Trematode Infections in *Littorina littorea* on the New Hampshire Coast

Author(s): Walter J. Lambert, Elise Corliss, Jasper Sha and Jaquay Smalls

Source: Northeastern Naturalist, 19(3):461-474.
Published By: Eagle Hill Institute
DOI: http://dx.doi.org/10.1656/045.019.0308
URL: http://www.bioone.org/doi/full/10.1656/045.019.0308

Trematode Infections in *Littorina littorea* on the New Hampshire Coast

Walter J. Lambert[1,*], Elise Corliss[1], Jasper Sha[1], and Jaquay Smalls[1]

Abstract - The prevalence of parasite infections in *Littorina littorea* (Common Periwinkle) was examined at 16 rocky intertidal sites along the New Hampshire coastline over three summers (2006 to 2008). We sampled over a relatively small spatial scale (21 km) and expected that the prevalence of infections in *L. littorea* would be similar between sites over this sampling area. In total, 1983 snails were collected from areas at mean low water during spring tides. Snail size (mm), gender, and type of parasitic infection were noted for all snails. Eleven percent of snails collected were infected with rediae and cercariae of the trematodes *Cryptocotyle lingua* or *Cercaria parvicaudata*; one snail had a double infection of both trematodes. The prevalence of infection at sites ranged from 1.9% to 30.1%. At all sites, female snails outnumbered male snails, and a greater proportion of females were infected than males. Large snails were more likely to be infected with trematodes at 3 sites, while a higher level of infection was found in small snails at 1 site. Snails at wave-protected sites were more likely to be infected than snails at wave-exposed sites. No relationship was found between the number of gulls at a site and the prevalence of infection. Although temporal variation in levels of prevalence in parasitic infections may explain some of our site-to-site differences, our data show large spatial variation of parasite prevalence in *L. littorea* over a minimum distance of 0.5 km and provide a foundation to test hypotheses concerning the susceptibility of female and immature (small) snails to infection.

Introduction

Parasites are common in marine animals, and many parasites have complex life cycles involving multiple hosts (Rohde 1993). Adult digenetic trematodes occur in the intestines of many marine fish and birds. Their eggs are shed with host feces, and typically infect prosobranch snails either by ingestion or by hatching into miracidia larvae that penetrate the snail directly (e.g., Stunkard 1930, 1950). Following asexual reproduction, cercariae shed from the snails may infect their definitive host either by direct penetration, e.g., avian schistosomes, or more commonly, by encysting in a second intermediate host, which is eaten as prey by the definitive host. Determining the percentage of infected snails, known as prevalence, at field sites over spatial and temporal scales is important because recent work has shown parasitism to impact the population biology, community structure, and food-web ecology of intermediate hosts (Davies and Knowles 2001, Gorbuskin and Levakin 1999, Huxham et al. 1993, Sorensen and Minchella 2001, Thompson et al. 2005, Wood et al. 2007). The prevalence and species richness of larval trematodes in host snails is spatially variable at regional scales (see Thieltges et al. 2009), thus documenting levels

[1]Department of Biology, Framingham State University, Framingham, MA 01701. [*]Corresponding author - wlambert@framingham.edu.

of infection in snail populations at a small spatial scale is important to assess local interactions between host and parasite as well as community dynamics.

Littorina littorea L. (Common Periwinkle) is a prosobranch gastropod that is an abundant and ecologically important grazer (reviewed by McQuaid 1996) in the mid-low intertidal and shallow subtidal zones (Carlson et al. 2006). Periwinkles are herbivores and preferentially consume leafy green algae (*Ulva* spp.) and sporelings of *Fucus* spp., and increased grazing intensity will decrease algal diversity (Lubchenco 1978, 1983). They are principally preyed upon by *Carcinus maenus* (L.) (Green Crab; Perez et al. 2009), and seastars (*Asterias* spp.) also consume periwinkles (W.J. Lambert, pers. observ.). Individuals reach sexual maturity after 1 yr (≥14 mm) and can attain a maximum size (30–35 mm) within approximately 6 yr (Moore 1937). Females release egg capsules from February through July into the water column; these capsules hatch to planktotrophic larvae.

In the Gulf of Maine, the parasite fauna infecting *L. littorea* has been examined along the coast of Nova Scotia (Lambert and Farley 1968), Maine (Pohley 1976, Sindermann and Farrin 1962), the Isles of Shoals (Hoff 1941), and Massachusetts (Pechenik et al. 2001, Stunkard 1983). These studies documented infections of up to five species of trematodes (*Cryptocotyle lingua* (Creplin) [Black-spot Parasite], *Cercaria parvicaudata* Stunkard and Shaw, *Renicola roscovita* (Stunkard), *Microphallus pygmaeus* (Levinsen), and *M. similis* (Jägerskiöld)) in *L. littorea* over relatively large spatial scales, with *Cryptocotyle lingua* as the most common infection.

In particular, *L. littorea* serves as the first intermediate host to the larval stages of *Cryptocotyle lingua* and *Cercaria parvicaudata*. Periwinkles ingest eggs of both parasites deposited in the feces of gulls (*Larus* spp.), the principle definitive host. Cercariae are released from infected snails and infect a second intermediate host; metacercariae of *Cryptocotyle lingua* encyst on fish skin (e.g., herring, *Pleuronectes putnami* (Gill) [Smooth Flounder], *Tautogolabrus adspersus* (Walbaum) [Cunner]), while *Cercaria parvicaudata* infects bivalve mollusks (e.g., *Mytilus edulis* L. [Blue Mussel]). Transmission to the definitive host is by ingestion of the second intermediate host (Galaktionov and Dobrovolsky 2003; Stunkard 1930, 1950).

