# BODY SIZE AND THE INTERACTION OF FISH PREDATION AND FOOD LIMITATION IN A FRESHWATER SNAIL COMMUNITY

By

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ABSTRACT

BODY SIZE AND THE INTERACTION OF FISH PREDATION AND FOOD LIMITATION IN A FRESHWATER SNAIL COMMUNITY

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The simultaneous effects of fish predation and food limitation were investigated in a natural assemblage of freshwater snails inhabiting lakes in southwestern Michigan. Using a combination of field and laboratory studies, I developed and tested a foraging model for the predator-prey interaction between pumpkinseed sunfish (Lepomis gibbosus) and snails, based on the ways in which encounter rates, size refuges and attack probabilities scaled with snail and fish size. The model explained 47-71% of the observed variance in prey selection by pumpkinseeds. Results from a large field experiment further showed that the population responses of snails to fish predation were similar to predictions from the foraging model: species with the largest body sizes during the time of the experiment incurred the greatest mortality rates from pumpkinseeds due mostly to their higher encounter rates.

Interactions between snails and epiphytic algae were explored by simultaneously altering fish density and primary productivity. Community changes were manifest through strong trophic connections that flowed up and cascaded down the food chain. For example, fertilization in the absence of fish led to increased biomasses of epiphytic algae and snails and a subsequent shift to algae that were resistant to grazing. In treatments with either high predator densities, poor quality algae, or low algal abundances, the snail community was dominated by small bodied taxa, which have lower encounter rates with predators and better

assimilation and metabolic efficiencies than larger taxa. Snail species with large adult body size only became abundant when predation intensity was low and food quality was high. Due to the dynamics of snails and epiphytes, this is typically a transient condition in natural lake communities.

Comparison of the effects of resources and predators on algae, snails and fish showed that both factors limit population growth. However, resource limitation appears to place more severe constraints on each trophic level than does predation. The greater importance of food limitation probably results from the dominance of relatively predator-resistant taxa at each trophic level. These taxa are able to establish large population densities in the presence of predators and thus impose food limitation throughout the trophic level.

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# CHAPTER 1

## THE EFFECTS OF BODY SIZE ON THE PREDATOR-PREY INTERACTION BETWEEN PUMPKINSEED SUNFISH (*LEPOMIS GIBBOSUS*) AND GASTROPODS

# INTRODUCTION

A predator's choice of prey serves as a primary link connecting the dynamics of species on different trophic levels (Brooks and Dodson 1965; Paine 1966; Hassel 1978; Murdoch and Oaten 1975). Prey choice and foraging rates not only determine the energy gained and therefore influence the growth rates, survivorships and fecundities of predators (Turnbull 1962; Osenberg et al. 1988; Mittelbach 1988), but, by definition, they also influence the mortality rates on the prey populations. These effects and the feedback between them remain a central focus for the understanding of population dynamics and community structure (Rosenzweig 1973; Holt 1977; Levins 1979; Oksanen et al. 1981).

Foraging theory, developed extensively since the seminal work by Holling (1959a,b) and Watt (1959), is a potentially powerful tool that can be used to link the mechanistic understanding of prey choice at the individual level with patterns that emerge at the population and community levels (Wilson 1976; Werner 1977; Werner and Mittelbach 1981; Tilman 1982). Clearly, this connection between different levels of organization is an important one to make in ecology, but it is often hindered by the complexity inherent in natural systems. For example, prey species each possess unique sets of traits that influence a predator's prey preferences (Schmitt 1981, 1982; Morgan 1987). Further, predators often exhibit strong preferences within a single prey species; these differences are often related to prey size (Mittelbach 1981, Bence and Murdoch 1986, Folkvord and Hunter 1986). The construction of a general framework in which to view prey selection, and the extension of this framework to population and community patterns, hinges upon determining the functional basis of this variation in the predator-prey

relationship. Because prey selection is equal to the relative mortality rate imposed on a prey type by the predator (Chesson 1978, 1983; Vanderploeg and Scavia 1979), prey selection by the predator and predation risk for the prey (i.e. the mortality incurred via the predator) can be viewed from similar perspectives within the same general framework.

Prey selection, or the relative vulnerabilities of prey to predators, is determined by the product of three important functions: the encounter rate between predators and prey, the probability that a predator attacks an encountered prey item, and the probability that the predator successfully consumes an attacked prey item (O'Brien 1979; Greene 1983). Previous studies in aquatic systems show that each of these three functions, which could be even further subdivided, are often related to prey (and predator) body size (Elner and Hughes 1978; Mittelbach 1981; Pastorak 1981; Wright and O'Brien 1984; Bence and Murdoch 1986; Wainwright 1987), although different prey (and predator) species often vary in the way the relationships scale with body size (Swift and Federenko 1978, Breck and Gitter 1983, Folkvord and Hunter 1983, Wainwright 1988). Thus, a general model of prey selection might consist of a few relatively simple functions, where complexity is present primarily in the way the parameters of these functions scale with body size for each of the interacting species. Because body size also influences individual fecundities (Bagenal 1978; Perron 1982; Chapter 2), it may well serve as a common variable linking models of prey selection with models of population dynamics based on size-specific birth and mortality rates (VanSickle 1977; Kirkpatrick 1984; Werner and Gilliam 1984; Kooijman 1986).

In this paper, I explore patterns of prey selection by pumpkinseed sunfish (Lepomis gibbosus). In field studies, I show that pumpkinseeds

feed primarily on gastropods (see also Keast 1978, Laughlin and Werner 1980, Mittelbach 1984), but that dietary patterns and prey selection among gastropods are highly variable from time to time (or site to site). I then use a series of laboratory studies to measure important size-related predator and prey traits that can influence encounter rates, attack probabilities, and capture successes. By incorporating these data into a series of general models, increasing in their level of complexity, I demonstrate how prey selection in the field is influenced by these components and how the effect of each key trait scales with body size.

## FIELD STUDIES

### Study Sites and Natural History

Diets of pumpkinseed sunfish were examined in three small (6-22 hectare) hardwater lakes (Culver Lake, Palmatier Lake and Three Lakes II) located within 25 km of the Kellogg Biological Station in southwestern Michigan (see Osenberg et al. 1988). The littoral zone of each lake is covered extensively by the macroalga Chara, which grows as a dense mat, approximately .25-.50 m thick, between depths of approximately 0-4.5 m. Other aquatic plants (e.g. Potamogeton and Myriophyllum) occur sporadically throughout the littoral zones.

The fish community of these lakes is typical of small glacial lakes in the northcentral United States. Centrarchids, notably bluegill (L. macrochirus), pumpkinseed (L. gibbosus) and largemouth bass (Micropterus salmoides), comprise well over half of the total fish biomass (Brown and Ball 1942; Hall and Werner 1977; Werner et al. 1977). Although approximately 20 species of fish occur in these lakes, pumpkinseeds are

the only fish that feed predominantly on gastropods (Osenberg, personal observation), due in part to their possession of modified pharyngeal jaws and associated musculature that aid them in crushing gastropod shells (Mittelbach 1984; Lauder 1983). Pumpkinseeds are active throughout the littoral zone from May through September when water temperatures are above approximately 15$^{o}$C.

Eleven gastropod species occur in the three study lakes (see Table 1), and these snails vary considerably in their shell morphologies and their maximum body mass. The snails feed primarily on epiphytic algae that grow on the surface of the littoral vegetation. Snails of several species however (i.e. Viviparus and large Helisoma) often occur deep within the Chara layer or on the sediments below other macrophytes.

The gastropods exhibit fairly repeatable patterns of growth and reproduction (Chapter 2). During ice-cover, the snails are inactive and lie on the surface of or just beneath the sediments below the decaying or senescent macrophytes. As the water warms, the snails become active and reproduction begins around late-April and continues through late-September. However, the reproductive patterns of each species is much more restricted. Prosobranchs (see Table 1) lay eggs (or give birth: Viviparus is live-bearing) between early-May and late-July. These species produce only one generation per year, and the adults typically die following reproduction (except for Viviparus, which can live up to 3 years). Pulmonate snails typically reproduce earlier than the prosobranchs (i.e. late-April through mid-June) and also die following reproduction (except for Helisoma, which can live up to two years). However, Physa and Gyraulus parvus often produce a second generation during August or September (Chapter 2). Therefore, during the period when fish are most active (May through September), the

Table 1. Gastropod species and pooling scheme for dietary analyses of pumpkinseeds. Also shown are the approximate adult masses (mg tissue dry mass) for each snail species. All species occur in each of the three study lakes, except Viviparus, which occurs only in Three Lakes II. Physa is probably represented by only one species in these lakes, but due to ambiguities and difficulties in the systematics, I do not refer to a specific epithet.

| Class | Family | Species | Prey Category | Adult Mass |
|---|---|---|---|---|
| Prosobranchia | | | | |
| | Hydrobiidae | | | |
| | | Amnicola limosa | Amnicola | 0.5 - 1.5 |
| | | Amnicola walkeri | Amnicola | 0.1 - 0.3 |
| | | Marstonia lustrica (<1.5mm) | Amnicola | 0.3 - 0.8 |
| | | Marstonia lustrica (≥1.5mm) | Marstonia | |
| | Valvatidae | | | |
| | | Valvata tricarinata | Valvata | 1.0 - 2.0 |
| | Viviparidae | | | |
| | | Viviparus georgianus | Viviparus | >20 |
| Pulmonata | | | | |
| | Physidae | | | |
| | | Physa | Physa | 2.0 - 10.0 |
| | Planorbidae | | | |
| | | Gyraulus parvus | Gyraulus | 0.1 - 0.4 |
| | | Gyraulus deflectus | Gyraulus | 0.6 - 3.0 |
| | | Promenetus exacuous | Gyraulus | 0.2 - 1.5 |
| | | Helisoma anceps | Helisoma | 10. - 20. |
| | | Helisoma campanulata | Helisoma | 10. - 20. |

size-structure and species composition of the snail community is extremely dynamic.

## Methods

Examination of dietary patterns and prey selection were based on 166 pumpkinseeds, ranging in size from 52-131 mm standard length (SL), that were collected from one of the three study lakes on six dates between August 1983 and June 1985 (Table 2). Smaller fish were not collected because they do not feed on gastropods (Mittelbach 1984). Fish were collected between 900 and 1100 hours; large fish (generally >80mm SL) were sampled by stomach pumping (Seaburg 1957), while smaller fish were preserved in 4% buffered formaldehyde due to difficulty of stomach pumping. Preserved fish were later dissected and the contents of their stomachs and intestines kept separate. On one date (17 August 1984), all fish were stomach pumped and then preserved. Fish collected from this date showed that stomach pumping was over 90% efficient in removing prey (#removed/total: $\bar{x}$=91.6%, 95% C.I = 84.5-96.7%, n=20, based on arcsin-square root transformed data), and snails and non-snails were removed with the same efficiency (paired t-test, $p>0.10$). Therefore, because of the very high efficiency and lack of bias, all fish were treated identically in the subsequent analyses (i.e. without regard to collection method).

Prey from the stomach samples were identified, counted and measured. Gastropods were identified to the lowest possible taxonomic level (see below), while other types of prey were identified to family or genus (only gastropod prey were identified from fish collected during 1983). Because pumpkinseeds crush the snails' shells, snail sizes could not be assessed directly by measuring the shell. For prosobranch snails, I

Table 2. Study sites and collection information. N is the number of fish, fish size is given in millimeters standard length, and each resource sample is 0.0324 $m^2$.

| Lake | Date | N | Size Range | No. of Resource Samples |
|---|---|---|---|---|
| Three Lakes II | 19 August 1983 | 9 | 56–80 | 8 |
| Three Lakes II | 4 September 1984 | 21 | 59–109 | 10 |
| Three Lakes II | 17 May 1985 | 63 | 54–131 | 16 |
| Three Lakes II | 6 June 1985 | 32 | 52–115 | 10 |
| Culver Lake | 30 August 1984 | 20 | 69–128 | 8 |
| Palmatier Lake | 17 August 1984 | 21 | 60–124 | 10 |

counted and measured opercula because they are not digested by the fish. In addition to the data from the stomach samples, I also counted and measured opercula collected from the intestines of preserved fish. Opercular diameter was converted to shell height or shell diameter using regressions based on snails collected in the resource samples (see below). Opercula could be identified to genus, with the exception of the opercula of Marstonia, which at small sizes closely resembled the opercula of Amnicola. Therefore, Marstonia smaller than 1.5 mm (shell height) were included in the Amnicola prey category (Table 1).

For pulmonate snails (which lack opercula), the length of the foot was measured. The foot has greater integrity than other soft parts of the snail and could be clearly identified and measured in the stomach samples. However, pulmonates could not be consistently identified or measured in the intestine samples. Thus, no data for pulmonates were taken from the intestine samples. Pulmonate snails were identified to genus, although P. exacuous could not be distinguished unambiguously from Gyraulus (Table 1). Foot lengths were converted to shell height or shell diameter using regressions of foot length on snail size.

All measurements of snail size were converted to tissue dry mass using length-mass regressions. Because pulmonates from the intestines could not be identified, data from intestine contents were not used whenever comparisons were being made among all snail categories. However, when comparisons were restricted to only prosobranchs, the data from the intestine samples were included in the analyses in order to increase sample sizes.

Immediately prior to collecting fish, snails were sampled from the same area of the lake. Snails were collected by gently creating an opening in the Chara mat and inserting a 20.3 cm diameter brass sieve (mesh size = 0.5 mm) under an undisturbed part of the Chara. I then

placed a similar diameter stovepipe above the Chara, and pushed the stovepipe down onto the sieve, thus capturing a 0.0324 $m^2$ core of vegetation. 8-16 cores were collected per sampling date (Table 2), and these were combined into one pooled sample. The collected vegetation was rinsed to remove the snails, the residue was preserved in 4% buffered formaldehyde, and the residue was later sorted and the snails removed. Snails from the resource samples were identified to species, counted, and all or up to approximately 300 snails per species were measured from each date. Prey taxa were pooled as required by the identification scheme used with the diet samples (Table 1).

Prey selectivities were calculated using Manly's index (Manly 1974, Chesson 1978, 1983) (see Table 3 for definitions of symbols used in this paper):

$$\alpha_i = g_i/d_i \; / \sum_{j=1}^{k} (g/d_j) \qquad (1)$$

where k is the number of prey categories, $g_i$ is the number (or proportion) of prey of type i in the diet sample and $d_i$ is the number (or proportion) of prey of type i in the resource sample. $\alpha_i$ ranges from 0-1, with random selection being indicated by $\alpha_i = 1/k$. The selectivity can also be interpreted as a relative mortality term, mediated through the predator, on the k prey types (Vanderploeg and Scavia 1979). Rare prey ($d_i < 20$) were excluded from calculations of the selectivities, and diet samples with few prey ($\Sigma g_j$) lower than some critical value) were also excluded. The critical values used depended on the particular analysis and will be provided along with the results.

Feeding observations of pumpkinseeds were conducted on ten dates in Three Lakes II and on three dates in Culver Lake. Fish were haphazardly selected and followed for 5-10 minutes (less time if they were lost). I

Table 3. Definition of symbols used in the text. Units are given parenthetically.

| | |
|---|---|
| $k$ | number of prey categories |
| $g_i$ | number of prey type i in a fish's diet or in a group of fishes' diet |
| $G$ | total number of prey in diet (summed over some specified set of prey types: $\sum g_j$) |
| $d_i$ | number of prey of type i collected and measured in the resource samples |
| $D_i$ | density of prey type i in the environment (no./$m^2$) |
| $_i$ | per capita encounter rate between a fish and prey type i ($s^{-1}$) |
| $P_i(a)$ | probability of attack given an encounter with prey type i |
| $P_i(g)$ | probability that a snail of type i can be taken into the fish's mouth given an attack |
| $P_i(c)$ | probability that a snail of type i can be crushed given it is taken into the fish's mouth |
| $P_i(s)$ | probability that an atack on prey type i is successful: $P_i(g)P_i(c)$ |
| $C_i$ | crushing resistance of prey type i (g) |
| $h_i$ | handling time per snail of prey type i: successful attacks (s) |
| $r_i$ | rejection time per snail of prey type i: unsuccessful attacks (s) |
| $H_i$ | total handling time per snail of prey type i including successful and unsuccessful attacks (s): $(P_i(s))h_i + (1-P_i(s))r_i$ |
| $m_i$ | tissue dry mass per snail of type i (mg) |
| $a$ | assimilation efficiency of fish feeding on snails |
| $c$ | energy content per unit snail dry mass (J/mg) |
| $M$ | fish mass (g) |
| $R$ | metabolic rate of a fish (J/s) |
| $e_i$ | energetic reward (gross or net) offered by an item of prey type i: $e_g=m_i caP_i(s)$, $e_n=e_g-RH_i$ |
| $e_i/H_i$ | profitability (using either $e_g$ or $e_n$ in the numerator) of prey type i |

Table 3 (cont'd.)

| | |
|---|---|
| S | time spent searching by a predator during a foraging bout (s) |
| E/T | rate of energy acquisition to a predator (see equation 10) (J/s): gross (without inclusion of metabolic losses) or net rates indicated as $E_g/T$ and $E_n/T$. Optimal foraging rates are indicated by E/T*. |

estimated the size of each fish to the nearest 5 mm and recorded their activities with a stopwatch (e.g. handling time, search time, time spent interacting with other fishes). 161 fish that ranged in size from 80–130 mm SL were observed.

For statistical analyses, patterns expected to follow allometric relationships were analysed by regression or analysis of covariance with fish size as the covariate (SAS Institute Inc. 1985: PROC REG or PROC GLM). Data were $\log_{10}$ transformed to achieve linearity. For responses that were not expected to follow simple allometric relationships, the fish were divided into four, approximately 20 mm, size categories (50–69, 70–89, 90–109, and 110–131 mm SL) and these categorical data were analyzed using SAS PROC GLM. Proportions were arcsin-square root transformed, while most other data were $\log_{10}$ transformed to reduce mean-variance correlations. Selectivity vectors were contrasted using multivariate analysis of variance (SAS PROC GLM with the MANOVA option). In order to test for deviations of a selectivity vector from the random expectation ($\alpha_i = 1/k$ for all i), Hotelling's $T^2$ statistic was calculated (BMDP3D, Dixon 1981).

## Results

Pumpkinseeds fed on a variety of littoral prey including gastropods, chironomids, other insect larvae and cladocera. Snails however, contributed over 80% of the total prey mass in the fish's diets (Table 4: averaged over all dates and fish sizes, $\bar{x}$=89.0%, 95%C.I.= 84.2-93.0%, n=157). Mittelbach (1984) obtained similar results for fish >50 mm SL, while fish < 50 mm SL fed very little on snails ($\bar{x}$=7.1%, 95%CI=0.5–20.4%, n=24). In general, the total mass of snails in the stomachs of fish increased with fish size (Figure 1), although the

Table 4. Percent of diet comprised by gastropods for four size classes of pumpkinseeds collected on six dates. Percents are based on dry mass. Means and 95% confidence limits are given based on arcsin($\sqrt{x}$) transformed data. Sample sizes (number of fish) are also given.

| Lake | Date | Fish Size-Class (mm) 50-69 | 70-89 | 90-109 | 109-131 |
|---|---|---|---|---|---|
| Three Lakes II | 4 September | 91.4 | 82.0 | 96.8 | --- |
| | | 29-100 | 66-94 | 87-100 | --- |
| | | 3 | 6 | 12 | 0 |
| Three Lakes II | 17 May | 15.8 | 93.5 | 99.8 | 97.0 |
| | | 0-80 | 82-99 | 99-100 | 88-100 |
| | | 6 | 18 | 21 | 18 |
| Three Lakes II | 6 June | 38.2 | 92.0 | 98.4 | 100.0 |
| | | 4-83 | 55-100 | 95-100 | 100-100 |
| | | 8 | 8 | 14 | 2 |
| Culver Lake | 30 August | 100.0 | 83.9 | 96.9 | 81.3 |
| | | --- | 26-100 | 91-100 | 39-100 |
| | | 1 | 3 | 9 | 7 |
| Palmatier Lake | 17 August | 100.0 | 73.1 | 80.0 | 38.2 |
| | | --- | 20-100 | 52-97 | 16-63 |
| | | 1 | 5 | 4 | 11 |

Figure 1. Biomass of snail prey in fish stomachs. Each point represents the mean for fish within 10 mm sizeclasses. Statistical summaries are given in Table 5. Symbols: ▲, ♦, ■, ● = 19 August 1983, 4 September 1984, 17 May 1986 and 6 June 1986 in Three Lakes II. O = 30 August 1984 in Culver Lake. □ = 17 August 1984 in Palmatier.

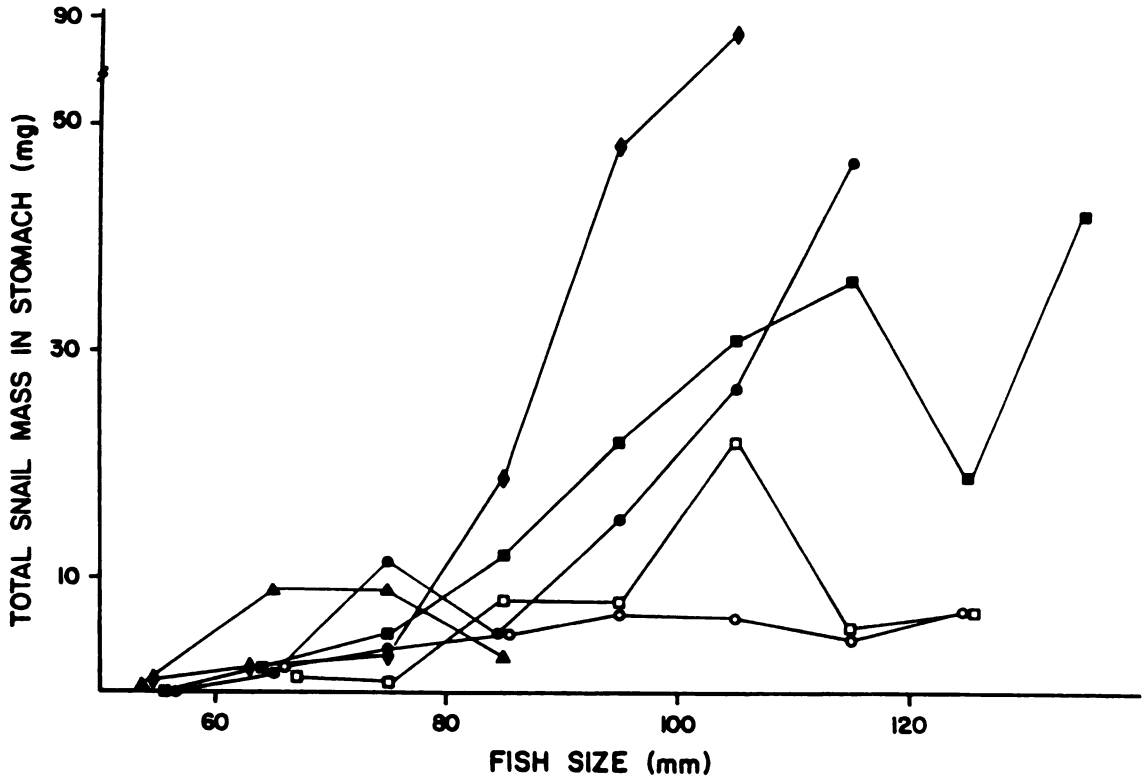
90
50
30
10
TOTAL SNAIL MASS IN STOMACH (mg)
60
80
100
120
FISH SIZE (mm)

Figure 1

Table 5. Regressions of snail mass in stomach ($Log_{10}(x + 0.1)$ on fish size ($log_{10}(SL)$ for each of six collection dates. Analysis of covariance showed that the six relationships differed significantly in slope ($F_{5,165}=3.04$, $p=0.012$). Sample sizes and ranges of fish sizes are given in Table 2.

| Lake | Date | $r^2$ | slope (s.e.) | Pr(slope=0) |
|---|---|---|---|---|
| Three Lakes II | 19 August | 0.30 | 4.73 (2.74) | 0.129 |
| Three Lakes II | 4 September | 0.84 | 8.78 (0.89) | 0.001 |
| Three Lakes II | 17 May | 0.40 | 5.07 (0.80) | 0.001 |
| Three Lakes II | 6 June | 0.41 | 5.34 (1.18) | 0.001 |
| Culver Lake | 30 August | 0.09 | 1.31 (1.00) | 0.206 |
| Palmatier Lake | 17 August | 0.06 | 1.91 (1.69) | 0.272 |

Figure 2. Mean individual mass of snails of four snail taxa in the diets of fish collected on six dates. A mean snail mass for each snail taxa in each fish was calculated, and the means of these means for 10 mm size classes of fish was plotted. Sample sizes (number of fish) and statistical analyses are given in Table 6. Symbols are the same as in Figure 1.

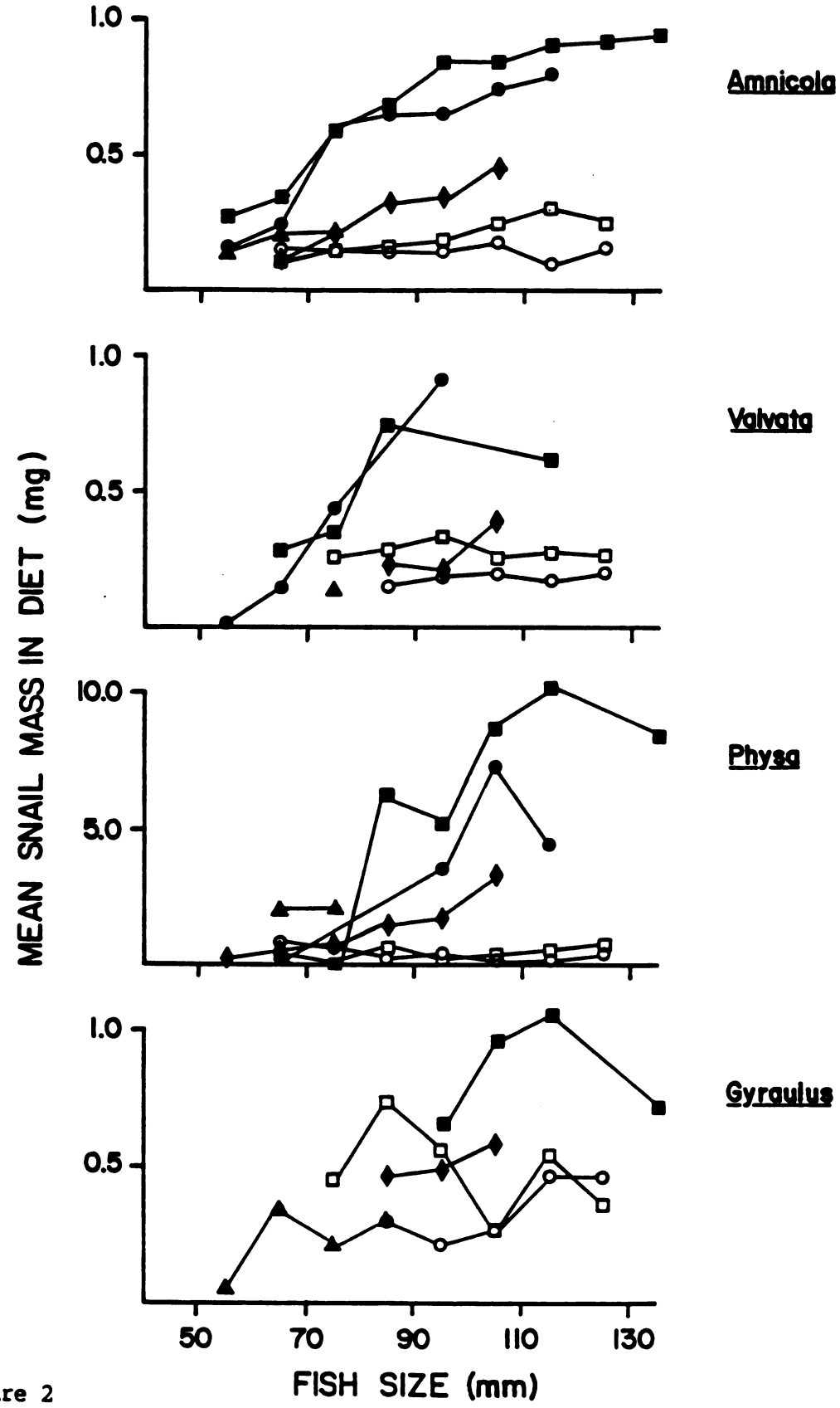
1.0
0.5
Amnicola
1.0
0.5
Valvata
10.0
5.0
Physa
1.0
0.5
Gyraulus
MEAN SNAIL MASS IN DIET (mg)
50
70
90
110
130
FISH SIZE (mm)

Figure 2

Table 6. Analyses of covariance and separate regressions comparing the effect of fish size on mean prey size among six collection dates for the four major snail taxa. Mean snail mass (mg) and fish size (SL) were $\log_{10}$ transformed for the analyses. The column headed Ancova gives the probability that the slopes of the relationship between mean prey mass and fish size were the same among the collection dates. The results from the separate linear regressions are given as slope (s.e.), number of fish, $r^2$, Pr(slope=0). See also Table 2.

| | | Linear Regressions | | | | | |
|---|---|---|---|---|---|---|---|
| | | Three Lakes II | | | | Culver | Palmatier |
| Prey | Ancova | 19 Aug | 4 Sep | 17 May | 6 June | 30 Aug | 17 Aug |
| Amnicola | 0.0001 | 1.67 (0.41) | 2.61 (0.40) | 1.30 (0.12) | 2.43 (0.20) | 0.16 (0.58) | 1.54 (0.20) |
| | | 8 | 16 | 54 | 34 | 19 | 21 |
| | | 0.73 | 0.75 | 0.70 | 0.83 | 0.00 | 0.75 |
| Valvata | 0.0001 | — | 3.35 (1.01) | 1.76 (0.95) | 8.15 (3.51) | 0.58 (0.40) | 0.03 (0.26) |
| | | 1 | 13 | 7 | 8 | 19 | 19 |
| | | — | 0.50 | 0.41 | 0.47 | 0.11 | 0.00 |
| | | — | 0.01 | 0.12 | 0.06 | 0.16 | 0.90 |
| Physa | 0.0001 | -1.07 (2.48) | 4.52 (0.70) | 7.74 (2.66) | 9.98 (1.09) | -1.30 (1.05) | 2.01 (1.15) |
| | | 6 | 16 | 15 | 7 | 13 | 14 |
| | | 0.04 | 0.75 | 0.39 | 0.94 | 0.12 | 0.20 |
| | | 0.69 | 0.00 | 0.01 | 0.00 | 0.24 | 0.11 |
| Gyraulus | 0.0690 | 5.19 (2.72) | 1.55 (0.88) | 1.88 (3.53) | — | 2.24 (1.07) | -1.70 (1.47) |
| | | 5 | 9 | 7 | 0 | 15 | 13 |
| | | 0.55 | 0.30 | 0.05 | — | 0.25 | 0.11 |
| | | 0.15 | 0.12 | 0.62 | — | 0.06 | 0.27 |

relationship varied among the six collection dates (Table 5). On three of the dates, there was no significant relationship between total snail mass in the stomach and fish size (although the sample size and range of fish sizes from 1983 was limited). Mean snail size in the diet also showed a general increase with fish size for the four major snail taxa (Figure 2), although the relationship varied among dates (Table 6). In general, there was no increase in total snail biomass or mean snail mass with fish size for fish collected in Culver and Palmatier Lakes, while there were increases for fish collected in Three Lakes II.

