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Periphytic food and predatory crayfish: relative roles in determining snail distribution

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Summary. In the laboratory and field, we examined how periphyton (food of snails) and predatory crayfish influenced snail distribution in Trout Lake, a permanent, northern Wisconsin lake. Laboratory experiments (with no crayfish) tested the importance of periphyton biomass in determining snail preference among rocks, and among rock, sand, and macrophyte substrates. Among rocks with four different amounts of periphyton, periphyton biomass and the number of *Lymnaea emarginata, Physa* spp., and *Amnicola* spp. were positively related. A similar, but non-significant, trend occurred for *Helisoma anceps*. A field experiment at a site in Trout Lake where predation risk was low confirmed the preference by snails for periphyton covered rocks; more snails colonized rocks with periphyton than rocks without. When given a choice of rock, sand, and macrophytes in the laboratory, *L. emarginata* preferred high periphyton biomass and rock. Laboratory and field results contrasted with the distribution of snails in Trout Lake; no snails occurred in areas with abundant periphyton-covered rocks, but snails were abundant nearby on scattered rocks with little periphyton. However, where snails were absent, crayfish were abundant (14.5 crayfish-trap^{-1}-day^{-1}), and where snails were abundant, crayfish were rare (3.2 crayfish-trap^{-1}-day^{-1}), suggesting that crayfish predation reduced snails. The hypothesis that the negative association between snail and periphyton biomass resulted from snail grazing was supported by the results of a field snail enclosure-exclosure experiment (1 m^2 cages; $n=3$). All experiments and observations therefore suggest that: 1) crayfish predation is more important than a preference for high periphyton biomass in determining snail distribution in Trout Lake; 2) periphyton biomass is negtively related to snail grazing; and 3) crayfish had a positive indirect effect on periphyton by preying on grazing snails.

Key words: Snail distribution – Crayfish predation – Periphyton – Substrate preference – *Lymnaea emarginata*

Whether community structure is controlled from the bottom-up or the top-down is an old question (e.g., Hairston et al. 1960). For freshwater communities, the traditional focus has been on bottom-up effects (Wetzel 1983). The positive correlations of water column phosphorus with standing crop of phytoplankton (Schindler 1978) and epilithon (Cattaneo 1987) are evidence of the important bottom-up influence of nutrients on pelagic and benthic communities. Stemming from earlier work (Brooks and Dodson 1965), though, many recent experimental manipulations of pelagic (Shapiro and Wright 1984; Carpenter et al. 1987; Mills et al. 1987; Mills and Forney 1988) and benthic (see Sih et al. 1985) food webs have demonstrated that top-down biotic interactions, may also have important effects on community structure and productivity. Among these top-down effects are the three-trophic-level (sensu Sih et al. 1985) or cascade (*sensu* Paine 1980; Carpenter et al. 1987) effect. The relative importance of bottom-up and top-down effects in different communities and under different conditions should be a major focus for freshwater ecologists (Crowder et al. 1988).

Lodge et al. (1987) proposed a comprehensive conceptual model including bottom-up and top-down mechanisms to explain the distribution of freshwater snails on a variety of spatial scales. In this paper, we test the part of the model that applies to snail distribution and abundance within permanent lakes. According to the model, where predators are absent, available habitats and periphytic food determine snail abundance and distribution. However, we predict that predators, e.g., fish and crayfish, which are often abundant in permanent lakes, limit snail abundance below potential abundance.

Specifically, we test the relative importance of predator and prey abundance in Trout Lake, Wisconsin in determining the abundance and distribution of snails and periphyton in a benthic food chain dominated by omnivorous crayfish, grazing snails, and periphyton. If bottom-up mechanisms predominate, we would predict positive correlations between i) crayfish and snail abundance, and ii) periphyton and snail abundance. If top-down mechanisms predominate, we would predict negative correlations.

To test the relative importance of crayfish predation and food availability in determining snail distribution, we first investigated the effect of periphyton on substrate choice by snails in the absence of predators (Section I). We then compared these substrate preferences to snail distribution in Trout Lake, which has a patchy distribution of crayfish (Section II). We used a field enclosure-exclosure experiment to test the impact of natural densities of snails on periphyton biomass (Section II). The results of all our experiments and observations suggested that topdown, cascading effects were of greater importance than bottom-up

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effects in determining the abundance and distribution of snails and periphyton in Trout Lake. Where crayfish were abundant, snails were absent and periphyton was abundant. Where crayfish were rare, snails were abundant and periphyton was in low abundance.