In general, the New Hampshire coast has been mostly ignored among studies investigating the prevalence of trematode parasites in *L. littorea.* We chose to direct our sampling effort along the New Hampshire coastline (21 km) with a minimum distance between sites of 0.5 km. Since the dispersal of these trematodes relies on the movements of their intermediate (fish) and definitive hosts (gulls), which appear to confer high levels of dispersal, we expected the prevalence of parasitic infections in populations of *L. littorea* to have similar levels of infection over relatively small distances. We focused on snail gender, shell size, and the presence of gulls as criteria that could potentially influence parasitic infections in snails, but do not directly assess seasonal and annual variation within and among the sites we visited. Our sampling over a smaller region compared to other studies shows a bias for infection in female and sexually mature snails in this area and establishes a foundation for future tests.

Methods and Materials

Fifteen rocky intertidal sites from Portsmouth to Seabrook, NH, and 1 site at Star Island, Isles of Shoals (see Fig. 1), were sampled at morning spring low-tide periods between June and September (2006, 2007, and 2008) (Table 1). Sampling

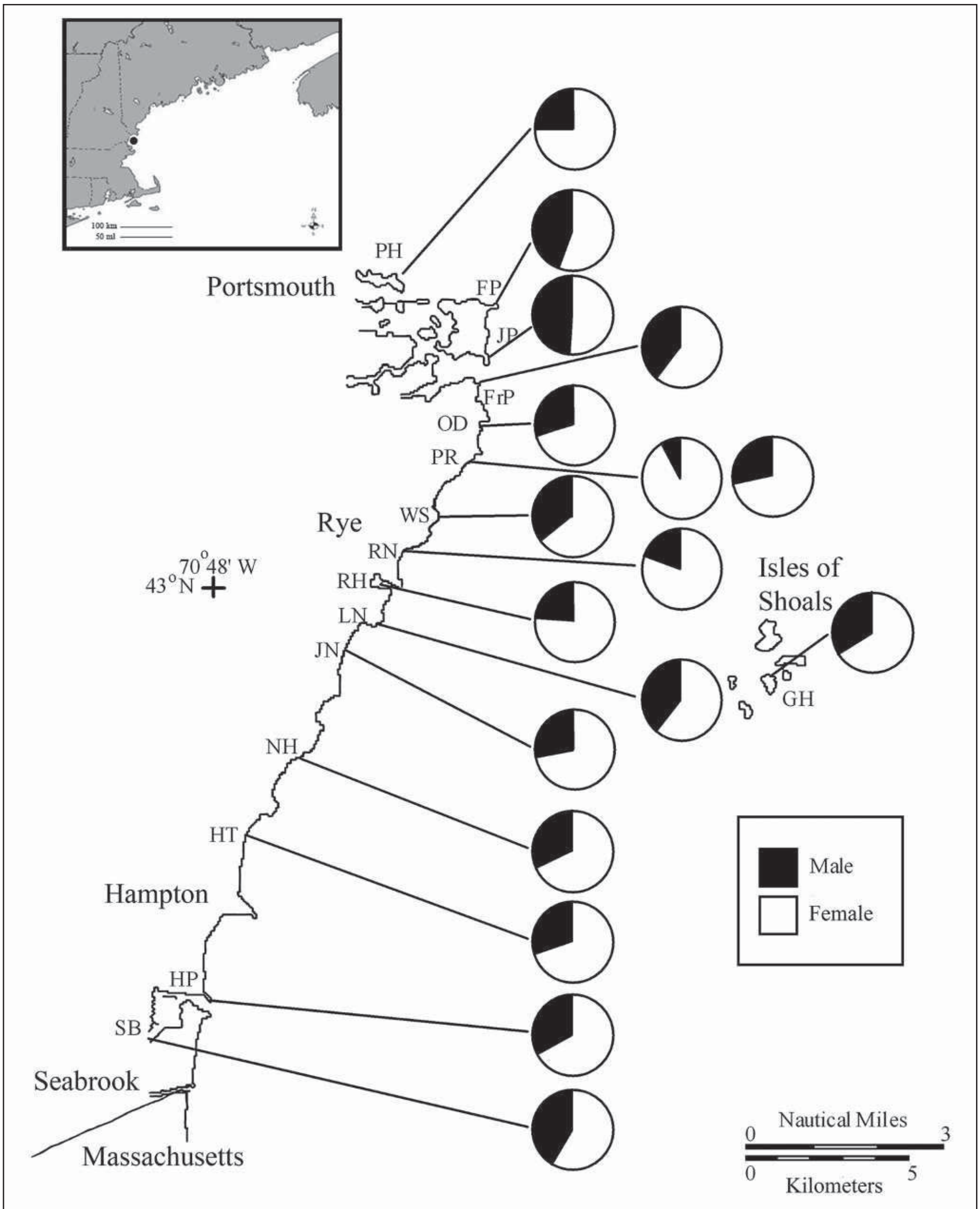

Figure 1. Gender ratios of *Littorina littorea* at sites along the New Hampshire coast. At all sites except FP, JP, FrP, and SB, female snails significantly outnumbered male snails. Site abbreviations: Gosport Harbor (GH), Portsmouth (PH), Fort Point (FP), Jaffrey Point (JP), Frost Point (FrP), Odiorne (OD), Pulpit Rock (PR), Wallis Sand (WS), Rye North (RN), Rye Harbor (RH), Lockes Neck (LN), Jenness (JN), North Hampton (NH), Hampton (HT), Hampton State Park (HP), Seabrook (SB).

