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Resource limitation, competition and the influence of life history in a freshwater snail community

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Summary. Previous work on a snail community occurring throughout lakes in southwestern Michigan showed that predation by molluscivorous sunfish had large impacts on only the rarest snail species. Thus, competition might play a major role in population limitation because dominant members of the snail community are relatively immune to predation. The present experiments were conducted to determine the extent to which the snail community depleted the abundance of food resources (epiphytes) and the extent to which epiphyte abundances limited snail production. An experimental gradient in snail densities showed that removal of snails increased epiphyte biomass by approximately 3-fold relative to that observed at natural snail densities. Enrichment of the environment with phosphorus fertilizer increased epiphyte biomass by approximately 20-fold and provided a test of food limitation in the snail community. All snail taxa exhibited positive numerical or growth responses to enrichment. The observations that snails depleted resources and that resources limited snail production demonstrated that snails competed exploitatively for epiphytes. The response of each snail species to increased food abundance differed depending on the timing of fertilization relative to the snails' life histories. Snails hatched before the experiment began were larger in fertilized treatments, due to increased growth, but their densities were similar among treatments. On the other hand, densities of snails born during the experiment were up to 15-fold greater in fertilized treatments, due in part to increased survival of newborn snails. Comparison of the responses of snails to food addition and to predator removals (based on prior experiments) suggested that food availability limits snail production more than predators do. Additionally, the large responses by algae and snails to fertilization demonstrated that both the producers and herbivores in this simplified food chain were strongly resource limited.

Key words: Resource depletion – Food limitation – Gastropods – Population limitation – Exploitative competition

There continues to be much debate regarding the importance of competition and resource limitation versus predation and disturbance in limiting population densities (e.g. Wiens 1977; Connell 1975; Schoener 1982; Sih et al. 1985). In many systems it is likely that populations are simultaneously limited by several interacting processes (e.g. Quinn and Dunham 1983; Sih et al. 1985). Historically however, work in freshwater lakes has focused primarily on the effects of predation (especially by fish) without comparable emphasis on the possible roles of resource limitation and competition (e.g. compare the paucity of competition studies in lake systems reviewed by Connell 1983 and Schoener 1983 with the numerous predation studies reviewed by Sih et al. 1985).

The bias towards studying predation in freshwater lakes may have resulted from the strong effects that fish have when introduced into previously fishless communities, where vulnerable prey taxa are initially present at high densities (Brooks and Dodson 1965; Hall et al. 1970; Zaret 1980; Hurlbert and Mulla 1981; Crowder and Cooper 1982). However, the effects of fish on their natural (i.e. coexisting) prey communities may be much smaller due to the rarity of relatively vulnerable prey (Thorp 1986; Vanni 1987; Mittelbach 1988; Osenberg 1988). If natural prey assemblages are dominated by relatively invulnerable prey taxa (as suggested by the above citations; see also Jeffries and Lawton 1984), then prey might be able to achieve densities at which resources become limiting even in the presence of predators, as recent studies on freshwater plankton suggest (Neill and Peacock 1980; Hessen and Nilssen 1985; Vanni 1987; Leibold 1988). There are almost no studies that permit evaluation of this idea for invertebrate populations inhabiting the littoral zones of freshwater lakes. Results from such tests could modify the ways in which ecologists view the relative importance of competition, resource productivity and predation as limits of population densities (Hairston et al. 1960; Connell 1975; Menge and Sutherland 1976, 1987; Oksanen 1988).

In previous work on freshwater snails, I showed that fish predation significantly reduced snail densities under natural conditions, but that these effects fell disproportionately on rare prey: the most abundant taxa (at ambient predator densities) were insensitive to predation by fish (Osenberg 1988). These results suggested that the presence of invulnerable taxa might create conditions in which competition was prevelant among all members of the snail community. In this paper I report on experiments designed to test for the influence of exploitative competition within the snail assemblage. Exploitative competition occurs when the abundances of resources (in this case epiphytes growing

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on the surface of aquatic macrophytes) are depressed by natural densities of consumers (i.e. snails), and when the consumers are simultaneously limited by the abundance of resources. These two components of competition are rarely separated in field experiments (but see, for example, Underwood 1984), and instead are often aggregated into general density-dependent relationships (e.g. Eisenberg 1966; Brown 1982; Schmitt 1985; Kerfoot et al. 1985). Separately assessing the roles of resource depletion and resource limitation in natural systems provides understanding of the processes that control consumer-resource interactions, and also provides insight into the mechanisms of competition.