The previous data presentations provide general descriptions of the dietary patterns observed among different size classes of fish during the six collection dates. Although these forms of presentation can be used to suggest the importance of particular processes (e.g. by comparing patterns across fish sizes), they do not provide a rigorous exploration of the selectivities of the predators because the data have not been adjusted for the abundance of each prey type in the environment. In the following section, I explore several levels of prey selection by pumpkinseed sunfish.

Collection date had a very strong effect on prey selection between prosobranch and pulmonate snails (Figure 3); no significant preference was detected in Palmatier or Culver Lakes, while prosobranchs were preferred on two dates in Three Lakes II, and pulmonates were preferred on the other two dates in Three Lakes II. Within dates, selection did not vary significantly among the four 20 mm size-classes of fish ($p>0.05$ for each of the six dates); thus, Figure 3 gives results averaged across all fish sizes. Evaluated at a finer level of resolution, there was also significant variation among dates in the pattern of selection among snail taxa (Figure 4), resulting in four different snail taxa being most preferred among the six different dates. The selectivities differed

Figure 3. Mean selectivities (±95% confidence intervals) between prosobranch and pulmonate snails for each of six collection dates. Preliminary analyses showed no differences among the four, 20 mm SL size classes of fish. These data are based on all fish collected within a date with ≥10 snails/stomach. Random prey selection (i.e. in proportion to the representation in the environment) would be indicated by selectivities equal to 0.5. Sample sizes and the probabilities that each vector differs from random are given.

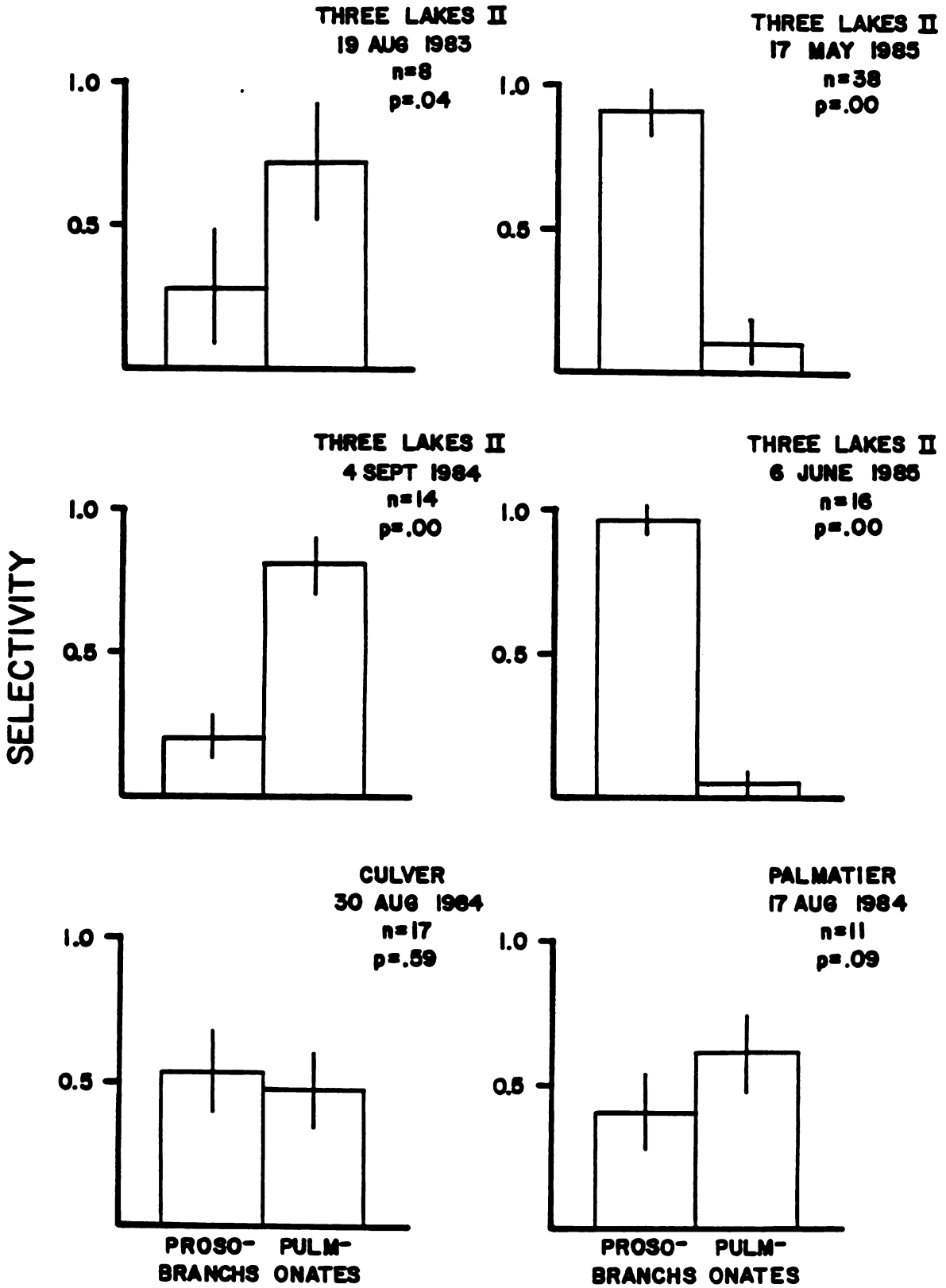
THREE LAKES II
19 AUG 1983
n=8
p=.04
THREE LAKES II
17 MAY 1985
n=38
p=.00
THREE LAKES II
4 SEPT 1984
n=14
p=.00
THREE LAKES II
6 JUNE 1985
n=16
p=.00
CULVER
30 AUG 1984
n=17
p=.59
PALMATIER
17 AUG 1984
n=11
p=.09
SELECTIVITY
1.0
0.5
PROSO-
BRANCHS
PULM-
ONATES

Figure 3

Figure 4. Mean selectivities (+95% confidence intervals) among snail species for each of six collection dates. Data are based on all fish collected within a date. Random selection would be indicated by selectivities equal to $1/k$ (i.e. the reciprocal of the number of prey categories). Sample sizes and the probabilities that each vector differs from random are given. Nd indicates that the snail species was absent or rare ($d_i$<20) on the given date.

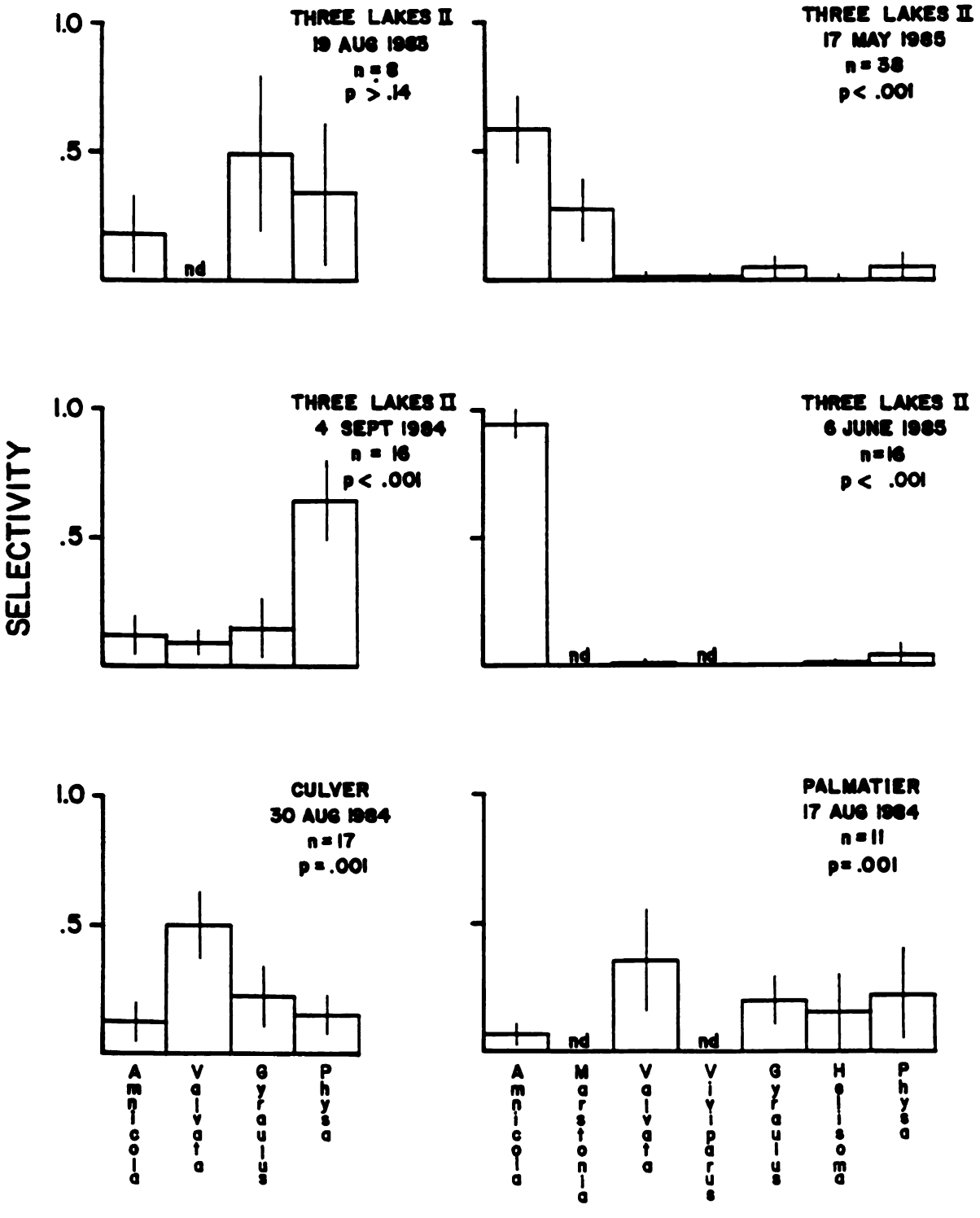
SELECTIVITY
1.0
.5
THREE LAKES II
19 AUG 1983
n = 8
p > .14
nd
THREE LAKES II
17 MAY 1985
n = 38
p < .001
THREE LAKES II
4 SEPT 1984
n = 16
p < .001
THREE LAKES II
6 JUNE 1985
n=16
p < .001
nd
nd
CULVER
30 AUG 1984
n=17
p=.001
PALMATIER
17 AUG 1984
n=11
p=.001
nd
nd
Amicola
Valvata
Gyraulus
Physa
Amicola
Marstonia
Valvata
Viviparus
Gyraulus
Helisoma
Physa

Figure 4

among fish size-classes on 2 of the 6 collection dates ($p<.05$ for 30 August 1984 and 17 May 1985); therefore, the selectivities shown in Figure 4 represent population averages and not necessarily the selection by any particular size class of fish.

Patterns of size selection, within species, also exhibited variation among dates (Figure 5). In addition, on several dates, fish size had a clear and consistent effect on size selection. In presenting these data, it was necessary to pool data from all fish within a size-class in order to obtain sufficient sample sizes (but see Chesson (1984) for a cautionary note); therefore, no statistical tests are given for the data in Figure 5. Notice in this figure that selectivity generally increased with snail mass, although the eight selection vectors for Amnicola from the two dates in 1985 in Three Lakes II were, by contrast, either hump-shaped or decreased with snail mass. On these two dates, the size-distributions of Amnicola were relatively broad and the largest snails may have entered a size refuge, thus causing the selectivity vectors to become hump-shaped (see below).

These data reveal that prey selection was extremely variable and depended, at least in part, on the effects of fish size, and on the size distributions of prey. It is not possible to describe a simple hierarchy of preference among the different snail taxa. Instead, the data suggest that any one of the available snail taxa could, on certain dates, be the most preferred. Because fish exhibit strong size selection within species and because size-distributions are extremely variable over the season, it is plausible that the large variation in prey selection might be produced by changes in the size distributions of snails within each taxonomic group. This suggests that the influence of fish size and snail size on the components of the predation process might help resolve these complex dietary patterns. In the following

Figure 5. Patterns of size selection for four size classes of fish. Each panel shows the size-selection for one snail taxa on one of the dates. Data are based on pooling data from all fish within four 20mm size-classes. Selectivity vectors were only calculated for fish classes with G>25 for prosobranch taxa and G>10 for pulmonate taxa. Fish classes are denoted by the size of the closed circle ( • = 50-69mm, • = 70-89mm, • = 90-109mm, ● = 110-131mm).

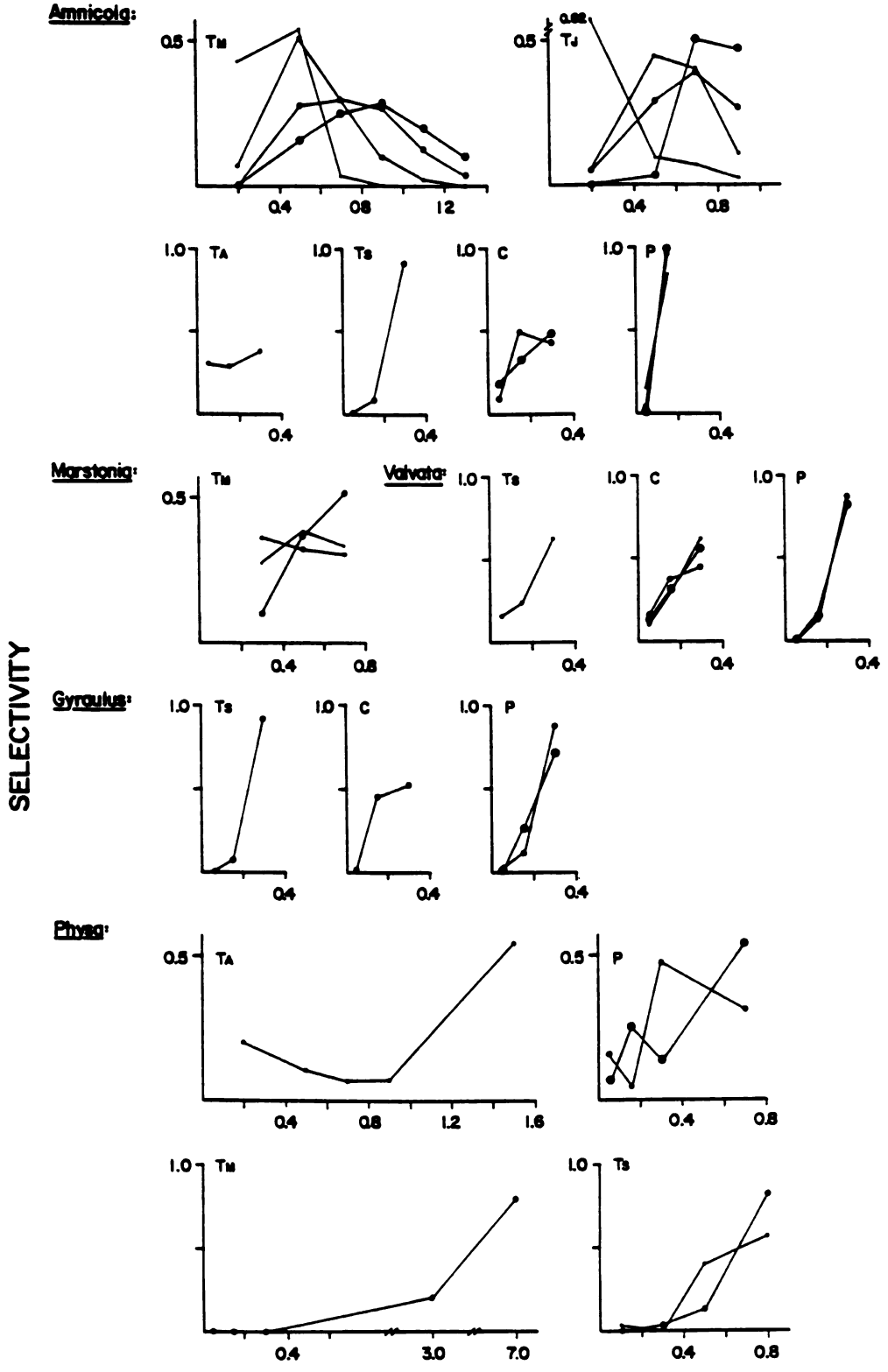
Amnicola:
Tm
Tj
TA
Ts
C
P
Marstonia:
Valvata:
Gyraulus:
Physa:
SELECTIVITY
SNAIL MASS (mg)

Figure 5

sections, I use laboratory studies to explore the effects of predator and prey size on specific components of the predator-prey interaction. I then synthesize these results into models of prey selection whose predictions I compare with observed patterns of prey selection.

## LABORATORY EXPERIMENTS

Primary components of standard foraging models include encounter rates, attack probabilities, capture successes, energetic gains and losses, and handling time constraints. Each of these was examined in a series of laboratory experiments, with the specific purpose of determining how the components scale with body size (of sunfish and snails) and how these might be functionally resolved into relatively simple and general relationships.

### Methods

Encounter rate (the number of prey detected per unit of predator search time) is probably the most fundamental component of any foraging model because it sets the initial baseline against which all other components of the predator-prey interaction operate. However, encounter rates are rarely measured and applied to field situations (but see Mittelbach 1981). At best, encounter rates have been modeled indirectly from consideration of the encounter process (e.g. Pastorak 1981; Wright and O'Brien 1984). In this study, I used laboratory experiments to directly measure encounter rates between pumpkinseed sunfish and snails. Direct measurement of encounter rates necessarily includes all of the potential effects of prey morphology and behavior (e.g. size, crypticity and movement) that might influence a prey's visibility to a predator.

One reason that encounter rates are rarely measured is because it is extremely difficult to determine when an encounter has occurred. For example, if predators ignore (i.e. do not attack) some prey that they encounter, then attack rates cannot be used to estimate encounter rates. However, if experiments are conducted with hungry predators feeding on a single prey type, then active selection by the predator should be minimized and attacks can be used to indicate encounters with prey (see Mittelbach 1981). Additionally, predators sometimes alter their search behaviors when they encounter prey, and these behavioral cues can also be used to ascertain when an encounter has occurred.

Throughout this chapter I focus on per capita encounter rates (i.e. total rates of encounter between a predator and a prey type divided by the prey density). I assume that total encounter rates are directly proportional to prey density, and thus, that per capita encounter rates are constant for a particular prey type.

Encounter rates were estimated in a large (214 L) aquarium into which a bottom layer of 10cm of rinsed Chara was placed: in the field, most snails occur within the top 10 cm of the Chara mat (Osenberg, personal observation). Two pumpkinseeds (109 mm SL each) were kept in the aquarium in two holding areas. The area of the experimental arena was 0.539 $m^2$. Fish were acclimated to feeding in the arena before the trials were begun, and each fish was starved at least 6 hours before being used in a trial. Snails were sorted by size and species, and a given density of a single snail type (defined by size and taxa) was introduced into the arena. Snail densities were 150 snails/arena (278/$m^2$) for A. limosa and V. tricarinata, and 50 snails/arena (93/$m^2$) for Physa and Gyraulus (both G. parvus and G. deflectus were used, but their representation in each trial varied depending on the size class). I used greater densities for the two prosobranchs because they were on

average smaller than the pulmonates and therefore I expected total encounter rates to be lower for these two species; thus greater densities were used to obtain adequate numbers of encounters per trial. In addition, the prosobranchs are more abundant than the pulmonates in natural lakes, and I could not collect greater numbers of Gyraulus. Physa were also rare but their numbers were supplemented with snails raised in laboratory cultures.

Snails were added to the experimental arena and given two hours to disperse within the Chara prior to the start of a trial. One pumpkinseed was released into the arena and each trial ran from 5–12 minutes depending on the amount of prey depletion. Depletion averaged 7% and never exceeded 37% (only 6% of trails had more than 20% depletion). During a trial I recorded each attack on a snail, how long it took, whether it was successful, and how much time the fish spent in non-foraging related activities. Following a trial, consumed snails were replaced, given about an hour to disperse, and the other fish was introduced into the arena and observed. After 1-3 trails/fish, the Chara and snails were removed. New Chara was rinsed and added to the arena along with a new snail type.

131 trials were run. During 7 of these trials, I observed encounters that were not followed by an attack. In these cases, I used the number of attacks plus these other encounters in the calculation of encounter rates. Encounter rates were estimated from these trials based on an exponential model that accounted for depletion (e.g. Murdoch et al. 1984):

$$\lambda = \ln(D_{start}) - \ln(D_{end}) \; / \; pS \qquad (2)$$

where $D_{start}$ and $D_{end}$ are the snail densities at the start and end of

the trial, p is the proportion of encounters that resulted in the consumption of a snail (i.e. depletion of the snail population), and S is the total search time during the foraging trail. Preliminary data analyses showed that the two fish did not differ in their encounter rates; therefore, encounter rates that were estimated from all trials within a set (i.e. sequential trials without complete replacement of the snails and Chara) were averaged (usually n=4, 2/fish) to obtain one estimate of the encounter rate per set. The 131 trails thus produced 36 independent estimates of encounter rates, which were examined for effects of snail size and taxa. These data are referred to as Experiment 1.

Results from Experiment 1 also yielded information on whether attacked snails were successfully consumed, how long it took a fish to handle a snail that it successfully consumed (handling time) and how long it took a fish to handle a snail that it eventually rejected (rejection time). Size refuges, handling times and rejection times were further examined in another laboratory study using four snail taxa: A. limosa, V. tricarinata, Gyraulus and Physa. Premeasured snails were offered individually to one of 26 fish that were kept in separate aquaria and ranged in size from 63-132 mm SL. If the fish attacked the snail, I recorded if the attack was successful or, if the attack was unsuccessful, I noted whether the snail was too big to fit into the fish's mouth or whether the fish spit the snail out (presumably indicating that the snail could not be crushed). I also recorded the time it spent handling or rejecting the snail. I refer to this data set as Experiment 2.

The final set of laboratory data (referred to as the Crushing Experiment) consisted of the description of the mechanical strength of the snail shells as functions of their sizes. Shell strength was

measured by placing a snail on a small platform on the bottom of a plexiglass tube. A slightly smaller tube, also with a bottom, was placed inside of the first and rested on top of the snail. Sand was slowly poured into the inner tube until the snail shell gave way and was crushed. The mass of the sand and tube was determined. A wide range of snail sizes was used for each species, and the relationship between crushing mass and snail mass was estimated using an allometric relationship for each of the species.

## Results: Encounter Rates

Encounter rates increased with snail mass (Figure 6). Analysis of covariance revealed no differences in the scaling of encounter rate with snail mass across species (based on regressions of $\log_{10}(\lambda)$ on $\log_{10}(m)$: $F_{3,28}=1.00$, pr(slopes equal among species)>0.40). However, the adjusted means did differ among the groups ($F_{3,31}=9.07$, $p<0.001$), due entirely to the greater adjusted mean of Gyraulus. As snails were transferred to the aquarium during the setup of the experiments, Gyraulus (but no other snails) trapped air bubbles under their shells. The air bubble, which was visible through the shell, reflected light and made the snails much more noticeable to the observer. In the study lakes, which generally lack emergent vegetation, Gyraulus rarely traps air within its pulmonary sac. Therefore, it is likely that the increased encounter rates of the fish with the Gyraulus was the result of a laboratory artifact. Repeating the Ancova with only Physa, Valvata and Amnicola, showed that the three species did not differ significantly in their relationships between encounter rates and snail mass (slopes: $F_{2,24}=1.33$, $p>0.25$; adjusted means: $F_{2,26}=1.15$, $p>0.30$; effect of mass: $F_{1,26}=54.58$, $p<0.001$).

Figure 6. Encounter rate as a function of snail mass for four snail taxa. Linear regressions for log-log transformed data are given. Each regression is significant at $p<0.02$.

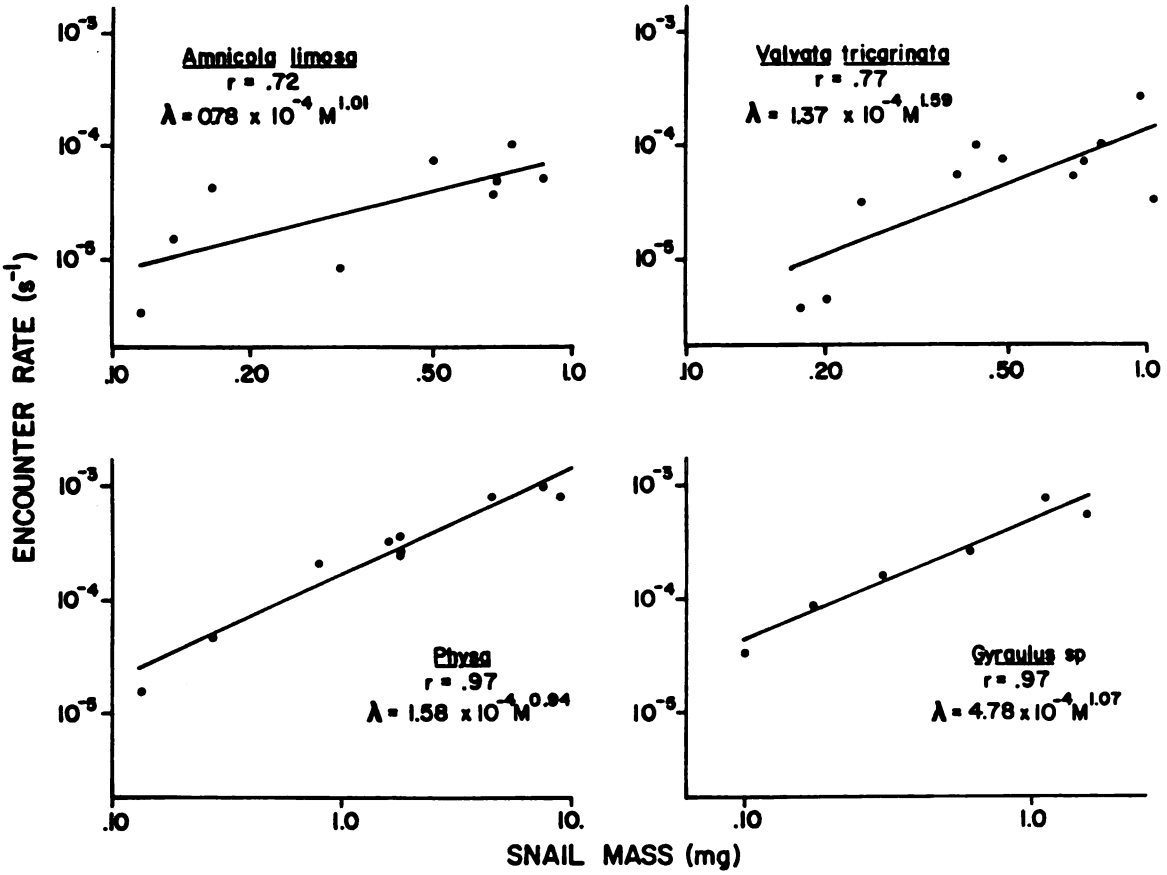
Amnicola limosa
r = .72
λ = 0.78 x 10⁻⁴ M^1.01
Valvata tricarinata
r = .77
λ = 1.37 x 10⁻⁴ M^1.59
Physa
r = .97
λ = 1.58 x 10⁻⁴ M^0.84
Gyraulus sp
r = .97
λ = 4.78 x 10⁻⁴ M^1.07
ENCOUNTER RATE (s⁻¹)
SNAIL MASS (mg)

Figure 6

## Results: Size Refuges and Crushing

Following an attack, a snail can escape death in two ways. First, the snail might be too large to be taken into the fish's buccal cavity: I refer to this type of size refuge as "gape limitation". Second, a snail that is taken into the fish's buccal cavity will be rejected if it cannot be crushed: I refer to this type of refuge as "crushing limitation". Gape and crushing limitation are functions of the snail size as well as the predator's size. In addition, because snail species differ in their morphologies and shell thicknesses, the effectiveness of crushing limitation might vary among snail species. My primary goal in analysing the size refuge data was to construct general functional relationships that appropriately scaled prey and predator sizes into simple models that transcended the differences among species.

Mouth gape in pumpkinseeds increases linearly with fish standard length (Laughlin 1979). Thus, the ratio of prey length to predator length should serve as a good way to scale the effect of gape limitation. However, because snail species vary in their shapes and because I measured only one aspect of the linear shape of each of the snail species, a unique relationship between gape limitation and the ratio of prey to predator length would probably exist for each snail species. On the other hand, the average linear dimension of a prey item should increase as the cube root of its mass (assuming mass is proportional to the cube of length) and this should be relatively independent of species identity. Thus the intensity of gape limitation should scale simply with the ratio of the cube root of snail mass to fish length. Indeed, as this index of the relative size of prey to predator increased, gape limitation became more severe and snails escaped a greater frequency of attacks (Figure 7). Among the five snail

Figure 7. Size refuge based on the occurrence of gape limitation during Experiment 2. The line is based on a logistic regression fit to the original binary data (n=1110): $P(g)=1/1+\exp(-41.95-26.45\log_{10}(m^{1/3}/SL))$.