was done during the summer because parasitic infections peak during summer months (Pohley 1976). Approximately 100 snails were collected by hand at areas near mean low water from each site. Snails were collected from a small area (<10 m^2) at each site without bias to size. We collected snails only once from each site except at North Hampton and Pulpit Rock, where samples were collected twice. Before entering the intertidal zone at each site, a survey and count of all birds roosting on the rocks within ≈37-m radius of the collection area was performed (Smith 2001). In the laboratory, individual snails were placed in jars with 100 ml seawater overnight. The next day, an Olympus dissecting microscope (at 10x) was used to examine each jar for swimming cercariae in order to identify patent infections. Snail length (mm) was measured from the apex to the lip of the shell with calipers. The visceral hump was dissected from all snails by crushing the shells; the tissue was squashed between 2 microscope slides and examined using an Olympus compound microscope (at 40x to 100x) to determine the presence of non-patent infections and the identity of the parasitic infections. When found, identification of cercariae was confirmed using descriptions and drawings by

Table 1. Sites surveyed for parasites of *Littorina littorea*. Sites are identified from N to S along the New Hampshire coast, except for Star Island. Rocks = large granite outcrops; rockweeds = substratum covered by *Fucus* spp. and *Ascophyllum nodosum* (L.) Le Jolis (Rockweed); cobble = small to moderate-sized rocks; wave exposure = subjective assessment of extent of wave-crash exposure.

Site	Date sampled	Wave exposure	Substratum type	GPS coordinates
Star Island, Gosport Harbor (GH)	08 June 2007	Protected	Rock + rockweeds	N42º58.69, W70º36.70
Pierce Island, Portsmouth (PH)	14 July 2006	Protected	Rock + rockweeds	N43º04.63, W70º44.89
Fort Point (FP)	14 June 2007	Exposed	Rock + rockweeds	N43º04.40, W70º42.52
Jaffrey Point (JP)	14 June 2007	Exposed	Rock + rockweeds	N43º03.51, W70º42.67
Frost Point (FrP)	09 June 2008	Exposed	Rocks + *Chondrus*	N43º03.14, W70º42.92
Odiorne (OD)	14 June 2007	Exposed	Rocks + rockweeds	N43º02.43, W70º42.76
Pulpit Rock (PR)	03 Aug 2007 09 June 2008	Exposed	Cobble	N43º02.06, W70º43.01
Wallis Sand, Seal Rock (WS)	03 Aug 2007	Exposed	Rocks + rockweeds	N43º01.69, W70º43.50
Rye North (RN)	19 June 2006	Exposed	Cobble	N43º00.71, W70º44.26
Rye Harbor (RH)	19 June 2006	Protected	Rock jetty + rockweeds	N43º00.15, W70º44.86
Lockes Neck (LN)	09 June 2008	Exposed	Cobble	N42º59.44, W70º45.12
Jenness (JN)	19 June 2006	Exposed	Cobble	N42º58.18, W70º46.25
North Hampton (NH)	17 July 2006 01 Sept 2006	Exposed	Cobble	N 42º57.46, W70º46.59
Hampton (HT)	03 Aug 2007	Exposed	Sand + cobble	N42º56.49, W70º47.48
Hampton (HP) State Park	17 July 2006	Protected	Rock jetty + rockweeds	N42º53.84, W70º48.75
Seabrook (SB)	17 July 2006	Protected	Rocks near boat landing	N42º53.24, W70º49.26

James (1968) and Stunkard (1930, 1950, 1983). Gender of each snail was determined by dissection and the presence of a fully formed penis or a remaining penis stub for males; all other snails were scored as female.

Chi-square contingency analysis (Zar 1984) was used to determine the existence of any association between infection and gender, and infection and size. The occurrence of double infections was tested against random expectations following Hurlbert's (1969) coefficient of association. Here we compared whether the frequency that both parasites occurred within a single host was more frequent or less frequent than expected by chance compared to the frequency of single infections by each parasite and to snails that were not infected.

Results

Overall, 1983 *L. littorea* were examined for parasitic infections from the 16 sites over the 3 summers. Of these, 219 snails (11.0% of snails collected) were infected with either *Cryptocotyle lingua* (71.4% of infections) or *Cercaria parvicaudata* (28.6% of infections) (Table 2). We found a single snail (at Pulpit Rock in 2008) infected with both *Cryptocotyle lingua* and *Cercaria parvicaudata*, which was well below expectations, and the negative association between the species of parasites was not significant (coefficient of association = -0.59, $\chi^2 = 2.74$, df = 1, $0.05 > P < 0.10$). Patent infections (cercariae released from snails) were found in 54.8% of snails infected with

Table 2. Parasitic infections (species and patency) and incidence of infection based on gender in populations of *Littorina littorea* at intertidal sites along the New Hampshire coast. One double infection was found at Pulpit Rock in 2008.

		Cryptocotyle lingua				*Cercaria parvicaudata*				
		Non-patent		Patent		Non-patent		Patent		% snails
Site	*n*	Female	Male	Female	Male	Female	Male	Female	Male	infected
Gosport Harbor	111	21	3	4	2	0	0	0	0	27.0
Portsmouth	90	7	1	3	0	2	0	0	0	14.4
Fort Point	113	4	0	0	0	0	0	0	0	3.5
Jaffery Point	113	2	0	2	0	0	0	0	0	3.5
Frost Point	93	1	0	1	0	0	0	0	0	2.2
Odiorne	91	0	0	1	2	0	0	0	0	3.3
Pulpit Rock										
(2007)	108	2	0	9	2	10	0	1	0	22.2
(2008)	216	6	3	14	5	23	7	8	0	30.1
Wallis Sand	106	2	2	0	0	0	0	0	0	3.8
Rye North	96	0	0	2	0	0	0	0	0	2.1
Rye Harbor	100	1	2	18	3	0	0	0	0	24.0
Lockes Neck	110	4	0	2	0	0	0	0	0	5.5
Jenness	120	0	0	0	0	4	0	0	0	3.3
North Hampton	210	2	1	6	3	6	1	1	0	9.5
Hampton	103	1	0	1	0	0	0	0	0	1.9
Hampton St. Park	103	3	0	1	0	0	0	0	0	2.9
Seabrook	100	3	0	4	1	0	0	0	0	8.0
Total	1983	59	12	68	18	45	8	10	0	11.0

Cryptocotyle lingua and 15.9% of snails infected with *Cercaria parvicaudata*. The visceral hump was gray when infected with *Cryptocotyle lingua* and orange when *Cercaria parvicaudata* infected the snails; in each case, sporocysts/rediae were seen protruding from the tissue.