Study site

The study site was along the east shore of the south basin of Trout Lake, in north central Wisconsin (Vilas County, 46°N, 89°W) (Fig. 1). North of Allequash Creek (NE Shore) a wide zone of abundant fist-sized cobble exists (0 to ≥ 2 m depth), with few open spaces of sand. At depths >40 cm, cobble has a thick, visibly fuzzy coat of periphyton during summer. Snails are absent and crayfish are plentiful (Lodge et al. 1987). South of Allequash Creek (SE Shore) patches of cobble, macrophytes, sand, and areas with scattered rocks and macrophytes across a sandy bottom exist. Snails are plentiful and crayfish are rare (Lodge et al. 1987), probably because of the scarcity of rock shelters.

I. Effect of periphyton on substrate choice by snails

Methods and materials

Experiments 1–3 tested the effect of periphyton on substrate choice by snails (Table 1). In Expts. 1 and 2, snails of a single genus were introduced into the center of replicate laboratory arenas containing lake water and 1 (rock) to 3 (rock, sand, and macrophyte) substrates that together covered the entire arena bottom. Each arena was a round, epoxy-coated pan (diam. = 30 cm, depth = 15 cm). The number of snails on each substrate was recorded at hourly intervals. Experiments ended when snail numbers on each substrate were relatively constant for 2–3 h and before periphyton was depleted by grazing. Experiment duration

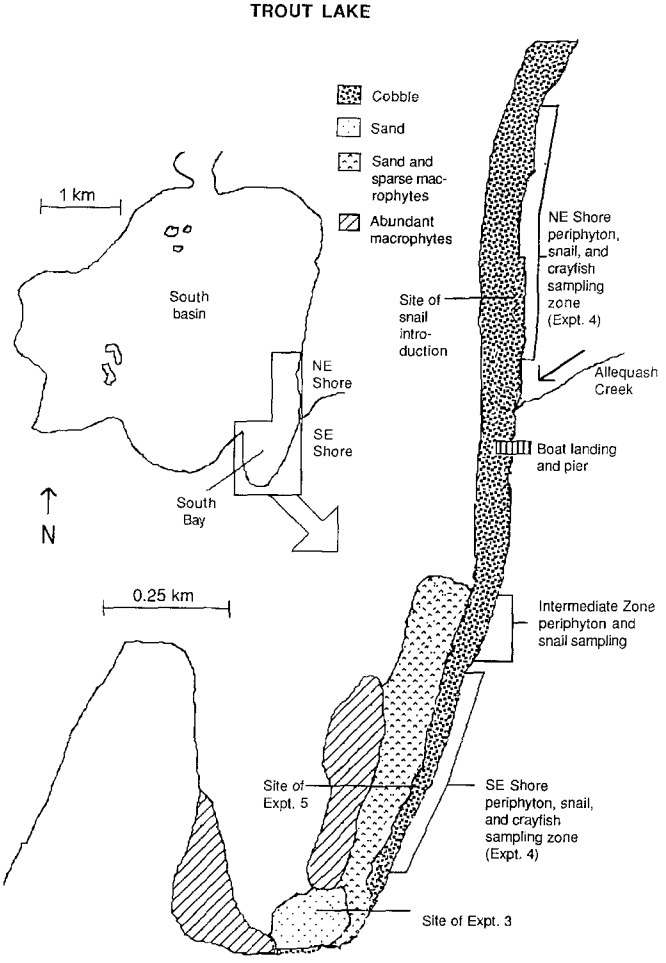


Fig. 1. South basin of Trout Lake, Wisconsin showing the east shore in detail, and location of experiments. Substrates are indicated to a depth of about 2 m

Table 1. Summary of experiments

Experiments	Snail spp. investigated	Range of snail size (mm)	Date (M/D/Y)	Replicates	Snails/rep
Section I					
1. Choice of three or four rocks, each with a different amount of periphyton.	*Amnicola* spp.	2–5	7/28/86	5	100
	H. anceps	3–10	7/22/86	5	30
	L. emarginata	12–24	6/20/86	5	30
	Physa spp.	4–9	5/30/87	3	100
2. Choice of rock, sand, and macrophytes.	*L. emarginata*	9.2–21.5	8/06/87	1	100
		8.2–20.0	8/12/87	2	100
		10.0–20.0	8/26/87	3	100
3. *In situ* choice of rocks with and without periphyton.	all species	>5	6/25/87	15	NA
Section II					
4. Survey of snails, crayfishes and periphyton.	all species	>5	6/06/87 6/20/87 6/22/87 6/24/87	NE S. = 16 Intmd Zn. = 12 SE S. = 17	NA
5. Snail Exclosure-Enclosure Experiment.	*L. emarginata* *H. anceps*	>5	7/01-15/87	3	NA