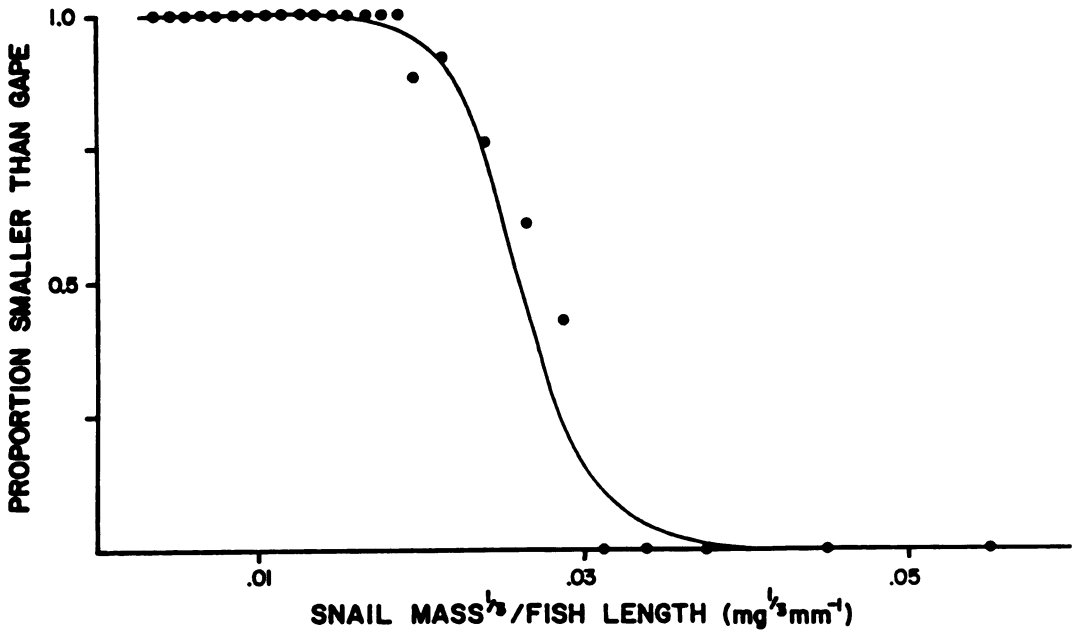
1.0
0.5
PROPORTION SMALLER THAN GAPE
.01
.03
.05
SNAIL MASS$^{1/3}$/FISH LENGTH (mg$^{1/3}$mm$^{-1}$)

Figure 7

taxa used in Experiments 1 and 2, only Physa in Experiment 2 ever escaped via gape limitation; the other snails were all too small. However, other species (e.g. Helisoma) occur in the lakes that can potentially escape predation through gape limitation, and I assume that the relationship shown in Figure 7 can be applied to these taxa as well.

The ratio of prey to predator size is commonly used to scale many aspects of the predator-prey relationship, for example handling times and size refuges (Werner 1977; Mittelbach 1981; Bence and Murdoch 1986). However, gape limitation is one of the few processes for which this scaling is a priori expected to be appropriate (see above). Crushing limitation on the other hand need not follow such a simple relationship. Indeed, unless crushing resistance of snail shells and crushing ability of fish increase linearly with size (of snails and fish) then the use of the ratio of prey to predator length will be incorrect and will mask important sources of variation in the data. In the following section I explore in detail, the relationships between snail size and crushing resistance and between fish size and crushing ability in order to develop a sound technique for scaling the simultaneous effects of snail size and fish size on crushing limitation.

Crushing resistance of snails increased significantly with snail size for all twelve prey types examined, though the relationship varied considerably among species (Figure 8). Linear regressions of log transformed data explained over 80% of the variation in crushing resistance for each species except Promenetus ($r^2$=44%). In Figure 8, two regression lines are shown for Physa: one for snails collected from lakes and one for snails collected from laboratory cultures. Both types of snails were used in the laboratory experiments and since the source for each snail used in Experiments 1 and 2 is not known, I assume that the average crushing resistance of Physa used in the laboratory trials

Figure 8. Crushing resistance as a function of snail mass for eleven snail species. Lines are based on linear regressions of $\log_{10}$ transformed data, and the endpoints denote the range of snail sizes used in the crushing experiment. Sample sizes ranges from 14-43, $r^2 > 0.80$ except for P. exacuous ($r^2=0.44$), and all regressions were highly significant. Two regression lines are shown for Physa: one for snails collected from lakes and one for snails obtained from laboratory cultures. Al=A. limosa, Aw=A. walkeri, Gd=G. deflectus, Gp=G. parvus, Ha= H. anceps, Hc=H. campanulata, Ml=M. lustrica, Pe=P. exacuous, Pf=Physa from field collections, Pl=Physa from lab cultures, Vg=V. georgianus, Vt=V. tricarinata.

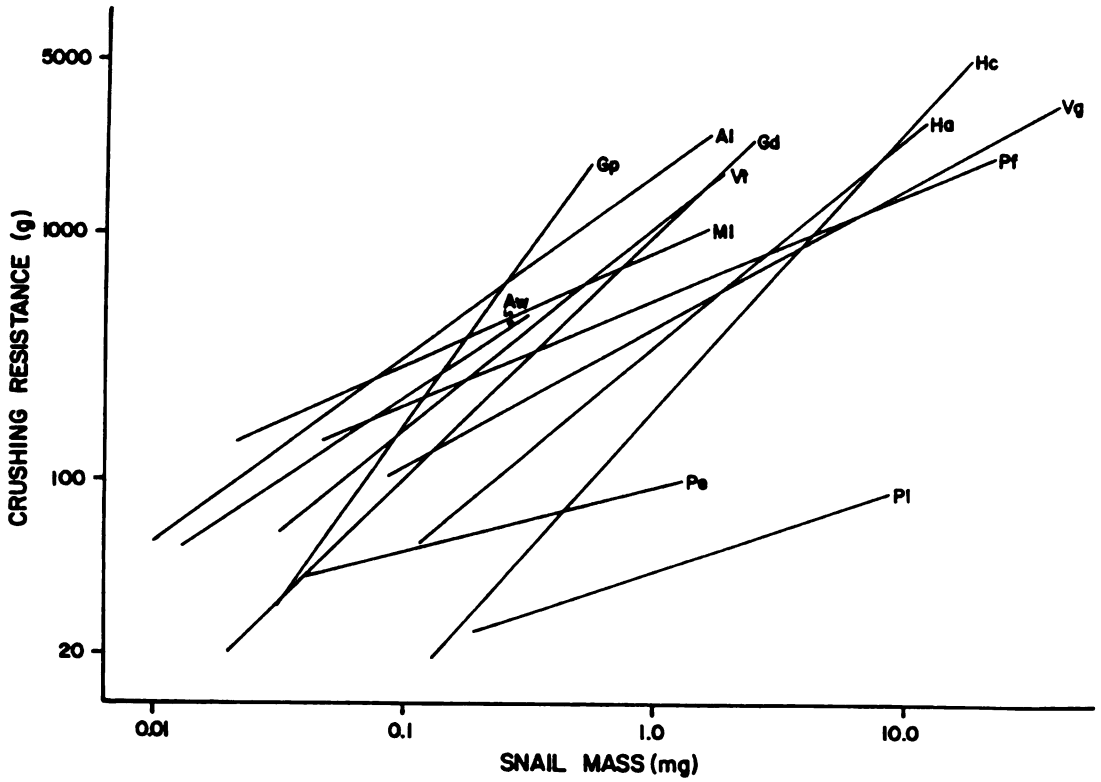
5000
1000
100
20
CRUSHING RESISTANCE (g)
0.01
0.1
1.0
10.0
SNAIL MASS (mg)
Hc
Vg
Ha
Pf
Al
Gd
Gp
Vt
Ml
Pe
Pl

Figure 8

was intermediate to these two extremes. The field equation was $C=90.9L^{1.15}$ (L is shell length) and the lab equation was $C=10.6L^{0.89}$, therefore I used $C=50L^{1.00}$ as a representative depiction of the actual, albeit variable, relationship between crushing resistance and snail size for Physa used in Experiments 1 and 2.

The data from Experiment 2, which were obtained with one size of fish (109 mm SL), show that the proportion of snails that were crushed declined with snail mass for each species except Physa, which were always successfully attacked (Figure 9a). Notice that the curves for each species appear to be unique when expressed in terms of snail mass: i.e. some species escaped at small body mass (e.g. A. limosa and G. parvus) while some escaped only at large body mass, if at all (e.g. Physa). However, when expressed with respect to crushing resistance, a general relationship was obtained that appeared to apply equally well to each of the species (Figure 9b). These data suggest that a single relationship between crushing limitation and crushing resistance can be used for all snail species.

To explore how crushing ability scaled with fish size, I used the data from Experiment 2, divided the fish into 10 g intervals and explored the relationship between crusing limitation (i.e. P(c), the probability that a snail could be crushed) and crushing resistance for each size class of fish. Logistic regression was used to fit an equation to the data (SAS PROC CATMOD), and from these equations I calculated the crushing resistance (for the snails) at which the fish were predicted to have P(c)=0.5. The regressions for the first six fish size classes (0-10 g up to 50-60 g) were significant, while those for the larger classes were not. The regressions for the larger classes failed to provide significant fits to the data because these fish could crush most of the snails, and the estimated point at which P(c)=0.5 was

Figure 9. Size refuge mediated through crushing resistance in Experiment 1. Given are the proportion of attacked snails in each size class that were successfully eaten (no snails escaped through gape limitation). a) Based on snail mass. b) Based on crushing resistance.

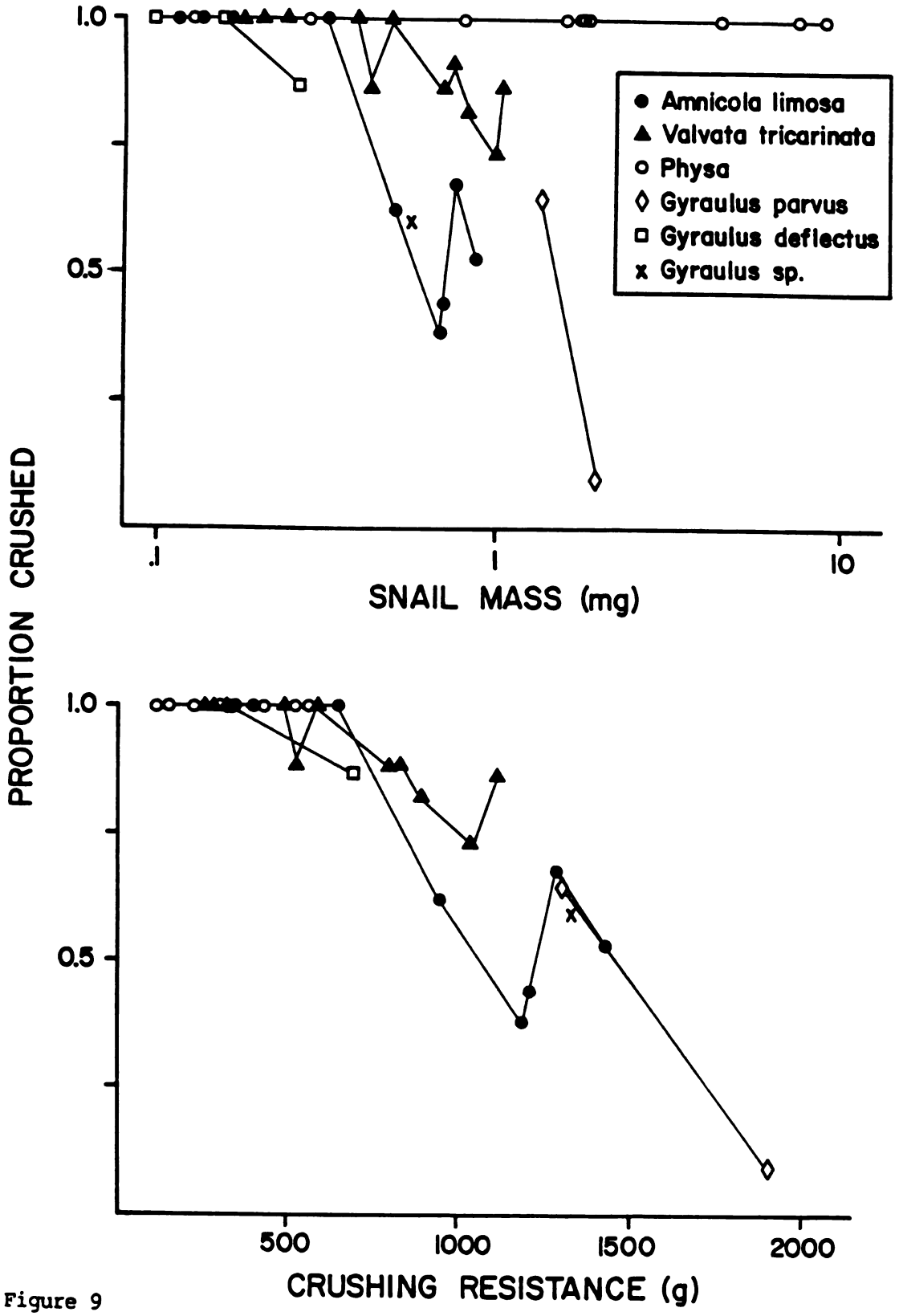
1.0
0.5
.1
1
10
SNAIL MASS (mg)
Amnicola limosa
Valvata tricarinata
Physa
Gyraulus parvus
Gyraulus deflectus
x Gyraulus sp.
PROPORTION CRUSHED
1.0
0.5
500
1000
1500
2000
CRUSHING RESISTANCE (g)

Figure 9

in all cases greater than the maximum presented to the snail. The relationship between the crushing resistances at which P(c)=0.5 and the mean masses of fish within the six smallest size classes was fit with a linearized power function. The relationship was approximately linear (exponent of power function=1.07, 95%CI=0.88-1.25, $r^2$=0.98), suggesting that the crushing ability of a fish was directly proportional to its mass. If a doubling in snail crushing resistance requires a doubling in fish crushing ability, in order to maintain a constant crushing probability, then a general index of crushing limitation can be expressed as the ratio of snail crushing resistance to fish crushing ability (i.e. fish mass). The proportion of attacked snails that were crushed in Experiments 1 and 2 declined with the ratio of crushing resistance to fish mass and the relationship was fit extremely well by logistic regression (Figure 10).

The efficacy of gape limitation and crushing limitation for each species exposed to different sizes of predators can be explored by combining the results shown in Figures 7 and 10. From these relationships, I determined the mass, for each species, at which it achieved a size refuge of P(c)=0.5 or P(g)=0.5 against a range of fish sizes (50-140mm SL). The predicted relationship for gape limitation was the same for each species, but the relationship for crushing limitation varied among the species due to differences in how crushing resistance scaled with snail mass (Figure 8). From Figure 11, it can be seen that crushing limitation was likely to occur at smaller snail masses than gape limitation. The only exception was Promenetus, which has the thinnest shell (Figure 8). Additionally, many snail species never escape from some size classes of sunfish because they rarely, if ever, achieve the neccessary body mass (compare Table 1 and Figure 11). For example, in order to escape (P(c)<0.5) from a 100mm SL fish, A. walkeri

Figure 10. Crushing success for data from Experiments 1 and 2 combined. Only snails that were taken into the fishes buccal cavity were used (n=1528). The line gives the results of the logistic regression: $P(c)=1/1+\exp(8.680-5.885\log_{10}(C/M)$.

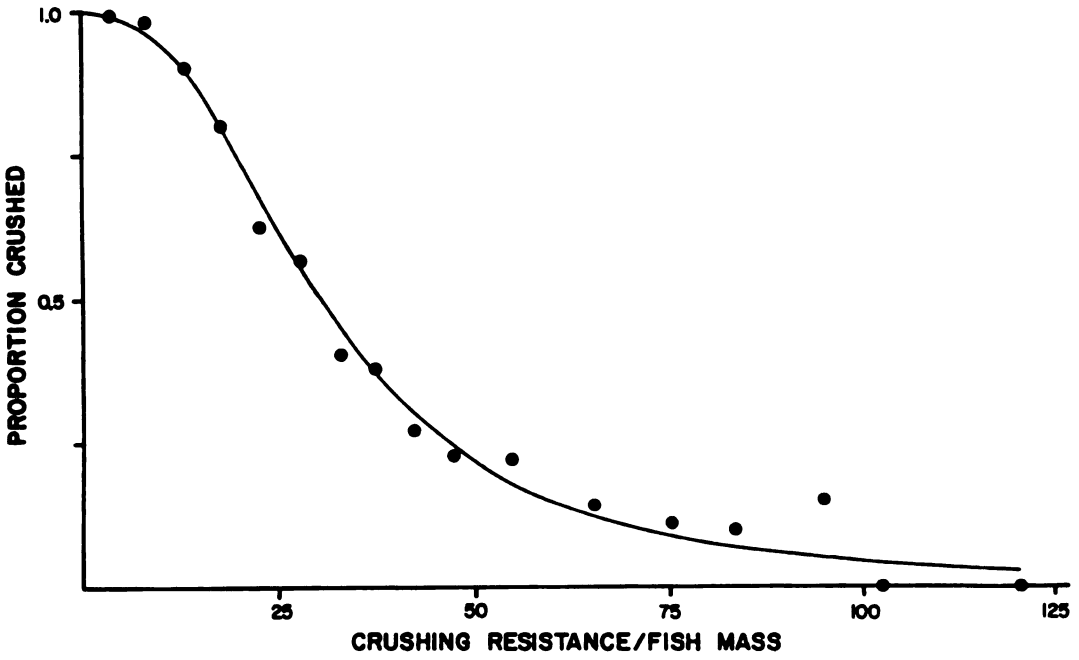
1.0
0.5
PROPORTION CRUSHED
25
50
75
100
125
CRUSHING RESISTANCE/FISH MASS

Figure 10

Figure 11. Relative importance of gape limitation and crushing limitation for snails in relationship to size of the predator. Lines show results from Figures 7 and 10 where snails have probabilities equal to 0.5 of being rejected by the predator due to gape limitation or crushing limitation. The line for Physa is based on the estimates of crushing resistance from lake collections; the line for the laboratory culture lies near the line for P. exacuous.

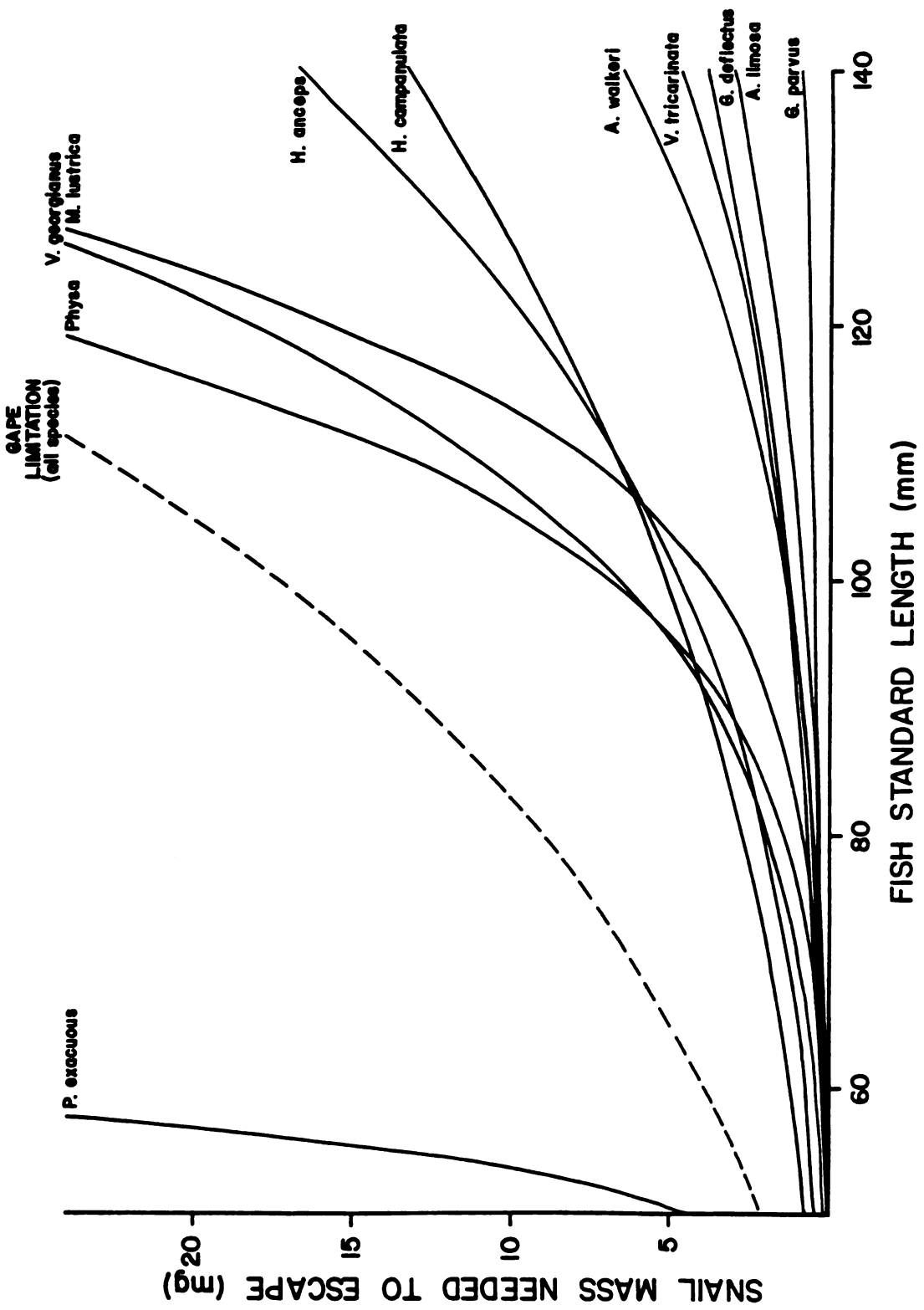
SNAIL MASS NEEDED TO ESCAPE (mg)
5
10
15
20
FISH STANDARD LENGTH (mm)
60
80
100
120
140
P. exacuous
GAPE LIMITATION (all species)
Physa
V. georgianus
M. lustrica
H. ancops
H. campanulata
A. walkeri
V. tricarinata
G. deflectus
A. limosa
G. parvus

Figure 11

must have a mass of at least 1.34 mg; however, I have never collected an A. walkeri larger than 0.5 mg.

## Results: Handling and Rejection Times

Data from Experiments 1 and 2 and from field observations were used to examine the effects of snail size and fish size on handling times and rejection times. Comparison of the handling times from Experiment 1 with handling times for comparably sized fish from Experiment 2 (100-119 mm SL), showed that the effect of snail size differed significantly between the two data sets for all four snail taxa (Figure 12). In each case, handling time increased more slowly when many snails were available (i.e. Experiment 1) than when only one snail was available (i.e. Experiment 2) (Table 7). Indeed, snail size explained, on average, only 7% of the variation in handling time in Experiment 1, while snail size explained an average of 33% of the variance in Experiment 2.

Two lines of evidence suggest that fish size probably has small effects on handling times under natural conditions (i.e. when several prey items are available to the fish). First, I analysed the handling times from the field observations with analysis of covariance (dates were treatment groups and fish size was the covariate): fish size had no significant effect on handling time ($F_{1,123}=0.11$, $p>0.70$). Second, the data from Experiment 1 were viewed in relation to the size refuge. As the proportion of snails that escaped attack increased, there was no change in the handling time of snails that were crushed (Figure 13). Snail classes that were sometimes rejected, incurred a relatively constant handling time. However, if the snails within the class were never rejected, then a more variable range of mean handling times was

Table 7. Analyses of covariance and separate regressions comparing the effect of snail size (mm) on handling times (s) between Experiments 1 and 2 for four snail taxa (see Figure 12). Fish sizes were 109 mm SL in Experiment 1 and 100–119 mm SL in Experiment 2. Both variables were $\log_{10}$ transformed for the analyses. Pr(equal slopes) gives the test that the effect of snails size on handling time was the same for the two data sets. The results from the linear regressions are given as slope (s.e.), number of snails, $r^2$, Pr(slope=0).

| Snail taxa | n | Pr(equal slopes) | Expt 1 | Expt 2 |
|---|---|---|---|---|
| Amnicola | 161 | 0.003 | 0.039 (0.068) | 0.389 (0.096) |
| | | | 86 | 75 |
| | | | 0.00 | 0.18 |
| | | | 0.57 | 0.00 |
| Valvata | 240 | 0.038 | 0.221 (0.077) | 0.598 (0.168) |
| | | | 209 | 31 |
| | | | 0.04 | 0.30 |
| | | | 0.00 | 0.00 |
| Physa | 285 | 0.000 | 0.101 (0.013) | 0.191 (0.019) |
| | | | 210 | 75 |
| | | | 0.24 | 0.57 |
| | | | 0.00 | 0.00 |
| Gyraulus | 119 | 0.001 | 0.035 (0.054) | 0.356 (0.087) |
| | | | 74 | 45 |
| | | | 0.01 | 0.28 |
| | | | 0.52 | 0.00 |

possible. The field data match these lab data quite well. Therefore, it appears that the fish set an upper limit to the amount of time they invest in attempting to crush a snail. If the snail is easily crushed (i.e. P(c)=1.0) then the handling time will be less than this upper limit. If the snail is not easily crushed (i.e. P(c)<1.0) then the fish expends a relatively constant amount of time attempting to crush the snail. If it is unsuccessful after this time, it rejects the snail, otherwise it completes processing the snail. Therefore, as the crushing resistance of snails increases, the fish simply rejects a greater proportion of snails, but handling times are relatively unaffected. Therefore, although larger fish might have lower handling times for very easily crushed snails, under most conditions handling times (for all fish) are probably close to the "asymptote" shown in Figure 13.

Rejection times were independent of snail mass (ANCOVA, $F_{1,125}=2.39$, $p>.10$) and snail taxa ($F_{2,125}=1.07$, $p>.30$) in Experiment 1. In Experiment 2, snail mass also had no significant effect on rejection times ($F_{1,255}=1.82$, $p>0.10$), although rejection times differed among snail species ($F_{3,255}=6.01$, $p<0.001$). In addition, fish size had no detectable effect on rejection times ($F_{1,255}=2.90$, $p>0.05$). Rejection times recorded in the field agreed very well with the laboratory data (Figure 14), although data were insufficient to permit analysis of fish size effects.

The results from Experiments 1 and 2 were not consistent. In particular, handling times increased strongly with snail size when snails were offered singly to fish (i.e. Experiment 2), but handling times were relatively size independent when many snails were available to the fish (i.e. in Experiment 1). Additionally, rejection times for Gyraulus and Physa were noticeably greater when offered singly (Figure 14). These results suggest that fish behaviors might have varied

Figure 12. Mean handling times (+95% confidence intervals) from Experiments 1 (●) and 2 (○). Fish sizes were 109mm SL in Experiment 1 and 100-119 mm SL in Experiment 2. Statistical analyses are summarized in Table 7.

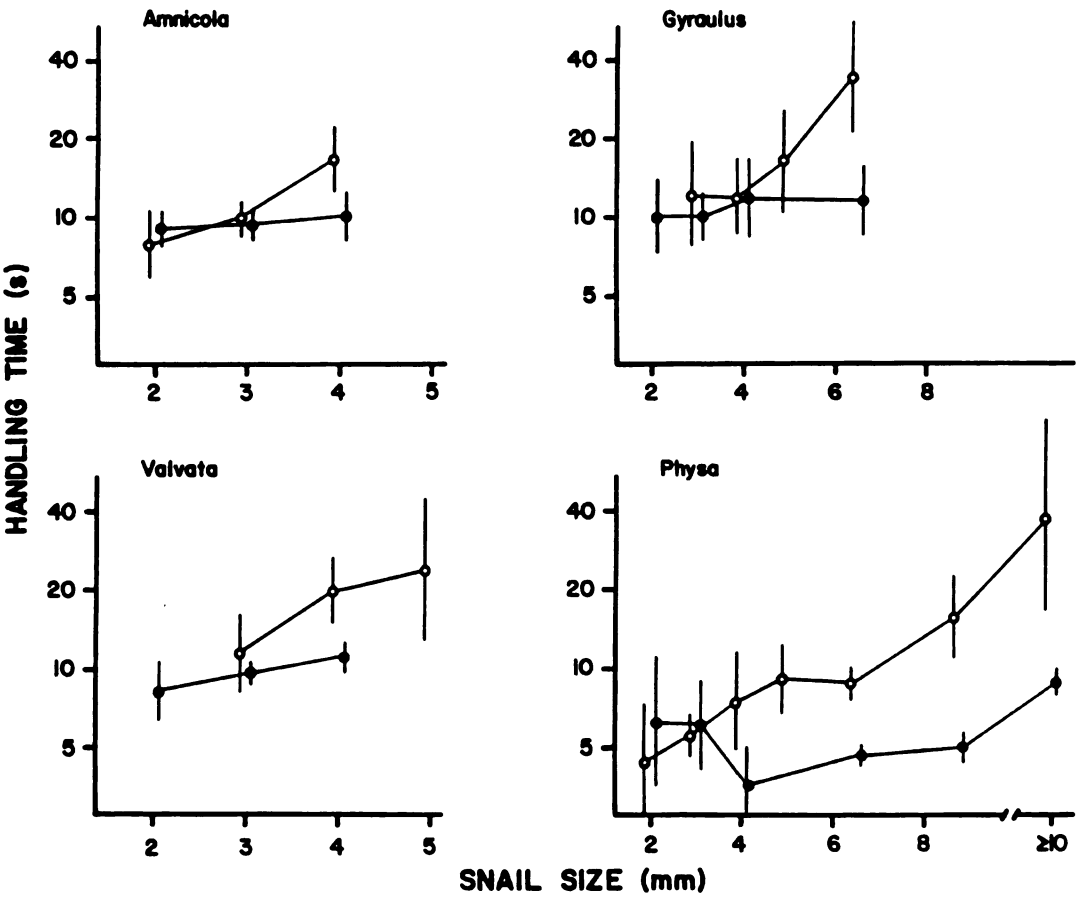
Amnicola
Gyraulus
Valvata
Physa
HANDLING TIME (s)
SNAIL SIZE (mm)
40
20
10
5
2
3
4
5
6
8
≥10

Figure 12

Figure 13. Mean handling times (±1 std. dev.) from Experiment 1 and field observations in relationship to the size refuge. Each set of trials from Experiment 1 ( ● ) are represented with one datum, although one point is excluded in which only 2 snails were eaten and both were probably swallowed without being crushed. Means from the field ( O ) are based on observations conducted within a single date. The data within the shaded region are sets (or dates) in which all attacks were successful (i.e. no snails were rejected). These data are ordered by increasing mean handling time.

