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# Parasitism and the burrowing depth of the beach hopper *Talorchestia quoyana* (Amphipoda: Talitridae)

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Talitrid amphipods spend their days burrowed in sand to avoid predators as well as desiccation and heat stress, although other factors may influence burrowing depth. We investigated the potential role of mermithid nematode parasites in determining burrowing depth in the amphipod *Talorchestia quoyana*. Mermithids grow as parasites inside amphipods until they reach adulthood, when they must emerge from their host into moist sand to complete their life cycle and reproduce. When allowed to burrow to a depth of their choice in experimental situations, large amphipods burrowed deeper than small ones. In addition, deep-burrowing amphipods were more likely to be infected by mermithid nematodes, and harboured longer worms, on average, than amphipods that burrowed close to the sand surface. This last result is not an artefact of the larger size of deep-burrowing amphipods: the increase in worm length with increasing depth was found after statistical correction for host size. In other words, amphipods that burrowed deeper harboured longer worms than expected based on their body size, whereas those that stayed near the surface of the sand column harboured worms shorter than one would expect based on host size. This implies that the greater burrowing depth of infected amphipods is a consequence, and not a cause, of infection. These results emphasize the importance of parasitism as a determinant of the small-scale spatial distribution of their hosts.



Talitrid amphipods, or beach hoppers, are among the most abundant supralittoral detritivores on temperate sandy beaches worldwide (Brown & McLachlan 1990). These semiterrestrial crustaceans spend the day burrowed in the sand, and come out at night to feed on plant and animal debris brought in by waves and tides and left on the sand surface. Studies on the temporal activity patterns (Scapini et al. 1992; Kennedy et al. 2000) and spatial distribution (Inglis 1989; Marsden 1991; Richardson et al. 1991; Scapini et al. 1992) of beach hoppers indicate that they are not uniformly distributed across their habitat, but instead aggregate under large pieces of debris, such as broken straps of kelp. The main determinants of their nocturnal activity patterns seem to be the avoidance of predation by birds, and of desiccation and heat stress; differences in peak activity periods between adults and juveniles may also serve to reduce intraspecific predation (Kennedy et al. 2000). In contrast, little is known of the determinants of burrowing depth during daytime, except for the influence of certain abiotic factors; for instance, high temperature and low humidity can result in deeper burrowing (Brown & McLachlan 1990).

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The talitrid amphipod *Talorchestia quoyana* is the most common beach hopper on New Zealand's beaches (Morton & Miller 1973). It frequently harbours two species of external symbionts, mites and small rhabditid nematodes (Poulin & Rate 2001). These beach hopper symbionts have no detectable effects on their hosts, and use them strictly as a means of dispersal from one patch of debris to another (Rigby 1996a, b; Pugh et al. 1997; Poulin & Rate 2001). In addition, *T. quoyana* is host to a parasitic mermithid nematode, which is superficially similar to *Thaumamermis cosgrovei*, a parasite of terrestrial isopods (Poinar 1981), but most certainly a different species (G. Poinar, personal communication). Mermithids are parasitic only as juveniles. They penetrate the cuticle of their host, usually a terrestrial arthropod, and they develop to large sizes in its body cavity, almost invariably killing it when they emerge from it as adults (Poinar 1983, 1991). Adult worms live freely in water or moist soil, where they mate and lay eggs. Because the hosts of mermithids often live in dry terrestrial microhabitats, timing emergence from the host during the latter's brief visits to suitably humid habitats poses a problem for the worm. In response to this difficulty, many mermithids have evolved the ability to modify the behaviour of their hosts to induce them to seek wet habitats that are suitable

for the survival and reproduction of adult worms (e.g. Poinar 1991; Maeyama et al. 1994; Vance 1996a). The mermithid worms harboured by the beach hopper *T. quoyana* face almost certain death if they emerge from their host close to the sand surface, where the sand is hot and dry. In view of what other mermithid species do, and of the ability of many other parasite taxa to manipulate the behaviour of their hosts to their own ends (Poulin 1995, 1998), we hypothesized that mermithid-infected beach hoppers will burrow deeper into the sand than uninfected conspecifics. This would place the hosts in the deeper, permanently wet sand layer and provide mature parasites ample opportunity to emerge into a habitat suitable for them. Clearly, this modification of host behaviour by the parasite should occur only once the worm has reached adult size.