Although some snails were infected at all sites, the level of infection in populations of *L. littorea* among these New Hampshire coastal sites was generally low (2–5%) and highly variable (Table 2). *Cryptocotyle lingua* was found at all sites except Jenness, where *Cercaria parvicaudata* was the only species parasitizing snails; both parasites were found at Portsmouth, Pulpit Rock, and North Hampton (Table 2). The proportion of snails infected exceeded 10% at four sites (Portsmouth, Pulpit Rock, Gosport Harbor, and Rye Harbor), and the prevalence of infection was between 5% and 10% at three other sites (Lockes Neck, North Hampton, and Seabrook).

The majority (68.1%) of snails sampled were female, and the number of female snails was significantly greater than males (Fig. 1) at all but 4 sites (Fort Point, Jaffrey Point, Frost Point, and Seabrook). A Chi-square heterogeneity test suggested that all samples came from a homogeneous population (heterogeneity $\chi^2 = 5.64$, df = 15, $P > 0.975$) and indicated that the sex ratio was similar across sites. A Yates correction (Zar 1984) to prevent overestimating a significant result with a small sample was used on the pooled data and indicated that female snails were more likely to be infected than male snails ($\chi^2 = 23.445$, df = 1, $P < 0.001$); 82.6% of all infected snails were female (Table 2).

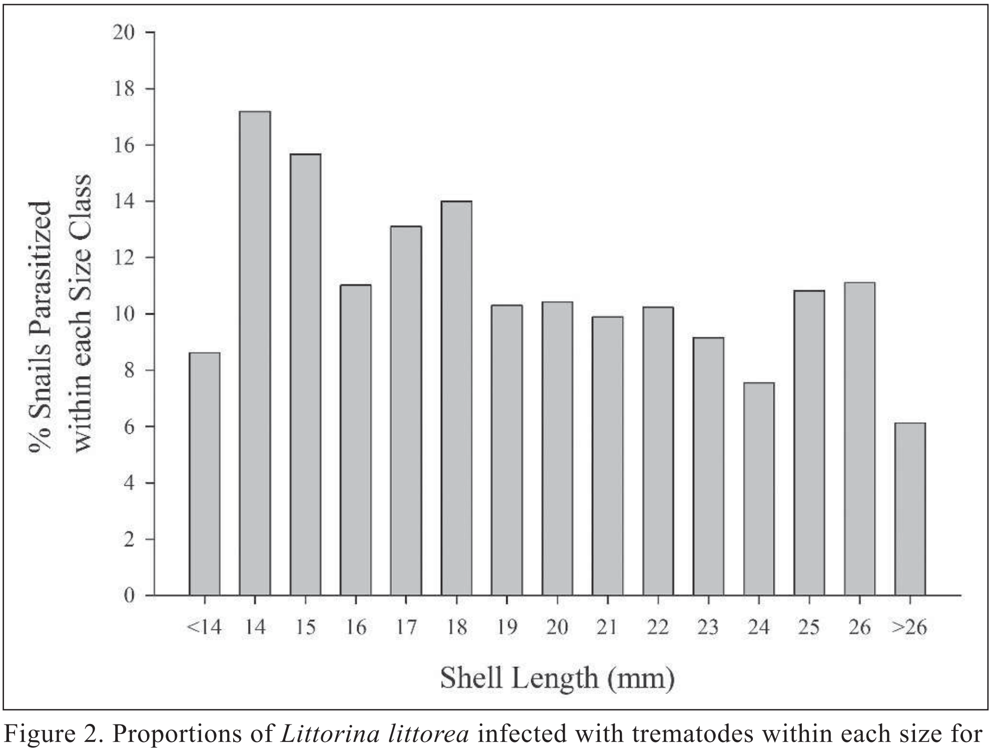

Figure 2. Proportions of *Littorina littorea* infected with trematodes within each size for all snails collected on New Hampshire rocky shores between Portsmouth and Seabrook. Snails <14 mm shell length are considered reproductively immature.

The vast majority (84.9%) of infected snails were between 14 and 23 mm (Fig. 2). No snails <10 mm were infected, and only 4.6% of infected snails were <14 mm. When all snails collected were combined, the proportion of infected snails from 14–26 mm was similar (χ^2 = 9.215, df = 12, P = 0.684; Fig. 2). However, four sites showed a significant association between snail size and infection. Snail size was partitioned based on Moore's (1937) estimates of annual size ranges: size class 1 = <14 mm, size class 2 = 14–18 mm, size class 3 = 19–23 mm, size class 4 = 24–26 mm, and size class 5 = >26 mm. At Pulpit Rock (2008) (χ^2 = 10.975, df = 4, P = 0.027), North Hampton (χ^2 =16.459, df = 4, P = 0.002), and Seabrook (χ^2 = 13.043, df = 4, P = 0.011), larger snails were more likely to be infected than smaller snails. In contrast, smaller snails had a higher prevalence of infection than larger snails at Rye Harbor (χ^2 = 6.657, df = 2, P = 0.036). Each of these localities was among the sites with snails showing the highest prevalence of infection observed.