NA = not applicable

(3–7 h) therefore depended on the periphyton quantity, and movement patterns of each snail species. Water covered the substrates and was deep enough (9–15 cm) to prevent access to the water surface by snails. Before adding other substrates, the bottom of each arena was covered with washed sand from Trout Lake.

Surface area determination. Surface area of rocks was estimated by covering all but the bottom of the rock with aluminum foil, and applying a measured area to weight ratio for foil around spheres. To measure surface area of macrophytes, leaves and stems of all shoots used of *Potamogeton amplifolius* Tuckerm. and *Vallisneria americana* Michx. were traced with a digitizer. Surface area of *Najas flexilis* (Willd.) Rostk. and Schmidt shoots were estimated from a wet weight-surface area regression formula derived from measurements with a stage micrometer of leaves and stems of six shoots (surface area = 58.8 (wet weight) + 3.93; $r^2 = 0.99$). Surface area of sand was considered to be equal to the flat area it covered.

Quantifying periphyton. Periphyton biomass was expressed as chlorophyll *a* (chl *a*) per unit substrate area. In Expt. 1, epilithon (periphyton on rock) was sampled by scraping with a razor blade within one or two 1 cm^2 quadrats on each rock in each replicate before grazing. In Expt. 2, one sample from each rock (area = 5.7 cm^2) was taken with a syringe sampler (Loeb 1981). In Expt. 3, periphyton biomass on rock, sand, and macrophytes was determined from substrates that were collected simultaneously with those used in experiments. Mean chl *a* values reported are means across dates.

Epiphyton (periphyton on macrophytes) was measured from 3–6 individual shoots of *N. flexilis, P. amplifolius,* and *V. americana* by uniform shaking in wide mouthed jars (Jones and Adams 1982).

Epilithon and epiphyton was collected on glass fiber filters (Fisher G4, 1.2 um nominal pore retention). Chl *a* was extracted from filters with 99% methanol and measured with a fluorometer, and corrected for pheopigments (Strickland and Parsons 1968; Holm-Hansen and Riemann 1978).

Chl *a* was extracted directly from known volumes of sand. Chl *a* per cm^2 of sand in Results is what would be extracted from a volume of sand of 1 $cm^2 \times 0.25$ cm depth. A depth of 0.25 cm was the estimated depth of *L. emarginata's* grazing as observed in a glass-sided dish.

To remove periphyton from substrates (Sets 1 and 2 of Expt. 3), rocks were scrubbed with a wire brush, macrophytes were gently rubbed by hand, and sand was ignited at 600° C for 0.25-1 h (Lind 1979).

Collection of materials. Substrates and snails used in laboratory experiments were collected from Trout Lake and nearby Plum Lake at depths of 0–1 m one or two days before each experiment and kept in lake water on a natural day-night light cycle. Rocks with different amounts of epilithon were collected from the Trout Lake NE Shore, while periphyton covered sand and macrophytes were collected from the SE Shore. Periphyton covered sand was collected by carefully taking the top 1–5 cm of sediment in shallow (0.5–1.5 m) areas of Trout Lake. Sand to this depth appeared to be uniformly mixed, and was green relative to washed or ignited sand.

Expt. 1. To determine if periphyton affected substrate preference, snails were given a choice among a rock scrubbed free of epilithon and two or three other rocks, each with a different amount of epilithon. While we were able visually to identify categories of periphyton abundance, we made no attempt to identify taxonomic composition of algae. For *Amnicola* spp. (we did not distinguish *A. limosa* (Say) and *Marstonia lustrica* (Pilsbry)), *Helisoma anceps* (Menke), and *Lymnaea emarginata* Say, four rocks were in each arena. For *Physa* spp. (*Physa gyrina* Say and one unidentified species), only three levels of epilithon were used because a fourth category with a noticeably different amount of epilithon was unavailable. The null hypothesis that equal numbers of snails would colonize equal substrate surface areas was tested by ANOVA and least significant difference tests (LSD) on log transformed snail numbers (SAS Institute Inc., Box 8000, Cary, NC).