We tested this hypothesis in a series of experiments on naturally infected beach hoppers. Our apparatus allowed amphipods to settle undisturbed at their chosen daytime depth in the sand, from where they were then removed and dissected. We examined two specific predictions: (1) the frequency and severity of infections should increase with depth, and (2) mermithid worms from deep-burrowing amphipods should be longer, both in absolute terms and relative to the size of the host, than those from hosts close to the sand surface.

## METHODS

We used naturally infected amphipods for our tests; experimental infections are presently not an option because we cannot get parasite eggs and infective stages under laboratory conditions. It is not possible to distinguish infected amphipods from uninfected ones, so we did all tests in ignorance of the infection status of individual amphipods. We obtained *T. quoyana* individuals from Long Beach, just north of Dunedin, South Island, New Zealand. The shore there consists of a sandy beach with a gentle slope, exposed to moderate wave action. We collected amphipods from the sand under piles of dead kelp, along the strandline of tidal debris. They were dug from the top 30 cm of sand, captured by hand, and immediately placed in a container with moist sand for their return to the laboratory. For each experimental series (see below), we collected amphipods from 5–10 patches, separated by 10–50 m, to avoid samples made up only of close kin. Taking into account the patchy distribution of amphipods, we estimate that amphipod density at the site is approximately 200/$m^2$. These amphipods live in a zone parallel to the waves that is about 10 m wide, over a beach >4 km long; since we depleted the equivalent of 6–7 $m^2$, our collections had no impact on the local population.

The apparatus we used to investigate the depth distribution of parasitized and unparasitized amphipods consisted of an opaque PVC tube (10 cm diameter, 45 cm long) standing vertically on a plastic base to which it was glued. We first filled the tube with 500 ml of seawater and then sand up to 1 cm below the top of the tube; we obtained the sea water and sand from Long Beach when we collected the amphipods. We placed two pieces of dead kelp (ca. 3 × 3 cm) on the surface of the sand, and then covered the tube opening with clear plastic after adding the amphipods. Along the height of the tube, at 11-cm intervals starting at the base of the tube, three thin slots stretched along half of the circumference of the tube. These allowed thin metal sheets that fitted the inner contours of the tube to be inserted quickly to separate the sand column into four depth zones, each 11 cm high. A total of five tubes could be used at any one time, and were cleaned after each usage.

We carried out five series of five replicates during November 2000, that is, on five occasions we used the five tubes with different groups of amphipods. We chose to do the study at this time of year because that is when most mermithids mature and emerge from their hosts (unpublished data). For each series of replicates, we made a separate collection of amphipods, clean sand and sea water at Long Beach. A series consisted of setting up the tubes on the afternoon of a collection day, and adding 50 randomly chosen amphipods to each tube. Thus, we used 50 individuals in five series of five replicates, for a total of 1250 amphipods. The density of amphipods in each tube corresponds to intermediate densities in the field, observed between the much higher densities seen immediately under stranded pieces of kelp and lower densities found away from kelp. The tubes were left undisturbed at room temperature, 18 ± 1°C (ca. 2°C warmer than field temperature during the night but the same as daytime field temperature), and under a natural photoperiod for 24 h before we separated the sand columns into the four depth zones. Given the circadian periodicity in beach hopper activity, 24 h is sufficient to allow them to settle at their preferred daytime depth. We then emptied the sand of each depth zone into separate plastic bags, and searched it for amphipods. All recovered amphipods were decapitated and then preserved in 70% ethanol. Later, we classified them as juveniles (≤10 mm), males (on the basis of their large specialized gnathopods) and females, and measured body length (anterior end of the cephalon to posterior tip of the telson). Each amphipod was also dissected. The number of mermithid worms, if any, inside each amphipod was determined, and each worm was straightened without stretching and measured to the nearest mm. We considered two measures in the analyses: (1) total worm length, which is the sum of the lengths of all worms in an amphipod, and (2) the length of the largest worm found in an amphipod. We also searched the sand of each depth zone for worms that may have emerged from amphipods; when found, we also measured these free worms.