A larger proportion of snails at wave-protected sites was infected with trematodes than snails at wave-exposed sites (χ^2 = 14.125, df =1, P < 0.001). Also, smaller snails (<18 mm) were more likely to be infected at protected sites compared to wave-exposed sites (Fig. 3).

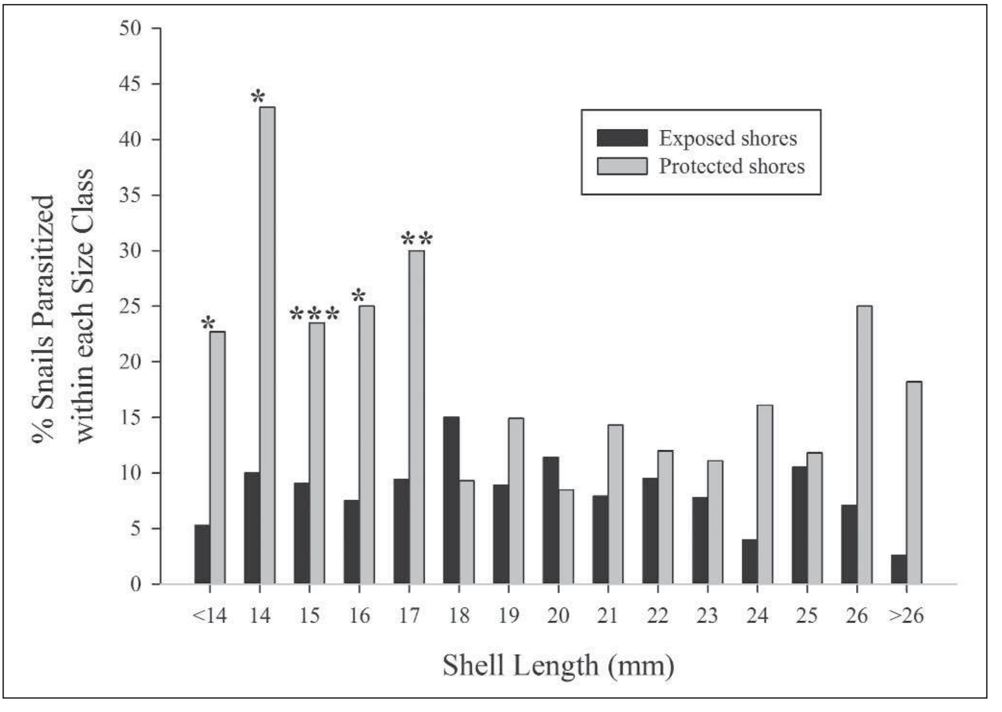

Figure 3. Proportions of *Littorina littorea* infected with trematodes by size-class (by mm) from exposed (n = 1479 snails) and protected (n = 504 snails) intertidal shores on the New Hampshire coast. Protected sites include: Gosport Harbor, Portsmouth Harbor, Rye Harbor, Hampton State Park, Seabrook. Exposed sites include: Fort Point, Jaffery Point, Frost Point, Odiorne, Pulpit Rock, Wallis Sands, Rye North, Lockes Neck, Jenness, North Hampton, Hampton). Proportions compared with chi-square test (*P < 0.05, ** P < 0.01, *** P < 0.001).

The most common birds observed roosting/grazing on the intertidal zone at the sites visited were *Larus marinus* Pontoppidan (Black-backed Gull), *Larus argentatus* L. (Herring Gull), and *Phalacrocorax auritus* Lesson (Double-crested Cormorant). Although we visited most sites only once to collect snails and make observations, we generally noted a low abundance of birds at these sites; fewer than five birds were observed at the time of collection at 11 of the 16 sites.

Discussion

Two trematode parasites were found to infect *L. littorea*: *Cryptocotyle lingua* and *Cercaria parvicaudata*. The species richness of trematodes infecting *L. littorea* was consistent with levels expected in field collections in the Gulf of Maine (Hoff 1941, Pechenik et al. 2001, Pohley 1976, Sindermann and Farrin 1962). Until Byers et al. (2008) surveyed periwinkle populations over a large regional scale, the New Hampshire coast was largely ignored among studies investigating the prevalence of parasites in periwinkles. They sampled 28 sites from northern Maine to southeastern Connecticut and included estuarine, coastal, and island populations within their survey, but assessed only 4 sites from coastal New Hampshire. They found 5 species of trematodes in *L. littorea* (*Cryptocotyle lingua*, *Cercaria parvicaudata*, *Renicola roscovita*, *Microphallus pygmaeus,* and *M. similis*), and >90% of infected snails contained *Cryptocotyle lingua*. Snails were predominantly infected with *C. lingua* in our study, but we found nearly 30% of infected snails with *Cercaria parvicaudata* (Table 2). The lack of other parasites in our survey is not surprising since >99% of parasitic infections in *L. littorea* recorded by Byers et al. (2008) were *Cryptocotyle lingua* or *Cercaria parvicaudata*. They recorded six infections other than *Cryptocotyle lingua* or *Cercaria parvicaudata*, and four of these infections were from sites at the Isles of Shoals, where the gull population is very high; in addition, none was found in coastal New Hampshire localities. Furthermore, at other locations in the Gulf of Maine, Hoff (1941) and Pechenik et al. (2001) found snails infected exclusively with *Cryptocotyle lingua*, and Pohley (1976) found only 4 of 2040 snails infected with trematodes other than *C. lingua* (*R. roscovita*, *M. pygmaeus*). The low species richness of parasites in *L. littorea* is unlikely due to the absence of other trematodes in the habitat because they are present in the other congeneric periwinkles (Byers et al. 2008, Pohley 1976), but may result from an inability of these parasites to recognize *L. littorea* as a suitable host due to its invasive history in North America (see Blakeslee and Byers 2008).