Expt. 2. We next determined whether colonization among rock, sand, and macrophytes by *L. emarginata* was affected by periphyton biomass and substrate type. *L. emarginata* (one of the most common species of large snails in Trout Lake), was given a choice of approximately 360 m^2 of each of the three substrates in a pan divided on the bottom into three equal areas. Just sand occurred in one third, and three rocks (diam. = approx. 10 cm) on top of sand in another third. In the macrophyte third, one *P. amplifolius* shoot, two rosettes of *V. americana,* and three shoots of *N. flexilis* were all anchored in sand. We chose this combination because it presented equal surface areas of three common macrophytes with diverse structure, representative of natural macrophyte assemblages. For rock and macrophytes, only snails on rock or macrophyte (not snails on the sand between rocks or under macrophytes) were included in the analyses.

In Set 1, periphyton was removed from all three substrates (rock, sand, and macrophytes) to determine of *L. emarginata* had substrate preferences unrelated to periphyton. Because in similar preliminary experiments, snails did not colonize macrophytes as densely as other substrates, in Set 2 we offered *L. emarginata* three substrates, with periphyton removed from sand and rock, but with natural epiphyton on macrophytes. To determine if snails avoided macrophytes because of macrophyte structure or because macrophytes had the least amount of periphyton, we selected macrophytes with high epiphyton biomass. In Set 3, all substrates had natural quantities of periphyton. Rock was collected from the Trout Lake NE Shore (high epilithon), and sand and macrophytes were collected from the Trout Lake SE Shore. Replicates were run on three dates and results were pooled across dates (Table 1). For selected comparisons, the null hypothesis that equal numbers of snails would colonize equal substrate surface areas was tested by ANOVA and LSD.

Exp. 3. This experiment gave snails a choice of rocks with and without epilithon *in situ,* where risk of predation was low, and determined whether responses observed in the laboratory also occurred in Trout Lake. A broad sandy area of South Bay without macrophytes or rocks (Fig. 1) was chosen as the study site because crayfish avoid open sand to escape fish predation (Stein 1977). Thirty rocks were placed in an oval area (20 × 10 m) at a depth of 40–60 cm. Rocks were separated by at least 1 m to eliminate crevices

that crayfish could use as refuges. Fifteen rocks with thick epilithon were alternated with 15 rocks from which epilithon was scrubbed. Rocks were collected from the NE Shore of Trout Lake, were uniform in size (12 cm diameter) and shape, and were without snails. Numbers of *Lymnaea, Helisoma,* and *Physa* greater than 5 mm (shell length) that had colonized the rocks were counted (using mask and snorkel) daily for the first three days and on day 20. The null hypothesis that equal numbers of snails colonized rocks with and without periphyton was tested with a *t*-test using Bonferroni's correction for multiple tests.

Results and discussion

Expt. 1. For *Amnicola, L. emarginata,* and *Physa,* number of snails that colonized rocks with different levels of epilithon differed, with the number of snails generally greater with greater epilithon (Fig. 2). However, these species did seem to respond somewhat differently to increasing epilithon. *Amnicola,* and perhaps *Physa,* exhibited threshold responses to epilithon chlorophyll, with *Amnicola*'s threshold chlorophyll level much lower than *Physa*'s. In contrast, *L. emarginata* had a near-linear or perhaps increasing positive response to greater epilithon abundance. *H. anceps* apparently showed a small near-linear positive trend between snail number and chlorophyll, but differences in snail number at different epilithon levels were not significant (Fig. 2).

Ideally, the same range of epilithon biomass should have been used for all snail species. For example, in the *Physa* and *H. anceps* trials, if a chlorophyll biomass treatment of 13 $\mu g \cdot cm^{-2}$ (the highest chl *a* value in the *Amnicola* trial) had been included, a threshold response like that of *Amnicola* might have occurred. However, *H. anceps* and *Physa* were tested over a similar (but narrower) range of epilithon abundance, and *H. anceps* responded much less than *Physa.* This difference and the difference in response of *Amnicola* and *L. emarginata* over a similar, wider range of chlorophyll suggest important biological differences exist among species. For example, the difference between *Amnicola* and *L. emarginata* may be explained by relative size of the snails.