Data on number of worms per amphipod did not meet the assumptions of parametric tests; they were either treated with nonparametric tests, or log transformed for parametric tests. All tests were two tailed. In the main analyses, differences between depth zones in amphipod length, prevalence (absence or presence of mermithids in each amphipod), number of worms per host, total worm length and length of the largest worm, were assessed with generalized linear models. Other factors included in the models were experimental series, tube and host sex; two-way interactions between factors were also included,

**Table 1.** Summary data on the amphipods used in each of the five experimental series

| Series | Total no. of amphipods | Juveniles | Males | Females (with offspring) | Length (mm, $\bar{X}$±SD) | Prevalence of infection (%) |
|---|---|---|---|---|---|---|
| 1 | 179 | 30 | 41 | 108 (6) | 12.9±2.8 | 33.5 |
| 2 | 250 | 20 | 92 | 138 (3) | 14.2±3.3 | 34.4 |
| 3 | 216 | 25 | 78 | 113 (1) | 13.3±2.8 | 28.2 |
| 4 | 244 | 8 | 83 | 153 (4) | 15.2±3.0 | 40.2 |
| 5 | 250 | 1 | 98 | 151 (3) | 15.2±2.2 | 20.4 |
| Total | 1139 | 84 | 392 | 663 (17) | 14.3±3.0 | 31.3 |

but only significant ones are reported. We used amphipod length as a covariate in analyses of the different measures of infection by mermithids.

## RESULTS

Of the 1250 amphipods used in the experiments, 13 were not found again and may have escaped during processing, 97 were dead at the end of the 24 h in the tubes, and one contained an encysted juvenile acanthocephalan parasite. These amphipods were all excluded from further analyses, leaving a total of 1139 amphipods in the study. Dead amphipods were common only in experimental series 1 and 3 (Table 1), most likely because it had rained shortly before collection in the other three series and the sand used on those occasions contained more water than in series 1 and 3. In those two series combined, live amphipods were slightly larger (two-tailed $t$ test: $t_{486}$=4.367, $P$=0.0001) and harboured more worms per host (Mann–Whitney $U$ test: $Z$=2.628, $N_1$=395, $N_2$=93, $P$=0.009) than dead amphipods, although they did not differ with respect to total worm length ($t_{135}$=0.523, $P$=0.602) or length of the largest worm harboured ($t_{135}$=0.195, $P$=0.846). Our main reason for excluding dead amphipods from the analyses was that there was no way of knowing whether they had just lost worms or not.

There were more females than males or juveniles among the amphipods we studied, with some of the females carrying offspring in their brood pouch (Table 1). Preliminary analyses suggested that whether amphipods were juveniles or adults had little impact on parasitism or burrowing depth. For instance, there was no difference between juveniles, males and females with respect to the number of worms per host (Kruskal–Wallis test: $H_2$=2.547, $P$=0.280). For this reason, we pooled all individuals irrespective of developmental stage because amphipod body size on its own appeared to be a much more important factor (see below).

Almost a third of the amphipods we examined harboured at least one mermithid worm (Table 1). The maximum number was 33 worms in one host, although the majority of parasitized amphipods harboured only one or two worms (Fig. 1). Host size appeared to be a key determinant of infection levels. Parasitized amphipods were significantly larger than unparasitized ones (two-tailed $t$ test: $t_{1137}$=6.674, $P$=0.0001), and amphipod