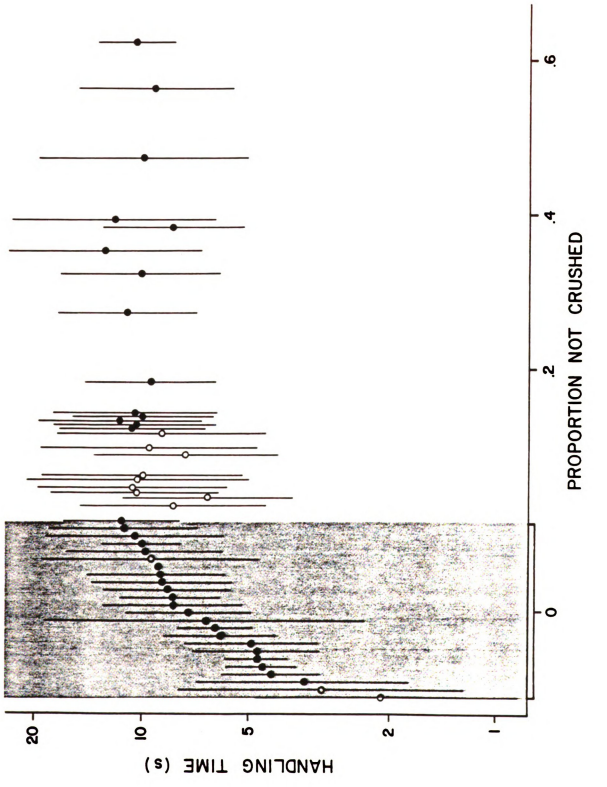


Figure 13

Figure 14. Mean rejection times (±95% confidence interval) for four snail taxa from Experiments 1 (●) and 2 (○) and from field observations (■). Physa were never rejected in Experiment 1.

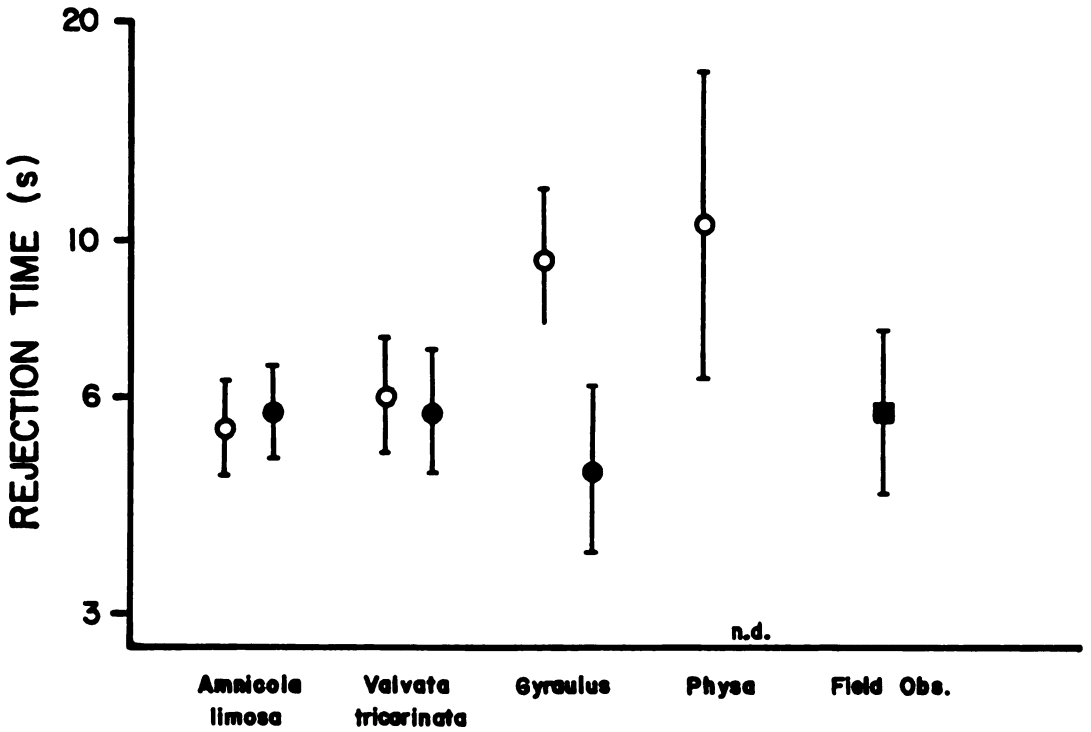
REJECTION TIME (s)
20
10
6
3
n.d.
Amnicola limosa
Valvata tricarinata
Gyraulus
Physa
Field Obs.

Figure 14

between the two experiments and that fish were more persistent during Experiment 2 when there were no other options (i.e. snails) available. Thus rejection and handling times might have been elevated, and crushing limitation might have been reduced in Experiment 2. Comparison of the two data sets however, reveal relatively small differences in crushing limitation: i.e. P(c) (Figure 15). Of the seven size categories shown in Figure 15, only one provides evidence that crushing limitation differed between data sets. This is based entirely on the largest size of Gyraulus used in Experiment 1, and is exacerbated by a slight hump in the data from Experiment 2 (i.e. the data for this category appear to be out of line compared to the smaller sizes and the next larger size). Thus, although handling time data differed appreciably between the two data sets (Figure 12), and rejection times differed somewhat (Figure 14), crushing limitation appears to have been relatively less affected (Figure 15).

## DEVELOPMENT AND TESTING OF THE FORAGING MODEL

The foraging rate of a predator on prey type i can be modeled according to

$$\text{Foraging rate} = D_i\lambda_i P_i(a)P_i(s) \;/\; 1 + \sum_{j=1}^{k} D_j\lambda_j P_j(a)H_j \qquad (3)$$

where foraging rate equals the number of snails of type i killed by a predator per unit foraging time, D is the density of the prey type, is the per prey encounter rate (i.e. $\lambda D$ is the total encounter rate), P(a) is the probability that the predator attacks an encountered prey item, and P(s) is the probability that an attack results in the successful consumption and death of the prey item. Therefore, the proportion of

Figure 15. Comparison of the size refuge based on crushing limitation from Experiments 1 ( ● ) and 2 ( O ). Proportion of snails that were successfully crushed (given they were taken into the buccal cavity) is plotted along with 95% confidence intervals based on the binomial distribution.

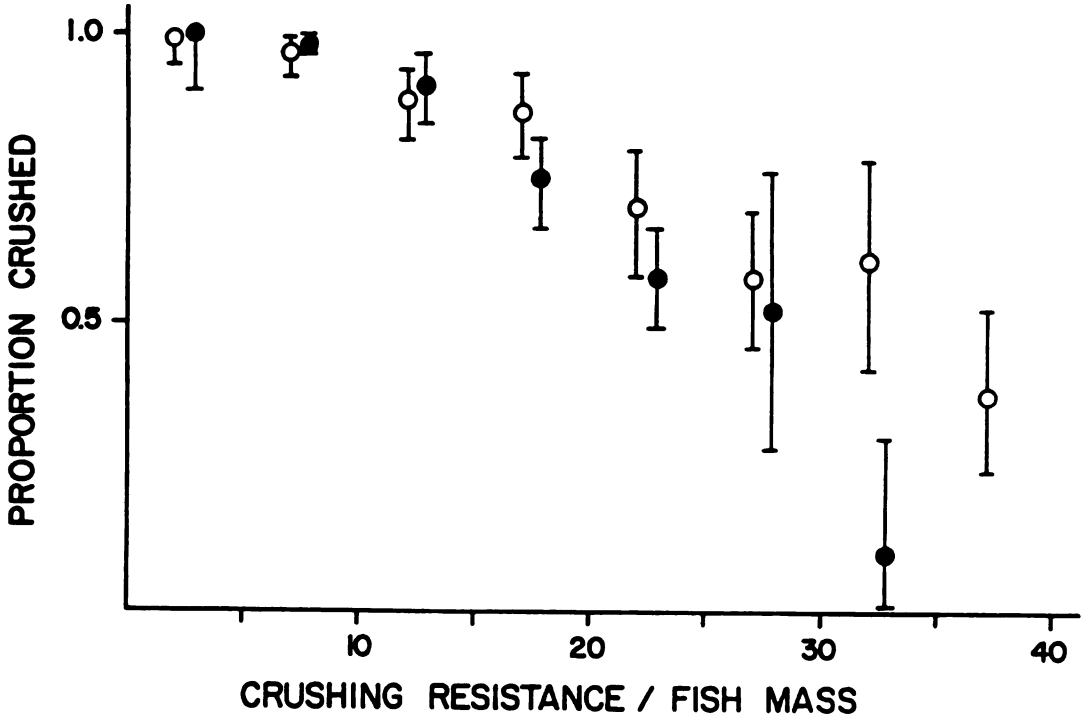
1.0
0.5
PROPORTION CRUSHED
10
20
30
40
CRUSHING RESISTANCE / FISH MASS

Figure 15

the diet comprised by prey type i is

$$\hat{p}_i = D_i\lambda_i P_i(a)P_i(s) \;/\; \sum_{j=1}^{K} D_j\lambda_j P_j(a)P_j(s) \qquad (4)$$

and prey selection, which is equal to the standardized ratio of the prey contribution in the diet compared to the environment (Chesson 1978, 1983), can be expressed as

$$\hat{\alpha}_i = \lambda_i P_i(a)P_i(s) \;/\; \sum_{j=1}^{K} \lambda_j P_j(a)P_j(s) \qquad (5)$$

In the following sections, I use the results from the laboratory experiments, and from the literature, to estimate the components in equation 5 as functions of snail and fish sizes. I then use these functions to predict patterns of prey selection based upon the densities and size-distributions of snails in resource samples. In particular, I am interested in determining to what extent each of the components of the predator-prey interaction (i.e. $\lambda$, P(a), and P(s)) contribute to observed patterns of prey selection.

I assessed the performance of the foraging model by using equation 5 to calculate predicted selectivities and calculating the reduction in the sums of squares of the observed selectivities due to the model:

$$R^2 = 1 - \sum_{j=1}^{n}\sum_{i=1}^{K}(\alpha_{j,i}-\hat{\alpha}_{j,i})^2/(\alpha_{j,i}-(1/k_j))^2 \qquad (6)$$

where $\alpha_{j,i}$ is the observed selectivity for the $i^{th}$ prey type in the $j^{th}$ selection vector, $\hat{\alpha}_{j,i}$ is the predicted selectivity, $k_j$ is the number of prey categories in vector j, $1/k_j$ is the mean selectivity for the $j^{th}$ vector (i.e. the expectation under non-selective foraging), and n is the number of selectivity vectors in the dataset. Theoretically, $R^2$ can

range from $-\infty$ to 1.0, the negative values arising when the mean selectivities represent the data better than the model does. Since the $\alpha_i$'s are not independent, I do not apply a statistical test to these $R^2$ values. Instead I use the $R^2$'s as a simple way to describe the relative performance of the model.

Encounter rates were assumed to increase with snail mass for all snail species according to the results of the analysis of covariance based on A. limosa, V. tricarinata and Physa. The results from this analysis yielded the following relationship

$$\lambda = 0.00001062m^{1.063} \qquad (7)$$

Since Viviparus and large Helisoma (greater than approximately 6mm shell diameter, or 2.1mg) are typically found deep within the Chara or on the sediments below other macrophytes, the encounter rates with these snails are probably much lower than for the other snail taxa, which occur much higher in the Chara and are more exposed to fish. Therefore, I assumed that encounter rates with Viviparus and large Helisoma were equal to 0.00. Furthermore, I assumed that encounter rates were independent of fish size, although for most of the following analyses, which are largely based on selection within single fish size classes, this assumption is not necessary. An earlier study investigating encounter rates between bluegill and prey dwelling on Chara found that fish size had no significant effect on encounter rates (Werner et al. 1983). This was probably a result of the highly structured aspect of the habitat which greatly reduced the effect of the increased reactive distances of larger fish (Li et al. 1985).

I initially assessed how well size-specific encounter rates could predict the observed patterns of size selection depicted in Figure 5, by

simplifying equation 5 to

$$\hat{\alpha}_i = \lambda_i / \sum_{j=1}^{K} \lambda_j \qquad (8)$$

(i.e. by assuming that P(a)P(s) in equation 5 was constant among all snail size classes). This simple model (Model 1: Table 8) explained 53% percent of the observed variation in selectivities among the entire data set (Figure 16). In addition, I divided the observed set of selectivity vectors into two categories: those in which the snails in the largest size class had, on average, a predicted size refuge with $P(s)<0.5$, and those in which the largest size class had, on average, a size refuge with $P(s)>0.5$. I refer to these two categories as invulnerable and vulnerable, respectively. Nine of the distributions (a total of 38 selectivity values) in Figure 5 were invulnerable (all vectors for Amnicola on 17 May and 6 June 1985 except the ones for the largest fish class, the vector for Amnicola in Palmatier Lake for the smallest fish class, and the vectors for Marstonia for the two smaller fish classes), while the other 27 vectors (90 selectivity values) were vulnerable (i.e. most snails in even the largest snail class could be eaten with probabilities exceeding 0.5). The encounter rate model explained 71% of the variation among the vulnerable vectors, but performed extremely poorly in predicting the selectivities for distributions that included invulnerable snails ($R^2$ = -33%, figure 16).

I next included the effects of size refuges in the model using the results shown in Figures 7 and 10 (Model 2: Table 8):

$$\alpha_i = \lambda_i P_i(s) / \sum_{j=1}^{K} \lambda_j P_j(s) \qquad (9)$$

Incorporation of the the size refuge into the model increased the total

Figure 16. Comparison of observed and predicted size-selectivities using Model 1 (incorporating size-specific encounter rates) and Model 2 (which additionally incorporated size-specific refuges) (see Table 8). The top panel gives the results from situations in which even the largest snail class had a $P(s)<.50$, while the middle panel gives the results from situations in which the largest snail class (and possibly smaller ones) had $P(s)\geq.50$. The bottom panel gives the results for all selectivity vectors. $\bar{R}^2$ is the proportion of total variation in observed selectivities explained by the predicted selectivities, and the diagonal line gives the expectation if the model was a perfect fit to the data. N = number of selectivity vectors. n = number of individual selectivities. The observed selectivities are plotted in Figure 5.

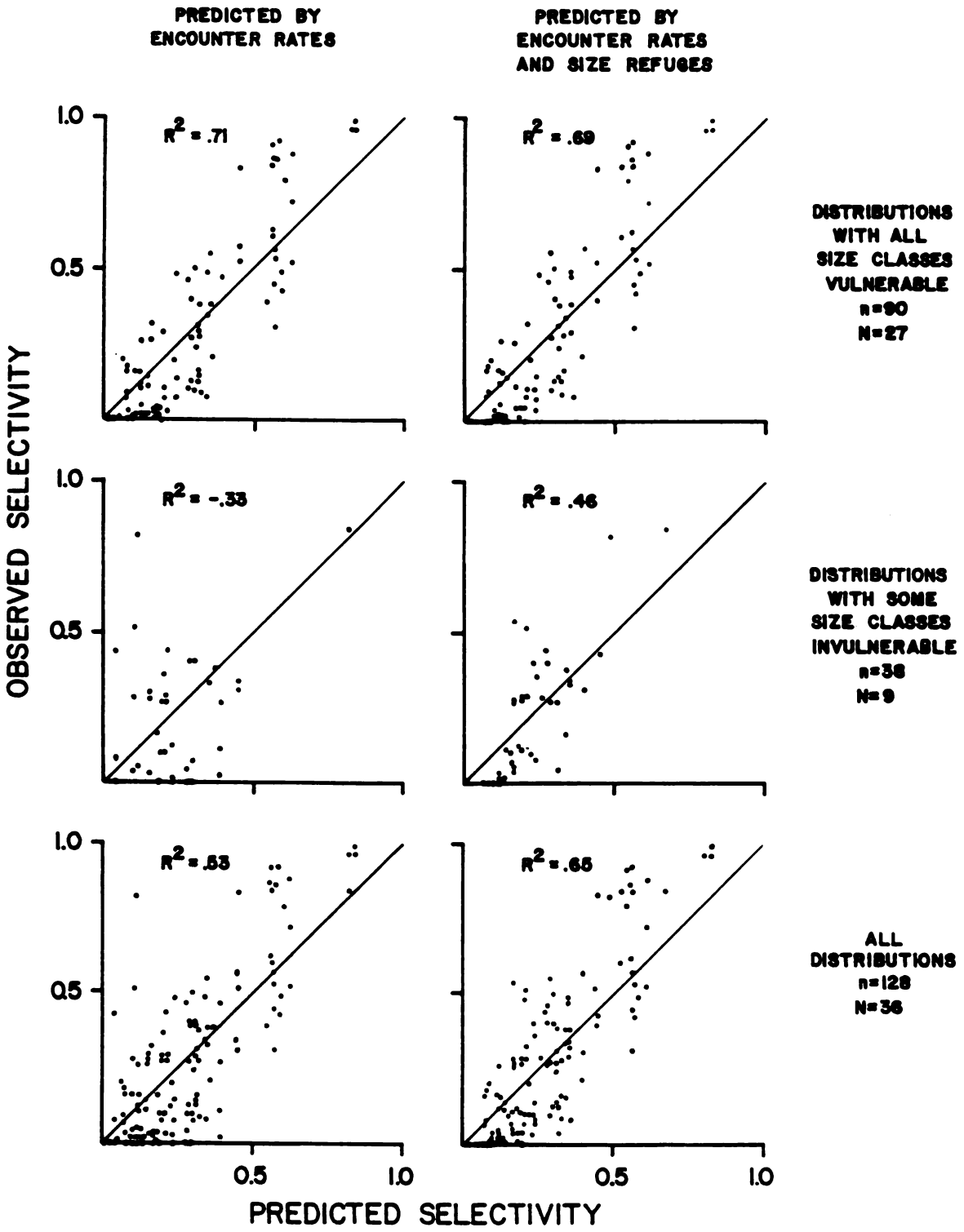
PREDICTED BY ENCOUNTER RATES
PREDICTED BY ENCOUNTER RATES AND SIZE REFUGES
OBSERVED SELECTIVITY
PREDICTED SELECTIVITY
1.0
0.5
$R^2$ = .71
$R^2$ = .69
$R^2$ = -.33
$R^2$ = .46
$R^2$ = .53
$R^2$ = .65
DISTRIBUTIONS WITH ALL SIZE CLASSES VULNERABLE n=90 N=27
DISTRIBUTIONS WITH SOME SIZE CLASSES INVULNERABLE n=38 N=9
ALL DISTRIBUTIONS n=128 N=36

Figure 16

Table 8. Constants and equations used in foraging models 1, 2 and 3 (see equations 5, 8 and 9. See Table 3 for descriptions of the terms.

| Function or constant | Source |
|---|---|
| $\lambda = 0.0001062m^{1.063}$ $(s^{-1})$ | Ancova, Figure 6 (without Gyraulus), equation 7 |
| $a = 20.0$ (J/mg) | (Stein et al. 1984) |
| $c = 0.70$ | (Elliot 1976, Ware 1975) |
| $R = 0.00105M^{0.73}$ (J/s) | (Evans 1984, using summer data and assuming 13.6J = 1 mg $O_2$ (Elliott and Davison 1975) |
| $h = 9.0$ (s) | See Figure 13 and text |
| $r = 6.0$ (s) | See Figure 14 and text |
| $P(g) =$ constant | Model 1 |
| $= 1/(1 + \exp(-41.95-26.45\log_{10}(m^{1/3}/SL))$ | Model 2 and Model 3 (Figure 7) |
| $P(c) =$ constant | Model 1 |
| $= 1/(1 + \exp(8.680-5.885\log_{10}(C/M))$ | Model 2 and Model 3 (Figure 10) |
| $P(a) =$ constant | Model 1 and Model 2 |
| $= 1/(1 + \exp(-2.332-6.579\log_{10}((e_g/H)/(E_g/T^*)))$ | Model 3 (Figure 18) |

variance explained from 53% to 65%. However, more importantly, this model increased the $R^2$ for invulnerable size distributions from -33% to 46%. As expected, the two models (equations 8 and 9) performed similarly when snails had not reached a size refuge (i.e. for vulnerable distributions, $R^2 \geq 69\%$). These data demonstrate that both encounter rates (which increase with snail size) and the ability of fish to consume attacked snails (which declines with snail size) can be important. Depending on the distribution of snail sizes in the environment and on the fish size, the resulting patterns of selection can be monotonically increasing, decreasing or hump-shaped, depending on the relative importance of these two processes (Figures 5, 16).

In developing these two models, I assumed that attack probabilities (P(a)) were equal among all snail sizes (e.g. $P_j(a)=1.0$ for all j). Some of the residual variation may be explained if fish adjust their attack probabilities. The best conceptual framework from which to generate an expected pattern for P(a) comes from optimal foraging theory (e.g. Charnov 1976). This theory predicts that predators should ignore encountered prey that offer less net energetic return than the environment on average (i.e. if $e_n/H < E_n/T^*$, then $P(a)=0$), and that predators should always attack prey that offer a greater net energetic return (i.e. if $e_n/H > E_n/T^*$, then $P(a)=1.0$). Two problems had to be resolved before I could examine the data and determine if attack probabilities were varied in qualitative accord with optimal foraging theory. First, I needed to specify an optimization model and decide upon the values of important parameters, notably handling times. Second, I needed to develop a technique to estimate attack probabilities from the laboratory and field data, neither of which directly yielded estimates of attack probabilities.

Optimal diet models have been published in many forms (e.g. Werner and Hall 1974; Charnov 1976; Mittelbach 1981). The model I use is similar to that developed for bluegill sunfish (Mittelbach 1981), where net energy gain per unit foraging time is estimated as:

$$E_n/T = \sum_{i=1}^{K} e_{gi} D_i \lambda_i P_i(s) - RT / T, \qquad (10)$$

$$\text{where } T = 1 + \sum_{i=1}^{K} D_i \lambda_i P_i(a) H_i,$$

$e_{gi}$ is the gross energy gain from an item of prey type i, R is the metabolic rate of the fish, $H_i$ is the expected total handling time per consumed item of prey type i (and includes the combined effects of handling time, rejection time and capture success: see Table 3); other terms have been defined previously (see Table 3). The optimal solution can be found by ranking the prey by increasing profitabilities (i.e. by the ratio of net energy gain per total handling time: $e_n/H$, where $e_n = e_g - RH$: see Table 3) and determining the diet breadth that maximizes $E_n/T$ (see Charnov 1976; Mittelbach 1981). Profitabilities were estimated for each prey item as the ratio of net assimilable energy to expected total handling time, H (incorporating rejection times). Assimilable energy was estimated as the product of the tissue dry mass of a snail times 20 J/mg (Stein et al. 1984) times an assimilation efficiency of 70% (Elliot 1976; Ware 1975). Energetic losses were based on Evan's (1984) study of metabolic rates of pumpkinseeds (Table 8) assuming that metabolism was similar during all phases of the foraging process. Rejection time was assumed constant and equal to 6 seconds, which is in good agreement with the field data and most of the laboratory data (Figure 14). Estimation of successful handling times posed a problem due to the variable results obtained in Experiments 1

and 2. I reasoned that pumpkinseed foraging in the field is more closely mimicked by Experiment 1, where a number of snails were simultaneously present in the aquarium (as they are in the field). Therefore, I set handling times equal to 9 seconds/snail (invariant among snail taxa, snail size and fish size) since 9 seconds was approximately equal to the mean handling time observed in the field and in Experiment 1 (Figure 13).

Using this model, I estimated $E_n/T^*$ for 60, 80, 100, 120 mm SL fish (corresponding to the midpoints for the four 20 mm fish size classes) on the six collection dates using the samples of snail density and size-structure. The predicted patterns of attack probabilities, based on optimal diet theory, are that prey with profitabilities greater than $E_n/T^*$ should always be attacked, while prey with lower profitabilities should always be ignored (i.e. if $e_n/H > E_n/T^*$ then $P(a)=1.0$, else $P(a)=0$).

Observed attack probabilities, though not directly available from the field data, can be inferred by applying Manly's index in the following manner. If feeding by fish reflects the combined effects of encounter rates, size refuges and attack probabilities and if the feeding rate on prey type i can be modeled according to equation 3, then a new index of selectivity can be defined as

$$\hat{\alpha}_i = D_i\lambda_i P_i(s)P_i(a)/D_i\lambda_i P_i(s) \Big/ \sum_{j=1}^{K} D_j\lambda_j P_j(s)P_j(a)/D_j\lambda_j P_j(s)$$
$$= P_i(a) \Big/ \sum_{j=1}^{K} P_j(a) \qquad (11)$$

Relative values of $D\,P(s)P(a)$ were estimated from the gut contents (as in previous calculations of selectivities), and $D\,P(s)$ were estimated using Model 2 (equation 9; Table 8). Thus, the standardized ratios of these two terms provide estimates of relative attack probabilities ($\alpha'$,

equation 11). In theory, if pumpkinseeds behaved optimally and the model was properly specified, relative attack probabilities ($\alpha'$) should vary discontinuously from zero for prey with low profitabilities (i.e. if $e_n/H < E_n/T^*$, then $\alpha'=0$ and $P(a)=0$) to $1/k^*$ for prey with greater profitabilities (i.e. if $e_n/H \geq E_n/T^*$, then $\alpha'=1/k^*$ and $P(a)=1.0$: $k^*$ is the number of prey classes within the optimal diet). In addition, the cut-off point between prey with $\alpha'=0.00$ and prey with $\alpha'=1/k^*$ should be equal to $E_n/T^*$. I defined prey types based on their profitabilities (using seven profitability classes, except when only fewer were available), and calculated selectivities among these classes for each of the four fish size classes on each of the six dates, which yielded 18 selection vectors (all with $G>25$: 6 combinations had sample sizes <10). I then compared the patterns of observed relative attack probabilities ($\alpha'$, equation 11) with the patterns predicted by optimal diet theory. To facilitate the comparison we grouped the 18 vectors into four categories based on their values of $E_n/T^*$.

Relative attack probabilities ($\alpha'$, equation 11) increased with profitability, and the transition between prey with low attack probabilities and high attack probabilities increased with $E_n/T^*$ (Figure 17). For example, in the situations with low $E_n/T^*$ (Figure 17d), snails with low or medium profitabilities were attacked as often as were snails with greater profitabilities. However, in the situations with the highest levels of $E_n/T^*$ (Figure 17a), the snails with low and medium profitabilities were ignored and only the most profitable snails were attacked. Therefore, it appears that fish varied their attack probabilities in qualitative accord with optimal foraging theory. However, as in previous studies of prey selection (e.g. Lacher et al. 1982; see also Stephens 1985) many prey with $e_n/H<E_n/T^*$ were included in the diet, and it appears that attack probabilities, rather than showing

Figure 17. Relative attack probabilities (calculated using equation 11) in relationship to prey profitability. $E_n/T^*$ values for each panel: a) >0.7, b) 0.4-0.7, c) 0.1-0.4, d) <0.1. Particular values of $E_n/T^*$ for each data set are indicated by the arrowheads. Data in panel d) were obtained from the smallest fish size class (which consistently had lower estimates of $E_n/T^*$), while data in each of the other three panels were obtained from at least two of the three larger size classes (which overlapped considerably in their estimates of $E_n/T^*$). Due to the lower range of profitabilities available to the fish in d), only five profitability classes were defined. Lines were fit to the equation $y=M/1+\exp(a+bx)$ using logistic regression.

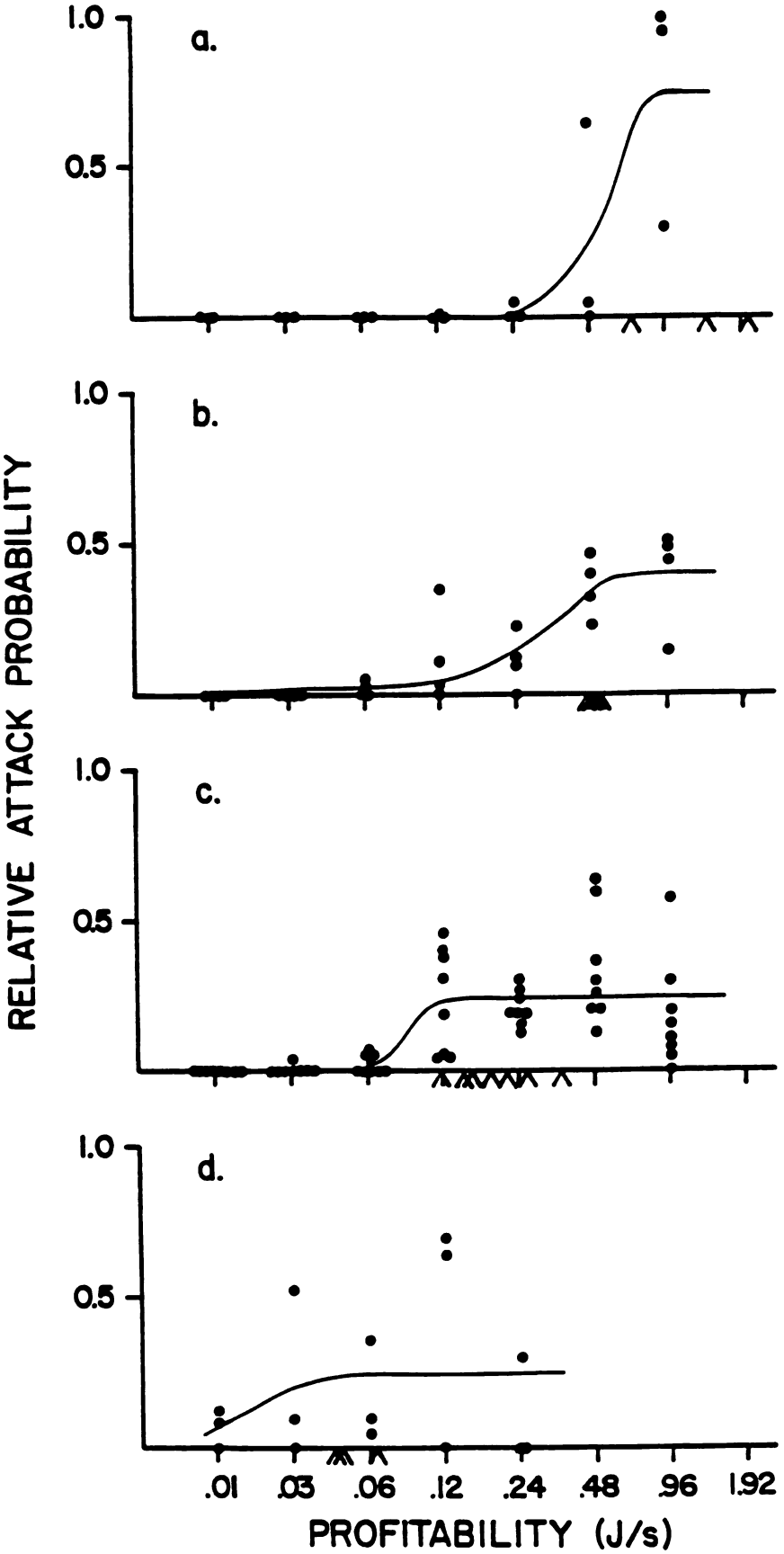
1.0
0.5
a.
b.
c.
d.
RELATIVE ATTACK PROBABILITY
.01
.03
.06
.12
.24
.48
.96
1.92
PROFITABILITY (J/s)

Figure 17

an abrupt increase from 0 to 1 showed a continuous increase (although it is difficult to assess this critically with the available data).

