments; the overall recapture success was 85.3% (384 recaptured out of 450 marked snails, 198 from the first replicate and 186 from the second). Their shell widths ranged from 10 to 23 mm, the same range as that of released snails. A multiple ANOVA revealed that snails from the first replicate experiment were smaller than those of the second replicate ($F_{[1,372]} = 5.728$, $P = 0.0172$) and that infected snails were larger than uninfected ones ($F_{[1,372]} = 5.889$, $P = 0.0157$). As was found along the transect samples from the previous section, there was significant variation in snail widths among the low, middle, and high zones from which the marked snails came ($F_{[2,372]} = 9.012$, $P = 0.0002$). None of the interactions was significant.

The overall prevalence of trematode infections among recaptured snails was 12% (46 snails with trematode sporocysts out of 384). The proportion of infected snails varied among the three zones in different ways in the two replicate experiments (contingency test, $\chi^2_{[2]} = 5.433$, $P = 0.0661$): prevalence of infection was highest away from the low-water mark in the first replicate and highest close to the low-water mark in the second replicate (Fig. 2).

Because shell widths differed between the two replicates, we analysed the data on distances travelled separately for each replicate as well as after pooling the replicates. Since the outcome of these analyses was the same, we only present here the results of the analysis of pooled data. Using shell width as a covariate in an analysis of covariance (ANCOVA), we found that the linear distance travelled by snails was dependent on their size ($r = 0.268$, $P = 0.001$). Larger snails tended to travel longer distances, although the relationship was not very strong (Fig. 3). Of the two main factors in the ANCOVA, only whether the snails were infected or not had a significant influence on the distances they travelled ($F_{[1,377]} = 6.095$, $P = 0.014$). Neither the zone from which they came ($F_{[2,377]} = 0.903$, $P = 0.4062$) nor the interaction between parasitism and zone of origin ($F_{[2,377]} = 0.031$, $P = 0.9693$)

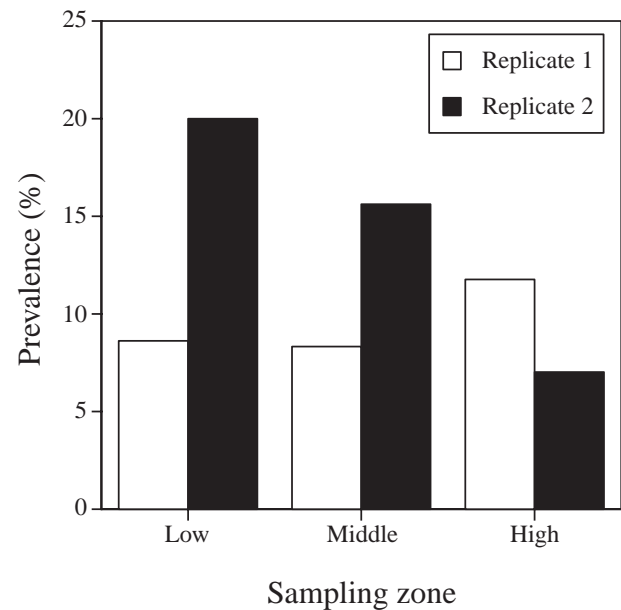
Fig. 1. Density and shell width (mean \pm SE) of the snail *Diloma subrostrata* as a function of distance from the low-water mark. Data are presented separately for each of three transects.



had a significant effect on how far marked snails moved following their release. Thus, after snail width was corrected for, infected *D. subrostrata* moved shorter distances than expected on the basis of their shell width, whereas noninfected conspecifics moved greater distances than expected on the basis of their shell width (Fig. 4).