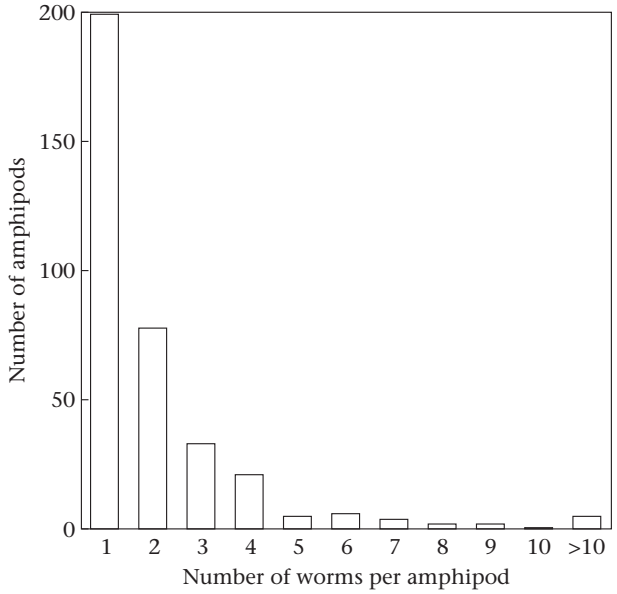


**Figure 1.** Frequency distribution of numbers of mermithid worms per amphipod host among the 356 infected amphipods found in the study.

length correlated with the number of worms per host (Spearman rank correlation: $r_S$=0.331, $N$=356 infected amphipods, $P$=0.0001). Amphipod length also correlated positively with total worm length (product–moment correlation: $r_{354}$=0.358, $P$=0.0001) and the length of the largest worm in a host ($r_{354}$=0.244, $P$=0.0001). There is much scatter in these relationships (Fig. 2), and the low $P$ values reflect the large sample sizes rather than strong effects. The patterns tend to become clearer, however, when examined separately for each experimental series (e.g. amphipod length versus length of the largest worm: series 1: $r_{58}$=0.411, $P$=0.001; series 2: $r_{84}$=0.421, $P$=0.0001; series 3: $r_{59}$=0.460, $P$=0.0001; series 4: $r_{96}$=0.216, $P$=0.033; series 5: $r_{49}$=0.513, $P$=0.0001).

Table 2 shows the results of the generalized linear models. There was significant variation among the five series in terms of amphipod length but no consistent differences in amphipod length between the five replicate tubes within each series. Across all series, amphipod length tended to increase with the depth at which they were recovered (Fig. 3), and males were longer than females (Table 2). When these analyses were repeated

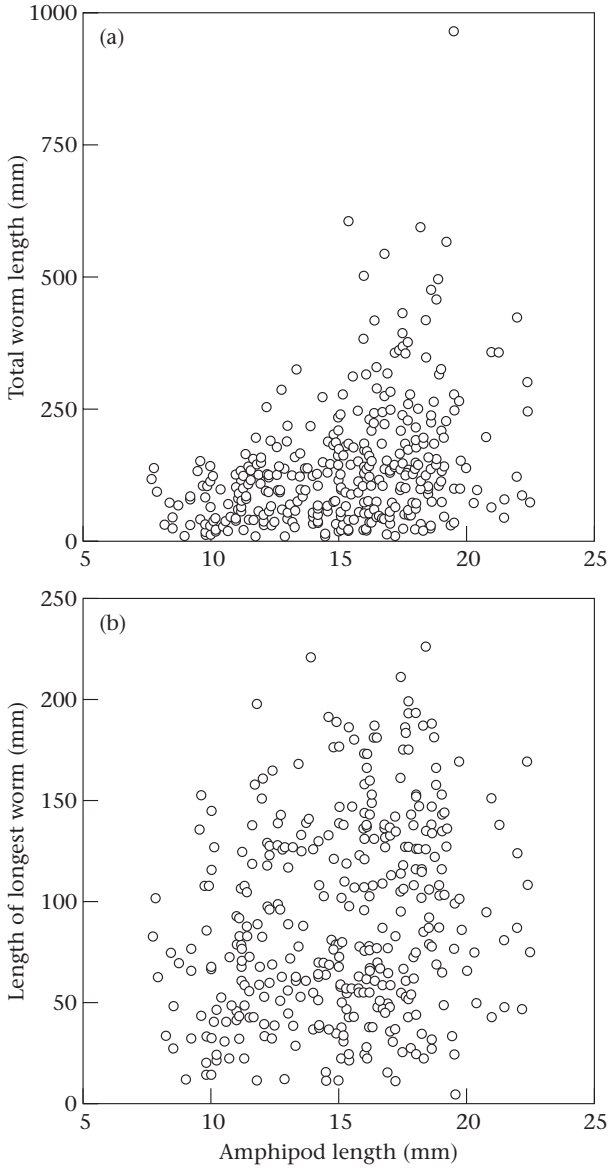


**Figure 2.** (a) Total mermithid worm length and (b) length of the longest worm as a function of the size of the amphipod host.