Using a series of field experiments, I show that snail grazing (as well as nutrient supply) limits the biomass of epiphytic algae. In addition, I show that the availability of epiphytes limits snail production. Thus exploitative competition occurs within this assemblage of freshwater herbivores. I further show that the particular nature of each species' response to increased epiphyte abundance depended on the timing of the snails' life histories relative to epiphyte dynamics. Based on the results of a previous field experiment (Osenberg 1988), I then compare the effects of resource limitation with the effects of predation by molluscivorous fish.

Methods

The system

Lawrence Lake is a hardwater oligotrophic lake with a maximum depth of 12.0 m, a surface area of 4.9 ha, and a littoral zone that is primarily vegetated by *Scirpus subterminalis* (Rich et al. 1971). Eight snail species occur in Lawrence Lake: three relatively small and numerically dominant prosobranch species (*Amnicola limosa*, *Marstonia lustrica* and *Valvata tricarinata*) and five pulmonate species (*Gyraulus parvus*, *G. deflectus*, *Physa*, *Helisoma anceps* and *H. campanulata*). During the spring and early summer, snails lay eggs on vegetation or debris. Hatching occurs within approximately two weeks and substantial somatic growth occurs during the summer and fall (Osenberg 1988). Two species (*Physa* and *G. parvus*) produce a second generation during late summer. All species, except *Helisoma*, are semelparous and die soon after egg production.

Snails feed primarily on the epiphytic community, which is a diverse assemblage of microalgae and bacteria lying within a matrix of calcium carbonate crystals and glycocalyx materials (Burkholder 1986). Small blue-green algae (e.g. *Synechoccus*) and diatoms (e.g. *Achnanthes*) comprise over 90% of the epiphytic biovolume (Burkholder 1986). Observational studies (Burkholder 1986) and an unreplicated fertilization experiment (R.E. Moeller, personal communication) suggest that epiphytic algae are phosphorus limited.

Snail effects on epiphyte biomass

In the first experiment, I tested whether the snail community significantly decreases the biomass of epiphytes. Eight sites were selected along the east shore of Lawrence Lake at a depth of 1.5 m. I collected snails at each site by sweeping a circular area (1.6 m diameter) with a 0.33 mm mesh net. Snails were easily dislodged from *Scirpus* with this technique and each site was swept twice to ensure adequate collection. I combined the snails from these sweeps and divided them into 21 approximately equal subsamples. I returned between 1 and 6 subsamples to each of six sites and returned no snails to the remaining two sites. Thus, the experiment consisted of a gradient in snail densities between 0X and 6X, where the '2X' and '3X' sites bracketed the natural density of snails (i.e. 21X/8 sites = 2.6X/site). The actual density at any one site consisted of any snails that were not collected by sweepnetting plus the snails that were returned to the site. Following the initial set-up, migration could have also modified snail densities. If snails influence the abundance of epiphytes, then epiphyte densities should have declined along this gradient of *relative* snail densities.

I established the gradient on 24 August 1985 and sampled epiphytes on 18 September. Two epiphyte samples were collected per site. Each sample consisted of several to a dozen pieces of the midsections of *Scirpus* leaves. Epiphytes were removed from the leaf sections by scraping each leaf with forceps. Lengths and widths of the leaf sections were measured to estimate the surface area sampled. Epiphytes were dried for 24 hours at 100° C and weighed to the nearest 0.01 mg. Mean epiphyte densities were calculated for each site based on the two samples and were expressed as dry mass per area of *Scirpus* sampled (mg/mm^2). In a subsequent study in Lawrence Lake (Osenberg, unpublished data), epiphyte densities expressed as dry mass per area (DM) and as ash-free dry mass per area (AFDM) were very closely linearly related ($r = 0.98$, $n = 240$, $p < 0.0001$, $AFDM = 0.150\ (DM) - 0.00015$, intercept not different from zero); therefore, results from this study can be converted to AFDM by multiplying by 0.15.

