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The Marine Gastropods *Crepidula plana* and *Crepidula convexa* Do Not Serve as First Intermediate Hosts for Larval Trematode Development

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ABSTRACT: Although it is commonly assumed that all gastropod species serve as hosts for larval stages of one or more trematode species, the marine gastropod *Crepidula fornicata* seems not to serve as such a host. In this study, we sampled populations of the related species *Crepidula plana* and *Crepidula convexa* from Rhode Island and Massachusetts, U.S.A., to determine if any individuals served as hosts for larval trematodes. No signs of parasitic infection were found, although up to 14% of co-occurring periwinkles (*Littorina littorea*) were so infected. Although most research has focused on known associations between larval trematodes and their gastropod hosts, we suggest that additional work focus on understanding why some gastropod species seem immune, or at least relatively immune, to infection by larval trematodes.

KEY WORDS: Calyptraeidae, *Crepidula*, *Cryptocotyle lingua*, Gastropoda, intermediate hosts, *Littorina*, Massachusetts, Rhode Island, periwinkles, trematode.

The trematode life cycle almost always requires at least 2 intermediate hosts (Hyman, 1951, p. 250), with the first intermediate host usually being a gastropod (Hyman, 1951, p. 256; Thieltges et al., 2008). Although it is commonly assumed that all gastropods serve as intermediate hosts for at least some trematode species (e.g., Hyman, 1967, p. 380; Fredensborg and Poulin, 2006), it is becoming clear that some gastropod species do not, or only rarely, serve such roles (reviewed by Pechenik et al., 2001). Less than 10% of marine gastropod families contain species that are known to serve as first intermediate hosts for trematodes (Pechenik et al., 2001).

The Calyptraeidae is a large group (more than 78 species; Collin, 2003) of suspension-feeding marine gastropods. The genus *Crepidula* alone has more than 60 species (Henry et al., 2010). Few species in this group have been examined as potential intermediate hosts for trematode infection. Pechenik et al. (2001) examined 136 individuals of *Crepidula fornicata* taken from field sites in both Massachusetts and Rhode Island and found no evidence of larval trematode infection in these snails. Similarly, Thieltges, Krakau, et al. (2006) found no evidence of infection among 124 individuals of *C. fornicata* taken from the Wadden Sea. In the present study, we examined 2 additional species of *Crepidula* from New England, *Crepidula plana* and *Crepidula convexa*, to determine whether these snails served as intermediate hosts for larval trematode development.

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MATERIALS AND METHODS

Individuals of *C. plana* and *C. convexa* were sampled in summer 2010, twice in July and once in August, at the same field sites sampled previously for *C. fornicata*: Bissell Cove, Rhode Island, U.S.A. (41°35′50″N, 71°25′53″W) and Nahant, Massachusetts, U.S.A. (42°26′10″N, 70°55′58″W). Because infected snails can be very patchy in their distribution (Curtis, 2007; Byers et al., 2010), we collected snails over dozens of meters of surface. In total, we examined 114 individuals of *C. plana* and 103 individuals of *C. convexa*, covering a wide range of shell lengths (Table 1). These 2 gastropod species are not found in high numbers at these field sites, so we believe that we sampled a substantial fraction of the local populations.

We also examined more than 264 individuals of the common periwinkle, *Littorina littorea*, collected from the same sampling sites. The periwinkles were collected to serve as positive controls for the presence of larval trematodes, as they are well-documented as hosts (e.g., Pohley and Brown, 1975; Pohley, 1976; Huxham et al., 1993; Galaktionov and Skirnisson, 2000; Pechenik et al., 2001; Curtis, 2002; Theiltges, Krakau, et al., 2006; Theiltges, Strasser, and Reise, 2006; Theiltges et al., 2009). In addition, most of the *C. convexa* individuals we collected were using periwinkles as substrate, and thus the periwinkles were collected along with *C. convexa*.

Snails of all 3 species were collected intertidally at low tide from Massachusetts and Rhode Island and then shipped to Lafayette College in Styrofoam coolers; the animals were wrapped in moist paper toweling and cooled with ice packs during transit.

