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J. Parasitol., 89(4), 2003, pp. 862–864

A Gastropod Scavenger Serving as Paratenic Host for Larval Helminth Communities in Shore Crabs

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ABSTRACT: The whelk *Cominella glandiformis* is an important predator–scavenger of New Zealand intertidal ecosystems; a few whelks can quickly eat all the soft tissues of recently dead crabs. In this study, we demonstrate that whelks can also ingest and act as paratenic hosts for at least 4 helminth species that use crabs as intermediate hosts: metacercariae of the trematode *Maritrema* sp. and of another unidentified trematode, larval acuariid nematodes, and cystacanths of the acanthocephalans *Profilicollis* spp. Large whelks ingest disproportionately more helminth larvae than small whelks, but the survival of parasites during their short stay in the whelks is not affected by whelk size. The majority of metacercariae and nematodes are passed out in whelk feces within 3 days of ingestion, whereas the few cystacanths found did not leave whelks until after that time; no parasite was left in whelks 5 days post-ingestion. Survival of all 4 helminth species was generally very high, though it decreased day by day in 2 species. Given that the avian definitive hosts of all 4 helminths also eat whelks, our results indicate that alternative transmission pathways exist and that parasites can take routes through food webs that are too often ignored.

Trophically transmitted larval helminths inside intermediate hosts face the prospect of being ingested by a range of predators or scavengers that are not suitable definitive hosts. Many helminths avoid this fate by manipulating the behavior or coloration of intermediate hosts in ways that specifically enhance capture by suitable predatory definitive hosts (Moore, 2002; Poulin, 2002). Often, though, the 'wrong' predator consumes the intermediate host. This can constitute a transmission dead-end, unless this predator also happens to be a prey of the definitive host. In such situations, the wrong predator becomes a paratenic, or transport, host for the parasite. In complex natural food webs, the use of alternate transmission pathways through paratenic hosts probably occurs much more frequently than what is recorded in the literature.

For instance, McCarthy et al. (1999) documented that metacercariae of the trematode *Maritrema arenaria* survive passage through the predatory snail *Nucella lapillus*, which feeds on the barnacles serving as second intermediate hosts of the trematode. Because the bird definitive hosts of the parasite feed on the snails as well as barnacles, the trematode can use *N. lapillus* as paratenic hosts. In this study, we investigate the potential role of another predatory snail, the whelk *Cominella glandiformis* (Buccinidae), as paratenic host for a diverse group of larval helminths using shore crabs as intermediate hosts. *Cominella glandiformis* is a common inhabitant of sheltered intertidal mudflats in New Zealand, where it preys on a wide range of invertebrates (Morton and Miller, 1973). Cockles are among its victims, and *C. glandiformis* has recently been shown to be a potential paratenic host for metacercariae of the trematode *Curtuteria australis* (Echinostomatidae), which are encysted in cockles (McFarland et al., 2003). Ironically, *C. glandiformis* is also the first intermediate host of *C. australis* (Allison, 1979); its occurrence in the diet of shorebird definitive hosts of *C. australis* (Fordham, 1970; Baker, 1974) allows it to play 2 distinct roles in the life cycle and transmission of this parasite. Whelks are also acting as scavengers in intertidal areas, feeding on recently dead organisms. Dead crabs are among the larger animals on which the whelk *C. glandiformis* feeds, and given the many larval helminths using shore crabs as intermediate hosts in New Zealand, it is likely that whelks act as paratenic hosts for these helminths as well.

The crabs *Macrophthalmus hirtipes* (Ocypodidae) and *Hemigrapsus crenulatus* and *H. edwardsi* (Grapsidae) are intermediate hosts of the acanthocephalans *Profilicollis* spp. (Polymorphidae), the trematode *Maritrema* sp. (Microphallidae), another unidentified trematode that is possibly a microphallid as well, and larval nematodes (Acuariidae). All these helminths complete their life cycles when ingested by shorebirds such as gulls or oystercatchers. Whelks feed on recently dead crabs, and because they are occasional prey of these same birds (Fordham, 1970; Baker, 1974), they may extend the functional lifespan of all 4 larval parasites beyond the death of the intermediate crab host. Indeed, this study was motivated by the finding of *Profilicollis* spp. cystacanths and *Maritrema* sp. metacercariae in field-collected whelks. The objectives of this study were to determine whether the whelk *C. glandiformis* can act as a paratenic host for the 4 larval helminths of New Zealand shore crabs and to quantify the effect of whelk size and passage time inside the whelk on the survival of the parasites.