Food limitation in the snail community

The best way to test for food limitation is to experimentally increase the density of food available to the population of interest. In Lawrence Lake this was easily accomplished by supplying phosphorus to the epiphytic community, which subsequently increased in biomass. The experimental test of food limitation consisted of a cross factored design: the presence or absence of phosphorus fertilizer was crossed with the presence or absence of a cage. Fertilization was done in caged sites so that results could be unambiguously assigned to changes in the local snail populations and not to differential snail migration. Uncaged (referred to as "open") sites were used to determine if qualitatively similar patterns were produced in caged and open sites because cages can have many unforeseen effects on enclosed populations (Virnstein 1978; Peterson 1979; Dayton and Oliver 1980).

Eight sites (2 replicates for each of the four treatments) were arrayed linearly along the shore of Lawrence Lake. Each site (2.5 m^2 in area) was located at a depth of approximately 1 m and was separated from the others by 2 m. Earlier results indicated that fertilization effects would not extend beyond 0.5 m from the edge of fertilized sites (R.M. Moeller, personal communication). Cages were made of wooden frames with nylon mosquito netting (1 mm mesh) attached to four sides. The netting was pushed into the sediments and projected approximately 10 cm out of the water. Fish were chased out of the cages as they were installed so that predation effects would not be confounded with effects of fertilization in caged sites. Open (i.e. un-

caged) sites were marked with flagging. Resin-encapsulated pellets of phosphorus fertilizer ("Osmocote" manufactured by Sierra Chemical Co., Milpitas, California) were glued to the top third of wooden dowels, and 25 dowels were stuck into the sediments of each fertilized site so that the ends with fertilizer projected throughout the *Scirpus* bed. Each dowel contained approximately 2.5 g of phosphorus in the form of calcium phosphate.

Cages were installed on 18 August 1985 and fertilizer sticks were added three days later. On 11 September I removed half of the fertilizer sticks from each fertilized site because the changes in epiphyte biomass were already very large. Epiphyte densities were sampled one month after the start of the experiment (18 September), and snails were sampled two days later. Methods for collecting and processing epiphyte samples were the same as in the first experiment, except that three samples (instead of two) were collected and pooled per site. The experiment was conducted for only a brief time period so that the direct effects of epiphytes on snail survival and growth could be isolated from the long-term effects associated with the secondary response of epiphytes to changes in the snail community.

I collected snails by using a square tray (area = 0.114 m^2) that I carefully slid along the surficial sediments as I cut the *Scirpus* plants at their bases. Directly above, I suspended a 0.33 mm mesh plankton net that was tied to a frame just slightly larger than the tray. The net collected the *Scirpus* that floated away, and after I had completely slid the tray along the sampled area, I carefully lowered the net onto the tray. Two of these samples were collected at each site. Prior to sampling the cages, I noticed that some snails had crawled onto the inside walls of the cages. Therefore, I supplemented the primary samples with samples taken from the sides of each cage with a fine-meshed aquarium net. 12 vertical sweeps were taken from the inside walls of each cage, corresponding to 17% of the interior surface area of the netting or an equivalent benthic area of 0.43 m^2 ($=2.5\ m^2 \times 0.17$). The samples were rinsed through a 0.5 mm sieve and preserved in 10% buffered formalin. Snails were identified to species, counted and measured, and linear measurements were converted to tissue dry masses using length-mass regressions (Osenberg, unpublished data). Data from the samples collected at each site were pooled; additionally, the samples from the caged sites were differentially weighted to properly combine the data from the net samples with that from the vegetation samples (i.e. snails collected on the vegetation were assigned a relative weight of $1.894 = 0.43/(0.114 \times 2)$).

I assumed that the response by snails would be expressed either in differential survival or reproduction, which would increase snail densities, or in differential growth, which would increase the size of individual snails. The responses were expected to vary depending on whether the snails reproduced before or during the experiment. Therefore, snails were classified by generation as well as species: e.g. *Physa* reproduced during the experiment and both adults and newborns were present in the samples. *G. parvus* also reproduced during the experiment; however, I could not distinguish the few surviving adults from the newborn snails due to the overlap in their size distributions. *H. anceps* and *H. campanulata* were very rare and because they have similar life histories, I combined data for these species into one taxonomic category, which I divided into adults (snails born during the previous year, 1984) and young of the year (snails born during the spring of 1985). All other taxa were represented only by young-of-year that had been produced prior to the start of the experiment. Data were $\log_{10}$ transformed (or $\log_{10}(x+1)$ for species with at least one $x=0$) and analyzed by two-way analysis of variance (SAS PROC GLM: SAS Inst. Inc. 1985).