The overall mean angle of direction for *D. subrostrata* parasitized by trematodes was 15.7°, which corresponds to movement almost parallel to the water's edge, whereas that for nonparasitized snails was 78.8°, which indicates movement almost straight toward the upper portion of the intertidal zone. The direction taken by parasitized snails did not differ between replicates (Watson-Williams test, $F_{[1,45]} = 1.318$, $P > 0.05$), nor did that taken by nonparasitized snails ($F_{[1,337]} = 3.503$, $P > 0.05$). There was a difference, however, between the mean angles of direction of parasitized and nonparasitized snails (Fig. 5), whether the data were pooled across replicates ($F_{[1,382]} = 28.283$, $P < 0.05$) or each replicate was treated independently (replicate 1: $F_{[1,196]} = 47.944$, $P < 0.05$; replicate 2: $F_{[1,184]} = 39.104$, $P < 0.05$). All mean vectors were relatively short, however (Fig. 5), indicating a weak concentration of angles around the mean angle. This

Fig. 2. Prevalence (percentage of snails parasitized) of trematode infections among individual *D. subrostrata* collected in three sampling zones located at different heights above the low-water mark. Data are presented separately for each of two replicates.



means that there was considerable dispersion within each group and no strong preference for the mean angle across individual snails within a group.

Discussion

Trematodes usually cause severe reductions in reproductive output, if not outright castration, in their snail hosts. Trematodes also act as major structuring forces in intertidal snail communities (Lauckner 1987). For these reasons they can act as strong selective agents and have driven the evolution of changes in snail life-history traits (Minchella 1985; Ruiz 1991; Lafferty 1993b). Their more proximate effects on snail behaviour and ecology are poorly understood, however. Here, we showed that *D. subrostrata* parasitized by a trematode move shorter distances than nonparasitized conspecifics, and also tend to choose a different direction.

The variation in sizes of snails between replicates in the mark-recapture experiment was very small; it may have been due to seasonal effects or some other factor, but it had no impact on our results. The larger size of parasitized snails observed here is consistent with the results of earlier studies. It may be due to an increased growth rate induced by the trematode, although the simplest explanation is that larger snails are older and have thus had longer to acquire parasites. Only detailed experimental studies can distinguish between these and other scenarios (e.g., Lafferty 1993a; Curtis 1995; Mouritsen and Jensen 1994; Mouritsen et al. 1999). Age or size of snails is often an important determinant of their movement or dispersal rates (e.g., Underwood 1977; Byers 2000). Here we observed that larger snails moved greater distances than smaller ones, and we had to control for shell width in an attempt to expose the influence of parasitism per se on snail movements. Our finding that parasitized snails move shorter distances supports earlier studies

Fig. 3. Distances travelled by marked *D. subrostrata* over 24 h following their release, as a function of their shell width. The regression line is also shown ($y = 0.05x + 1.066$, $r^2 = 0.072$). Each symbol denotes a different snail.