Eighty whelks were collected at low tide (mean low water level) from an area of approximately 50 × 50 m at Waipuna Bay, Otago Harbour, South Island, New Zealand (45°47′S, 170°42′E), on 23 September 2002. Whelks were divided into 4 groups (each n = 20) of different size classes (shell height <14 mm, 14–17 mm, 18–21 mm, >21 mm). They were then returned to the laboratory, placed in 4 separate aquaria (24 × 19 cm) containing approximately 10 cm of seawater, and starved for 72 hr. All whelks stopped passing feces after this 72-hr period.

At the end of the starvation period, the whelks were fed similarly sized (approximately 30-mm carapace width) crabs (*M. hirtipes*) collected from Waipuna Bay on 26 September 2002. We killed the crabs by pithing their brain (located directly posteriorly between the crab's eyes); freshly killed crabs were necessary because we required viable parasites. The carapace of each crab was lifted slightly to allow the whelks easy access to the body cavity of the crabs. Two crabs were placed in each of the 2 aquaria containing whelks from the 2 smaller-size classes, whereas whelks from the 2 larger-size classes were fed 3 crabs. Whelks were allowed to feed on the crabs for 3 hr, before being removed from their aquaria and placed in individual petri dishes each containing a small amount of seawater.

Whelk feces were examined every 24 hr (for 120 hr) under a stereomicroscope for the presence of acanthocephalan cystacanths, trematode metacercariae, or nematode larvae. Once the feces had been examined, they were removed from the petri dishes, the dishes were washed, and clean seawater was added. Whelks were never seen feeding on their feces, and thus egested parasites were not reingested by the whelks between fecal examinations. The viability of metacercariae and nematode larvae was assessed during the examination of whelk feces, i.e., if they were intact and moving they were deemed to be viable. Many metacercariae had excysted in the feces but were still active. To validate our assessment on the viability of cystacanths and encysted metacercariae after their passage through the whelk's digestive system, in vitro excystment was carried out. Cystacanths and a sample of metacercariae were incubated for 1 hr at 40 C in petri dishes containing an excystment solution that mimics the chemical conditions inside a bird's intestine (see Irwin et al., 1984). The solution consisted of 5 ml of bicarbonate saline (0.8% w/v sodium chloride and 1.5% w/v sodium bicarbonate) containing 0.8% w/v sodium taurocholate, 0.3% w/v trypsin, and 5 ml 0.02 M hydrochloric acid containing 0.8% w/v L cysteine (Irwin et al., 1984). After incubation, parasite larvae were examined under a stereomicroscope; because they excysted and were viable, our assessment based on movement was validated. At the close of the final fecal examination (120 hr), all whelks were dissected to see whether any crab parasites had remained in the whelk's digestive system.

Our results show that larvae of all 4 helminths survive passage in whelks. Mean numbers of trematode metacercariae and nematode larvae egested by whelks during the experiment varied significantly among the whelk size classes (Kruskal–Wallis test, all $P < 0.0001$). As a rule, more parasites passed out of larger whelks (Fig. 1). The differences are too pronounced to be the mere outcome of the fact that we fed 1 extra crab to the 2 largest size classes. There was no difference among whelk size classes, however, with respect to the percentage of metacercariae or nematodes that were viable (Kruskal–Wallis test, all $P > 0.25$). The patterns also apply to the acanthocephalan *Profilicollis* spp., although only 5 whelks passed out cystacanths, all of them viable: 1 of the whelks was in the 18- to 21-mm size class, whereas the other 4 were >21 mm.

In total, 133 *Maritrema* metacercariae, 1,200 metacercariae of the unidentified trematode, and 115 larval acuariid nematodes were recovered. Of all trematode metacercariae and nematode larvae passed out by whelks, the greatest proportions were recovered 48 hr after ingestion, followed by 72 hr postingestion; very few were recovered after that (Fig. 2). Although only 7 *Profilicollis* cystacanths were recovered, none came out of whelks before 72 hr postingestion (Fig. 2). At the end of the experiment, no parasite was found during the dissection of the whelks.