Results and discussion

Snail effects on epiphyte biomass

Epiphyte biomass decreased significantly across the manipulated snail gradient (Fig. 1). Epiphyte biomass at reduced snail densities (i.e. 0–1X) was two to four times greater than the biomass at natural (i.e. 2–3X) and elevated (i.e. 4–6X) snail densities. These data suggest that natural densities of snails reduce the abundance of epiphytes in Lawrence Lake. The relationship in Fig. 1 might be biased with respect to the quantitative relationship between epiphyte biomass and snail density because the epiphyte community was disturbed by sweeping while setting up the snail gradient. Additionally, snails might have migrated among sites, thus altering snail densities. However, a subsequent experiment in Lawrence Lake, in which snail densities were reduced 50–85% below natural levels by high densities of molluscivorous fish, showed that epiphyte biomass increased approximately 2-fold in response to decreased snail densities (Osenberg 1988). The results of these two experiments demonstrate that snails reduce epiphyte biomass, and suggest that the removal of snails would lead to a 2 to 4-fold increase in epiphyte biomass. Results from other field experiments involving snail-algae interactions in littoral systems show similar reductions of algal biomass due to grazing (Hunter 1980; Higashi et al. 1981; Cuker 1983a, b), as do studies of grazer-algae interactions in streams (Lamberti and Resch 1983; Jacoby 1985; Hart 1987; Hill and Knight 1988) and the rocky intertidal (Nicotri 1977; Underwood 1984).

Food limitation in the snail community

Because natural snail densities significantly depress the biomass of epiphytes (Fig. 1), competition can be demon-

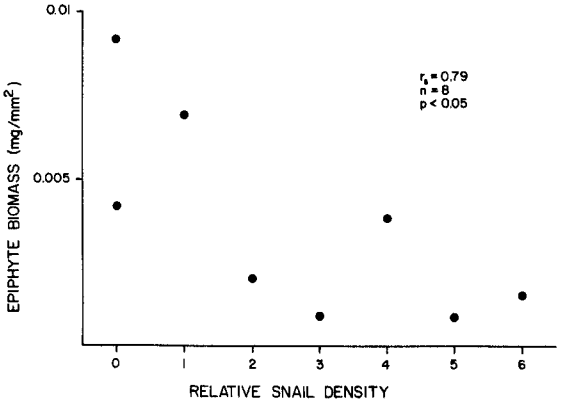

Fig. 1. Epiphyte density measured along a gradient in snail density. Snail density represents a relative measure (see text) where natural density corresponds to a value of 2.6. Spearman's rank correlation coefficient and the associated probability of no relationship are shown

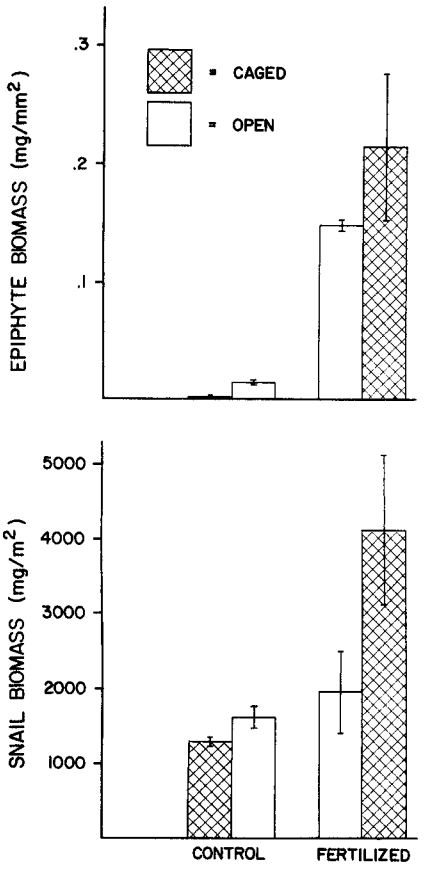

Fig. 2. Epiphyte and snail densities in the four experimental treatments. Ordering of the treatments is based on epiphyte biomass. Means and ranges are indicated (n = 2). *A posteriori* contrasts were performed using Duncan's method: for epiphytes, cage-cont < open-cont < open-fert = cage-fert; and for snails, cage-cont = open-cont = open-fert < cage-fert