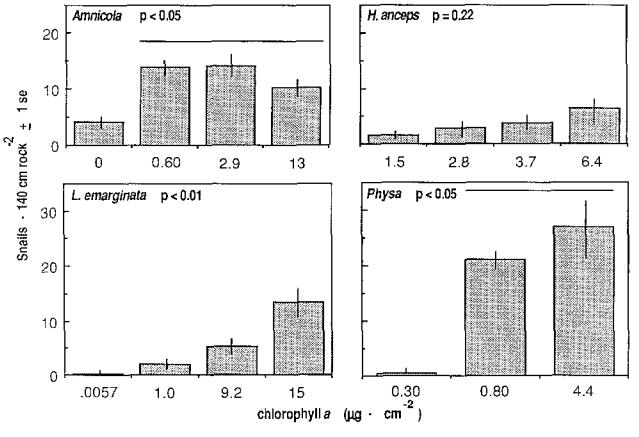


Fig. 2. Mean number of snails on rocks with different periphyton biomasses (chlorophyll *a*) in Expt. 1. For each snail species, ANOVA p values are indicated. Except for *H. anceps*, horizontal bars links treatments that are not significantly different ($P < 0.05$, least significant difference tests). No least significant difference test was performed for *H. anceps* because ANOVA $P > 0.05$

Amnicola is smaller (range 2–5 mm) than *L. emarginata* (range 12–24 mm). At higher epilithon biomasses, feeding rate of *Amnicola* may be limited by mouth size; at the same epilithon biomass, feeding of larger snails may be limited by epilithon abundance. Therefore, *Amnicola* may not have derived any advantage at higher epilithon biomasses.

We did not measure epilithon species composition, although epilithon color and texture among rocks and dates were similar. Therefore, we cannot tell if snails were responding to epilithon biomass or to differences in algal species composition.

In either case, the mechanism of substrate selection may involve distant chemoreception (Sterry et al. 1983, Bronmark 1985). The most parsimonious explanation for the apparent preferences, though, is that snails move randomly and slow down to feed when they encounter a substrate they like.

Expt. 2. In Set 1 (periphyton removed from all substrates), *L. emarginata* preferred rock over sand and macrophytes, and preferred macrophytes over sand (Fig. 3). In Set 2 (periphyton removed from rock and sand, natural quantity on macrophytes), snails preferred macrophytes over rock and sand, but expressed no significant preference between rock and sand (Fig. 3). Thus, snails preferred rock when all substrates had periphyton removed, but preference switched to macrophytes when macrophytes had natural periphyton and rocks did not.

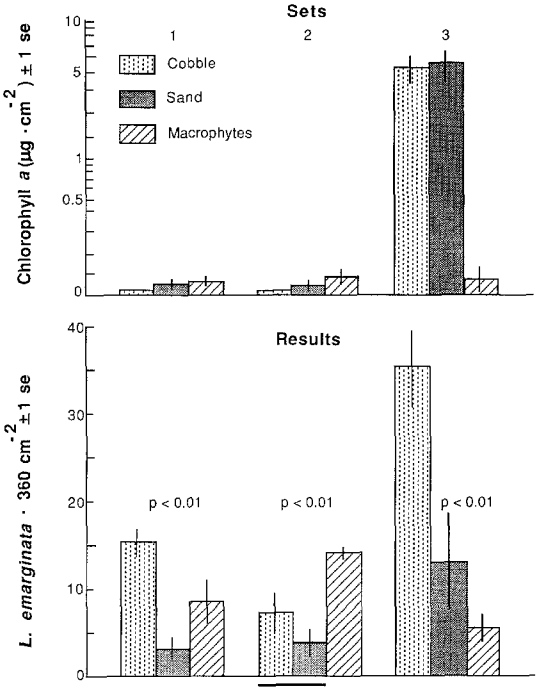


Fig. 3. Periphyton chlorophyll *a* (top) and mean number of *L. emarginata* (bottom) on three different substrates in Expt. 2 when periphyton was removed from all substrates (*Set 1*), when periphyton was removed from rocks and sand but at a natural level on macrophytes (*Set 2*), and when given the choice of NE Shore rocks, SE Shore sand, and macrophytes, all with natural periphyton (*Set 3*). P values for ANOVA comparing numbers of snails among substrates within each set are indicated. Horizontal bars links treatments within sets that are not significantly different ($P > 0.05$, least significant difference test)

While epiphyton biomass did not differ significantly between Sets 1 and 2 ($t=1.37$, $P>0.05$), mean values and our visual observations suggested there was more epiphyton on macrophytes in Trt. 2 than Trt. 1. The epiphyton that remained on macrophytes after our removal efforts probably consisted of tightly adhering taxa like adnate diatoms. These groups are not as grazable to snails (see Lamberti and Moore 1984). Thus, while hand rubbing clearly did not remove all periphyton, it probably did remove most grazable biomass. The response of the snails suggests our efforts to reduce epiphyton produced results that may be biologically meaningful.