A single snail (at Pulpit Rock in 2008) was infected with both *Cryptocotyle lingua* and *Cercaria parvicaudata*. This result does not provide evidence of competitive trematode interactions within *L. littorea*. Since both *Cryptocotyle lingua* and *Cercaria parvicaudata* are acquired by the snails from ingesting eggs delivered in the feces of gulls and the delivery of these infective stages by gulls is unpredictable, the typical co-occurrence of the two parasites in any snail would be rare (see Curtis 2002). The predominance of infections by one parasite

(*Cryptocotyle lingua*) could suggest that *C. lingua* determines the outcome of interactions by arriving first and deterring other infections (Sousa 1992) or that *C. lingua* is the competitive dominant regardless of which parasite infects the host first. But the level of prevalence in these populations of *L. littorea,* and the absence of *Cercaria parvicaudata* at most localities, indicate that antagonism between the parasites within the snails is not evident (Fernandez and Esch 1991, Kuris 1990). Studies attempting to infect snails containing *Cryptocotyle lingua* or *Cercaria parvicaudata* with eggs from other trematodes and observing subsequent release of cercariae along with dissection of the snail could provide insight regarding trematode interactions within this host.

The level of infection in populations of *L. littorea* among these New Hampshire coastal sites was generally low and highly variable (Table 2). For populations of *L. littorea* in New England, the levels of parasitism we observed (1.9% to 30.1%) are similar to other studies documenting the prevalence of parasitism during summer months (Byers et al. 2008, Pechenik et al. 2001, Pohley 1976). Only Sindermann and Farrin (1962) found higher levels of infection (45% to 65%) in populations of *L. littorea* in Boothbay, ME. Byers et al. (2008) made single collections of *L. littorea* at 8 sites at the Isles of Shoals and 4 sites along the New Hampshire coast between May and September 2002 and documented prevalence of parasitic infections in *L. littorea* between 7.2% to 47.1% and 1.2% to 11.8%, respectively. Where our sampling sites overlapped with those of Byers et al. (2008:Appendix 2), we found a higher prevalence of parasites at Gosport Harbor (Star Island; 27.0% vs. Byers et al. 17.8%) and Rye Harbor (24.0% vs. Byers et al. 5.9%) and a lower prevalence at Odiorne (3.3% vs. Byers et al. 11.7%). These differences could be attributable to annual variation in the delivery of eggs to populations of snails by the definitive bird hosts (Byers et al. 2008, Poulin and Mouritsen 2003).

Although seasonal variation in the prevalence of parasitic infections in intertidal snails is common (*L. littorea*: Hughes and Answer 1982, Lauckner 1987, Pohley 1976, Robson and Williams 1971, Sindermann and Farrin 1962; *Hydrobia* spp: Field and Irwin 1999, Kube et al. 2002), we sampled during summer because a higher prevalence of infection occurs during summer months compared to winter months. Poulin and Mouritson (2003) attribute low prevalence of infection during winter months to ambient water temperatures. Embryonic development in *Cryptocotyle lingua* is halted at 0 °C and slowed at 5 °C (Möller 1978), and Sindermann and Farrin (1962) showed that cercariae were not released from periwinkles at temperatures <10 °C; thus, we would expect a similar decrease in prevalence in these populations if sampled between December and February. On the 2 occasions when an additional sample was collected from the same sites, similar levels of infection were observed. The North Hampton population was sampled twice over a 6-week period in 2006, and both samples contained 10 infected snails (17 July, $n = 99$; 01 Sept, $n = 111$), thus we decided to pool these data. The 2 collections of the population at Pulpit Rock, sampled in August 2007 and June 2008, both showed high levels of infection (Table 2).

A bias for females to be infected by trematodes in populations of intertidal snails was also shown for *Ilyanassa obsoleta* (Say) (Eastern Mudsnail; Curtis and Hurd 1983), *L. littorea* (Hughes and Answer 1982, Pohley 1976), *L. saxatilis* (Olivi) (Rough Periwinkle), and *L. obtusata* (L.) (Yellow Periwinkle) (Pohley 1976). However, Pohley (1976) also found more male *L. saxatilis* and *L. obtusata* than female snails infected in populations in Eastport, ME. Pechenik et al. (2001) did not find any male *L. littorea* infected with trematodes in populations at Nahant, MA and Wickford, RI, but their sample sizes were very small. The increased prevalence in female snails may be due to different activity patterns of females (foraging) and a decreased resistance to infection by females (see Tétreault et al. 2000). If the probability of infection is similar for male and female *L. littorea*, then males could be less tolerant to the infection and experience increased mortality compared to infected female snails.

Generally, larger (typically assumed to be older) snails are more likely to be infected with parasites than smaller snails due to an increased opportunity to become infected over time (Hughes and Answer 1982, James 1968, Kube et al. 2002, Matthews et al. 1985, Pohley 1976). We found few small snails (<14 mm) to be infected. Since reproductive maturity in *L. littorea* is reached within 12–18 months of metamorphosis at a shell size of ≥14 mm (Moore 1937), immature snails may be less susceptible to infection due to development of the gonad (Fernandez and Esch 1991, Hughes and Answer 1982). An equally small proportion (10.3%) of large snails (>24 mm) were infected, which could indicate that large infected snails are rare due to an increased risk of mortality from physiological stress/intolerance due to the parasitic infection (Huxham et al. 1993), decreased mobility (Williams and Ellis 1975) leading to an increased risk of predation, or parasite-induced behavioral changes causing different distribution patterns (Curtis 1987).