In order to incorporate variable attack probabilities into the foraging model, I derived a general empirical relationship (since the quantitative predictions of the optimal diet model were not met) relating the probability of attack to the profitability of the prey. I first fit non-linear regressions ($\alpha' = M/1+\exp(u)$, where $u = c1+c2(e_n/H)$) to the four data sets in Figure 17. The asymptote of this equation, M, is an estimate of the maximum relative attack probability, which should be equivalent to an absolute attack probability of 1.00. Therefore, absolute attack probabilities (P(a)) were estimated as $\alpha'/M$ for the data in Figure 17. Prey value was standardized across the different levels of $E_n/T^*$ by using the the ratio of gross prey profitability to the gross foraging rate: i.e. $(e_g/H)/(E_g/T^*)$. In other words, this provided an index of relative prey value. Operationally, the use of gross rewards (rather than net rewards) has little effect on the model but was necessary to avoid problems with logistic regression that could arise if both terms had negative values. I then submitted these data to non-linear regression ($P(a) = 1/1+\exp(u)$, $u = c_1+c_2\log_{10}(e_g/H)/(E_g/T^*)$). This method, justified for its empirical use, provided an excellent description of the data (Figure 18).

I incorporated this new function for attack probabilities into the foraging model (Model 3, equation 5, Table 8), although unlike the previous models, this model used field data in its development and is therefore not independent of the field patterns. The new model explained somewhat more of the variance in selectivities than did the model without variable attack probabilities ($R^2$=69% in Figure 19 versus $R^2$=65% in Figure 16), although the improvement was slight considering the strong patterns evident in Figures 17 and 18. Most noticeably,

Figure 18. Probability of attack as a function of the relative value of the prey items. Data were taken from Figure 17 and transformed as described in the text. The curve was fit to the equation $P(a)=1/1+\exp(a+b\log_{10}X)$ using nonlinear regression: a=-2.332 , b=-6.579.

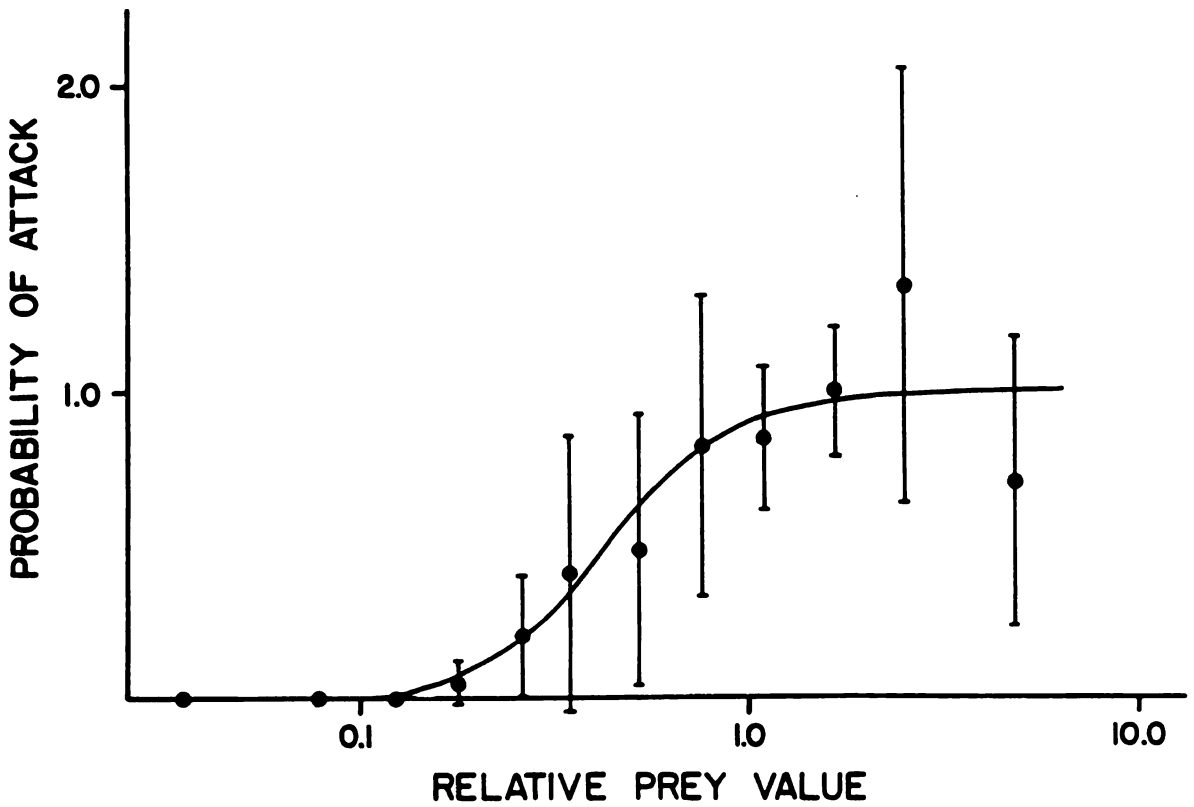


Figure 18

Figure 19. Comparison of observed and predicted size-selectivities using Model 3 (see Table 8).

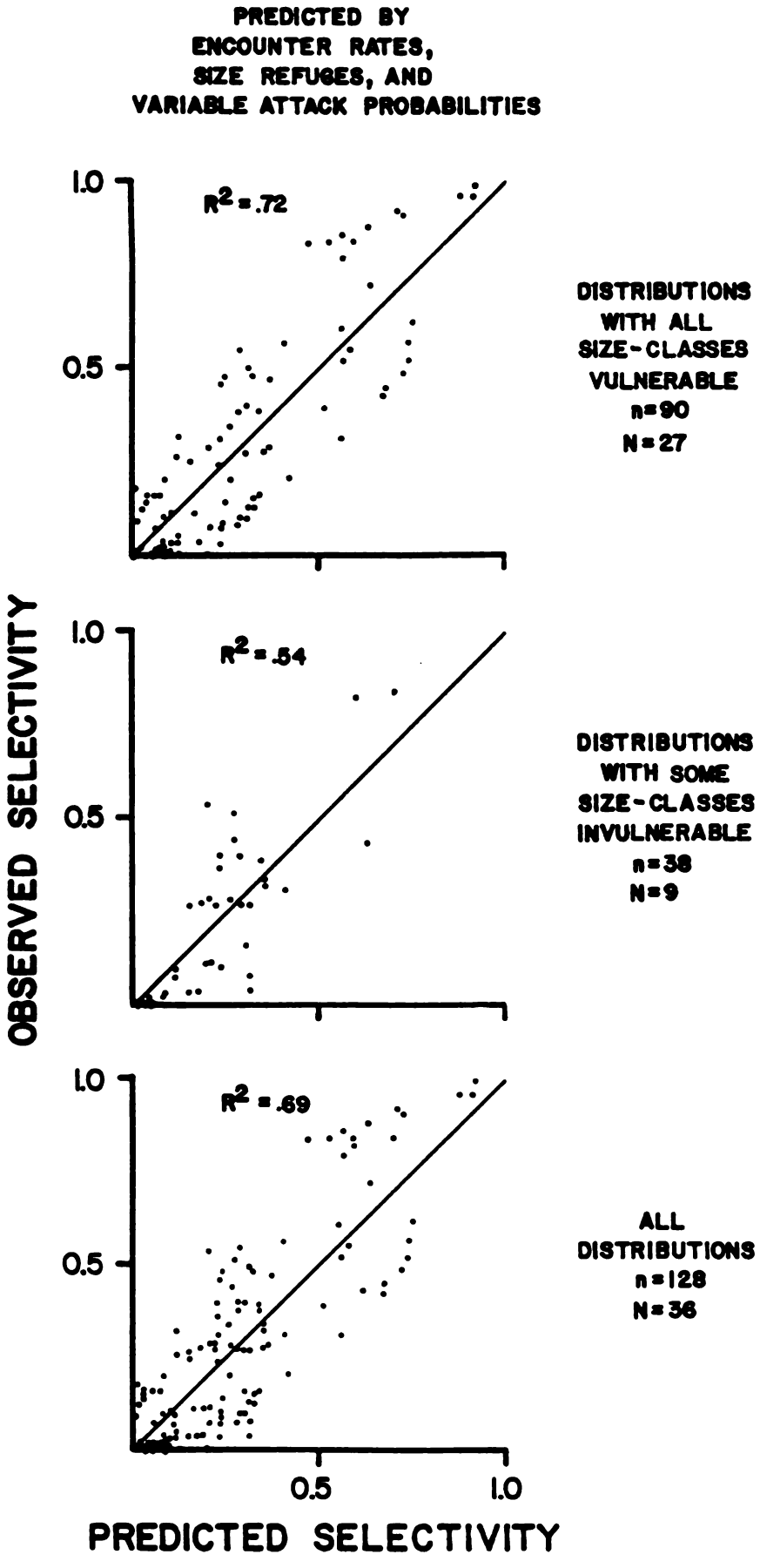
PREDICTED BY
ENCOUNTER RATES,
SIZE REFUGES, AND
VARIABLE ATTACK PROBABILITIES
1.0
0.5
$R^2$ = .72
DISTRIBUTIONS
WITH ALL
SIZE-CLASSES
VULNERABLE
n=90
N=27
OBSERVED SELECTIVITY
1.0
0.5
$R^2$ = .54
DISTRIBUTIONS
WITH SOME
SIZE-CLASSES
INVULNERABLE
n=38
N=9
1.0
0.5
$R^2$ = .69
ALL
DISTRIBUTIONS
n=128
N=36
0.5
1.0
PREDICTED SELECTIVITY

Figure 19

incorporating variable attack probabilities improved the predictions for invulnerable size distributions ($R^2$=54% versus 46%) and it reduced the apparent bias in the model; notice that the points in Figure 16 tend to fall along a line with slope >1, whereas the data in Figure 19 fall much closer to a line with slope=1. These improvements in fit came largely from the prey classes with observed and predicted selection fairly close to zero and therefore had little effect on the calculation of $R^2$.

As a final, and more complete test of Model 3, I compared predicted and observed selection based on prey taxa as well as size. Each prey item was assigned to a taxonomic category as well as a size class (i.e. <.5mg, .5-1.0mg, 1.0-2.0mg, 2.0-4.0mg, etc), and selectivities were calculated among all taxa and size classes with d>20. Due to the relatively broad size categories, most taxa were represented by only one size-class on any particular date. Thus, this served largely as a test of species selection. The foraging model (Model 3) explained 47% of the variation in selectivities (Figure 20).

Rather than calculating a single $R^2$ based on the entire data set, as done in previous analyses, I calculated the $R^2$ for each of the available selectivity vectors (i.e. for each j in equation 4 rather than over all j). There was considerable variation in the fit of Model 3 to each particular vector of size selection and species selection ($R^2$'s ranged from below zero to 99%). However, there was also considerable variation in the observed selectivities within each vector, and the model was fairly good at predicting the magnitude of this variation (Figure 21a). As would be expected, the observed variance had a strong impact on the values of $R^2$. When there was little variation in selectivities (due to small differences in selectivity or risk among the prey groups), the model provided little additional information beyond the prediction that there should be little variation (and $R^2$ was therefore very small, or

Figure 20. Comparison of observed and predicted selectivities using Model 3. Observed data were based on patterns of species and size-selection (see text).

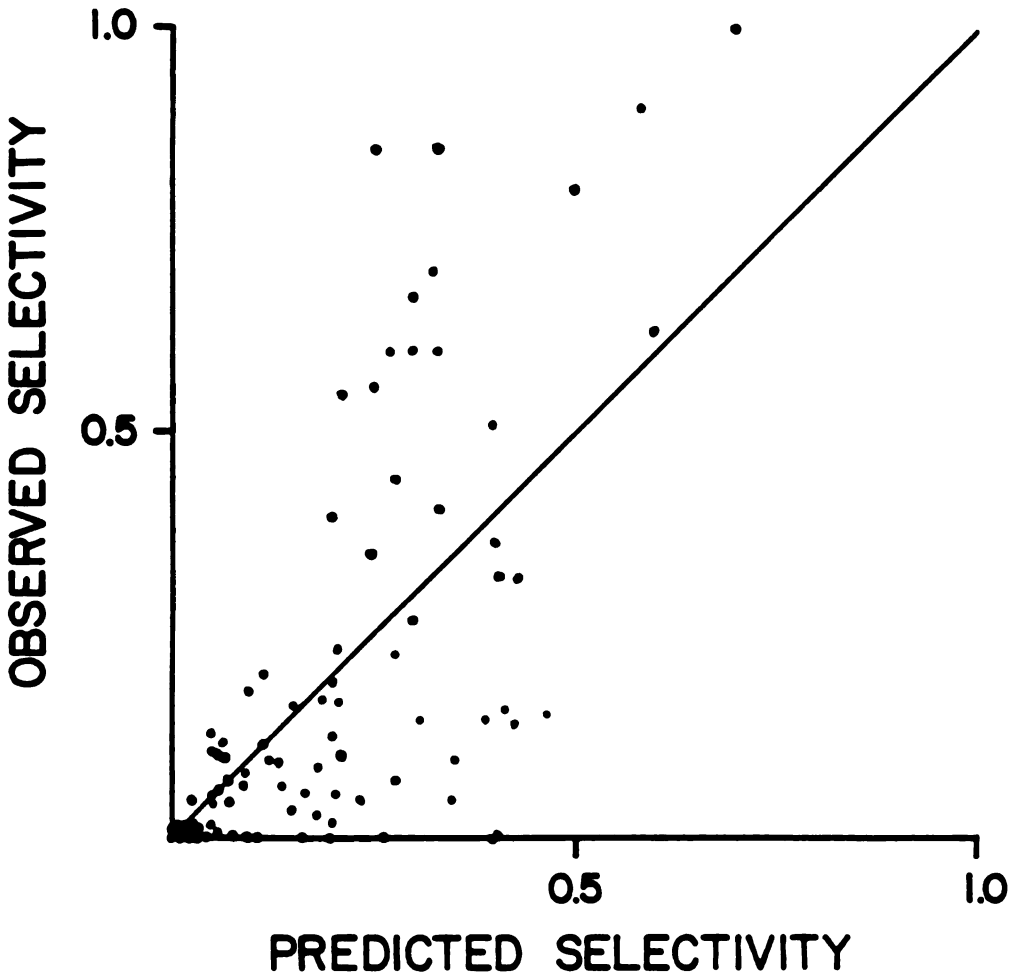


Figure 20

Figure 21. Performance of Model 3 as a function of the variance in selectivities within a selection vector. Closed symbols are for data from the size-selection vectors (i.e. Figure 21). Open symbols are for data from the species selection vectors (i.e. Figure 22).
a) Proportion of variance explained by Model 3 in relation to the amount of observed variation in selectivities (based on within vector comparisons). Data from two vectors with $R^2$<-10.00 were plotted at $R^2$=-1.00 for clarity. The curve was drawn by eye. Both variables were significantly correlated, although the correlation is higher using $\log_{10}$(Observed Variance): r=.66, n=53, p<.0001. b) Variance in the predicted selectivities as related to the observed variance. The two variables are significantly correlated: r=0.78, n=53, p<0.0001. The correlations in a) and b) are still highly significant if the three points with large variances (>0.30) are excluded (p<0.003 in both cases).

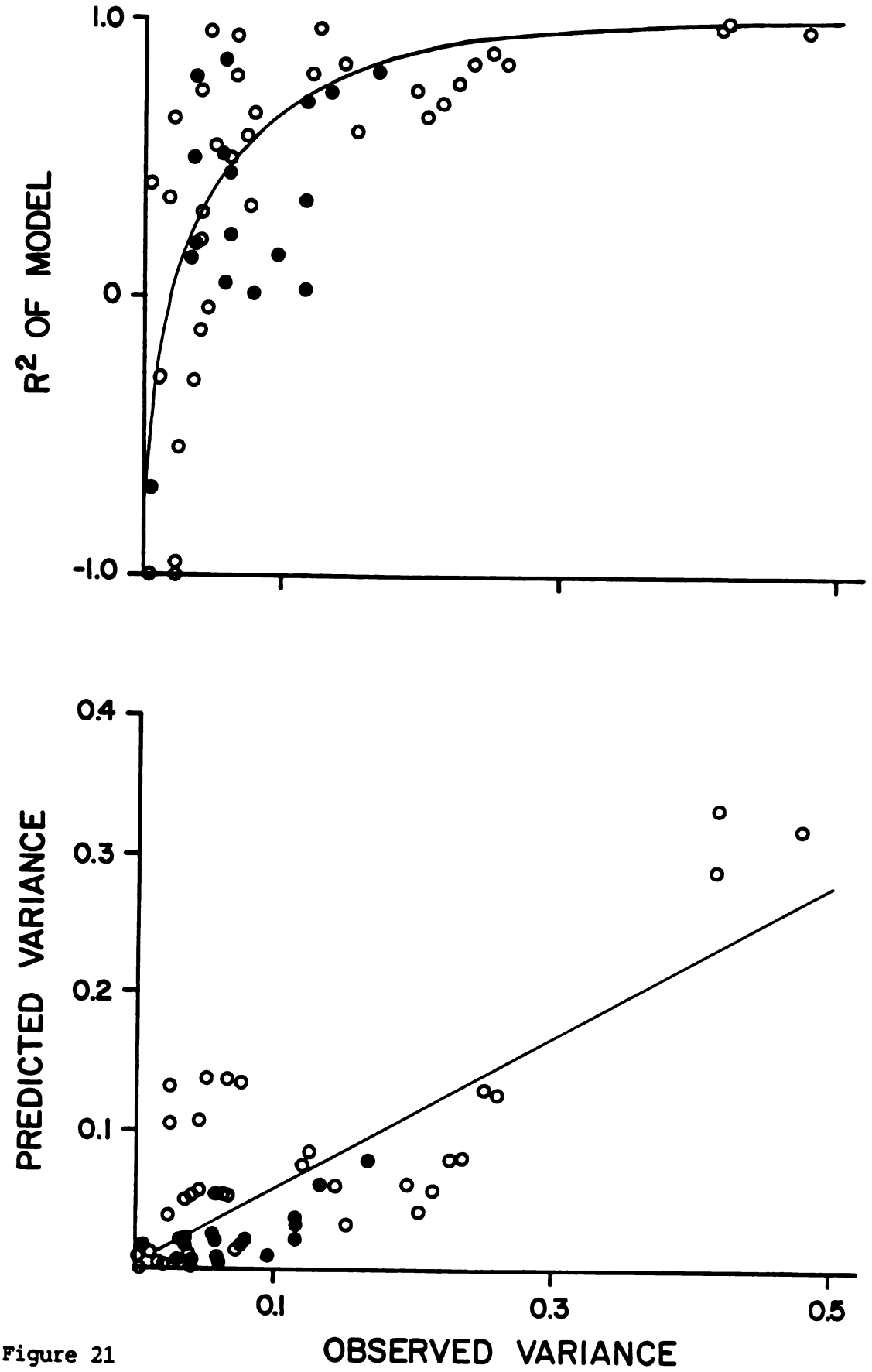
1.0
0
-1.0
$R^2$ OF MODEL
0.4
0.3
0.2
0.1
PREDICTED VARIANCE
0.1
0.3
0.5
OBSERVED VARIANCE

Figure 21

negative). However, as the variation in selectivities increased (i.e. some prey groups stood out as being more or less at risk than others), then the model explained a greater portion of the observed variance: i.e. $R^2$ increased (Figure 21b). These results show that the model actually provided quite a good predictor of dietary patterns: when little variation in selection was observed, the model predicted low variation in selectivity (Figure 21a), and as the observed variation increased, the predicted variation increased along with a rapid increase in the $R^2$ (Figure 21b).

## DISCUSSION

The components of the pumpkinseed-snail interaction that were measured in the laboratory were quite successful in predicting and explaining observed patterns of prey selection under natural conditions. Each of the three primary foraging components (encounter rates, attack probabilities and capture successes) were found to scale with body size of the prey, and each component increased the explanatory power of the model. Encounter rates, which increased with snail size, played a major role in determining prey selection. However, on dates when some snails had grown into the size refuge, only a model incorporating both encounter rates and capture successes could predict selection. Together, these two functions create a risk curve that is humped-shaped, with intermediate size snails at greater risk than smaller or larger snails of the same species (Pastorak 1981; Greene 1983, 1986; Figure 22). Of course, the predator's size affects the location of this hump (e.g. due to changes in the predator's crushing ability), and different snail species also differ in the location of the hump due to differences in the way crushing resistance scales with body size among the snail

Figure 22. a) The three primary components of the foraging models (encounter rates, capture probabilities and attack probabilities) as functions of prey size. b) Predictions of prey selection (or prey risk) as functions of prey size for the three foraging models (see Table 8).

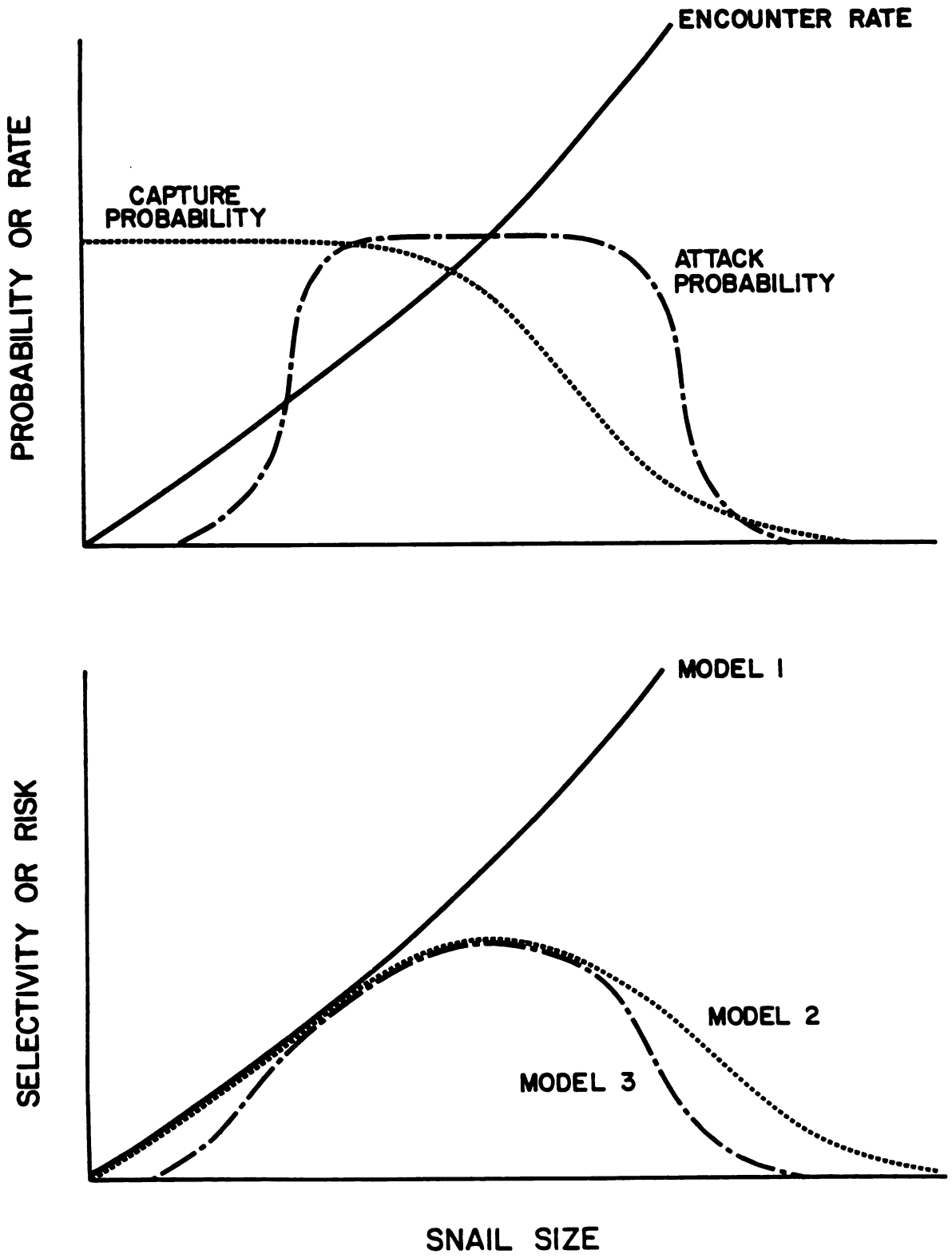
ENCOUNTER RATE
PROBABILITY OR RATE
CAPTURE PROBABILITY
ATTACK PROBABILITY
MODEL 1
SELECTIVITY OR RISK
MODEL 2
MODEL 3
SNAIL SIZE

Figure 22

species. Similarly, prey profitability is a humped shaped function of snail size because of the conflicting effects of snail size on the components of profitability: energy content and total handling time (H). Small snails have very low energy content, and therefore very low profitabilities, while very large snails offer large potential energetic rewards but they can only rarely be successfully eaten, thus producing a very low profitability also. Therefore, P(a) will also be hump-shaped, although its position will depend on $E/T^*$, which is determined by many factors, including the the densities and size-distributions of the snails. These processes are summarized in Figure 22. Notice that Models 1 and 2 differ qualitatively in their predictions of size-selection (monotonic vs. humped), but that Models 2 and 3 both predict hump-shaped selection curves: incorporating variable attack probabilities simply shaves off the tails of the hump-shaped curve.

Several recent papers have suggested that size-selection should, in theory, be hump-shaped, but that natural distributions of prey may not provide enough range in prey sizes to permit the detection of humped-shaped selection under field conditions (Scott and Murdoch 1983, Schmitt and Holbrook 1984, Bence and Murdoch 1986). The data on size selection by pumpkinseeds confirms this suggestion. Theoretically, size selection is hump-shaped, due largely to the conflicting effects of different components of the predator-prey interaction (e.g. prey capture and prey retention (Wankowski 1979) or encounter rates and capture success (Bence and Murdoch 1986; Pastorak 1981; Greene 1983; this study). However, in the present study, hump-shaped selection curves were rarely observed in the field data; selection was usually monotonically increasing, due to the rarity of large prey (a point also stressed by Scott and Murdoch 1983). Only on rare occassions, when the snail size distributions were broad relative to the feeding abilities of

the fish, could the underlying hump-shaped relationship be documented under field conditions. Therefore, it appears that a complete understanding of prey selection can best be understood from a perspective that simultaneously considers the feeding abilities of the predator, the scaling of risk to prey size, and the dynamics of prey size-distributions in the environment.

Variation in size-structure of the snail community can have major effects on the dietary patterns of pumpkinseeds (Figures 1-5). For example, in Figure 23, I show the size frequency distributions for two dates in Three Lakes II and the associated selectivities of 90-109 mm SL fish. Notice that the selectivities were extremely different between the two dates, but that this is easily understood by the shifts in the size distributions of the snails. On the first date, Physa were relatively large and therefore had a high selection coefficient due to the large encounter rate. On the second date, Amnicola was selected (i.e. incurred the highest risk) because all other species were smaller (having recently hatched out from eggs) and thus incurred much lower encounter rates. The size refuge enjoyed by the large Amnicola was not enough to reduce its selection in the face of high encounter rates.

Thus the dynamics of size-structure in the snail community can have profound effects on the prey selection by pumpkinseeds. Differences in the snail community among sites can also influence dietary patterns. For example, the snail communities in Culver and Palmatier Lakes tend to be dominated by smaller snails than occur in Three Lakes II. In addition, the snail community is biased toward smaller snails during August (which is when Culver and Palmatier Lakes were sampled). On these two dates, there were only small effects of fish size on total snail biomass in the diet (Figure 1) and on mean snail mass in the diet (Figure 2). Data from Three Lakes II showed consistent effects of fish

Figure 23. Size-frequencies of major snail taxa on two collection dates in Three Lakes II. Also given are the per capita encounter rates ($\lambda$), probabilities of successful attack (P(a)), predicted selectivities ($\hat{\alpha}$), and observed selectivities ($\alpha$) for 90-109 mm SL pumpkinseeds.