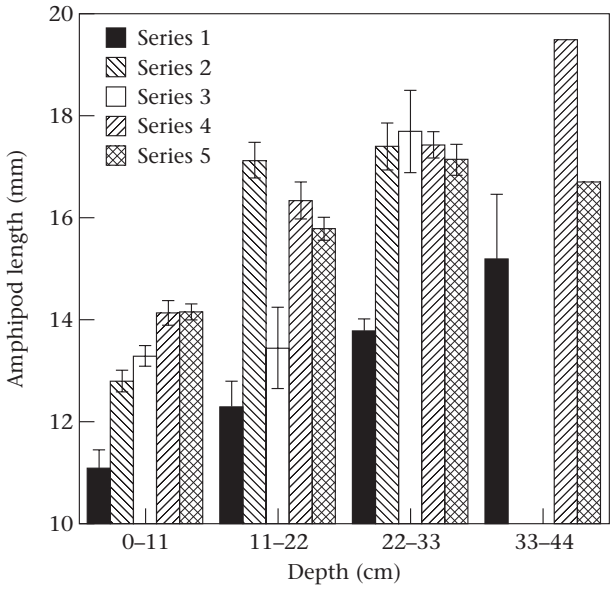


**Figure 3.** Amphipod length ($\bar{X}\pm$SE) as a function of the depth zone in which they were found. Data are presented separately for each of the five experimental series. Sample sizes for each depth, pooled across series, are 698, 218, 214 and 9 amphipods, respectively.

including only unparasitized amphipods, exactly the same pattern emerged, and thus the size segregation of the amphipods at different depths was independent of mermithid infection. There were no significant interactions between any pair of factors in analyses of amphipod length.

The prevalence of infection (or the percentage of amphipods parasitized) and the mean number of worms per amphipod tended to increase with depth (Fig. 4); experimental series, tube and host sex also influenced these variables (Table 2). In both these models, there were significant interaction terms between experimental series and tube, and between depth and sex (all $P<0.01$). These results are independent of amphipod body size, which was included as a covariate in both models (both $P<0.001$).

For analyses of mermithid length, we used only data from infected amphipods. Total worm length did not increase significantly with depth in the sand ($P=0.057$; Fig. 5a), perhaps because of variability among experimental series (Table 2). The length of the largest worm in parasitized amphipods, however, increased significantly with depth in the sand, and was not influenced by any other factor (Fig. 5b, Table 2). All interaction terms were

**Table 2.** Summary of the generalized linear models testing for the effects of four factors on amphipod length and different measures of infection by mermithids

| Variable | Experimental series | Tube | Depth | Host sex |
|---|---|---|---|---|
| Amphipod length (mm) | $F_{4,1107}=39.21$** | $F_{4,1107}=1.73$ | $F_{3,1107}=79.10$** | $F_{1,1107}=10.47$** |
| Prevalence (presence/absence) | $F_{4,1106}=11.10$** | $F_{4,1106}=5.76$** | $F_{3,1106}=19.31$** | $F_{1,1106}=15.58$** |
| No. of worms per host | $F_{4,1106}=17.30$** | $F_{4,1106}=5.58$** | $F_{3,1106}=18.99$** | $F_{1,1106}=19.42$** |
| Total worm length (mm) | $F_{4,326}=2.82$* | $F_{4,326}=0.28$ | $F_{3,326}=2.53$ | $F_{1,326}=2.92$ |
| Largest worm length (mm) | $F_{4,326}=1.44$ | $F_{4,326}=0.02$ | $F_{3,326}=3.21$* | $F_{1,326}=0.02$ |

*$P<0.05$; **$P<0.005$.