In Set 3 (natural levels of periphyton on all substrates), *L. emarginata* preferred NE Shore rock over SE Shore sand and macrophytes, and preferred sand over macrophytes (Fig. 3).

In summary, for *L. emarginata,* both substrate type and amount of periphyton contributed to substrate preference. *L. emarginata* preferred rock regardless of the presence of periphyton, but an increase in periphyton biomass on macrophytes could override preference for rock. When no predators were present, NE Shore rock was preferred over SE Shore sand and macrophytes at natural periphyton biomasses.

Expt. 3. In Trout Lake, more snails were on rocks with epilithon than rocks without epilithon on days 1 (unpaired $t=5.19$ $P<0.001$), 2 ($t=7.01$ $P<0.001$), and 3 ($t=5.41$ $P<0.001$), but not on day 20 (Fig. 4). By day 20, our visual observations clearly indicated that algal levels on rocks that initially had epilithon were reduced, apparently by snail grazing.

Like our Expts. 1–3, previous studies also showed that substrate type and the presence of periphyton were important in laboratory substrate selection. When there was no periphyton on rock or sand, *Physa integra* and *P. parkeri* preferred rock over sand (Clampitt 1973), but *Helisoma antrosa percarinata* (Clampitt 1973), *Viviparus bengalensis* and *Melania scabra* (Vaidya 1979) preferred sand over rock. However, periphyton also altered substrate selection for these same species; the presence of periphyton enhanced colonization both on rock and sand for every species (Clampitt 1973; Vaidya 1979). In addition, Clampitt (1974) inferred from field observations of snail size that snail growth rate in Douglas Lake was higher on periphyton-covered stones than on wave-washed sand, suggesting that nutrition is better on the periphyton covered stones. However, previous investigators did not quantify the periphyton, measure substrate surface area, or include macrophytes in their experiments.

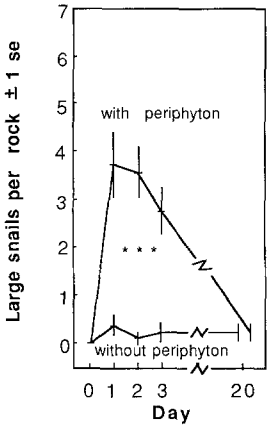


Fig. 4. Mean number of large snails (>5 mm axial shell length) on rocks with and without periphyton over time on a sandy area of South Bay, Trout Lake in Expt. 3. Significance of difference between numbers of snails on rocks with and without periphyton is indicated (*t*-Test, * = $P<0.001$). Because we conducted four *t*-tests (for days 1, 2, 3 and 20), the critical alpha value is 0.0125 (after applying the Bonferroni correction)

In summary, Expts. 1–3 indicate that snails are positively associated with periphyton biomass in the absence or near absence of predators, and that in the absence of periphyton, *L. emarginata* prefers rock over sand and macrophytes. Therefore, we would expect snails to be abundant on the NE Shore of Trout Lake because rocks and periphyton are more abundant there than on the SE Shore.

II. Trophic interactions among crayfish, snails, and periphyton in Trout Lake

Methods and materials

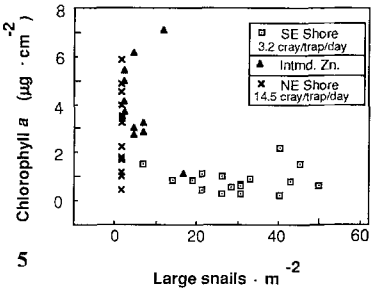
Expt. 4. To determine whether experimental results of substrate preference were consistent with snail distribution in Trout Lake, snails and epilithon were sampled simultaneously from the scattered cobble along the SE Shore, abundant cobble along the NE Shore, and in an area intermediate between the two sites (see Fig. 1). Snails (>5 mm long) were counted (using snorkel and mask) in quadrats (0.4 m^2) at a depth of 40–70 cm on four dates (see Table 1). From each quadrat, one (all dates except 6 June) or two (6 June) epilithon samples were taken from the rocks in each quadrat with a syringe sampler, as described earlier.