We noted a single population (Rye Harbor) where the largest proportion of the population that was infected was small snails. There, no snails with a shell length of >23 mm were collected. The collection site was a small jetty within the harbor where gulls perch at low tide and populations of *Carcinus maenus* and *Hemigrapsus sanguineus* (De Haan) (Asian Shore Crab) are abundant (W.J. Lambert, pers. observ.). All of these predators could eliminate snails from the population, thus impacting the sizes of snails in the population.

We noted 3 species of birds roosting/grazing on the intertidal zone: *Larus marinus*, *L. argentatus*, and *Phalacrocorax auritus*. Although the predominant factor impacting the number of snails infected at any particular site is the presence of the definitive host, especially gulls (Byers et al. 2008, Hoff 1941, Huxham et al. 1993, Pohley 1976, Poulin and Mouritsen 2003), we noted a low abundance of birds at all sites we visited; at 11 of the 16 sites, fewer than 5 gulls were observed at the time of collection. Given the prevalence of parasites in the periwinkles and since gulls may have been offshore foraging over open water during the early morning, these observations are "snapshots" and probably do not completely reflect the number of birds that visit particular sites. In addition, four of the sites sampled with the highest level of infection were wave-protected (Gosport Harbor, Portsmouth, Rye Harbor, and Seabrook), a small fishing fleet resides at 3 sites (Portsmouth, Rye Harbor, and Seabrook), and Gosport Harbor is a protected area for recreational boats that could entice marine birds with easy opportunities for food. Furthermore, the archipelago at the Isles of Shoals contains nesting colonies of gulls, which ensure large numbers of gulls likely feeding on fish hosting *Cryptocotyle lingua* (Annett and Pierotti 1989) and providing snails with parasite eggs at Star Island (Gosport Harbor). The other 2 sites (Pulpit Rock and North Hampton) we sampled that had a high prevalence of parasitism also had the highest number of gulls observed.

We show that infection by the trematodes, *Cryptocotyle lingua* and *Cercaria parvicaudata*, in the Common Periwinkle, *L. littorea*, varies tremendously over a relatively small spatial scale. Importantly, we show that patterns over small geographic scales may not meet expectations predicted by observations from larger spatial scales based on dispersal capabilities of larvae (in this case tied to the second intermediate hosts [fish] and definitive host [gulls] of the trematodes). Although the contribution of temporal variation within and among sites to the prevalence of infections we observed cannot be assessed because we visited all but 2 sites on a single occasion over 3 consecutive summers, the ecological impact that trematodes exert on host populations and intertidal community dynamics is important to understand (Curtis and Hurd 1983). Our data provide a foundation to test hypotheses regarding the susceptibility of immature snails as well as female snails to infection.

Acknowledgments

We thank P. Richardson for assistance in the field, L. Oak for assistance with figures, and J. Dijkstra, L. Harris, G. Muller, and E. Wetzel for comments on drafts of the manuscript. Partial financial assistance was provided by the Biology Department at Framingham State University.

Literature Cited

Annett, C., and R. Pierotti. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. Colonial Waterbirds 12:4–11.

Blakeslee, A.M.H., and J.E. Byers. 2008. Using parasites to inform ecological history: Comparisons among three congeneric marine snails. Ecology 89:1068–1078.

Byers, J.E., A.M.H. Blakeslee, E. Linder, A.B. Looper, and T.J. Maguire. 2008. Controls of spatial variation in the prevalence of trematode parasites infecting a marine snail. Ecology 89:439–451.

Carlson, R.L., M.J. Shulman, and J.E. Ellis. 2006. Factors contributing to spatial heterogeneity in the abundance of the Common Periwinkle, *Littorina littorea* (L.). Journal of Molluscan Studies 72:149–156.

Curtis, L.A. 1987. Vertical distribution of an estuarine snail altered by a parasite. Science. 235:1509–1511.

Curtis, L.A. 2002. Ecology of larval trematodes in three marine snails. Parasitology 124:S43–S56.

Curtis, L.A., and L.E. Hurd 1983. Age, sex, and parasites: Spatial heterogeneity in a sandflat population of *Ilyanassa obsoleta*. Ecology 64:819–828.

Davies, M.S., and A.J. Knowles. 2001. Effects of trematode parasitism on the behavior and ecology of a common marine snail (*Littorina littorea* (L.)). Journal of Experimental Marine Biology and Ecology 260:155–167.

Fernandez, J., and G.W. Esch. 1991. Guild structure of larval trematodes in the snail *Helisoma anceps*: Patterns and processes at the individual host level. Journal of Parasitology 77:528–539.

Field, L.C., and S.W.B. Irwin. 1999. Digenean larvae in *Hydrobia ulvae* from Belfast Lough (Northern Ireland) and the Ythan Estuary (northeast Scotland). Journal of the Marine Biological Association, UK 79:431–435.

Galaktionov, K.V., and A.A. Dobrovolskij. 2003. The Biology and Evolution of Trematodes: An Essay on the Biology, Morphology, Life Cycles, Tranmissions, and Evolution of Digenetic Trematodes. Springer, The Netherlands. 602 pp.

Gorbuskin, A.M., and I.A. Levakin. 1999. The effect of trematode parthenitae on the growth of *Onoba acaleus*, *Littorina saxatilis*, and *L. obtusata* (Gastropoda: Prosobranchia). Journal of the Marine Biological Association, UK 79:273–279.

Hoff, C.L. 1941. A case of correlation between infection of snail hosts with *Cryptocotyle lingua* and the habits of gulls. Journal of Parasitology 27:539.

Hughes, R.V., and P. Answer. 1982. Growth, spawning, and trematode infection on *Littorina littorea* (L.) from an exposed shore in North Wales. Journal of Molluscan Studies 48:321–330.