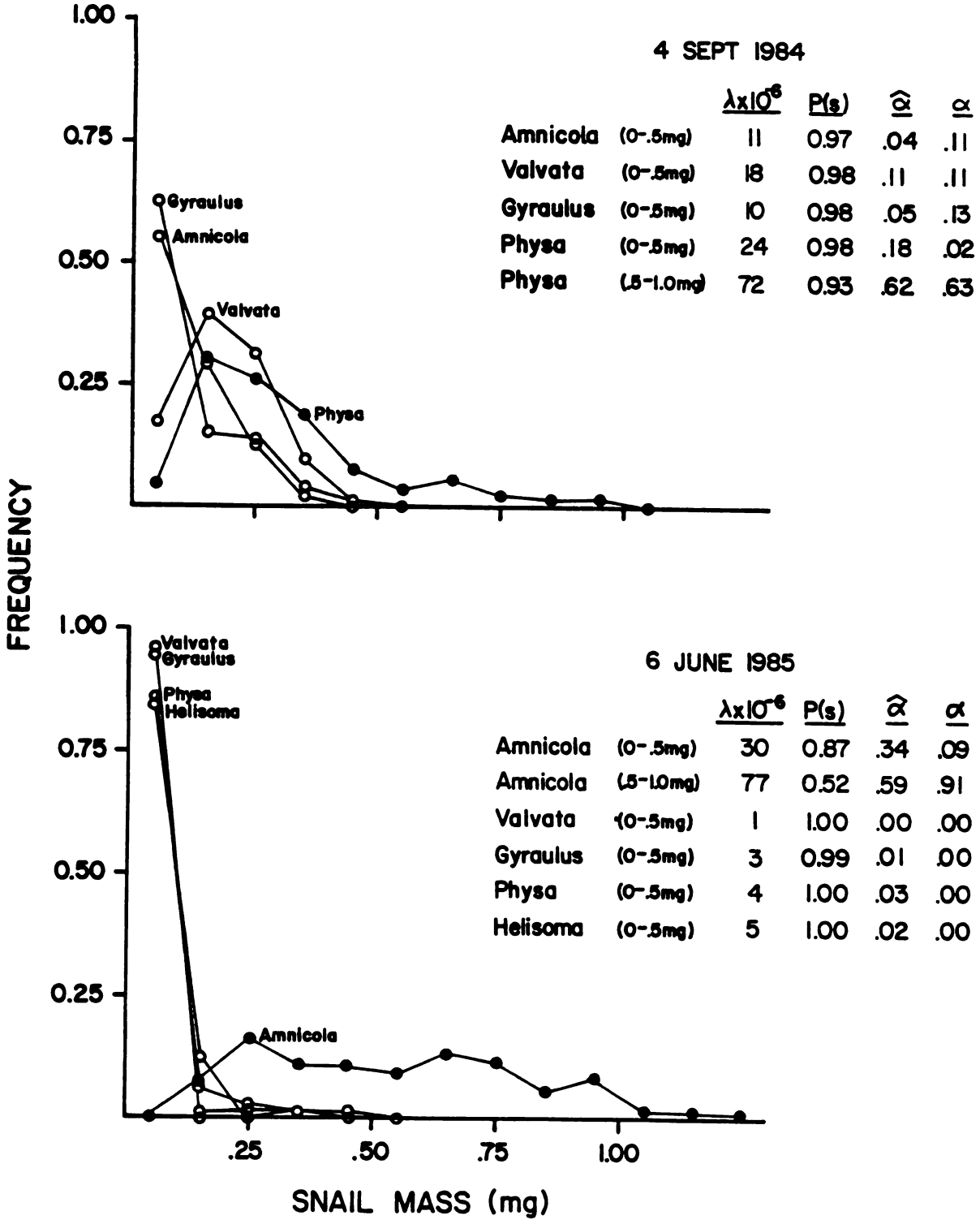
4 SEPT 1984
λx10^6 P(s) α̂ α
Amnicola (0-.5mg) 11 0.97 .04 .11
Valvata (0-.5mg) 18 0.98 .11 .11
Gyraulus (0-.5mg) 10 0.98 .05 .13
Physa (0-.5mg) 24 0.98 .18 .02
Physa (.5-1.0mg) 72 0.93 .62 .63
Gyraulus
Amnicola
Valvata
Physa
6 JUNE 1985
λx10^-6 P(s) α̂ α
Amnicola (0-.5mg) 30 0.87 .34 .09
Amnicola (.5-1.0mg) 77 0.52 .59 .91
Valvata (0-.5mg) 1 1.00 .00 .00
Gyraulus (0-.5mg) 3 0.99 .01 .00
Physa (0-.5mg) 4 1.00 .03 .00
Helisoma (0-.5mg) 5 1.00 .02 .00
Valvata
Gyraulus
Physa
Helisoma
Amnicola
1.00
0.75
0.50
0.25
.25
.50
.75
1.00
FREQUENCY
SNAIL MASS (mg)

Figure 23

size. These differences arose for at least two reasons. First, because snails were larger in Three Lakes II, size refuges were more important than in Culver and Palmatier Lakes; thus larger fish should have consumed larger snails because of their better crushing ability. Second, the effects of the size refuges caused E/T* to increase more rapidly with fish size in Three Lakes II than in Culver and Palmatier Lakes; thus, larger fish dropped a greater range of small snails from their diets, further increasing the trends in mean snail mass. The data in Figures 1 and 2 also indicate a greater role of size refuges than was revealed in the patterns of size-selectivity (Figure 5). This discrepancy apparently arose because large prey in Three Lakes II were extremely rare, although they were eaten occassionally by large fish. These data however, were excluded from the selectivity analyses because the sample sizes were too small. The complex dietary patterns and selectivities observed in this system were only understood as a result of the simultaneous consideration of how prey and predator morphologies influenced key components of the predator-prey interaction and how shifts in the size-structure of the snail community altered the relative importance of these processes.

These relatively simple foraging models succeeded in predicting the diets of fish despite assuming that encounter rates could be modeled only as a function of snail mass. Clearly, this was an oversimplification. For example, fish size is known to influence encounter rates with zooplankton (O'Brien et al. 1976; Mittelbach 1981) because larger fish generally possess better visual acuity (Li et al 1985); however, in highly structured environments, such as the littoral zone of lakes, this fish size advantage can disappear (Werner et al. 1983). Microhabitat use by snails might also modify their encounter rates with predators, as suggested earlier for Helisoma and Viviparus.

A more comprehensive model would need to explore and possibly incorporate these (and other) additional sources of variation in encounter rates. Two other ways in which encounters could vary is through the formation of search images or through patch selection, both of which should produce encounter rates that are density and/or frequency-dependent. The possible role of these two factors is seen in Figure 20 where prey with low risk tended to be avoided more than predicted, while prey at high risk were selected more than predicted. These biases were not seen in the size selection patterns, suggesting that unexplained sources of variation in risk might be greater among species than among size-classes within species. This might also explain the poorer performance of the model when predicting species selection, although this might also be explained by the lower variance in risk among snail species as compared to size classes (Figure 21b).

The difference in the accuracy of the model in predicting size selection versus species selection might be the result of the different spatial scales over which snail densities and size-distributions vary. Using data collected over several months in 1983 from a study site in Three Lakes II, I examined how the coefficients of variation (one simple way to express patchiness) varied when measured for density and for mean snail size for each species. The CV's for densities were three to eight times greater than the CV's for mean size (or mass) of snails (Table 9). These data suggest that small patches of the littoral zone are likely to differ more with respect to snail densities than with respect to average snail sizes. Furthermore, for each date I examined the correlations between the densities of the common snail species; of 24 correlations, only 2 were significant at $p<0.05$. Therefore, species were relatively independently distributed within this study site. If a fish concentrated its search in one particular patch, it was likely to see a

Table 9. Coefficients of variation among samples for density and mean size of snails. CV's are based on snail samples (from 5–14/date) collected during 1983 in Three Lakes II. For each snail species, CV's (100s/x) were calculated for density, mean size (shell height or diameter) and mean mass among samples on each date. Results were summarized over all species and dates. Sample sizes are 47.

| Variable | CV | 95% confidence limit |
|---|---|---|
| density | 128.4 | ± 18.6 |
| mass | 44.7 | ± 9.9 |
| size | 16.0 | ± 3.3 |

very different species composition compared with a nearby patch, although the size-distributions of any snail species would be fairly similar between the patches. This suggests that investigation of patch selection might provide additional insights into the determinants of prey selection by pumpkinseeds. Schluter (1981) reached a similar conclusion after reviewing studies that tested optimal diet theory under field conditions in which multiple prey types were available.

Most studies of prey selection make no attempt to quantify encounter rates, probably because encounter rates are often difficult and time consuming to measure. However, as this and other studies have shown (Mittelbach 1981; Wright and O'Brien 1984), the explicit consideration of prey encounter rates can be critical in accurately explaining patterns of selection. For example, Stein et al. (1984) studied prey selection by another molluscivorous sunfish (L. microlophus), and concluded that optimal foraging theory was not useful in predicting the patterns of prey choice they observed in the laboratory. In one sense, I agree with Stein et al. that foraging profitability alone might not explain a large fraction of the observed variation in prey selection by predators (indeed, it did not in my study; Figure 16 versus Figure 19), and that the "optimal" aspect of many foraging models might be unnecessary. However, Stein et al. did not measure encounter rates and capture probabilities, and without accurately assessing the effects of these components of the foraging process, the additional role of prey profitability cannot be easily assessed. Indeed, this focuses on the general problem of testing optimal foraging predictions by examining the correlation betwen diet selection and prey profitability. In many situations, components of the predator-prey interaction are correlated; e.g. enounter rates and prey profitabilities often increase with prey size under many conditions (Werner and Hall 1974; O'Brien et al. 1976;

Mittelbach 1981; this study). Thus, the observation that a predator's diet is biased, for example, in favor of larger prey cannot be interpreted as evidence that the predator only attacked more profitable (i.e. larger) prey. The effects of encounter rates and other "passive" components of the interaction (e.g. capture success) must first be incorporated into the model.

Foraging models can also be useful (even if the underlying mechanisms and assumptions are shown to be incorrect or violated) if the models capture enough of the salient features of the predator-prey interaction to be useful tools for understanding population dynamics and/or individual performance of predators and prey. For example, I used the foraging model (Model 3) to predict the rates of ingestion for fish on each of the six collection dates. The predicted ingestion rates were strongly correlated with the snail biomass in the stomachs of fish (Figure 24: $r=.84$, $n=21$, $p<.0001$), suggesting that the model correctly predicted relative feeding rates of the fish. However this correlation is somewhat suspect because of the use of different size classes of fish. That is, stomach capacity increases with fish size and predicted ingestion rate generally increases with fish size; therefore prey mass in the stomach and predicted ingestion rate might be correlated but not functionally related. To factor this out, I performed an analysis of covariance (on $\log_{10}$ transformed data) using the three largest size classes of fish, which overlapped in their predicted ingestion rates. Slopes (i.e. the effect of ingestion rate) were similar among the three groups ($p>.75$), and adjusted means did not differ among the fish size-classes ($p>.20$), although the predicted ingestion rate (the covariate) did explain a significant portion of the variation in snail mass in the stomachs ($p=0.03$). Therefore, the model provided a good description of the relative feeding rates of fish and might be useful as

Figure 24. Total snail mass in stomach as a function of predicted gross feeding rate. Data are based on means for fish within four size classes. Analysis of covariance for the three larger classes, which overlap in their predicted feeding rates, showed that the three relationships were similar. The regression analysis for the complete data set was highly significant and the relationship was not different from linear (log-log regression: $r^2$=0.71, n=21, p=0.0001, slope=0.86 $\pm$ 0.26). Symbols denote fish size classes: ■ = 50-69 mm SL, ● = 70-89 mm SL, ▲ = 90-109 mm SL, ♦ = 110-131 mm SL.

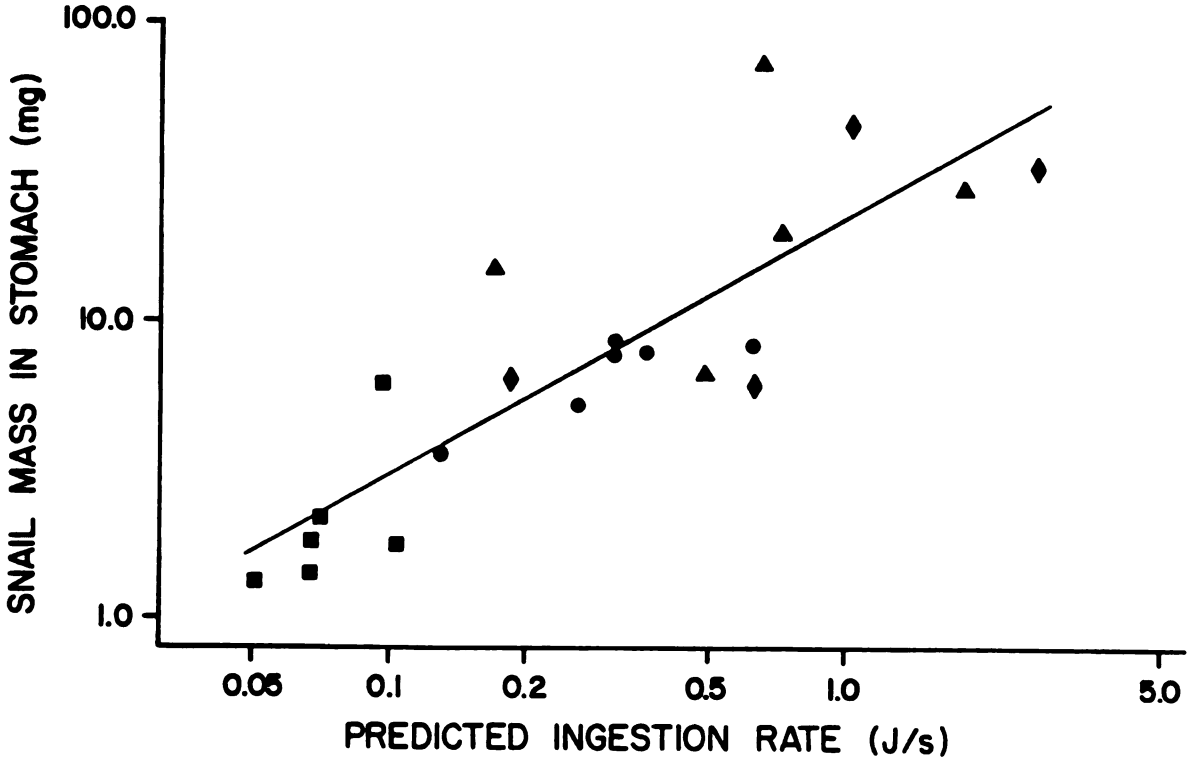
100.0
10.0
1.0
SNAIL MASS IN STOMACH (mg)
0.05
0.1
0.2
0.5
1.0
5.0
PREDICTED INGESTION RATE (J/s)

Figure 24

a tool to predict the degree of food-limitation or growth rates of fish based on resource samples (Osenberg et al. (1988), Mittelbach (1988) and Mittelbach et al. (1988) provide similar examples for bluegill, L. macrochirus). In another study (Chapter 2), I have also used the model to predict relative mortality rates of snails exposed to predation by pumpkinseed sunfish. The predictions of the model were significantly correlated with the observed effects of pumpkinseeds in a field experiment in Palmatier Lake.

Due to the important role of prey size in determining the prey selection by predators (and the predation risk of prey), individual growth rates of prey should have large influences on the survival of prey because growth rates determine the time spent at each size and therefore how long prey incur each level of risk (Werner et al. 1983, Werner and Gilliam 1984). The shape of the risk curve (e.g. Figure 22) determines the effect that growth rate has on the survivorship of prey during a particular time interval. For example, if risk decreases with prey size, then an increase in growth rate will result in a greater survivorship over a time interval (Craig 1982, Travis 1983). However, if risk increases with prey size (as it does under many situations (Figure 6; Mittelbach 1981, 1988; Li et al. 1985), then the survival during a time interval will necessarily decrease with increasing growth rate. Thus, by increasing the prey's growth rate (e.g. by increasing the abundance of its resources), the mortality of the prey could actually increase. This is neither a numerical nor, strictly speaking, a functional response by the predator, but rather a simple consequence of the simultaneous effect of growth rate on prey size and of prey size on risk.

This interaction between growth and predation risk could have important consequences for population dynamics of size-structured prey

(Botsford 1981). In these populations, the survival rate of cohorts from birth to reproduction will be simultaneously determined by growth rates and size-specific risk (see VanSickle 1977; Werner et al. 1983). The integration of these survival rates with fecundities, which are also often strongly influenced by body size and therefore individual growth rates, will describe the population dynamics. This argument suggests that in size-structured populations, the factors that directly affect growth rate (e.g. temperature, food abundance, or competitor density) and the factors that directly affect mortality rates (e.g. predator density) are inextricably linked: it is not possible to dichotomize population regulation into being governed by one of these sets of factors versus another set. There has been, and continues to be, debate over whether populations and/or communities are affected by, for example, competition vs. predation (Connell 1983; Shoener 1983; Sih et al. 1985), or bottom-up vs. top-down processes (McQueen et al. 1986). Indeed, in size-structured populations, where mortality rates are typically size-specific, the effects of bottom-up and top-down processes will necessarily interact, and it is this interaction that demands attention from ecologists. Because body size provides a simple way to scale many processes that influence a species' ecology, and because body size can be used as a common variable uniting separate demographic components that determine population dynamics, an explicit focus on body size might provide a powerful way to develop ecological models that necessarily incorporate the simultaneous effects of diverse processes and interactions.

# CHAPTER 2

## BODY SIZE, FISH PREDATION AND PATTERNS OF MORTALITY AND FECUNDITY IN A FRESHWATER SNAIL COMMUNITY

# INTRODUCTION

Predation is known to influence the abundances of prey populations and the structure of prey communities in aquatic ecosystems (Brooks and Dodson 1965; Paine 1966; Connell 1970; Hall et al. 1970). However, experiments that manipulate predator densities often yield variable results (Gilinsky 1984) or results that change across environmental gradients (Lubchenco and Menge 1978). For example, different prey species often exhibit different responses to predator manipulations (Paine 1966; Lubchenco 1978; Crowder and Cooper 1982; Morin 1984a,b), and even the same species is known to exhibit different responses at different sites or during different times (Lubchenco and Menge 1978; Gilinsky 1984; Keough 1984). A primary goal of community ecology is the development of general models that help resolve this variation in prey responses. Mechanistic foraging models (e.g. Mittelbach 1981a; Chapter 1) of predator-prey interactions are one possible tool that can be used to explore how different traits of the predator, prey or environment alter the dynamic processes that determine the effects of predators on their prey.

Prey body size is one of the most useful single parameters that can be used to model prey preferences of a predator and therefore the effects of predators on prey mortality rates, due to the ways in which encounter rates (Mittelbach 1981a; Pastorak 1981; Chapter 1), escape abilities (Pastorok 1981; Wright and O'Brien 1984; Wainwright 1987, 1988; Chapter 1) and energetic profitabilities (Elner and Hughes 1978; Mittelbach 1981a; Werner et al 1983; Chapter 1) scale with prey size. Since most populations are size-structured (Werner and Gilliam 1984), especially in aquatic systems, the influence of body size on predator-prey relationships must be understood from an intraspecific as

well as an interspecific perspective: e.g. in comparing the predicted predator-mediated mortality rates of two prey species, the analysis must incorporate differences among the two prey species as well as the size distributions of individual's within each species and the temporal changes in the size distributions that arise through growth and recruitment (VanSickle 1977). Additionally, because body size influences other demographic processes (e.g. fecundity (Baegenal 1978; Perron 1982) and other sources of mortality (e.g. environmental stress, Oliver et al. 1979)), body size might serve as a principal link between models of individual performance and population dynamics (Botsford 1981; Kirkpatrick 1984; Kooijman 1986).

The role of body size is probably best understood in freshwater planktonic systems, where foraging studies have been used in conjunction with field experiments to understand how shifts in the prey community are mediated by size-selective predators (Brooks and Dodson 1965; Lynch 1979; Murdoch et al. 1984). In many other systems, however, the mechanistic basis of predator preferences is less well understood, and experimental studies of predation in these systems often do not include appropriate data on predator preferences. This is especially true in studies of freshwater littoral communities where less is known about the particular processes that influence predator preferences (but see Mittelbach 1988).

In this study, I examine the effects of a molluscivore, the pumpkinseed sunfish (Lepomis gibbosus), on the population densities of freshwater snails. These snails differ in several aspects of their morphologies (e.g. body size and shell thickness), and these features are critical in determining their vulnerabilities to the shell-crushing predator (Chapter 1). I begin this chapter by exploring seasonal patterns in body size, and natural patterns of mortality and fecundity

in the snail community. I then report the results from a large-scale field experiment in which I assessed the effect of pumpkinseed sunfish on snail densities. In addition, I use a quantitative foraging model of the pumpkinseed-snail interaction (Chapter 1) to explain the variation in fish effects that I observed among the snail species during the field experiment. I also use the results of this experiment to estimate the proportion of the natural mortality rate that was contributed by pumpkinseeds. This work demonstrates the importance of body size in determining patterns of mortality, natality and relative abundance, and suggests that mechanistic foraging models can provide useful insights into the processes that determine prey responses to predators.

## NATURAL PATTERNS

### The System

The study was conducted in Palmatier Lake, a small (6 ha.) hardwater lake with a maximum depth of 12 m located in Barry County in southwestern Michigan. Vegetation completely covers the littoral zone and is dominated by the macroalga Chara vulgaris. Lesser amounts of C. golbularis also occur as do small amounts of Potamogeton sp. (primarily P. pectinatus), Utricularia vulgaris and U. purpurea.

The fish community is dominated by bluegill (Lepomis macrochirus), pumpkinseed sunfish (L. gibbosus), largemouth bass (Micropterus salmoides), and yellow perch (Perca flavescens) (Osenberg and Werner, unpublished data; see also Werner et al. 1977, Hall and Werner 1977 and Osenberg et al. 1988 for descriptions of Palmatier Lake and/or similar lakes in the region). The pumpkinseed is the only member of the fish community whose diet includes a large number of snails (Osenberg,

personal observation); diets of pumpkinseeds larger than 50 mm standard length (SL) contain greater than 75% snails on a dry mass basis (Mittelbach 1984; Chapter 1). Pumpkinseeds are present and active in the littoral zone from May through September, when water temperatures are above approximately 15°C (Hall and Werner 1977; Osenberg, personal observation).

The snail community consists of ten different species, all of which feed predominantly upon epiphytic constituents (e.g. algae, bacteria and detritus) that occur on the surfaces of the littoral vegetation. Snails can also be found on the surface sediments in isolated patches of the littoral zone where there is no vegetation (e.g. in old fish nests), but since Chara covers well over 95% of the littoral habitat, these microhabitats are relatively unimportant. During ice cover however, the snails drop off the plants and lie on the surface of or just beneath the sediments. As the lake warms in the spring, the snails become active and crawl back onto the plants. During the warmer months of the year (e.g. April-October) the sediments below the Chara are anaerobic and no snails are found there.

The four prosobranch species (Amnicola limosa, A. walkeri, Marstonia lustrica and Valvata tricarinata), which are relatively small in body size, are numerically dominant compared with the six pulmonate species (Helisoma anceps, H. campanulata, Gyraulus deflectus, G. parvus, Physa sp., and Promenetus exacuous). In Palmatier Lake, the four prosobranch species, and two pulmonates (Promenetus, and G. deflectus) are univoltine and lay eggs during the spring or early summer. Physa and G. parvus appear to be bivoltine, with their first generations appearing in the spring and their second generations appearing in the early fall (see also Brown 1979). Unlike the other species, Helisoma is iteroparous and

can survive after it reproduces in the spring. These patterns will be explored in more detail in the following sections.

## Methods

Natural patterns of population dynamics were assessed at one site in Palmatier Lake that was approximately 190 $m^2$ in area and extended from the shore to a depth of 3.5m where the littoral vegetation ended. This site was monitored as part of the field experiment (see below) and therefore much of the sampling protocol was developed specifically for that aspect of the study. Snails were sampled on thirteen dates between 20 July 1984 and 29 September 1985. To collect a sample, I carefully created an opening in the Chara mat, which rests loosely atop the sediments, and inserted a 20.3 cm diameter brass sieve (mesh = 0.5 mm) under an undisturbed part of the Chara. I pushed a stove pipe (with the same diameter) down onto the sieve, thus collecting a 0.0324 $m^2$ core of vegetation. Eight cores were collected and pooled from the site on each collection date. On the final sampling date, 29 September 1985, two samples (eight cores each) were collected. The vegetation from each sample was rinsed to remove snails, and the remaining debris was concentrated through a 0.5mm sieve and preserved in 10% buffered formalin. Snails were later picked from the debris, identified to species, counted and measured (all snails up to a maximum of approximately 300 per species per sample were measured). Linear measurements of snail size were converted to tissue dry mass using length-mass regressions. H. anceps and H. campanulata were very rare, and since they exhibit similar morphologies and life histories, they were combined into a single Helisoma category.

In addition to providing information on the size-distributions of each species through time, the data were also used to estimate mortality rates of juvenile snails of each taxa under natural conditions during 1984 and 1985. I followed the density of each new cohort through time beginning with their first appearance in the samples until the last sample of each year. Initial densities were not defined until snails had grown enough to be reliably sampled (i.e. retained on the 0.5mm sieve). For Physa and G. parvus, I stopped each analysis approximately 3 weeks before the second generation of newborns appeared in order to isolate the effect of juvenile mortality from reproduction-associated mortality of adults. In addition, cohorts for Physa and G. parvus were difficult to define due to the broad and unclear size-frequency distributions. In 1984, the first cohort could be followed for each species, but in 1985 G. parvus did not produce a clearly defined pulse of young. The other seven taxa exhibited clear patterns of reproduction and growth. Mortality rates for each cohort were estimated as the slope in the regression of the logarithm of density on time.

The combined effects of mortality and natality determine population dynamics. To assess the role of natality, I obtained information on patterns of size-specific reproduction from field experiments in which a known number of snails of a specific size and species (either Helisoma, Physa, V. tricarinata, or A. limosa) were placed into glass jars (0.95 L) fit with small mesh lids. Included with the snails was approximately 10g (wet mass) of Chara that was free of snail eggs. At approximately weekly intervals, the number of eggs and surviving snails were counted, the old Chara, dead snails and eggs were removed, and fresh Chara was placed into each jar. These experiments were conducted during the spring and/or early summer when the snails were reproducing. The majority of data came from trials conducted in Palmatier Lake, where the

jars were laid within the Chara (so that water quality, light and temperature were similar to natural conditions). For each jar, I calculated the number of eggs produced per snail-day (the sum of snail density over all days of the experiment).

## Results

All snail species underwent cycles in mean individual snail mass during the study (Figure 1). These patterns were similar to those I have observed in other lakes (Osenberg, personal observation) and represent the natural cycle of growth and reproduction for these predominantly semelparous species. In general, snails were at their maximum individual masses during the spring, corresponding to a predominance of adults that were beginning to reproduce. Following reproduction in the spring or early summer, mean mass of each species declined as adults died and young hatched out of eggs. The univoltine species then showed clear patterns of growth (and mortality: see below) as these young snails grew dramatically in size. Even Helisoma, which can survive and reproduce during two springs showed a clear cycling due to the relative rarity of adult snails. Two species showed less clearly defined patterns of growth and reproduction, Physa and G. parvus. The changes in the size-distributions for Physa showed that two generations were produced: one in the spring and a second during late August or early September. Detailed inspection of size-frequency distributions showed that the adult snails died following both periods of reproduction. G. parvus showed the most ambiguous patterns due, in part, to its small size which made it difficult to distinguish adult and young snails. Based on these data as well as patterns from other similar lakes, it appears that G. parvus also goes through two generations per

Figure 1. Seasonal patterns in mean individual body mass of snails in Palmatier Lake. The scales for all species except Helisoma are the same: the scale for Helisoma is given on the inside of the axis on the lower panel. The means are based on the entire populations that were sampled and therefore sometimes include adults as well as young snails. Thus, the cycles denote changes in mean mass for the population and not for particular cohorts.

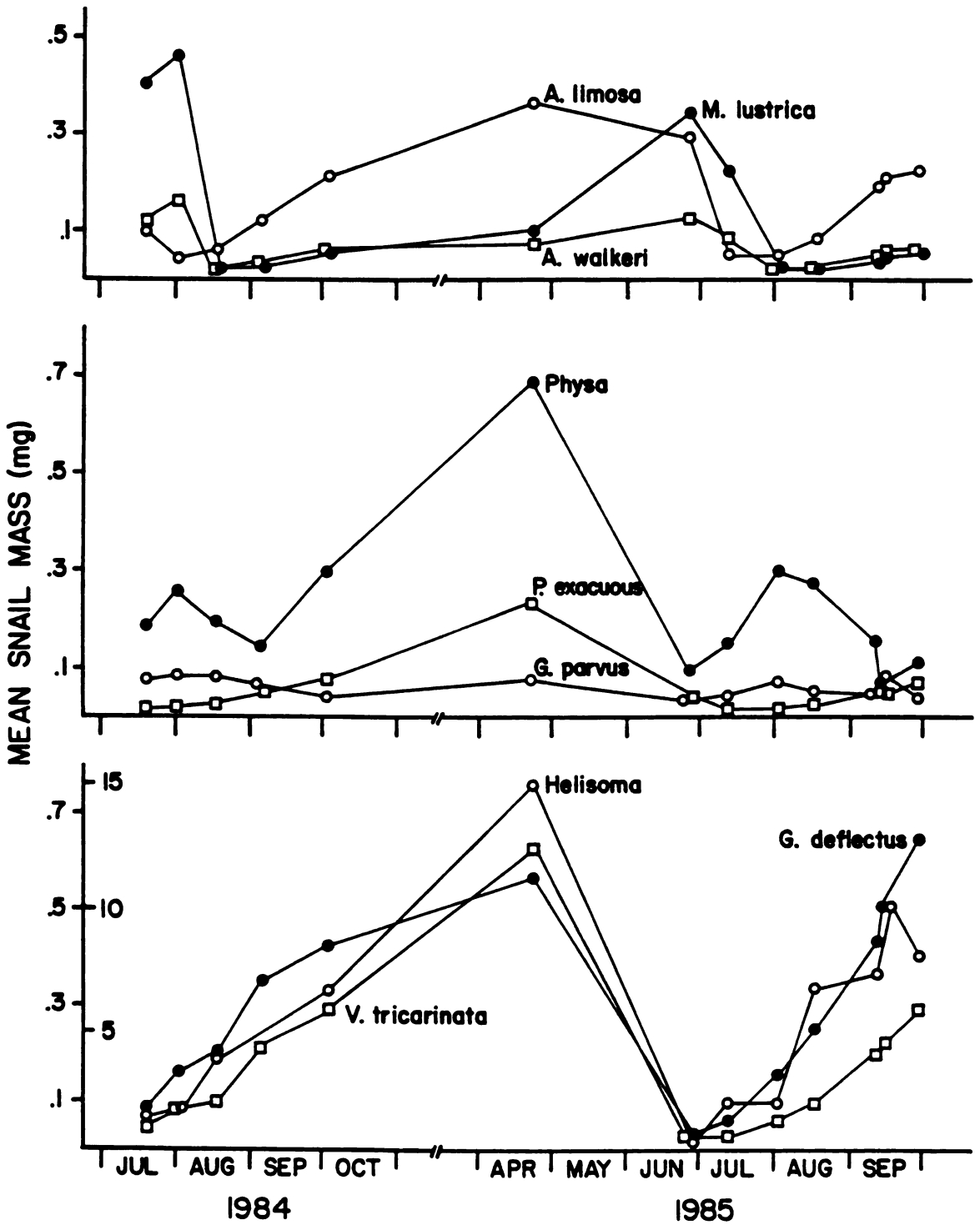
MEAN SNAIL MASS (mg)
.5
.3
.1
A. limosa
M. lustrica
A. walkeri
.7
.5
.3
.1
Physa
P. exacuous
G. parvus
15
.7
10
.5
.3
5
.1
Helisoma
G. deflectus
V. tricarinata
JUL
AUG
SEP
OCT
APR
MAY
JUN
JUL
AUG
SEP
1984
1985

Figure 1

year. In later sections I show that these temporal dynamics in snail size have consequences for predator-mediated mortality, and that the differences in snail mass among species influences the species-specific effects of predation by pumpkinseed sunfish.

During periods of juvenile growth in 1984 and 1985, all cohorts decreased in density (Table 1). In addition, the mortality rates estimated during 1984 were significantly correlated with the mortality rates estimated from the 1985 data ($r=0.87$, $n=8$, $p<0.01$), suggesting that patterns of mortality were a repeatable feature of the snail community. Helisoma and Physa, the two largest snails in the community, incurred mortality rates that were 2-7 times greater than those for the other species. A. walkeri and Promenetus incurred the lowest mortality rates and they are two of the smallest species in the community (Table 1). Since mortality analyses were not initiated until the snails had grown large enough to be reliably sampled, these estimates do not include mortality that occurred during the egg or early juvenile stages.