To determine how crayfish abundance related to snail abundance and epilithon biomass, crayfish were trapped in modified minnow traps (as described by Lodge et al. 1986) on 10–11 Aug on the NE and SE Shores (Fig. 1). Ten traps on the NE Shore and 11 traps on the SE Shore were baited with 120 g of beef liver and placed in water 1–3 m deep. After one night, the number of crayfish (*Orconectes virilis* (Hagen), *O. propinquus* (Girard), and *O. rusticus* (Girard)) in each trap were counted.

Expt. 5. To determine whether snail grazing reduced epilithon (as suggested by results of Expt. 3), loss of epilithon biomass on rocks in snail enclosures was compared to loss in snail exclosures (Table 1) using *t*-test on arcsine-transformed ratios of final over initial biomass. Cages constructed of galvanized steel frames covered with fiberglass window screen (1.5 mm mesh) enclosed an area of 1.05 m × 0.87 m × 0.8 m deep. Cages had neither tops nor bottoms and were seated into the sand (with no rocks) of the SE Shore in water 45–55 cm deep. Large snails (>5 mm) were removed from all cages by hand. Sixteen epilithon covered rocks from the NE Shore were placed in a 4 × 4 grid in each cage. Five rocks in the grid were selected randomly for epilithon sampling. One syringe sample was collected from each of the five rocks in each cage before snails were put into enclosures. Fifteen adult *L. emarginata* and 12 *H. anceps* (average densities for these two species on the SE Shore from June 20 to June 25, L. Weber, unpubl. data) were put into three cages on 1 July, 1987. Different locations on the same five rocks in each cage were sampled seven and 14 days later.

Results and discussion

Expt. 4. In our survey, crayfish and snail numbers were inversely related, as were snails and epiphyton biomass



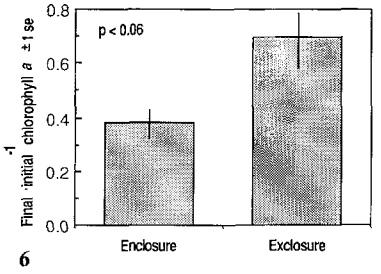


Fig. 5. Number of snails greater than 5 mm (axial shell length) in Expt. 4 quadrats compared to periphyton chlorophyll *a* on rocks in the same quadrats in three areas along the East Shore of Trout Lake

Fig. 6. Epilithon loss (final/initial chlorophyll) in Expt. 5 snail enclosures ($N=3$) and exclosures ($N=3$) after 14 days. Result of *t*-test is indicated

(Fig. 5). The mean number of crayfish on the NE Shore (14.5 crayfish-trap^{-1}-day^{-1}, sd = 5.38) was greater than on the SE Shore (3.2 crayfish-trap^{-1}-day^{-1}, sd = 2.23, $t=6.19$, $P<0.0001$). Although only large snails were counted, the abundance of small snails (*Amnicola*, young *Lymnaea* and *Physa*) seemed to be proportional to that of large snails.

These data suggest that crayfish predation was more important than epilithon biomass in determining snail distribution in Trout Lake. Snails were absent on abundant cobble which was thickly coated with epilithon (where crayfish were numerous); snails were abundant on scattered cobble which had little epilithon (where crayfish were rare). The results also suggest that instead of periphyton biomass controlling snail distribution, snail abundance controlled periphyton abundance.

Expt. 5. As suggested by the survey results, grazing by large snails appeared to reduce epilithon in cages. After 14 d, there was greater epilithon loss in snail enclosures than snail exclosures, although the difference was not quite significant ($t=2.54$, $P=0.06$; Fig. 6). Part of the decline in epilithon in both enclosures and exclosures (final over initial ratios were <1 in both treatments; Fig. 6) was probably the result of grazing by abundant small snails (<3 mm), many of which were *Amnicola*. In a previous caging study in a Rhode Island pond, enclosures with *Amnicola limosa* had lower standing crop of periphyton than exclosures (Kesler 1981). In our experiment, small snails were not removed because they were so abundant (about 6000·m^{-2}, Lodge, Weber, and K.M. Brown, unpubl. data) and so many were burrowed in the sand.