Hurlbert, S.H. 1969. A coefficient of interspecific association. Ecology 50:1–8.

Huxham, M., D. Raffaelli, and A. Pike. 1993. The influence of *Cryptocotyle lingua* (Digenea:Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda:Prosobranchia): An ecological approach. Journal of Experimental Marine Biology and Ecology 168:223–238.

James, B.L. 1968. The distribution and keys of species in the family Littorinidae and of their Digenean parasites, in the region of Dale, Pembrokeshire. Field Studies 2:211–224.

Kube, S., J. Kube, and A. Bick. 2002. Component community of larval trematodes in the mudsnail *Hydrobia ventrosa*: Temporal variations in prevalence in relation to host life history. Journal of Parasitology 88:730–737.

Kuris, A. 1990. Guild structure of larval trematodes in molluscan hosts: Prevalence, dominance, and significance of competition. Pp. 69–100, *In* G.W. Esch, A.O. Bush, and J.M. Aho (Eds.). Parasite Communities: Patterns and Processes. Chapman and Hall, London, UK.

Lambert, T.C., and J. Farley. 1968. The effect of parasitism by the trematode *Cryptocotyle lingua* (Creplin) on zonation and winter migration of the Common Periwinkle, *Littorina littorea* (L.). Canadian Journal of Zoology 46:1139–1147.

Lauckner, G. 1987. Ecological effects of larval trematode infestation of littoral marine invertebrate populations. International Journal of Parasitology 17:391–398.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. American Naturalist 112:23–39.

Lubchenco, J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

Matthews, P.M., W.I. Montgomery, and R.E.B. Hanna. 1985. Infestation of littorinids by larval Digenea around a small fishing port. Parasitology 90:277–287.

McQuaid, C.D. 1996. Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. Oceanography Marine Biology Annual Review 34:263–302.

Möller, H. 1978. The effects of salinity and temperature on the development and survival of fish parasites. Journal of Fish Biology 12:311–323.

Moore, H.B. 1937. The biology of *Littorina littorea* Part 1. Growth of the shell and tissues, spawning, length of life, and mortality. Journal of the Marine Biological Association, UK 21:721–742.

Pechenik, J.A., D. Fried, and H.L. Simpkins. 2001. *Crepidula fornicata* is not the first intermediate host for trematodes: Who is? Journal of Experimental Marine Biology and Ecology 261:211–224.

Perez, K.O., R.L. Carlson, M.J. Shulman, and J.C. Ellis. 2009. Why are intertidal snails rare in the subtidal? Predation, growth, and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 369:79–86.

Pohley, W.J. 1976. Relationships among three species of *Littorina* and their larval Digenea. Marine Biology 37:179–186.

Poulin, R., and K.N. Mouritsen. 2003. Large-scale determinant of trematode infections in intertidal gastropods. Marine Ecology Progress Series 254:187–198.

Robson, E.M., and E.C. Williams 1971. Relationships of some species of Digenea with the marine prosobranch *Littorina littorea* (L.). I. The occurrence of larval Digenea in *L. littorea* on the North Yorkshire coast. Journal of Helminthology 44:153–168.

Rohde, K. 1993. Ecology of Marine Parasites, 2nd Edition. CAB International Press, Walllingford, UK. 298 pp.

Sindermann, C.J., and A.E. Farrin. 1962. Ecological studies of *Cryptocotyle lingua* (Trematoda:Heterophyidae) whose larvae cause "pigment spots" of marine fish. Ecology 43:69–75.

Smith, N.F. 2001. Spatial heterogeneity in the recruitment of larval trematodes to snail intermediate hosts. Oecologia 127:115–122.

Sorensen, R.E., and D.J. Minchella. 2001. Snail-trematode life history interactions: Past trends and future directions. Parasitology 123:S3–S18.

Sousa, W.P. 1992. Interspecific interactions among larval trematode parasites of freshwater and marine snails. American Zoologist 32:583–592.

Stunkard, H.W. 1930. The life cycle of *Cryptocotyle lingua* (Creplin), with notes on the physiology of the metacercariae. Journal of Morphology and Physiology 50:143–191.

Stunkard, H.W. 1950. Further observations on *Cercaria parvicaudata* Stunkard and Shaw 1931. Biological Bulletin 99:136–142.

Stunkard, H.W. 1983. The marine cercariae of the Woods Hole, Massachusetts region. A review and a revision. Biological Bulletin 164:143–162.

Tétreault, F., J.H. Himmelman, and L. Measures. 2000. Impact of a castrating trematode, *Neophasis* sp., on the common whelk *Buccinum undatum* in the northern Gulf of St. Lawrence. Biological Bulletin 198:261–271.

Thieltges, D.W., M.A.D. Ferguson, C.S. Jones, L.R. Noble, and R. Poulin. 2009. Biogeographical patterns of marine larval trematode parasites in two intermediate snail hosts in Europe. Journal of Biogeography. 36:1493–1501.

Thompson, R.M., K.N. Mouritsen, and R. Poulin. 2005. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. Journal of Animal Ecology 74:77–85.

Williams, I.C., and C. Ellis. 1975 Movements of the Common Periwinkle, *Littorina littorea* (L.) on the Yorkshire coast in winter and the influence of infection with larvae Digenea. Journal of Experimental Marine Biology and Ecology 17:47–58.

Wood, C.L., J.E, Byers, K.L. Cottinham, I. Altman, M.J. Donahue, and A.M.H. Blakeslee. 2007. Parasites alter community structure. Proceedings of the Natural Academy of Sciences 104:9335–9339.

Zar, J.H. 1984. Biostatical Analysis, 2nd Edition. Prentice-Hall, Inc., Upper Saddle River, NJ. 718 pp.