The survival of *Maritrema* sp. metacercariae appeared unaffected by passage time through the whelk (Fig. 2). In contrast, the survival of both the other trematode and the larval nematodes tended to decrease with time in the whelks, suggesting that the extra transmission time they achieve by using whelks as paratenic hosts is more limited than that for *Maritrema* sp. metacercariae. In addition, a negative relationship was found between the total number of larval nematodes passing out

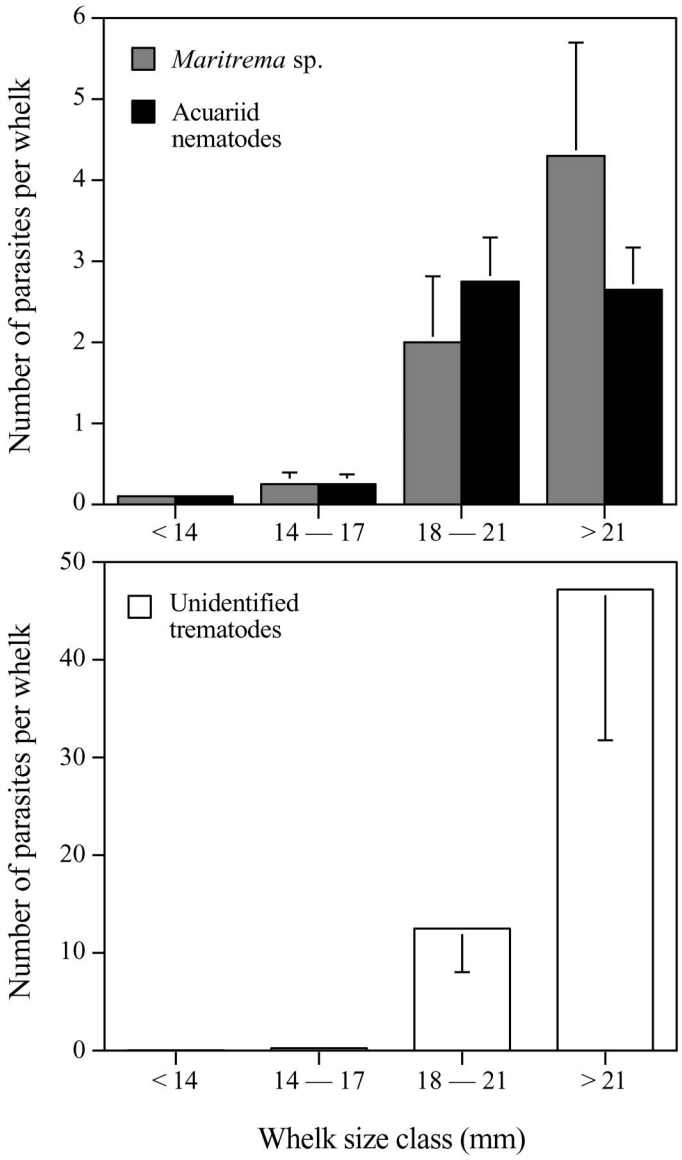

FIGURE 1. Mean (±SE) number of parasites passed out by whelks, *Cominella glandiformis*, of different sizes during the experiment. Data are presented separately for 3 parasite species and include whelks that did not egest any parasites (n = 20 whelks in each size class).

of a whelk and the percentage that were alive (Spearman rank correlation: $r_s = -0.362$, n = 40 snails that passed out nematodes; $P = 0.0236$). This density-dependent mortality suggests that ingestion of large numbers of nematodes by a whelk may be associated with greater likelihood of damage to these nematodes. Indeed, most dead nematodes recovered in whelk feces had visibly damaged cuticle, possibly as a result of the whelk's mode of feeding. No such relationship was observed for the 2 trematode species (both $P > 0.60$), whereas all acanthocephalans recovered were viable.

Preliminary observations indicated that all larval helminths found in crabs are viable; it is clear that if any of them die in a crab, they do not persist for very long. Therefore, we can assume that all larval helminths ingested by whelks in this study were viable. It is not clear whether the metacercariae that excysted inside whelks would still be infective to birds should the latter feed on whelks. Even if they were not, our experiment demonstrates that a substantial proportion of larval helminths survive passage through whelks.