At 14 d, epilithon biomass in enclosures was reduced to just slightly more than on the natural rocks in the experimental area (4.78 µg·5.7 cm^{-2}, sd = 2.85, $n=18$, on the SE Shore during June; no measurements of ambient epilithon were taken in July).

This experiment suggests that ambient densities of large SE Shore snails can reduce epilithon on NE Shore rocks to near SE Shore epilithon levels in 14 days. Although epilithon loss in the cages without large snails is attributed to small snails, a cage or environmental effect cannot be ruled out because there was no small snail exclosure for comparison. However, our interpretation is consistent with previous studies which demonstrate reductions in periphyton biomass by snails and other lotic (Lamberti and Moore 1984) and lentic grazers (Cattaneo and Kalff 1986).

General discussion

Our experiments and observations support the hypothesis that top-down mechanisms (predation by crayfish and grazing by snails) are important determinants of Trout Lake benthic community structure. In addition to supporting the hypothesized strong interaction between crayfish and snails (Lodge et al. 1987), our study suggests that predation by crayfish cascades through the food chain, producing an indirect mutualism between crayfish and periphyton. This indirect facilitative effect parallels many examples from pelagic food webs (Kerfoot 1987), and parallels the positive effect that fish predation on large benthic invertebrates has on small invertebrates (Crowder and Cooper 1982; Gilinsky 1984; Morin 1984).

In our laboratory experiments, *L. emarginata* preferred NE Shore rocks over SE Shore sand and macrophytes. Yet in Trout Lake, snails were absent on NE Shore rocks (where crayfish were abundant) and abundant on SE Shore substrates (where crayfish were rare). That these patterns result from a strong predation effect is supported by our experimental introduction of 100 *L. emarginata* to the NE Shore (site indicated on Fig. 1). Within 15 min of introducing the snails, crayfish began to remove snails from their shells and eat them and to remove entire snails to rock crevices. After one night, 51 empty snail shells were recovered, two snails were recovered alive, and 47 snails were unaccounted for. In a concurrent control, 100 *L. emarginata* were put into a wire cage that excluded crayfish. Ninety-nine snails survived, and one snail died. While these results suggest that crayfish predation is an adequate explanation for the absence of snails from the Trout Lake NE Shore, we cannot asolutely rule out two alternative hypotheses.

The two alternative hypotheses are that i) snails have not clonized the NE Shore, and ii) wave exposure causes high snail mortality on the NE Shore. Given the high density of snail populations within 250 m of the NE Shore (Fig. 1), the diverse dispersal mechanisms of snails (Boag 1986), and the rapid dispersal of snails in other lakes (Haynes et al. 1985; Ribi 1986), we are confident that the first alternative is not very plausible.

Because the SE Shore is in a bay, we thought wave exposure there might be less than on the NE Shore. However, our *in situ* measurements on three different summer dates showed wave height was greater on the NE Shore only when wind came from the S–SW. When the wind came from the N or NW, which it does during the highest winds of the year (unpubl. observations), waves were higher on the SE Shore. In addition, we placed about 20 *L. emarginata* and *L. stagnalis* (Say) on rocks in a large mesh (0.6 cm) cage (80 cm × 50 cm × 60 cm), and placed the cage in areas of high wave action. Although the cage did not seem to reduce significantly the force of the waves, no snails were dislodged. Some snails did move to the lee sides of the rocks. Therefore, our observations suggest i) that at times of high wind, waves would be higher on the SE Shore, where snails were more abundant, and ii) snails showed an effective defensive response to high waves. While snail activity and growth might be reduced in areas of high

waves, it seems unlikely that exposure could explain the absence of snails on NE Shore rocks in Trout Lake.

While potential periphyton production and biomass may be a function of nutrient availability (Cattaneo 1987), our results suggest that in Trout Lake, actual periphyton biomass is largely a function of grazing pressure by snails, which is, in turn, determined by predation pressure by crayfish. Earlier work suggests predation pressure by crayfish is strongly determined by the abundance of fish predators (Stein and Magnuson 1976; Stein 1977). The similarity of this lentic trophic cascade (fish-crayfish-snails-periphyton) with lotic cascades (piscivores-grazing fishes periphyton; see Power 1987) suggests that top-down effects are important in many freshwater benthic communities.

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