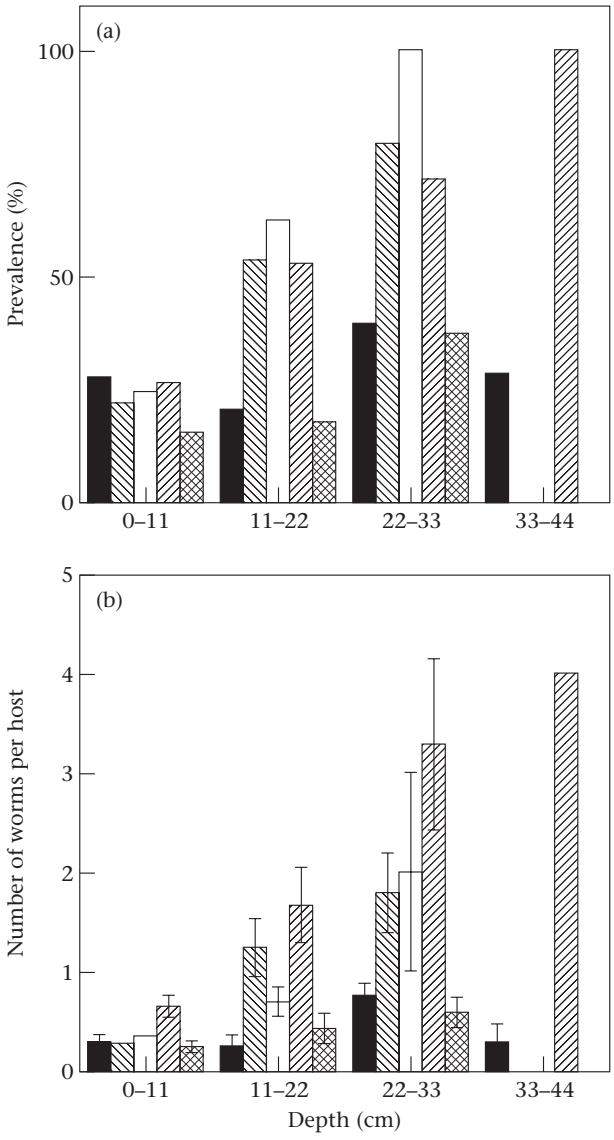


**Figure 4.** (a) Prevalence (percentage of infected amphipods) and (b) number of mermithid worms per host ($\bar{X}$±SE) as a function of the depth zone in which amphipods were found. Data are presented separately for each of the five experimental series (see legend in Fig. 3). Sample sizes for each depth, pooled across series, are 698, 218, 214 and 9 amphipods, respectively.