strated if the depleted resource limits the snail populations (e.g. through reduced growth, survival and/or reproduction). In the experiment testing for resource limitation, phosphorus addition had detectable effects on epiphyte biomass after one week of fertilization, and by the end of the experiment epiphyte biomass was 13–500 times greater in fertilized sites compared to controls (Fig. 2). Analysis of variance showed that fertilization and caging had significant effects on epiphyte biomass ($F_{fert} = 184.6$, $p < 0.001$; $F_{cage} = 20.5$, $P = 0.01$) as did the interaction between the two factors ($F = 31.5$, $P = 0.005$): epiphyte biomass in unfertilized treatments was greatest in open sites, while in fertilized treatments epiphyte biomass was greatest in caged sites (although the latter difference was not significant based on *a posteriori* tests: Fig. 2). This differential response was probably attributable to the effect of cages on water circulation.

Total snail biomass showed a response that was very similar to the response by epiphytes (Fig. 2). Snail biomass was greatest in the caged-fertilized sites and least in the caged-control sites, although only the effect of fertilization was significant ($F_{fert} = 11.3$, $P = 0.03$; $F_{cage} = 2.01$, $P = 0.23$; $F_{cage \times fert} = 5.2$, $P = 0.09$). Thus the depletion of epiphytes by snails (Fig. 1) coupled with the observation that epiphyte biomass limits snail production (Fig. 2) demonstrated that competition occurs within the snail community. I next explore how the survival, recruitment and growth of particular snail species were influenced by the experimental treatments.

Snails born prior to the start of the experiment showed no significant variation in density among treatments (Fig. 3), suggesting that survival was not influenced by epiphyte productivity or caging. By contrast, densities of *Physa* and *G. parvus* born during the experiment, were approximately 15-fold greater in the treatments with the most epiphyte biomass compared to the treatment with the least (Fig. 3). Mean individual masses of snails showed almost the reverse pattern. The second generations of *Physa* and *G. parvus* did not show significant increases in mean mass in response to fertilization (Fig. 4). However, the mean mass for all but one of the other species was greater in the fertilized treatments (Fig. 4). The only exception was *Helisoma* that were over a year old at the time of the experiment. During its first winter, *Helisoma* thickens its shell by greatly increasing the deposition of calcium. This might limit a snail's ability to increase its shell size during its second year of life. The snails can however continue to change in body mass (Russell-Hunter and Eversole 1976); I would not have detected these changes because I estimated body mass based on measurements of shell size.

The dramatic numerical response by *Physa* and *G. parvus* could have been caused by several processes involving effects of algal biomass on adult and/or newborn snails: 1) increased food might have increased the size of adults, and because fecundity (daily egg production) is strongly related to snail size (Brown 1979; Perron 1982; Osenberg 1988), adults would have produced more eggs; 2) additional food might have increased the size-specific fecundities of adults; 3) adults might have survived longer during reproduction when food was more abundant, thus increasing their overall production of eggs; and 4) very young snails might have survived better when food was more plentiful.

It is very difficult to isolate the effects of these different mechanisms with the available data. Eisenberg's (1966, 1970) work on food limitation in another species of freshwater snail demonstrated that density-dependence in adult fecundities was largely responsible for adjustments in population density. The responses observed by Eisenberg were produced over a longer time period than in the present study, and were primarily attributable to changes in the size of adults and not in size-specific fecundities (analysis of Table 2 in Eisenberg (1970)). It is unlikely that large changes in adult size (or size-specific fecundity) could have accrued during the experiment in Lawrence Lake. The experiment lasted only four weeks, there was a time lag of approximately one week before fertilization had a noticeable effect on epiphyte biomass, and eggs require 1.5–2.5 weeks to hatch (Heard 1963; Eisenberg 1966; Osenberg, personal observation). Therefore, any effect mediated through adults (e.g. explanations 1, 2 and 3 above) must have occurred during the second week of the experiment. One week is insufficient time for adult snails to accrue differences in size necessary to produce the putative 15-fold variation in egg production (Osenberg 1988). I conclude that the effects of differential adult fecundity were probably small, and I suggest that early survival of young snails may have been responsible for the large numerical response by *Physa* and *G. parvus*.