These data suggest that mortality rates were greatest on the larger bodied taxa. The data on egg production suggests that these same species also had the greatest fecundities. Daily egg production increased with adult mass (Figure 2), although there appeared to be a threshold for A. limosa and V. tricarinata below which no eggs were produced (i.e. 0.4 mg). Using the data obtained from adults with mass >0.4 mg showed that snail species did not differ in their relationships between egg production rate and mass, although there was little overlap in the size-distributions of species used in the experiments (analysis of covariance of log-log transformed data: equal slopes, $F_{3,55}=1.61$, $p=0.2$; equal intercepts, $F_{3,58}=1.30$, $p>0.2$; effect of mass, $F_{1,58}=38.93$, $p<0.0001$). This analysis suggests that larger snails (independent of species identity) produce a greater number of eggs per unit time. I

Table 1. Patterns of natural mortality and egg production. Natural mortality is expressed as a per capita daily rate. Mortality rates could not be estimated in 1985 for G. parvus. Mean adult masses (mg/snail) and estimated per capita daily egg productions (eggs/snail/day) are given. Relative fecundity was obtained as the ratio of the per capita daily egg production and generation time (see text). In this and subsequent tables, snail taxa are ordered by decreasing adult mass.

| Snail Taxa | Natural Morality $\times 10^{-3}$ | | | Mean Adult Mass | Per Capita Production | Relative Fecundity |
|---|---|---|---|---|---|---|
| | 1984 | 1985 | Mean | | | |
| Helisoma | 35.44 | 46.93 | 41.19 | 11.51 | 5.06 | 3.37 |
| Physa | 43.01 | 57.82 | 50.41 | 2.03 | 1.34 | 2.68 |
| G. deflectus | 21.07 | 18.67 | 19.87 | 0.64 | 0.55 | 0.55 |
| A. limosa | 17.75 | 13.03 | 15.40 | 0.62 | 0.54 | 0.54 |
| V. tricarinata | 14.32 | 11.88 | 13.10 | 0.62 | 0.53 | 0.53 |
| M. lustrica | 26.43 | 8.98 | 17.71 | 0.40 | 0.38 | 0.38 |
| P. exacuous | 7.74 | 10.15 | 8.93 | 0.24 | 0.25 | 0.25 |
| G. parvus | 19.69 | --- | 19.69 | 0.12 | 0.16 | 0.32 |
| A. walkeri | 4.84 | 9.69 | 7.28 | 0.12 | 0.15 | 0.15 |

Figure 2. Daily per capita egg production as a function of snail mass. The regression line ($Y=0.79X^{0.77}$) was obtained from the log-log regression using data from snails with mass >0.4 mg.

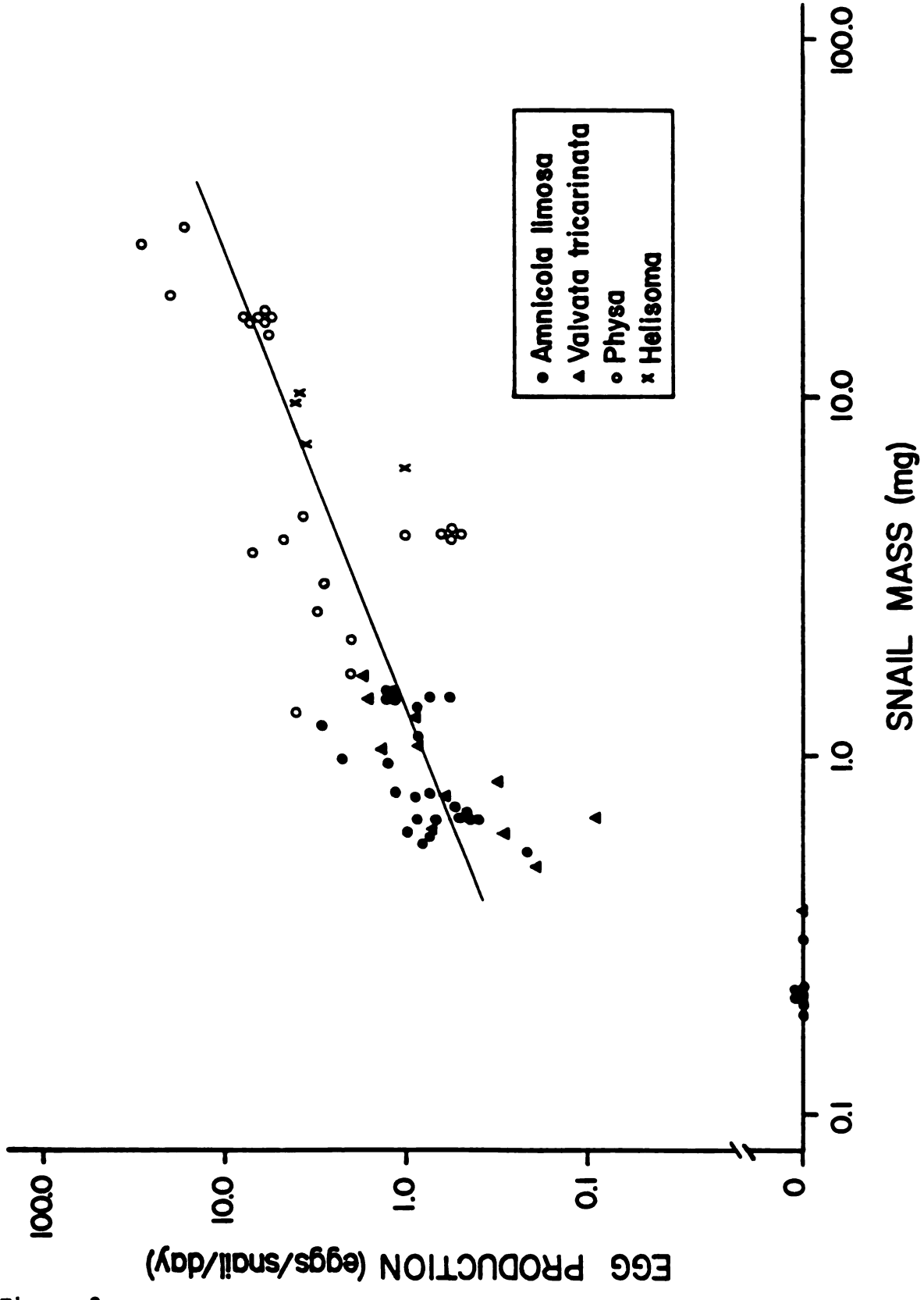
EGG PRODUCTION (eggs/snail/day)
100.0
10.0
1.0
0.1
0
0.1
1.0
10.0
100.0
SNAIL MASS (mg)
• Amnicola limosa
▲ Valvata tricarinata
○ Physa
× Helisoma

Figure 2

used the egg production-mass relationship ($E=0.79M^{0.77}$) to calculate average daily egg productions for adult snails of each species (adult size-distributions were defined from the size-frequency data collected on dates just prior to the appearance of newborns) (Table 1). In order to compare these measures of egg production with the observed patterns of mortality, I adjusted them for the amount of time that snails must survive before reproduction (i.e. their average age at reproduction), by dividing each average adult daily egg production rate by the generation time for that species (i.e. 1.5 years for Helisoma, 0.5 years for Physa and G. parvus, and 1.0 for the other taxa). I assume that all species lay eggs for approximately the same number of days and that I can use this index as an estimate of relative total egg production by a species. This index of relative per capita fecundity is highly correlated with the observed per capita daily mortality rates ($r=0.92$, $n=9$, $p<0.001$, Table 1), suggesting that differences among species in birth rates compensated for differences in mortality rates incurred by the snails. In particular, Helisoma and Physa, which incurred the greatest mortalities, also had the greatest relative fecundities.

The compensation observed in mortality and birth rates suggests that the relative abundances of species should be relatively constant from year to year: e.g. no species should be dramatically increasing in relative abundance as would have been indicated by a species with disproportionately low mortality rates and high birth rates. Of course it is difficult to make comparisons among different years due to the extreme seasonal dynamics that occur within years, but comparison of relative abundances on 3 October 1984 and 29 September 1985 suggest that the snail community was not undergoing dramatic alterations in relative abundances (Figure 3). Indeed, birth rates and death rates were

Figure 3. Relative abundance of each snail taxa during the final sampling dates in 1984 and 1985. Data are from two sites in Palmatier Lake. One of the sites was the one monitored during 1984 and 1985. The other site was sampled only on these two dates and will be explained in the section of the field experiment (see text). The mean and range are shown. Species are ordered in decreasing relative abundance. Al=A. limosa, Aw=A. walkeri, Gd=G. deflectus, Gp=G. parvus, He=Helisoma, Ml=M. lustrica, Pe=P. exacuous, Ph=Physa, Vt=V. tricarinata.

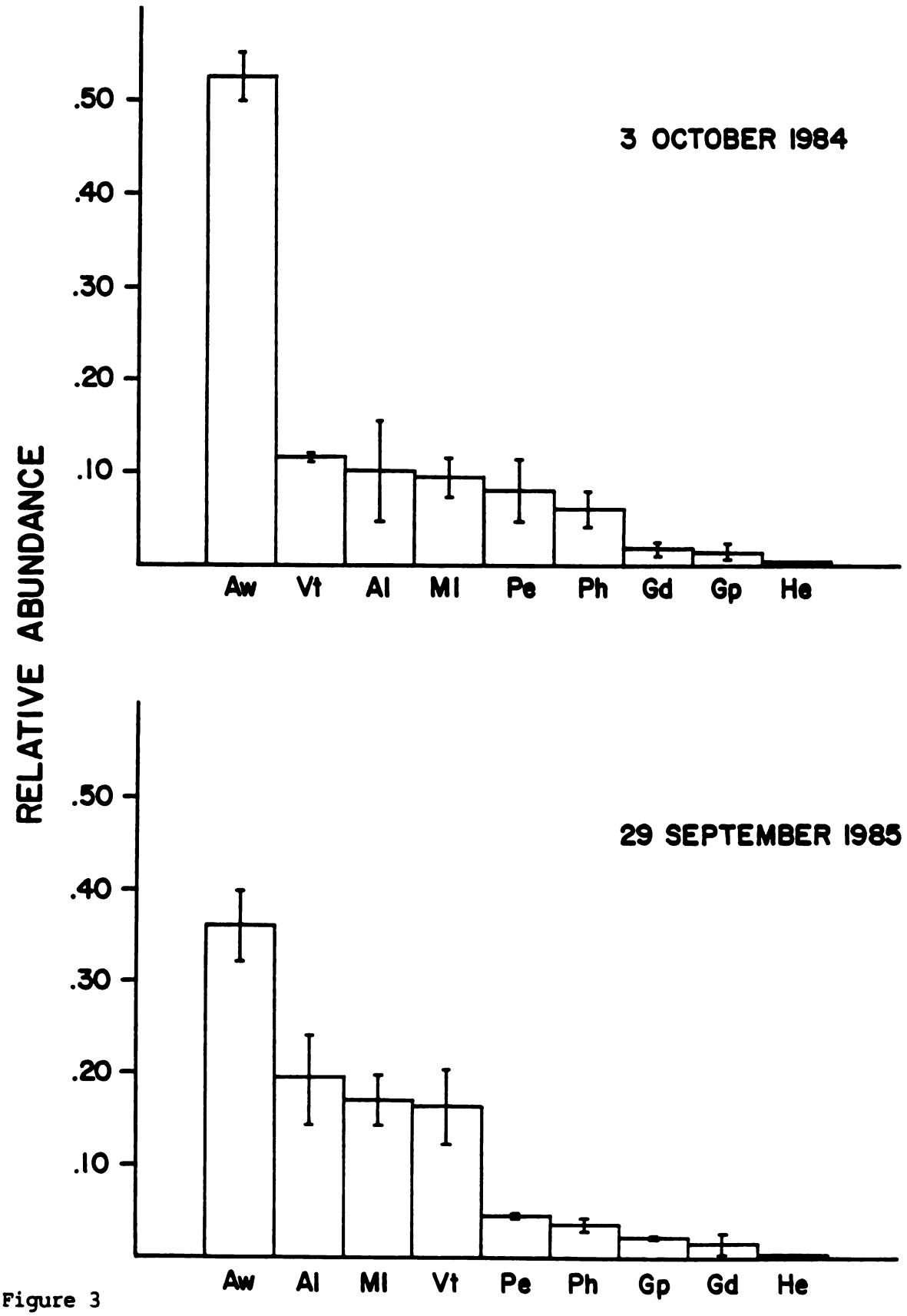
RELATIVE ABUNDANCE
.50
.40
.30
.20
.10
3 OCTOBER 1984
Aw
Vt
Al
Ml
Pe
Ph
Gd
Gp
He
.50
.40
.30
.20
.10
29 SEPTEMBER 1985
Aw
Al
Ml
Vt
Pe
Ph
Gp
Gd
He

Figure 3

relatively balanced and led to similar species compositions in the snail community from one year to the next.

## FIELD EXPERIMENT

### Methods

In this section, I test the hypothesis that pumpkinseed sunfish contributed to the observed mortality rates on the snail populations by conducting a field experiment in which I manipulated the densities of pumpkinseeds. In particular, I document statistical effects of pumpkinseeds on the densities of snails. In a subsequent section, I explore, with the aid of a foraging model developed for the pumpkinseed-snail system, the differential effects that pumpkinseeds had on different snail species, and I show how these effects depended on snail size.

I tested for the effects of pumpkinseeds on the snail community by conducting a large enclosure/exclosure experiment in Palmatier Lake. Each "cage" measured approximately 12 m x 21 m, and was made of nylon netting (1.27 cm mesh) that extended vertically from the lake sediments to the lake surface, where it was strung with bouyant rope and floats. Each enclosure extended perpendicularly from the shoreline of the lake out past the deepest edge of the Chara to a depth of 5.0-5.5 m. Approximately 190 $m^2$ of the total 250 $m^2$/enclosure consisted of littoral vegetation, owing to the inclusion of 60 $m^2$ of deeper profundal sediments. Four enclosures were installed on one shore of Palmatier Lake. Due to their large size, enclosures were constructed parallel to each other with each enclosure sharing one or two sides with adjacent enclosures.

The experimental treatments consisted of removing pumpkinseeds from two of the four enclosed sites, while maintaining all other fish species at their natural densities. In the other two sites, all fish species, including pumpkinseeds, were maintained at their natural densities. Thus, the design isolated the effects of pumpkinseeds, without introducing possible indirect effects that might have resulted from removal of the entire fish community (e.g. removal of bluegills might have caused an increase in the densities of other invertebrate grazers that might compete with snails). In addition, two sites to the east and west of the caged areas were mapped out and sampled to assess pumpkinseed and snail densities under under natural conditions (the east site corresponds to the site where I followed the natural dynamics of the snail community—see previous section).

Installation of the cages began on 22 June 1984 and the treatments were imposed on 2 July. On 2 October, the floats were removed and the netting was sunk to avoid destruction from ice during the winter. The net was raised and scrubbed clean from 19-23 May 1985, although because of recurring damage to the nets, treatments were not successfully reimposed until 16 June. I maintained the same treatment at each site during the two phases of the experiment. The experiment was concluded on 29 September 1985.

I estimated pumpkinseed densities in each of the six sites (in the four cages and at the two adjacent lake sites) by swimming for five minutes on scuba in the deeper parts of each site and counting all the fish that I encountered. Fish densities in the shallower areas were similarly estimated by snorkeling for five minutes. The counts from the shallow and deep areas of a site were summed and translated into absolute numbers of fish per site by the following method. Between 21 and 23 May 1985, I swam transects in the enclosed sites that had been

cleaned and repaired. Following these transects I counted and removed all pumpkinseeds that occurred in each site. After ensuring that all of the pumpkinseeds had been removed, I returned a known number of pumpkinseeds to each site and then swam additional transects. Transect counts and absolute densities were highly correlated and the data were fit quite well with a power function ($r=0.98$, $n=10$, number/site = 1.81 x (number counted)$^{0.85}$, exponent different from 1.00 at $p<0.05$). This equation was used to translate all pumpkinseed counts into density estimates (number/site). Fish were counted on four dates during 1984 and on eight dates during 1985 while the nets were raised. Pumpkinseeds were also counted on 15 May 1985 before the net was refloated.

Snails were sampled in the same manner as discussed in the preceding section. One sample (consisting of eight pooled vegetation cores) was collected per site on 3 October 1984. On 29 September 1985, two samples were collected per site. Thus, these data provided two snapshots of the snail community at each site near the end of the primary growth stanza for juvenile snails. Due to the large size of the enclosures, I assumed that snail migration was negligible among the sites and that adjacent sites did not influence one another.

Treatment effects were generally analyzed by analysis of variance with orthogonal contrasts (SAS Institute, Inc. 1985: PROC GLM). Contrasts included the comparison of the control treatment versus the lake treatment, and the pumpkinseed exclusion treatment versus the combined response of the control and lake treatments (which had pumpkinseed densities at their natural levels). As I show below, statistical tests of treatment effects on a species by species basis were generally insignificant (due, in part, to low replication ($n=2$) and high variation among replicate sites). Therefore, I used principal components analysis to conduct a more powerful test of the effect of

pumpkinseeds on the entire snail community. Details of this analysis are given along with the results.

## Results

Manipulations of pumpkinseed densities successfully achieved the desired treatment levels (Figure 4). Orthogonal contrasts show that the density of pumpkinseed sunfish was significantly reduced in the exclusion sites compared to the densities in the other sites (testing the combined 1984 and 1985 densities in the exclusion treatment against the combined densities in the control and lake treatments: $F_{1,6}=91.2$, $p<0.0001$), while there was no difference between the densities in the control and lake sites ($F_{1,6}=0.26$, $p>0.60$). There were also no differences between 1984 and 1985 in the control or lake treatments ($p>0.5$ for both cases), but the densities in the exclusion sites were greater during 1985 than during 1985 ($F_{1,6}=6.98$, $p<.05$). Thus, the natural densities of pumpkinseeds were stable across years, the control sites mimicked the lake sites well, and the densities in the exclusion sites were reduced, albeit to varying degrees in the two years.

Snail densities (and biomasses) of all nine species tended to increase in the absence of pumpkinseeds (Table 2), although Anova did not reveal many significant effects. In particular, orthogonal contrasts showed that of the 18 tests (nine taxa in two years) comparing snail densities in the control sites with densities in the lake sites, only one was significant (at $p<.05$), suggesting the absence of an "enclosure effect" (see also below). Therefore, the snail densities from the lake and control sites were combined for presentation in Table 2. However, there were also very few differences in snail densities between sites with low densities of pumpkinseeds and sites with natural

Figure 4. Pumpkinseed densities in the three treatments during 1984 and 1985 while the treatments were being imposed. The mean and range for the means of the two replicates are given (the mean for each site is based on n=4 in 1984 and n=8 in 1985). LAK=lake sites, CON=control sites, EXC=pumpkinseed exclusion sites.

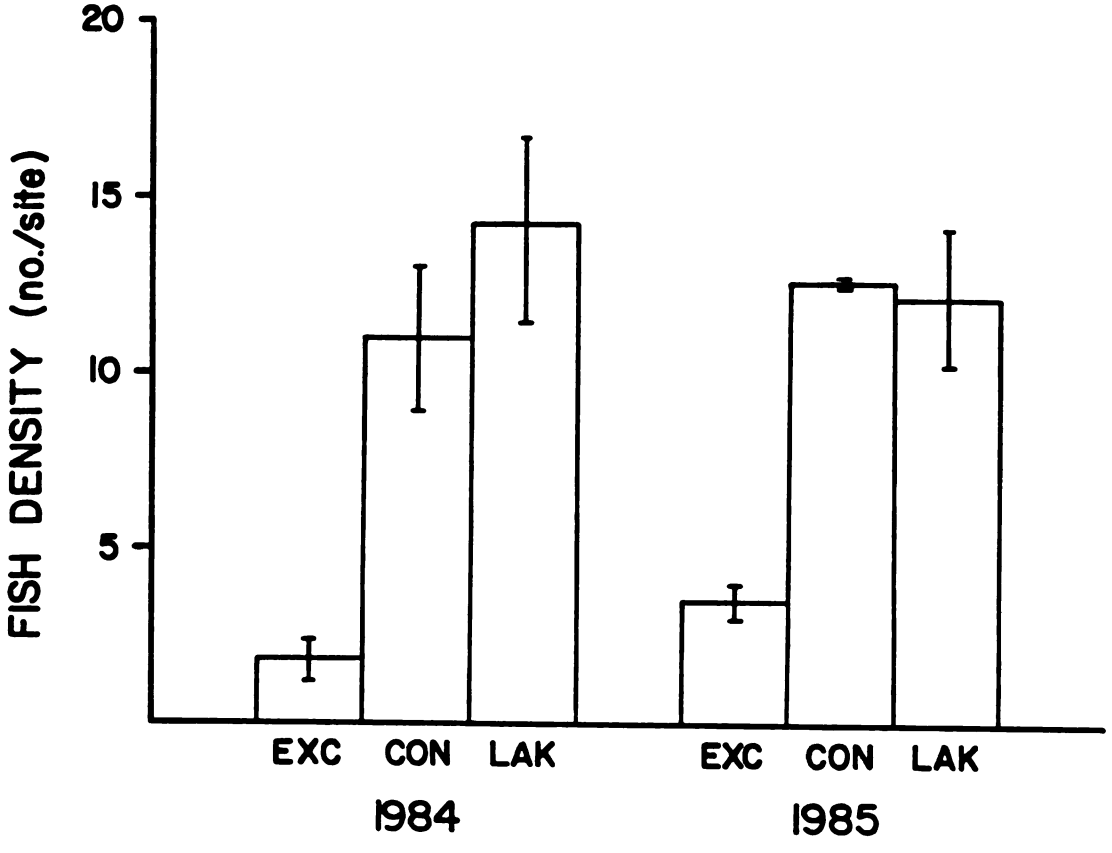
FISH DENSITY (no./site)
20
15
10
5
EXC
CON
LAK
1984
EXC
CON
LAK
1985

Figure 4

Table 2. Snail densities in Palmatier Lake on 3 October 1984 and 29 September 1985 in sites with natural pumpkinseed densities (n=4) and in sites with reduced pumpkinseeds densities (n=2). Means and ranges are given and densities are expressed as number/$m^2$. Densities in the control and lake sites were combined into a single category for presentation. An asterisk between the two fish density columns indicates that the orthogonal contrast of the sites with reduced pumpkinseed densities differed significantly ($p<0.05$)from the sites with natural densities. An asterisk following the second column indicates a significant difference between the two treatments with natural densities of pumpkinseeds.

| | 1984 | | | 1985 | | |
|---|---|---|---|---|---|---|
| Snail taxa | Reduced | Natural | | Reduced | | Natural |
| Helisoma | 13<br>7-19 | 6<br>0-12 | | 10<br>6-14 | | 7<br>4-12 |
| Physa | 496<br>459-532 | 299<br>216-382 | | 406<br>380-432 | | 322<br>243-388 |
| G. deflectus | 231<br>177-285 | 87<br>54-116 | | 214<br>204-224 | | 99<br>17-189 |
| A. limosa | 615<br>509-721 | 610<br>228-938 | | 1534<br>1427-1638 | | 1809<br>1063-3007 |
| V. tricarinata | 594<br>540-648 | 745<br>444-1262 | | 700<br>602-799 | * | 1169 *<br>764-1512 |
| M. lustrica | 926<br>899-953 | 637<br>347-926 | | 2157<br>1809-2504 | | 1663<br>1439-1792 |
| P. exacuous | 478<br>478-478 | 443<br>278-629 | | 616<br>529-704 | | 546<br>322-745 |
| G. parvus | 150<br>116-185 | 132<br>23-235 | | 484<br>411-557 | * | 225<br>174-264 |
| A. walkeri | 4008<br>3665-4352 | 3230<br>2681-3993 | | 4208<br>4028-4389 | | 3745<br>2386-5033 |

densities. Only 2/18 comparisons were significant, and one of these showed a negative reponse to the removal of pumpkinseeds (V. tricarinata, Table 2). Similar results were obtained using biomass ($mg/m^2$) rather than density.

Due to the lack of power in the previous analyses, I used principal components analysis to conduct a more sensitive test in which the responses of all the snail species were combined into a simple metric that provided a good description of the entire variation in the snail community and could be analyzed with univariate Anova. Two principal component analyses were performed (one for each of the two data sets, 3 October 1984 and 29 September 1985) using the snail density and total biomass for each species in each site (a total of 18 variables in each of the two analyses). The data were submitted to two separate principal components analyses (SAS Inst Inc. 1985: PROC FACTOR), from which all five principal components were obtained for each of the two datasets. The first two components accounted for over 70% of the variation in each year's data, while additional components each explained less than 16% of the variation. Therefore, I restricted further analyses to the first two components and determined the scores for each site on these two components. These scores are the new variables that represent how the six sites were ordered in multivariate space with respect to the observed variation in the snail community. Assuming that responses of snail species were monotonic over the snail gradient, then the scores from only one of the principal components should be related to the experimental treatments. Theoretically, at the start of the experiment, none of the variation in the snail community should be attributable to the pumpkinseed treatments, and the principal component scores should represent other (i.e. unknown) factors that created spatial variation in the snail community. However, as the experiment progressed, an

increasing amount of variation (i.e. one of the principal components) should have become associated with the variation in pumpkinseed density.

I initially analyzed the scores on the first two principal components (for each years' data) by performing separate analyses of variance with orthogonal contrasts. Thus four analyses were performed (two contrasts each) using the scores from 1984 on PC1 and PC2 and the scores from 1985 on PC1 and PC2 (recall that PC1 and PC2 in 1984 and PC1 and PC2 in 1985 are not the same principal components since each years' data were analysed separately). In no case were there differences in the principal component scores in the contrast of the lake sites against the control sites ($F_{1,5}<3.25$, $p>0.15$ for all four tests), indicating the absence of an "enclosure effect". Contrasts comparing the response of the exclusion sites with the sites with natural pumpkinseed densities showed significant differences in their scores on PC2 during 1984 ($F_{1,5}=28.90$, $p<0.05$) and on PC1 during 1985 ($F_{1,5}=13.63$, $p<0.05$), but not on PC1 during 1984 or on PC2 during 1985 ($F_{1,5}<1.00$, $p>0.50$ in each test). The absence of an "enclosure effect" and presence of a "pumpkinseed effect" suggests that the data can be examined simply with respect to the density of pumpkinseeds. In 1984, a site's score on the first principal component (PC1) was not correlated with the pumpkinseed density at the site (averaged over all preceeding dates) ($r=0.13$, $n=6$, $p>0.50$), while the score on the second principal component (PC2) was significantly correlated with pumpkinseed density ($r=-0.97$, $n=6$, $p<0.01$) (Figure 5a). In the analysis for 1985, the scoring on PC1 was correlated with pumpkinseed density ($r=-0.83$, $n=6$, $p<0.05$), while the scoring on PC2 was not ($r=0.41$, $n=6$, $p=0.40$) (Figure 5b). These analyses indicate that the snail community was not influenced by the enclosure method, but that the snail community did respond significantly to variation in pumpkinseed densities. Importantly, for each year only

Figure 5. Relationship between scores on principal components and pumpkinseed densities. a) Scores for each of the six sites on the second principal component for the 3 October 1984 snail data. b) Scores for each of the six sites on the first principal component for the 29 September 1985 snail data. Fish densities are the means from all dates prior to the collection of the snail data. ● = pumpkinseed exclusion, O = control, □ = lake.

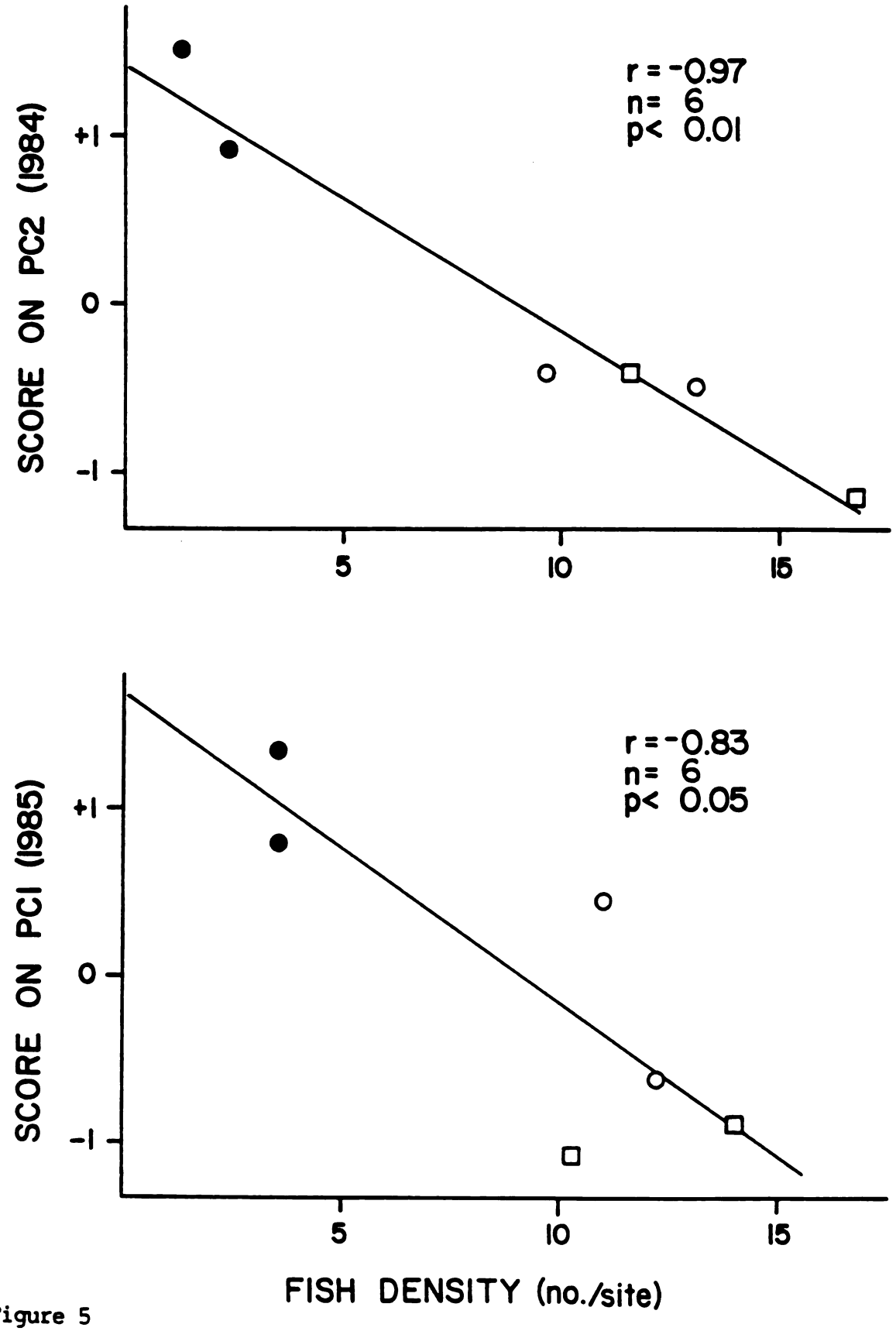
r = -0.97
n= 6
p< 0.01
SCORE ON PC2 (1984)
+1
0
-1
5
10
15
r = -0.83
n= 6
p< 0.05
SCORE ON PC1 (1985)
+1
0
-1
5
10
15
FISH DENSITY (no./site)

Figure 5

one of the two primary descriptions of the variation in the snail community (i.e. the principal components) was associated with the experimental treatments. The other principal components presumably represent additional (i.e. unknown) factors that produced site-to-site variation in the snail community. Thus, the pumpkinseed removal produced significant changes in the snail community, and as the experiment progressed, the amount of variation in the snail community that could be attributed to the pumpkinseed gradient increased from 33% (the variation explained by PC2 in 1984) to 42% (the variation explained by PC1 in 1985) (Table 3).