Snails were examined as described in Curtis (1997). In brief, shell length was measured with vernier calipers to the nearest 0.1 mm. The snail's shell was then opened with a hammer, and the body was removed to a Petri dish half-filled with artificial seawater (~30 ppt). We were not able to determine unequivocally the sex of the individual littorines from this population.

Our examinations emphasized the gonad and the digestive gland, but the other organs were also examined. Tissues or

Table 1. Sampling information for the periwinkle *Littorina littorea* and 2 *Crepidula* species collected intertidally from Rhode Island (RI) and Massachusetts (MA), U.S.A., in 2010.

		L. littorea			*C. plana*			*C. convexa*		
			Shell length (mm)			Shell length (mm)			Shell length (mm)	
Sampling date	Location	*N*	Mean ± SD	Range	*N*	Mean ± SD	Range	*N*	Mean ± SD	Range
14 July 2010	RI	66	15.0 ± 1.1	12.9–17.50				70		6.0–13.0
19 July 2010	MA	100	20.92 ± 2.37	15.2–27.6	14	14.29 ± 8.44	7.2–38.1	33	10.8 ± 3.0	5.4–16.9
10 August 2010	MA	50	22.5 ± 2.36	17.7–26.9	100	15.78 ± 7.58	5.8–34.9			

organs containing larval trematodes or suspected of having larvae were examined further by placing tissues between a slide and cover slip with a drop of salt water, and then viewing the preparation at either ×100 or ×400 using a compound microscope.

RESULTS

We found no evidence of larval trematode infection in either of the 2 *Crepidula* species sampled from either of the 2 locations. In contrast, periwinkles collected from the same locations were infected with larval trematodes: 3% of snails from Rhode Island were infected, 11% of snails from Massachusetts in the first sampling were infected, and 14% of Massachusetts snails in the second sampling (10 August 2010) were infected.

Infected individuals of *L. littorea* mostly harbored *Cryptocotyle lingua*, although a few individuals from Massachusetts were infected with unidentified armatae cercariae. As reported earlier (Pechenik et al., 2001), these unidentified cercariae had a small stylet and oral and ventral suckers of about equal size. The cercarial tail was simple and lacked finfolds. The cercariae also lacked a virgula organ, as is typical of virgulate xiphidocercariae.

DISCUSSION

This study supports the growing impression that species in the genus *Crepidula* do not serve as first intermediate hosts for larval trematodes. For example, Linton (1915) sampled individuals of *C. fornicata* and *C. plana* from Cape Cod, Massachusetts, without finding larval trematodes, although he did find infected individuals of the mudsnail *Ilyanassa obsoleta* in his samples. Similarly, Pechenik et al. (2001) found no trematode infection in 136 individuals of *C. fornicata* sampled from the intertidal zones of Rhode Island and Massachusetts, although mudsnails (*Ilyanassa obsoleta*) and periwinkles from the same sampling areas had substantial trematode infections. Finally, Thieltges, Krakau, et al. (2006) examined 124 individuals of *C. fornicata* from 2 sampling sites in the Wadden Sea (northern Europe) and found no infected individuals, even though more than 10% of individuals of *Hydrobia ulvae* and *L. littorea* sampled from those same sites served as first intermediate hosts for a variety of trematode species. Although Cable (1954) suggested that *C. convexa* in Puerto Rico served as a first intermediate host for trematodes in the family Megaperidae, we now know that he misidentified the host; it was certainly not *C. convexa* (R. Collin, personal communication), but as Cable deposited no specimens for further study, we cannot know what the intermediate host actually was. It may have been *Crepidula navicula* (R. Collin, personal communication).

Although no individuals of *C. fornicata*, *C. plana*, or *C. convexa* so far sampled have been found to be acting as first intermediate hosts for any trematode species, Aitken-Ander and Levin (1985) found metacercarial cysts, juveniles, and adults of the digenetic trematode *Proctoeces maculates* in individuals of *Crepidula convexa* collected from Jamaica Bay, New York, and metacercarial cysts in specimens of *C. convexa* collected from Quissett Harbor, Massachusetts (Cape Cod); those individuals of *C. convexa*, however, contained no cercariae. Thus, *C. convexa* can apparently serve as a host for the trematode *P. maculates*, but not as the first intermediate host.