This explanation requires that there be a dramatic shift

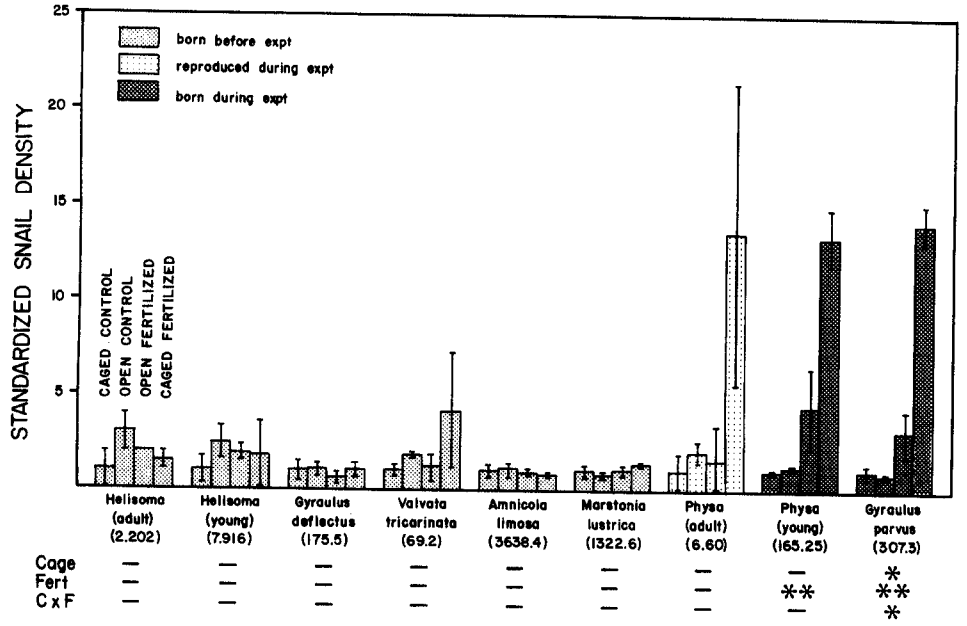

Fig. 3. Standardized densities for each snail species in the four experimental treatments. Standardized densities are the ratio of a site's density and the mean from the caged-control sites (the treatment with the lowest density of epiphytes: Fig. 1). The mean densities (no./m^2) from the caged-control sites are shown parenthetically below each species label. Data for different generations of the same species are shown separately. Generations were distinguished by the timing of their life-histories relative to the experiment (e.g. born before or during the experiment). Adult *Physa* were born before the experiment, but they reproduced during the experiment; therefore they were further distinguished. The data for *G. parvus* are primarily based on young born during the experiment, but probably also include a few adults that could not be clearly distinguished due to the overlap in size-distributions. Within each of the three life history categories, species are ordered approximately by age. For each species, treatments are ordered by epiphyte biomass (see Fig. 1). Means and ranges are indicated (n = 2). Asterisks indicate significant effects from analysis of variance (* = $P<0.05$, ** = $P<0.01$, --- = not significant)

in the resource-dependent survival of recently hatched snails compared to older snails (e.g. >1 month) (Fig. 3). Work on other size-structured aquatic organisms suggests that this is plausible. Small animals incur greater mortality rates than larger conspecifics under conditions of low food (Oliver et al. 1979; Borchers and Hutchings 1986; Tessier et al. 1983), due to the way metabolic rates and stored energy scale with body size (Threlkeld 1976; Shuter et al. 1980). Thus, snails are most likely to die due to food limitation during early stages of their life histories. Furthermore, Berg and Ockelmann (1959) have shown that pulmonate snails (e.g. *Physa*) tend to have higher mass-specific metabolic rates than prosobranchs (e.g. species related to *Amnicola* and *Marstonia*). Thus, pulmonates should starve to death faster than prosobranchs under conditions of low food (all else being equal). These data suggest that *Physa* and *G. parvus* exhibited strong numerical responses to epiphyte