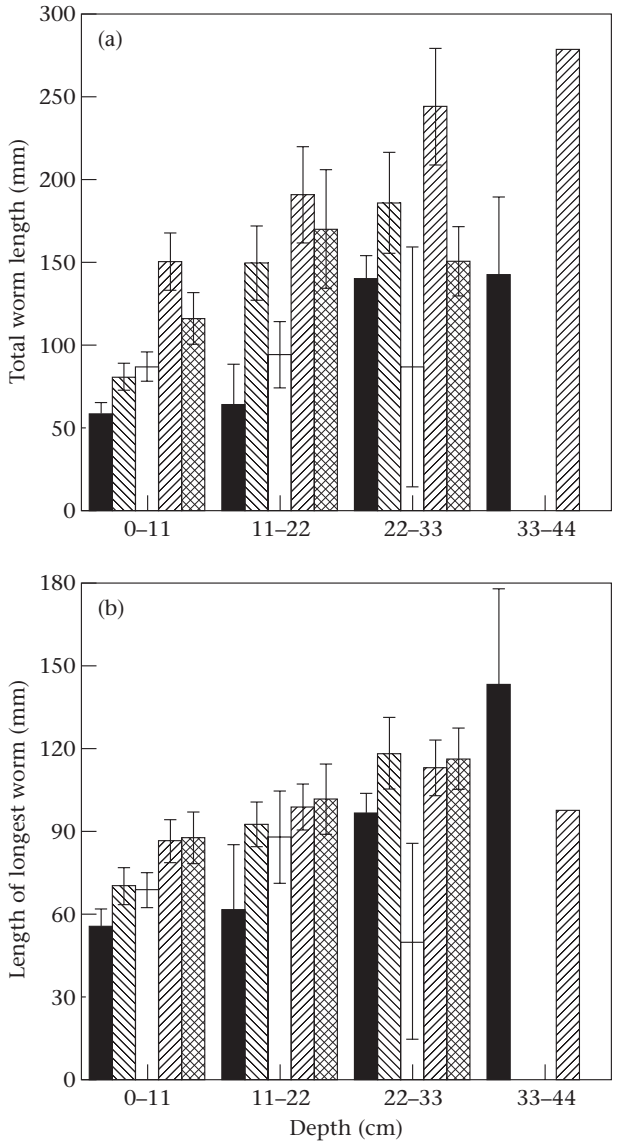


**Figure 5.** (a) Total mermithid worm length and (b) length of the longest worm per amphipod ($\bar{X}$±SE), as a function of the depth zone in which amphipods were found. Data are presented separately for each of the five experimental series (see legend in Fig. 3). Sample sizes for each depth, pooled across series, are 161, 84, 108 and 3 infected amphipods, respectively.

nonsignificant in the two analyses of worm length. The models account for amphipod length as a covariate ($P$=0.0001 and $P$=0.032, respectively), and thus indicate that amphipods that burrowed deeper tended to harbour longer worms than expected based on their body size, whereas those that stayed near the surface of the sand column tended to harbour worms shorter than one would expect based on host size.

Three worms were found free in the sand from two tubes in series 4. They measured 95, 136 and 160 mm. In the distribution of worm lengths of all mermithids found in amphipods, these three worms would fall in the 77th, 90th and 95th percentiles, respectively; in the distributions of lengths of the longest worms per host only, they would be in the 57th, 81st and 91st percentiles. This suggests that there is considerable flexibility in the size at which these mermithid worms mature and leave their amphipod hosts.

## DISCUSSION

The ability of parasites to manipulate the behaviour of their hosts in ways that facilitate the completion of their life cycle has evolved separately in many parasite lineages (Poulin 1995, 1998), including mermithid nematodes (Maeyama et al. 1994; Vance 1996a). The beach hopper *T. quoyana* is parasitized by a mermithid that must emerge in moist sand in order to survive and reproduce. Here we found that the frequency of infection and the

mean number of worms per host increased with the burrowing depth chosen by beach hoppers. More importantly, the length of the longest worm also tended to increase with depth in the sand. This was true after correction for host size. The trend is statistically significant across all five experimental series despite the variability in sand moisture among series, owing to varying weather conditions prior to collections, and the small number of amphipods that settled in the deepest zone in the experimental apparatus (perhaps because the sand there was saturated with water). The fact that total worm length did not increase significantly with burrowing depth suggests that the longest worm may be driving changes in host behaviour, and that other worms are essentially passengers with no additional impact on the host.

Parasitism by mermithids may thus be an important biotic factor influencing burrowing depth in beach hoppers. In a previous study on this host–parasite system, the prevalence of infection varied significantly among patches of stranded kelp where the densities of beach hoppers are highest (Poulin & Rate 2001). Therefore, the importance of parasitism can vary spatially, even on small spatial scales. In samples collected at Long Beach in November 1999, Poulin & Rate (2001) found an overall prevalence of infection of slightly less than 10%, three times lower than that found in this study, from a sample collected at the same location exactly 1 year later. The reasons for this dramatic increase are not clear, but since mermithids kill their host when they emerge from it, parasitism appears to have somehow become a major mortality factor in the beach hopper population in just 1 year.

Although the increase with burrowing depth in the length of the largest worm per host supports the existence of parasite-induced changes in host behaviour, there are still significantly more infected amphipods, regardless of worm sizes, deeper in the sand than at the surface. This could reflect a higher exposure to mermithids for beach hoppers that intrinsically prefer to burrow deep in the sand, or it could also be the product of parasite manipulation of host behaviour. What could be the benefits of inducing the host to burrow deeper during the daytime for a small worm not even close to being ready for emergence? Benefits for the host are probably not an issue: arthropods harbouring these fast-growing worms are soon castrated, and eventually destined to die (Wülker 1964; Poinar 1991). It is evolutionarily dead from the moment it is castrated, and soon becomes nothing more than a vehicle for the parasite genes. Some host behaviour may still be expressed, however; there is no selection on amphipods to stop doing what they did prior to infection, and they may still display some of their former normal behaviour. This residual host behaviour may create noise in the expression of any parasite-induced behavioural alteration. Potential benefits for small, growing mermithids that induce their hosts to burrow a few cm deeper include avoiding desiccation and heat stress. In addition, oystercatchers (*Haematopus unicolor* and *H. ostralegus*) are commonly seen during the day probing the sand around stranded kelp. Because of the length of their bill, any beach hopper and its parasites deeper than 10 cm are probably safe from these predators.