These same researchers (Aitken-Ander and Levin, 1985) found no trematodes of any developmental stage in individuals of either *C. plana* or *C. fornicata* (100 individuals sampled of each species), which were serving as substrate for the infected individuals of *C. convexa*. Why were trematode larvae unable to utilize *C. convexa* as a first intermediate host but able to use them as a second intermediate host? Why were they unable to utilize adjacent individuals of the 2 other snail species in the same genus even as second intermediate hosts? Interestingly, Epstein (1972) reported *C. plana* serving as a second intermediate host in the waters near Galveston, Texas.

Failure of *C. fornicata* to serve as a second intermediate host—and the rarity of *C. plana* serving as such a host—is especially surprising when considering that trematodes are generally less host specific as free-living cercariae (e.g., Ginetsinskaya, 1988; Gibson and Bray, 1994). Possibly the cercariae fail to invade the snails, either through failure of recognition, failure to penetrate, or failure to survive following penetration. Alternatively, they may invade the snail successfully but then fail to encyst. Additional studies are needed to evaluate these possibilities.

Although no *Crepidula* species have so far been documented as first intermediate hosts for trematodes, individuals of a related species *Crepipatella dilatata* (formerly *Crepidula dilatata*—Collin et al., 2007) apparently serve as a first intermediate host for some members of the Microphallidae in Puerto Madryn, Argentina; sporocysts were found in approximately 40% of intertidal individuals of *C. dilatata* that were sampled by C. Gilardoni (C. Ituarte, personal communication). More calyptraeids should be sampled to determine whether any other species serve as first intermediate hosts. This should enable future studies of the factors that make only some species vulnerable to infection, and of the factors that prevent infection in other species.

A large body of literature focuses on the utilization of gastropods as first intermediate hosts by trematode larvae (e.g., Kuris and Lafferty, 1994; Fried, 1997) and on the ways in which trematodes evade host immune defenses (e.g., Cheng, 1967; Bayne and Yoshino, 1989; Adema and Loker, 1997). Much less attention has been paid to gastropods that do not serve as hosts for the first larval stage, and reasons for this situation. As summarized by Pechenik et al. (2001), *C. fornicata*, *C. convexa*, and *C. plana* may simply not release attractants recognized by trematode miracidia, or the miracidia might be attracted to the snails but then may be unable to penetrate through the snail's epithelium, or be unable to survive within the snail after infection.

Negative results always provoke skepticism: Perhaps evidence of primary infection would have been found if more populations had been sampled, or if sample sizes had been larger. However, even if an individual of *C. fornicata*, *C. plana*, or *C. convexa* is eventually discovered serving as a first intermediate host, we would still have to explain why infections in these species are so very rare, even when trematode infections are common in snails of other species sampled from the same habitats.

Crepidula fornicata, *C. convexa*, and *C. plana* are all native to the east coast of the United States. Both *C. fornicata* and *C. convexa*, however, are now widely distributed along the west coast of the United States and elsewhere in the world (Blanchard, 1997; Thieltges et al., 2004; Collin et al., 2006). Over time, it will be important to see whether individuals in some of these invasive populations acquire larval trematode infections that the species apparently avoid in their native range.

The unidentified armatae cercariae that we found in *L. littorea* from both sites fit the description given by Schell (1985, fig. 37). Such cercariae are found in at least 5 diverse families of trematodes. They are not easy to characterize without additional morphological and life history studies. This one seems to be an undescribed cercarial species from *Littorina*; it does not fit the description of other "small cercariae" reported from littorines globally (e.g., Galaktionov and Skirnisson, 2000). The parasite *C. lingua* is found in *Littorina* hosts globally (e.g., Stunkard, 1930; Pohley, 1976; Huxham et al., 1993; Lysne et al., 1998; Curtis, 2002; Thieltges, Krakau et al., 2006) but is understudied in the United States; our collection sites in Rhode Island and Massachusetts, U.S.A., could be useful for future studies on medically and economically important heterophyid trematodes.

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