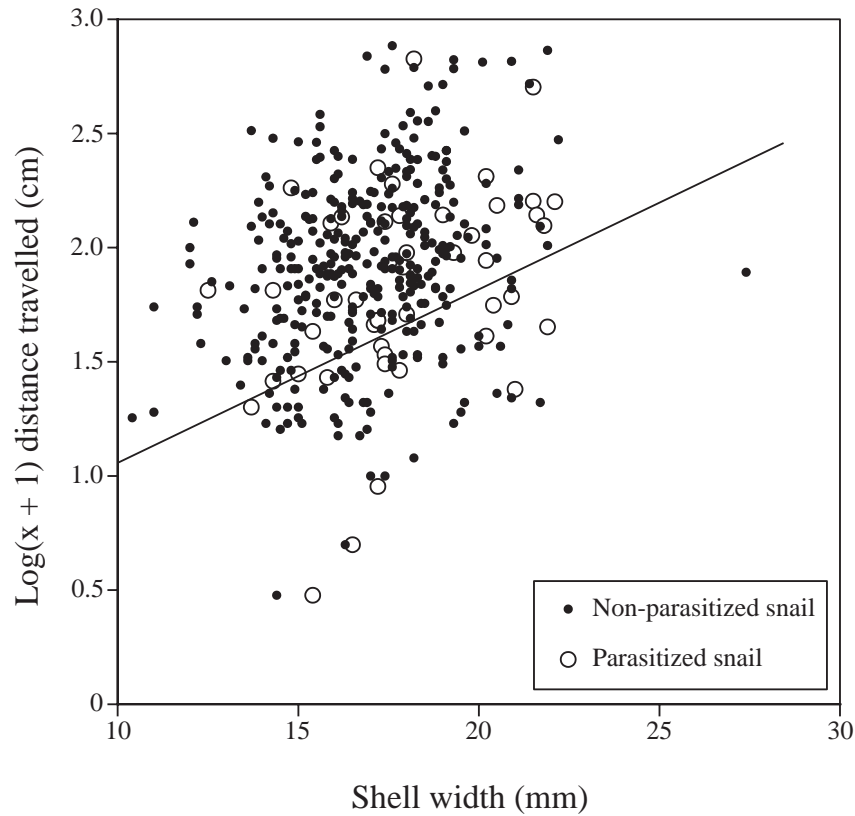


Fig. 4. Distances travelled (mean \pm SE) by 46 parasitized and 338 nonparasitized *D. subrostrata*, after correction for shell width. Data shown are the residuals from the regression in Fig. 3; negative values indicate snails that moved shorter distances than expected on the basis of their shell width, whereas positive values indicate snails that moved longer distances than expected. The difference between the two groups is significant ($t = 2.553$, $df = 382$, $P = 0.0111$).

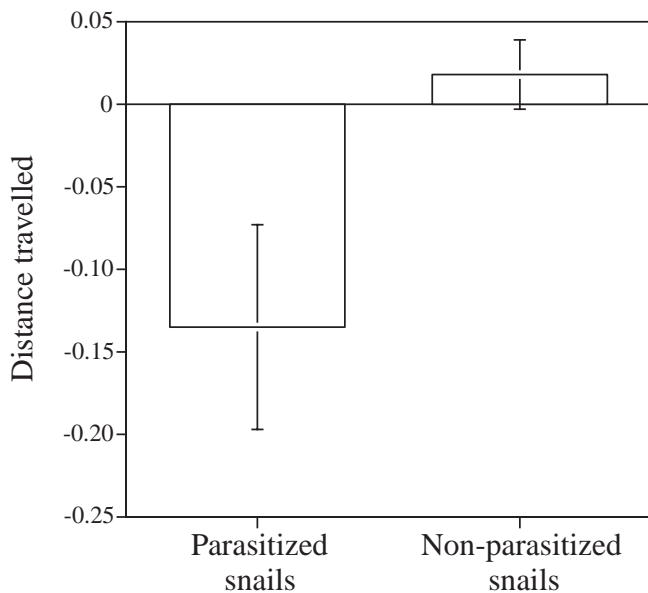
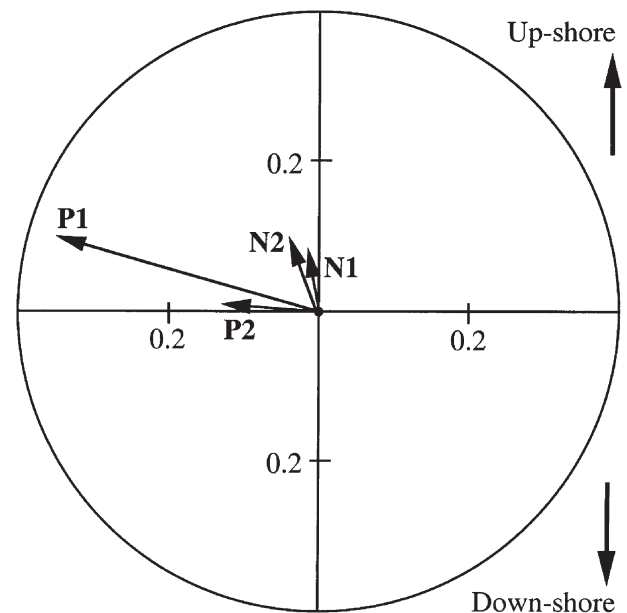


Fig. 5. Mean angles of direction taken by marked parasitized (P) and nonparasitized (N) *D. subrostrata* from two replicates (1 and 2) in the 24 h following their release. The length of the arrows indicates the strength of the mean vectors according to the scale on the axes (0 indicates maximum dispersion and 1 indicates maximum concentration of directions taken by individual snails).



that reported similar observations (Lambert and Farley 1968; Mouritsen and Jensen 1994). This is most likely a pathological result that may have important indirect repercussions for parasitized snails, given the role of mobility in resource acquisition and avoidance of competition or predation by intertidal snails (Underwood 1977; Fairweather 1988; Byers 2000).