Most studies using naturally infected hosts to investigate parasite-induced changes in behaviour face a common shortcoming (Poulin 1995). These studies compare the behaviour of infected and uninfected hosts; without experimental infection, it is difficult to determine whether the difference in behaviour is the consequence of infection, or its cause. In our case, it could be argued that beach hoppers that have an intrinsic preference for burrowing deeper into the sand are exposed to a higher risk of infection by mermithids than those that stay close to the sand surface. If mermithids lay their eggs in the deeper, moist sand layers, this is where their freshly hatched larvae will be seeking hosts. This phenomenon could lead to levels of infection being highest among deeply burrowed hoppers without the need to invoke parasite-induced changes in behaviour. In our study, however, one line of evidence strongly supports the parasite manipulation hypothesis: the size of the longest mermithid per host, even corrected for host size, increased with host burrowing depth. One obvious way to explain this is to postulate that the size of the parasite harboured by an infected beach hopper determines how deep it will burrow, and thus that the pattern we observed is a consequence of the influence of the parasites on host behaviour. There was also a size segregation by burrowing depth among the hoppers, with large uninfected individuals burrowing deeper than their small uninfected conspecifics. This may represent a strategy to reduce interactions among size classes and maybe even intraspecific predation, a factor responsible for differences in the circadian activity patterns of juvenile and adult beach hoppers (Kennedy et al. 2000). In other words, small individuals may remain closer to the sand surface and risk desiccation to avoid intraspecific predation. Growing conditions may also be better for beach hoppers deeper in the sand, and the parasites harboured by deep-burrowing hosts may benefit from this and reach larger sizes, without host manipulation being involved. Whether or not the effect of parasitism acts in parallel with this segregation by host size cannot yet be resolved. If mermithids drive hoppers of all sizes to burrow deeper than usual once the worms reach a certain size, what that size might be is difficult to determine. The fact that the shortest worm we found moving freely in the sand was smaller than many worms found still in their hosts suggests that adult size is a plastic trait in mermithids. The size and condition of the host, and the number and sizes of other worms sharing the same host, possibly combine to determine the final size at maturity. It must benefit the parasite, however, to reach a large size before emerging from the host, because in the lifetime of nematodes fecundity is typically proportional to body size (Poinar 1983).

Effects of mermithid nematodes on the behaviour of their hosts have not been studied in detail but have been reported from a few other systems. For instance, ants harbouring mermithids are driven to throw themselves in open water by their parasite, which must emerge in water as an adult (Meayama et al. 1994). Male mayflies infected

by mermithids adopt a behaviour (and morphology) very similar to female conspecifics, including a mock oviposition in water which ensures the safe return of the worm to an aquatic habitat (Vance 1996a). Other effects of mermithids on host behaviour have also been reported, although they are not directly related to the completion of the parasite's life cycle (e.g. Benton & Pritchard 1990; Vance 1996b). Our results are therefore in line with these earlier investigations.

In summary, we have shown that the daytime burrowing depth chosen by beach hoppers is influenced by parasitism by mermithid nematodes. Other reports in the literature indicate that the spatial distribution of animals can be influenced by parasites, particularly invertebrates in marine systems. For example, the vertical distribution of planktonic chaetognaths (Pearre 1979), the distribution of snails from the lower to the upper intertidal zone (Lambert & Farley 1968; Curtis 1987), the burrowing ability and depth of bivalves (Thomas & Poulin 1998), and the depth distribution of free-swimming gammarid amphipods (Thomas et al. 1995) are all markedly modified by parasitic infection. These earlier studies and the present one all point to an important role for parasites in determining the small-scale spatial distribution of invertebrates in natural systems.

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