Our results also show that considerable numbers of larval helminths

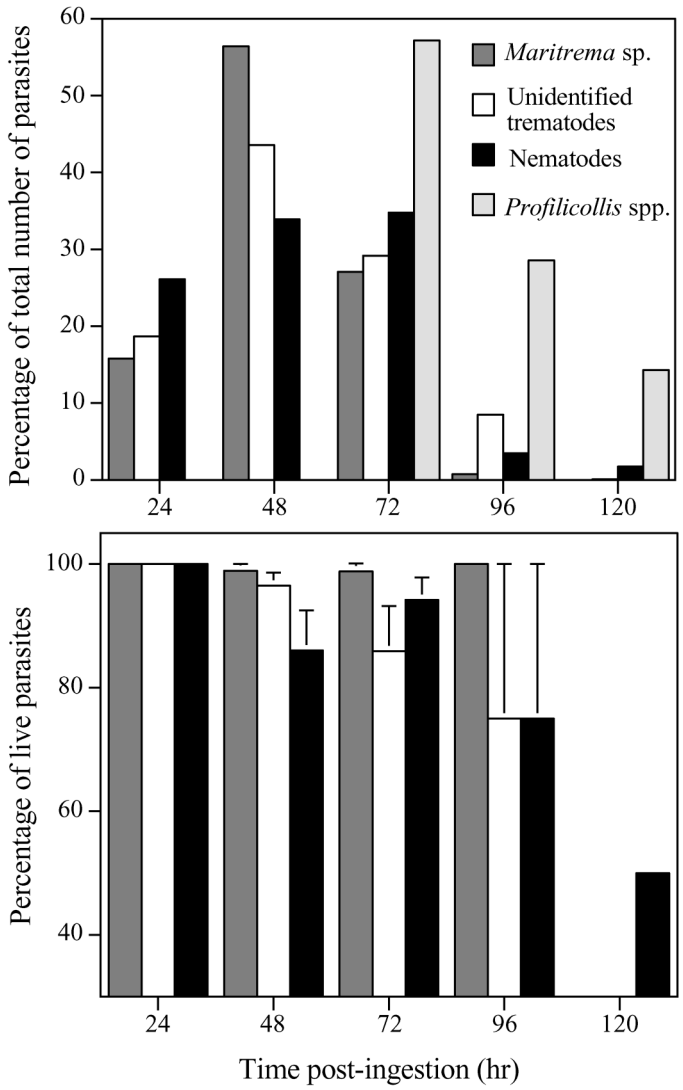

FIGURE 2. Percentage of the total number of parasites passed out by whelks, *Cominella glandiformis*, at different times after ingestion (top), and mean percentage (±SE) of live parasites passing out of whelks as a function of time postingestion (data on *Profilicollis* spp. not shown). Data include only whelks that egested parasites: n = 26 for *Maritrema* sp., n = 37 for the unidentified trematode, n = 40 for acuariid nematodes, and n = 5 for *Profilicollis* spp.

can be ingested by whelks feeding on dead crabs and that these helminths can survive up to 5 days inside the whelks. To our knowledge, this is the first report on predator–scavenger snails acting as paratenic hosts for larval nematodes or acanthocephalans. Given the large size (approximately 1.5 × 1 mm) of *Profilicollis* cystacanths, it is remarkable that they can be ingested intact by *C. glandiformis*. Only a fraction of the acanthocephalans present in the crabs was ingested by whelks; large numbers were found scattered over the remains of the crabs after the whelks had finished feeding. Their ingestion appears possible only by the largest whelks, most likely because of size constraints. Acanthocephalans also tended to take longer to be passed out of whelks; it is possible that their size causes them to remain temporarily lodged inside the whelk's digestive tract.

This study and that of McFarland et al. (2003) show that whelks extend the transmission window of at least 5 helminth species for a few days beyond the death of their intermediate hosts. This list should probably also include a sixth species, *Ascarophis* sp. (Nematoda: Cystidicolidae), a parasite of the same crabs in adjacent areas (Moravec et al., 2003). This nematode is a fish parasite, and several fish species are known to regularly prey on the crabs (McLay, 1988), some of which may also feed on whelks. Given that whelks also feed on many other invertebrates that may serve as intermediate hosts to other helminths, they may harbor a rich community of temporary residents in their gut. Shorebirds regularly feed on whelks and other gastropods (Fordham, 1970; Baker, 1974), and thus these whelk passengers still have a chance of completing their life cycles. For certain invertebrates, the probability of predation or scavenging by whelks is relatively high (e.g., cockles; Ansell, 2001). Our own field observations suggest that every dead crab is within minutes the focus of a group of feeding whelks; often this involves a gull abandoning a partially eaten crab. After the death of the intermediate host, there is thus a second-chance possibility of transmission for all crab parasites if they have not been initially ingested by bird definitive hosts.

The finding of cystacanths and metacercariae in field-collected whelks that inspired the present study gives an indication of the importance of the phenomenon in nature. Of the 62 whelks dissected (also originating from Waipuna Bay), 2 harbored *Profilicollis* spp. cystacanths and 5 harbored between 3 and 7 *Maritrema* sp. metacercariae. From these data, it appears that only a small proportion of the total parasite populations is passing through whelks at any one time. For survival in a whelk to increase the parasites' transmission success, they would need to adapt to this second-chance transmission, by increasing their residence time in whelks, for instance. Whether or not this is the case, our results illustrate the existence of alternative routes of transmission for many helminths, and they emphasize the need to consider parasite life cycles in the context of complex food webs and not merely as part of simple predator–prey systems.

We thank Jane Duthie for technical assistance. This research was partially supported by a grant from the Marsden Fund.

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