Perhaps more interesting than how far parasitized snails move is the issue of where they go. The variation in trematode prevalence observed in marked snails across the three intertidal levels from where they were collected was not consistent between replicates. A consistent pattern could have meant either that infections were more likely to occur at a certain intertidal level or that following infection, snails tend to migrate to that level. The former scenario is always a likely one, because in molluscs that are not mobile, such as buried bivalves, variation in infection levels across the intertidal zone is commonly observed and can only result from variation in the risk of infection or differential predation on parasitized hosts, and not from host movement (Lim and Green 1991; Poulin et al. 2000). However, in the absence of a consistent pattern, the best indication of the area chosen by infected and uninfected snails comes from the recapture data.

Based on the observed density and shell-width distributions of *D. subrostrata* at our study site, the preferred habitat of the snails appears to lie between 10 and 60 m from the low-water mark. Within the lower part of that area, they achieve their largest sizes, whereas they occur at their highest densities (and at only marginally smaller sizes) higher up within that area. In the mark-recapture experiments, the snails were released approximately 60 m above the low-water mark, and thus in an area of high density. There was therefore no reason to expect a marked migration away from that area. Indeed, the weak mean vectors suggest that the directions chosen by dispersing snails, whether they were parasitized or not, showed no strong consistency. The difference in directions chosen between parasitized and nonparasitized snails was statistically significant, but it is difficult to evaluate the biological importance of this result. On the one hand, the results of the two replicates were relatively consistent. This is compelling evidence that snails harbouring trematodes tended to remain at the level where they were released, whereas uninfected snails moved higher up the intertidal zone. Having their snail host remain at midshore may facilitate the transmission of trematodes to their next host, but only if it lives in the lower shore. On the other hand, the considerable dispersion in angles of direction chosen by snails in all groups suggests that their movements included a random element, or that the effect of parasitism was masked by some other environmental factor. So many other variables can influence snail movement (Underwood 1977; Fairweather 1988; Underwood and Chapman 1989; Chapman and Underwood 1994; Byers 2000) that only marked consistency in the directions taken by parasitized and nonparasitized snails can be accepted as evidence for a parasite-induced bias in dispersal direction.

Knowing which intertidal invertebrate serves as the next host for the trematode might serve in assessing whether or not the weak but statistically significant result of the mark-recapture experiments represents adaptive manipulation of snail behaviour by the parasite. At this point the parasite is

only known from its larval stages in *D. subrostrata*. The morphology of the cercariae suggests that it is a member of the family Opecoelidae, therefore its next host would most likely be a crustacean. Large numbers of crabs (the grapsids *Hemigrapsus crenulatus* and *Hemigrapsus edwardsii* and the ocyropodid *Macrophthalmus hirtipes*) from Company Bay and adjacent soft-sediment shores have been dissected and none has been found to harbour trematode metacercariae (A.D.M. Latham and R. Poulin, unpublished data). Other likely candidates include corophiid amphipods. Studies on the North American snail *Ilyanassa obsoleta* have shown how observed biases in habitat preference or direction of dispersal can be matched with a knowledge of the parasite's life cycle (Curtis 1987, 1990; but see McCurdy et al. 2000). When the next host is identified, the results of our mark-recapture experiments can be reinterpreted in the light of its observed spatial distribution. Meanwhile, our results show that the trematode reduces the mobility of infected snails, and possibly also affects their direction of movement and hence their eventual distribution within the intertidal zone. Given that more than 10% of the dissected snails harboured trematodes, the parasite can clearly have important impacts on the population. Our results reinforce Sousa's (1991) call for the inclusion of parasites in models of intertidal community structure.

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