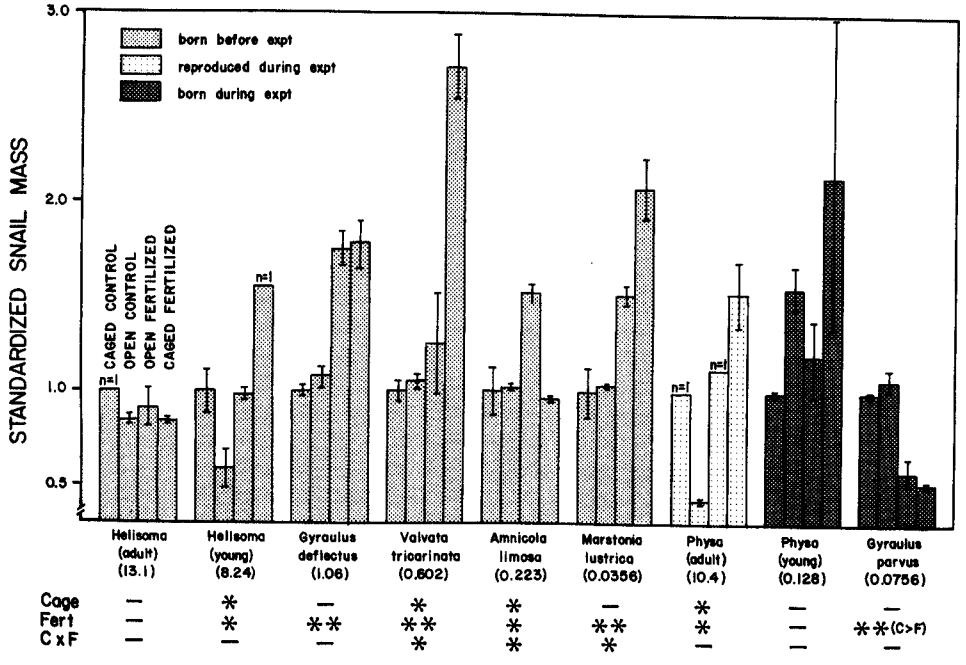

Fig. 4. Standardized mean snail mass for each species in the four experimental treatments. See legend to Fig. 3. Means and ranges are indicated ($n = 2$, except where indicated)

biomass due to the increased susceptibility of newborns to starvation, which might have been exacerbated by the greater mass-specific metabolic rates characteristic of some pulmonates.

The qualitative effects of fertilization were similar among caged and uncaged sites, although caging appeared to exaggerate the effects of fertilization on epiphyte and snail responses (Fig. 2). In caged-control sites, phosphorus (and/or other nutrients) may have been relatively depleted due to the limited exchange of water with the lake. However, where fertilizer was added, cages probably inhibited the dispersion of phosphorus to the lake, leading to an enhancement of available phosphorus relative to open-fertilized sites. These effects on primary production may have created a parallel pattern in snail biomass (Fig. 2). Of course, other differences attributable to cages may have also contributed to these patterns. For example, predators were excluded from caged but not open sites. However, a previous experiment (Osenberg 1988; see below) and the lack of density effects in the present experiment (Fig. 3) suggest that predators played at best a minor role in determining results of this study.

The only species that did not show the same qualitative response to fertilization in caged and open sites was *Amnicola*, which did not increase in size in the caged-fertilized treatment (Fig. 4). Instead, I observed that a number of *Amnicola* (probably 5–10%) were deformed in samples from caged-fertilized sites but not in any other samples. In these specimens, the whorls were not completely fused and the shells often had gaps between successive whorls. I do not know the cause of this although in a subsequent experiment in Lawrence Lake (Osenberg 1988), where I fertilized inside cages but also transferred lake water to each cage on a weekly basis, *Amnicola* did not show these deformities and its mean mass increased relative to controls.

Comparison of resource limitation and predator limitation

These data demonstrate that the availability of epiphytes severely limited snail populations in Lawrence Lake. During the 30 day fertilization experiment in Lawrence Lake, *Physa* and *G. parvus* increased their densities by 15-fold and the mass of other snails increased by approximately 2-fold. It is unclear how these short-term growth responses would eventually translate into numerical responses, but the responses by *Physa* and *G. parvus* suggest that the effects could be very large. Total snail biomass, which combines the numerical and growth responses into a simple community metric, was approximately 3-fold greater in caged-fertilized sites relative to control sites (Fig. 2).

On the other hand, predation by large predators (e.g. fish) appeared to have little effect on snail abundances, as suggested by the absence of cage effects on snail densities (Fig. 3); the only exception was *G. parvus*, which recruited during the experiment and was probably influenced by the greater epiphyte biomasses in the caged-fertilized treatment. Additionally, I experimentally altered the density of pumpkinseed sunfish (*Lepomis gibbosus*) in another lake (Palmatier Lake) and observed minor effects on total snail biomass. Pumpkinseed sunfish are the most conspicuous molluscivore in these lakes, and because their densities are similar in both lakes (Osenberg et al. 1988), the effects of pumpkinseeds are probably comparable. Over a 93 day period (three times the duration of the fertilization experiment), removal of pumpkinseeds had very little effect on 6 of the 9 snail taxa, but did produce stronger effects on the three most vulnerable snail taxa, which approximately doubled in density (Osenberg 1988). However, the natural density of these vulnerable species was only 1/10 the density of the six less vulnerable species, leading to only a 50% increase in snail biomass in the absence of fish predation.

Table 1. Sizes of snails in Lawrence Lake and Palmatier Lake during September 1985. Mean snail masses from two sites per lake are given in milligrams dry mass. The data for Lawrence Lake are from the two open-control sites. *Physa* sizes are based on young snails (second generation) in Lawrence Lake. Although age classes of *Physa* were not distinguished in Palmatier Lake, it appeared that adults had completely died by the sample date. *Helisoma* data are not included because adults and young-of-year were not distinguished in the Palmatier Lake study. Snails were sampled on 20 September 1985 in Lawrence Lake and on 29 September 1985 in Palmatier Lake

Snail taxa	Mean snail mass (mg)				
	Lawrence Lake			Palmatier Lake	
Marstonia lustrica	0.047	0.041		0.038	0.055
Gyraulus parvus	0.078	0.086	*	0.046	0.045
Physa	0.183	0.214	*	0.123	0.112
Amnicola limosa	0.230	0.229		0.191	0.210
Valvata tricarinata	0.655	0.613	**	0.289	0.267
Gyraulus deflectus	1.234	1.305	*	0.640	0.347

t-tests were used to compare snail sizes in the two lakes: * = $P < 0.05$, ** = $P < 0.01$

I compared the degree of food limitation in Lawrence Lake with that in Palmatier Lake by comparing the mean mass of snails collected from two sites in Palmatier Lake on 29 September 1985 with the mean mass of snails collected from Lawrence Lake in open-control sites on 20 September 1985 (Table 1). Snails of each species were consistently smaller in Palmatier Lake compared with Lawrence Lake (phenologies of snails in the two lakes were similar, as were water temperatures, which averaged 23.5° C in each lake based on four dates in August and September). Thus, growth rates were slightly poorer and food limitation was probably greater in Palmatier Lake. These comparisons suggest that resource limitation is much more important than predation (at least by pumpkinseed sunfish) in limiting the total biomass of snails in Lawrence and Palmatier Lakes. In addition, results from the fertilization experiment suggest that epiphytes are also strongly resource limited, based on the 20-fold increase in biomass following additions of phosphorus fertilizer.

These results stand in contrast to predictions made by several general models of trophic-level limitation that have been proposed. For example, Hairston et al. (1960) (see also Slobodkin et al. 1967) suggested that herbivores are maintained at such low densities by predators that biomass of primary producers does not limit the herbivore trophic level; this was clearly not the case in Lawrence and Palmatier Lakes. Although Hairston et al.'s predictions were based on a particular set of observations from terrestrial ecosystems, the model has been recently extended to other systems (Connell 1983; Schoener 1983, 1985; Sih et al. 1985; Persson et al. 1988). Another prediction of Hairston et al. (1960)

is that the importance of resource limitation should "flip-flop" up the food chain. However, the results of this study show that snail biomass and algal biomass were both limited by the availability of their resources (algae and phosphorus). The strong resource limitation present at the base of the food chain was transmitted to the herbivore trophic level. Using correlative data, McQueen et al. (1986) recently argued that freshwater pelagic systems are strongly resource limited at both the primary producer and herbivore levels, and similar arguments have been made for terrestrial systems (Sinclair 1975; White 1978). At present it is difficult to assess how the relative importance of different processes vary with trophic position (or other ecologically important characteristics). Much additional insight is likely to come from experimental studies that simultaneously address different modes of limitation in several trophic levels within the same ecosystem.

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