Although the principal components analysis demonstrates that the exclusion of pumpkinseeds had a significant effect on the snail community, it does not indicate how each species was affected by the experiment. One way to assess this is to examine the correlations of the original density and biomass variables with the principal components (Table 3; see also Table 2). As expected, density and biomass for each species gave very similar patterns, and most species exhibited positive correlations with the principal components (Table 3), suggesting that the principal components represented simple overall measures of snail abundance: i.e. snail abundance of most species increased in response to the removal of pumpkinseeds. The few negative correlations were generally small and mostly associated with A. limosa and Valvata, suggesting that they might have been affected favorably by the presence of pumpkinseeds (see also Table 2).

An additional and compelling line of evidence suggesting that pumpkinseeds significantly influenced the snail community came from observations of site selection by pumpkinseeds. On 15 May 1985, before the nets were refloated, I conducted fish transects in the six sites. These density estimates represent preferences for sites by the

Table 3. Results of principal components analyses on snail densities and biomasses sampled on 3 October 1984 and 29 September 1985 at six experimental sites in Palmatier Lake. See text (and Figure 5) for additional information.

Percent Variance Explained:

| | 1984 | 1985 |
|---|---|---|
| Principal Component 1 | 39.5 | 41.6 |
| Principal Component 2 | 32.9 | 30.9 |
| Total | 72.4 | 72.5 |

Scores On The First Two Principal Components From Each Year:

| | 1984 | | 1985 | |
|---|---|---|---|---|
| Treatment | PC1 | PC2 | PC1 | PC2 |
| Lake | 0.41 | -1.14 | -0.89 | 1.46 |
| Lake | -1.34 | -0.40 | -1.08 | -1.58 |
| Control | 1.51 | -0.50 | -0.63 | 0.14 |
| Control | -0.82 | -0.40 | 0.46 | 0.46 |
| Exclusion | 0.00 | 0.91 | 0.79 | -0.20 |
| Exclusion | 0.23 | 1.52 | 1.35 | -0.28 |

Correlation Between Variables and Important Principal Components:

| | 1984: PC2 | 1985: PC1 |
|---|---|---|
| Snail taxa | density/biomass | density/biomass |
| Helisoma | +0.70/+0.61 | +0.56/+0.41 |
| Physa | +0.81/+0.86 | +0.80/+0.93 |
| G. deflectus | +0.81/+0.89 | +0.56/+0.38 |
| A. limosa | -0.24/-0.28 | -0.36/-0.38 |
| V. tricarinata | -0.24/-0.08 | -0.84/-0.72 |
| M. lustrica | +0.52/+0.57 | +0.78/+0.71 |
| P. exacuous | +0.33/+0.27 | +0.69/+0.47 |
| G. parvus | +0.17/-0.25 | +0.87/+0.90 |
| A. walkeri | +0.72/+0.79 | +0.39/+0.00 |

Figure 6. Habitat selection by pumpkinseeds on 15 May 1985 in relationship to the average fish densities that had been confined to each site during 1984. Symbols as in Figure 4.

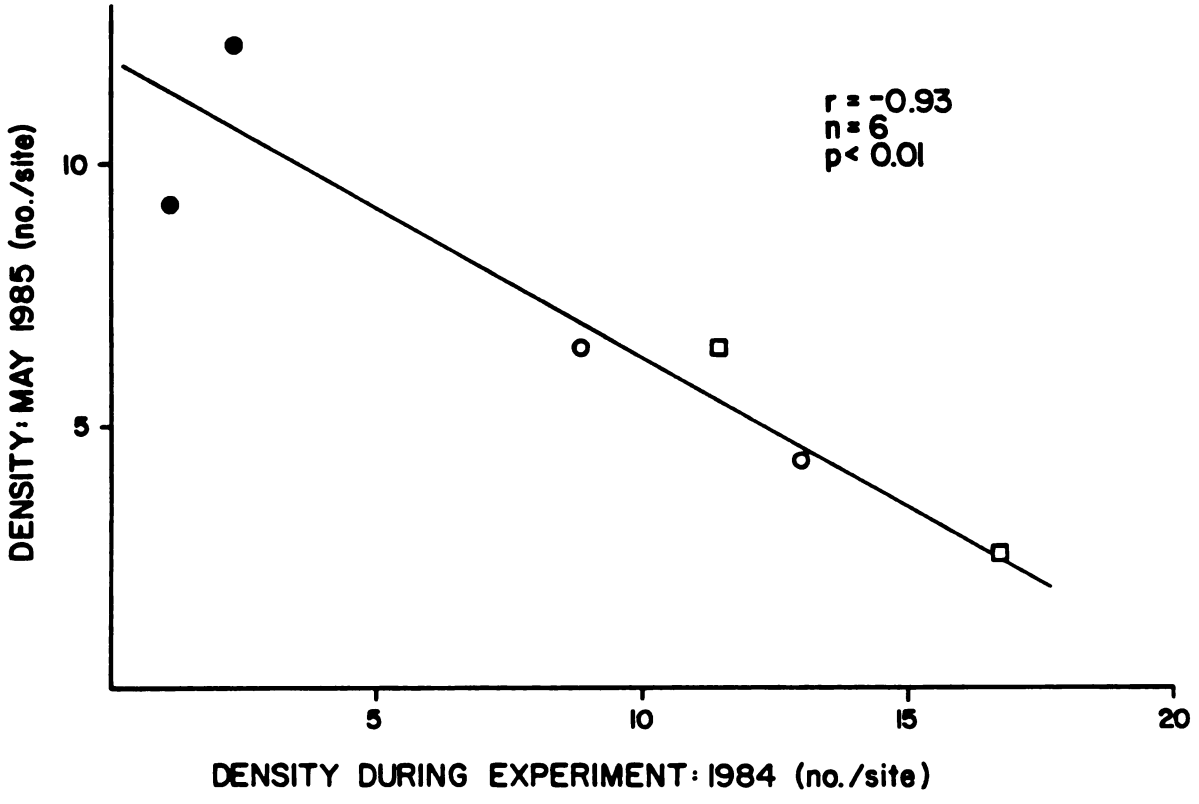
r = -0.93
n = 6
p < 0.01
DENSITY: MAY 1985 (no./site)
10
5
5
10
15
20
DENSITY DURING EXPERIMENT: 1984 (no./site)

Figure 6

pumpkinseeds since the fish were free to feed in any of the six sites. Densities in the sites were negatively correlated with the densities that had been imposed on the sites during the preceding phase of the experiment (Figure 6), suggesting not only that pumpkinseeds had altered their prey community during the previous summer and fall, but that those differences persisted and led to strong site selection by the pumpkinseeds.

The preceding analyses demonstrate that fish density had significant effects on the snail community and that most species increased their abundances following the removal of pumpkinseeds. These analyses however only address the significance of the observed community response and at best provide a qualitative index of the reponse of each snail species to the fish treatments. In the following section I estimate the species-specific effects that fish had on snail populations, and I compare these effects with those predicted from a foraging model previously developed for the pumpkinseed-snail system (Chapter 1).

## PREY RISK AND FISH EFFECTS

### Methods

The best estimate of the effect of fish on the mortality rates of snail populations would be the difference between the mortality rates of snails in the presence and absence of fish. However, I do not have data on the temporal dynamics of snails in each of the six sites, and therefore I cannot directly estimate mortality rates under the experimental treatments. I can however use an indirect approach. I assumed that the snail density at a site after t days could be modeled according to

$$N_t = N_0 e^{-rt} = N_0 e^{-t(uF+m)} \quad (1)$$

where $N_0$ is the snail density at the start of the study, r is the per capita mortality rate, t is the duration of the study, u is the per fish mortality rate imposed on the snails, F is the fish density (number/site), and m is the effect of all other factors that contributed to the mortality rate (e.g. other predators or food limitation). Throughout the paper I define mortality rates as positive values (thus the use of the negative sign in equation 1). Additional terms for birth rates and migration could be incorporated into equation 1, but because I focus primarily on periods of juvenile growth (see below) and because the enclosures were very large, the influence of birth and migration rates should be negligible (see below for a further qualification). In addition, I assume that the per capita effects of different mortality agents are additive and that uF represents the direct effect of pumpkinseeds on snails: i.e. I assume that indirect effects are negligable. However, if pumpkinseeds reduced snail densities, which increased resources and therefore reduced starvation rates, then uF would include the direct effect of fish (the consumption of snails) as well as the indirect effect of fish (mediated through the increase in resources).

Application of equation 1 requires that several other conditions be satisfied. First, $N_0$ must be estimated from each site, or assumed to be equal among sites. Second, among sites, the gradient in F must be maintained during the entire time period. The first phase of the experiment (between 2 July 1984 and 3 October 1984) best satisfied these requirements: F was reliably maintained among sites (Figure 4) and $N_0$, although not sampled (and certainly not equal) was at least random with respect to the assigned fish treatments. In addition, indirect effects

were likely to be least important early in the experiment and therefore uF and m were most likely to be independent during the first phase of the experiment. Thus I used the snail densities on 3 October 1984 as estimates of $N_t$, and I estimated the effects of fish, u, by regressing $\ln(N_t)$ on fish density, F. The slope of this regression provides an estimate of -ut, which when divided by -t (i.e. -93 days), yields the effect of one fish/site on the per capita daily mortality rate of the snails, u. Because Physa and G. parvus reproduced between the start of the experiment and the October sample, use of this approach for these two species requires the additional assumption that per capita birth rates were independent of fish densities. Since mean snail size, which is a good predictor of individual fecundity (Figure 2), was not related to pumpkinseed density (see below), this assumption is probably valid.

If fish effects, u, represent direct effects on the mortality rate of snails, then estimates of u should be correlated with the predicted mortality rates derived from the foraging model of the pumpkinseed-snail interaction (Chapter 1). Therefore I used this model to calculate the average risk to predation for each snail species during the 1984 phase of the experiment. Ideally, risk should be based on a series of samples from each site. However, in the absence of such detailed information, I used the data from the east lake site and assumed that these data provided a good relative measure of risk for the snails in each site. I defined risk as the expected per capita mortality rate imposed by a predator (while it was foraging) on a prey population. Using notation from Chapter 1,

$$RISK_i = L_i P_i(a) P_i(s) \;/\; 1 + SUM(D_i L_i P_i(a) H_i) \qquad (2)$$

where $L_i$ is the prey's per capita encounter rate with the predator

(defined at a predator density of 1/site), $P_i(a)$ is the probability that the predator attacks an encountered snail of type i, $P_i(s)$ is the probability that an attacked snail of type i is successfully consumed (i.e. killed), $D_i$ is the density of snails of type i, and $H_i$ is the handling time for snails of type i (which includes time spent on successful as well as unsuccessful attacks). Relative values of LP(a)P(s) determine the prey preferences of a pumpkinseed feeding on several snail types and thus risk and prey preference are directly related (Chesson 1978, 1983; Vanderploeg and Scavia 1979; Chapter 1). A detailed discussion of the pumpkinseed-snail foraging model can be found in Chapter 1, where it was shown that encounter rates (L) increased approximately linearly with snail mass (although because of differences in microhabitat use, encounter rates with large Helisoma (>6mm shell diameter) were assumed equal to 0.00 (Chapter 1)); capture success, P(s), was determined primarily by the relative shell crushing ability of the fish and the relative crushing resistance of the snail shell; and attack probability, P(a), was derived from the predictions of optimal foraging theory. In general, risk for each species was a hump-shaped function of snail size due predominantly to the opposing effects of encounter rates and size refuges. Theoretically, risk (equation 2) and u (equation 1) should be directly proportional, differing only by a factor representing the amount of time per day spent foraging by a fish.

The risk of any particular snail depends on the size of the predator because shell crushing ability increases with fish size. In order to keep the analyses simple, I report risk estimated for only one size of pumpkinseed (100 mm SL); using other sizes yielded relatively similar results. Pumpkinseeds collected in Palmatier Lake were primarily between 90 and 130 mm SL (Figure 7). The rarity of fish <40 mm SL is

Figure 7. Size-frequency distribution of pumpkinseeds collected in Palmatier Lake during 1984 and 1985.

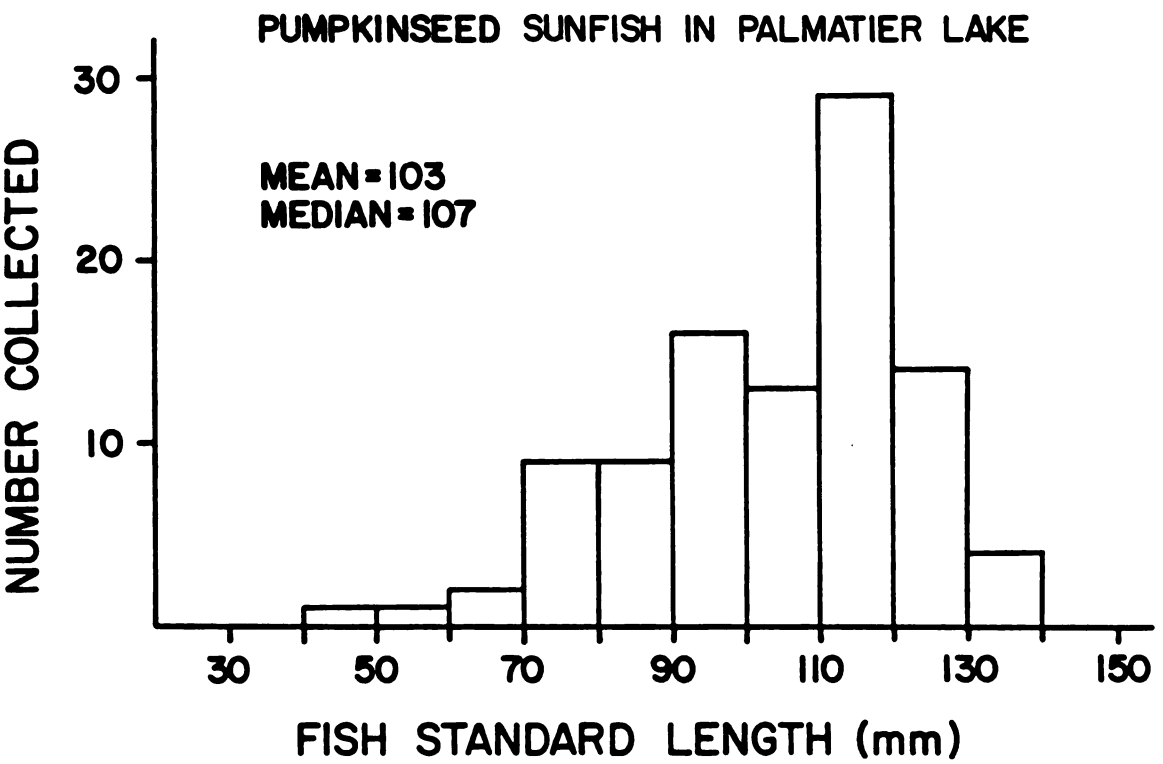
PUMPKINSEED SUNFISH IN PALMATIER LAKE
MEAN=103
MEDIAN=107
NUMBER COLLECTED
30
20
10
30
50
70
90
110
130
150
FISH STANDARD LENGTH (mm)

Figure 7

probably due to a sampling bias as well as the rapid growth of small fish (Osenberg et al. 1988). These small fish however, do not feed on snails (Mittelbach 1984); therefore, 100mm SL appears to be a relatively good single description of the portion of the pumpkinseed population that feeds on snails.

## Results and Discussion

Regressions of ln(snail density) on pumpkinseed density provided estimates of the effect of fish on snail mortality rates (u), and suggested that Helisoma, Physa and G. deflectus were most affected by fish predation, while other taxa were less affected (Table 4). The mean risk of snails during the period from 2 July-3 October 1984 showed patterns that were very similar to the observed fish effects: i.e. the three species at greatest risk were the same three that exhibited the greatest declines across the fish gradient (Table 4). In fact, the observed fish effects and the predicted snail responses were significantly correlated, as expected ($r=0.61$, $n=9$, $p_{1\text{-tail}}<0.05$).

If the densities of the three species that were most at risk (Helisoma, Physa, and G. deflectus) are summed, and the densities for the other species are summed, then we can compare the response of these two classes of snails to the fish gradient. The density of the three species that incurred highest risk were significantly negatively affected over the pumpkinseed gradient ($r=-0.81$, $n=6$, $p=0.05$), while the density of the species that were relatively safe from pumpkinseed predation did not show a significant decline ($r=-0.47$, $n=6$, $p>0.10$). Indeed, the total density of snails was not significantly correlated with fish density ($r=-0.59$, $n=6$, $p>0.10$), nor was the total biomass of snails ($r=-0.56$, $n=6$, $p>0.10$). The reason for this seems to be that the

Table 4. Species-specific estimates of the fish effect, u, and the predicted risks based on the foraging model of Chapter 1 (equation 1). Fish effect is defined as a per capita daily mortality rate attibutable to one fish per site. Risk is the average for each species based on samples that were collected during the 1984 phase of the experiment from the east lake site. Risk is defined as a per capita mortality rate (per second of foraging time) evaluated at a fish density of 1/site. Also given is the mean mass (mg) for each species from the same samples used to calculate risk.

| Snail Taxa | Fish Effect $x10^{-4}$ | Risk $x10^{-8}$ | Mass |
|---|---|---|---|
| Helisoma | 6.20 | 10.74 | 2.641 |
| Physa | 4.20 | 6.34 | 0.211 |
| G. deflectus | 9.65 | 6.34 | 0.203 |
| A. limosa | -1.20 | 1.36 | 0.066 |
| V. tricarinata | -2.37 | 2.96 | 0.110 |
| M. lustrica | 2.74 | 2.07 | 0.077 |
| P. exacuous | 3.17 | 0.64 | 0.038 |
| G. parvus | 2.40 | 1.92 | 0.084 |
| A. walkeri | 2.38 | 0.75 | 0.040 |

three species at highest risk, which exhibited the strongest response to the fish, were also three of the four rarest members of the natural snail community (Figure 3; Table 2). These species were also the three largest members of the snail community (Tables 1,4) and they possess shells that are easier to crush than are those of most of the other species (Chapter 1).

To assess the relative importance of encounter rates (which are highest for large snails) and the size refuges (which are least effective for easily crushed snails) as determinants of the risk of snails to fish predation, I calculated the mean risk for snails of each species on each collection date in the east lake site, and plotted this mean against the mean mass of those same snails (from Figure 1). If encounter rates primarily controlled the predator-prey interaction, then there should be a positive relationship between risk and mass: i.e. the data for each species should appear on the ascending portion of its risk curve. The data in Figure 8 show that mean risk increased monotonically with mean snail mass for each species, demonstrating the importance of encounter rates in determining risk. However, collapsing each snail size distribution into a single mean risk (and mass) per species obscures the potential affect that the size refuge could play for the larger snails of each species. Therefore, I also calculated and plotted the risk curves for each species and extended each curve out to the point corresponding to the <u>largest</u> snail <u>ever</u> collected during the experiment for that species (based on the east lake samples). In order to clearly present these patterns, I redefined risk so that it was density and frequency independent by setting $P_i(a)=1.0$ and $H_i=0.0$ (for all i) in equation 2. Therefore, risk reflects the effects of differential encounter rates and size refuges, but not the additional density dependent effects of attack probabilities and handling times.

Figure 8. Mean risk as a function of mean snail mass. a) Data based on the samples collected during 1984 and 1985 from the east lake site. b) Risk curves for each of the species shown in a). Each risk curve was terminated at the point corresponding to the largest snail ever collected of that species. The curve for Physa continues monotonically to the point (8.59, $4.18 \times 10^{-4}$). Data for Helisoma are not included because of the assumption that encounter rates equal 0.00 for large snails. Species abbreviations as in Figure 3. Risk was defined slightly differently in the two panels (see text).

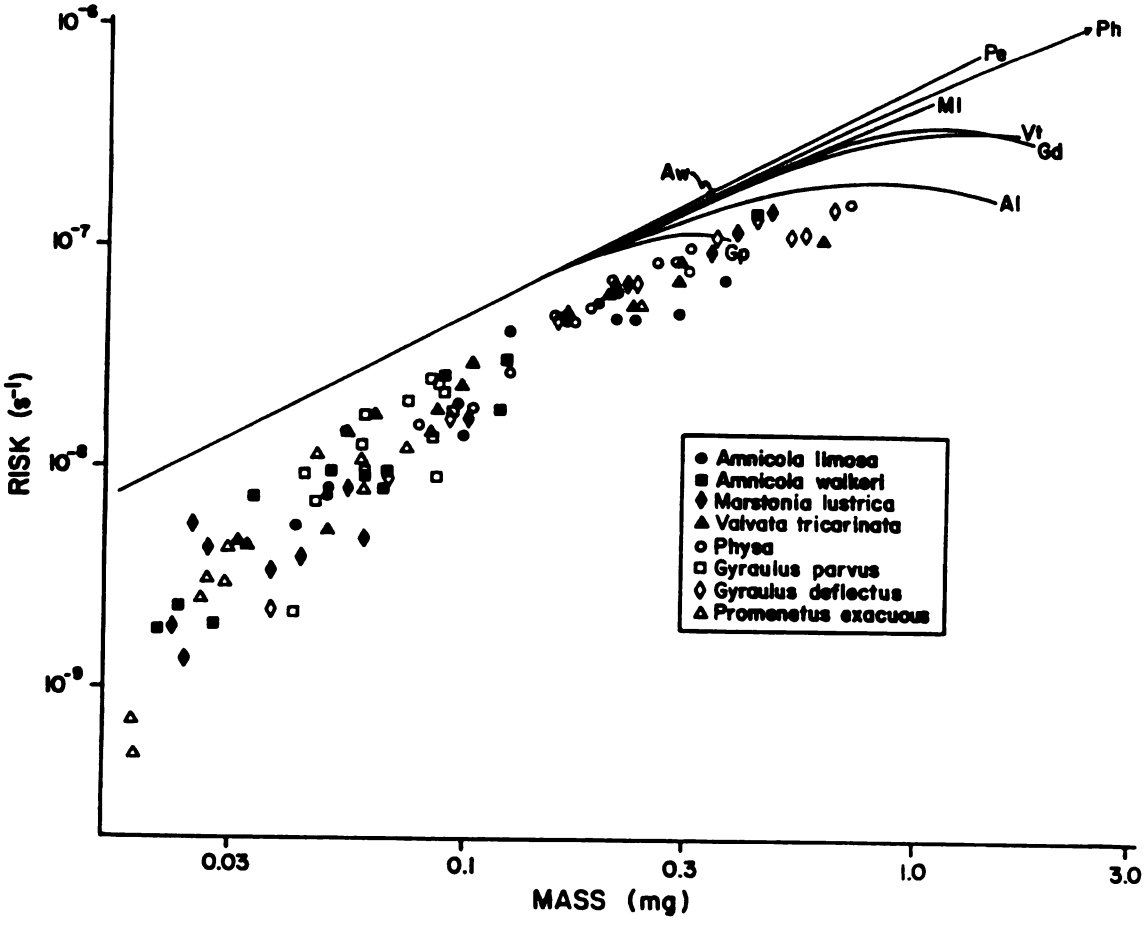
RISK ($s^{-1}$)
$10^{-6}$
$10^{-7}$
$10^{-8}$
$10^{-9}$
0.03
0.1
0.3
1.0
3.0
MASS (mg)
Ph
Pe
Ml
Vt
Gd
Aw
Al
Gp
Amnicola limosa
Amnicola walkeri
Marstonia lustrica
Valvata tricarinata
Physa
Gyraulus parvus
Gyraulus deflectus
Promenetus exacuous

Figure 8

This analysis shows that even the largest snails of the thick-shelled species (e.g. A. limosa and G. parvus) benefitted little from the size refuge (Figure 8). Therefore, differential size refuges played a minimal role in determining relative risks of the snail taxa. The large, easily crushed species (e.g. Physa and Helisoma) were at higher risk and incurred greater fish mortality than smaller thick-shelled taxa because they spent more time at larger sizes during the experiment (Figure 1; Table 4) and were therefore encountered more frequently by pumpkinseeds. In this case, large body size, per se, and not correlated traits (e.g. thin shells) caused increased risk to fish predation.

Interestingly, mean snail size showed little response to the very strong size-selective predation by pumpkinseeds (Figure 8; Chapter 1). Based on the 1984 and 1985 data, no taxa showed a significant decrease in its mean mass across the fish gradient. One species (A. walkeri) significantly increased its mean mass with fish density based on the 1985 data ($r=0.90$, $n=6$, $r<.05$), which because it was the most abundant species (Figure 3) caused a significant increase in the mean snail mass averaged over the entire snail community in 1985 ($r=0.82$, $n=6$, $p<.05$). It is possible that the increase in the mean mass of A. walkeri (as well as the lack of response by other species) was a result of increased growth in response to decreased snail densities.

The estimates of natural mortality from the east lake site and the results from the fish gradient experiment were used to estimate the amount of natural mortality that was attributable to sources not involving predation by pumpkinseeds. The natural mortality data provided estimates of r in equation 1 (total per capita mortality rate), while the data from the fish gradient provided estimates of u (per capita mortality rate attributable to one pumpkinseed/site). Therefore the effect of other sources of mortality was estimated as $m = r - uF$,

where F was the pumpkinseed density observed at the east lake site. Since r was not measured during periods of reproduction, m consists predominantly of environmental sources of mortality not associated with direct pumpkinseed effects (e.g. food limitation or predators other than pumpkinseed sunfish). The relative importance of predation by pumpkinseeds was estimated as the percent of r contributed by uF (i.e. 100(uF/r)). Helisoma and Physa incurred the greatest mortality that could not be attributed to pumpkinseeds (Table 5). The ranking of species by this measure of mortality is very similar to the rankings based on the previous measures of fish effects, risk, total mortality and fecundity (Tables 1, 4: Kendell's coefficient of concordance, $W=.72$, $p<.001$). Despite the documentable and predictable effects of pumpkinseed predation, mortality caused by pumpkinseed predation never accounted for more than 60% of the estimated total snail mortality and averaged only 21% (Table 5).

The unexplained sources of mortality could be due to a number of sources. For example, other vertebrates, such as turtles, feed on snails, as do many invertebrate predators, such as leeches and insect larvae (Michelson 1957; Eckblad 1973; Bronmark and Malmqvist 1986). However, many of the invertebrate predators are rare in lakes like Palmatier because of the well developed fish populations which reduce the densities of these predators much below their abundances in fishless ponds (Crowder and Cooper 1982) and therefore probably have limited effects on snail abundances (Brown and Strouse 1988). Another possible source of mortality includes food limitation. In subsequent experiments conducted in a nearby lake, I increased the density of epiphytes and documented increased growth, recruitment and/or survival of snails. Comparisons of the size distributions of snails in that lake with those in Palmatier Lake (Chapter 3) suggest that food is at least as limiting

Table 5. Sources of mortality and the relative importance of predation by pumpkinseed sunfish. Data are from the east site in Palmatier Lake during the period 2 July - 3 October 1984. Mortality is defined on a daily per capita basis. Mortality rates from pumpkinseeds were taken from Table 2 and multiplied by the pumpkinseed density at the east lake site during 1984 (11.5 fish/site).

| Snail Taxa | Mortality $\times 10^{-3}$ | | | Percent from Pumpkinseeds |
|---|---|---|---|---|
| | Total | Pumpkinseeds | other sources | |
| Helisoma | 35.44 | 7.13 | 28.30 | 20 |
| Physa | 43.01 | 4.83 | 38.18 | 11 |
| G. deflectus | 21.07 | 11.10 | 9.97 | 53 |
| A. limosa | 17.75 | -1.38 | 19.13 | - 8 |
| V. tricarinata | 14.32 | -2.73 | 17.06 | -19 |
| M. lustrica | 26.43 | 3.16 | 23.28 | 12 |
| P. exacuous | 7.74 | 3.65 | 4.08 | 47 |
| G. parvus | 19.69 | 2.76 | 16.92 | 14 |
| A. walkeri | 4.84 | 2.74 | 2.10 | 57 |

in Palmatier Lake. Furthermore, Physa and Helisoma, which incurred the greatest amount of unexplained mortality, were the species that I found to be most sensitive to reductions in food abundance and quality (Chapter 4). These data suggest that food limitation may have been an important factor that contributed to the unexplained sources of mortality to snails inhabiting Palmatier Lake.

The field experiment was conducted during a particular time of the year that coincided with particular stages in the life-histories of the snails (Figure 1). Different effects of pumpkinseeds (with respect to the magnitude of u or u/r, or with respect to the relative effects among the different snail species) might have been obtained had I established the experiment during another period. For example, during June and the beginning of July, the smallest prosobranchs (Amnicola and Marstonia) attain their largest sizes and hence incur their greatest risk to pumpkinseeds. During that same time, pulmonates (and Valvata) have just recently hatched from eggs (Figure 1) and hence incur their lowest risk. Thus an experiment conducted during June should produce results in which Amnicola and Marstonia would show the greatest change in density across the pumpkinseed density gradient; the pulmonates (e.g. Helisoma and Physa) and Valvata would be relatively unaffected due to their small sizes. However, June appears to be the only month in which these generally "low risk" species would incur greater mortality effects via pumpkinseeds. At most other times, snails of other species are larger, and therefore at greater risk (Figure 1).

Between late fall and early spring, most snail species are at their greatest masses and might therefore be expected to incur their greatest pumpkinseed-mediated mortality rates. However, pumpkinseeds densities in the littoral zone are very low during this time (Figure 9) because the pumpkinseeds overwinter in deeper parts of the lake (Hall and Werner

Figure 9. Pumpkinseed abundances in Palmatier Lake during 1984 and 1985. Data are based on transect counts that were converted to absolute densities (see text) at the east and west lake sites. Dotted lines are based on the observations that pumpkinseeds are absent from the littoral zone when water temperatures are below approximately 15°C (see also Hall and Werner 1977).

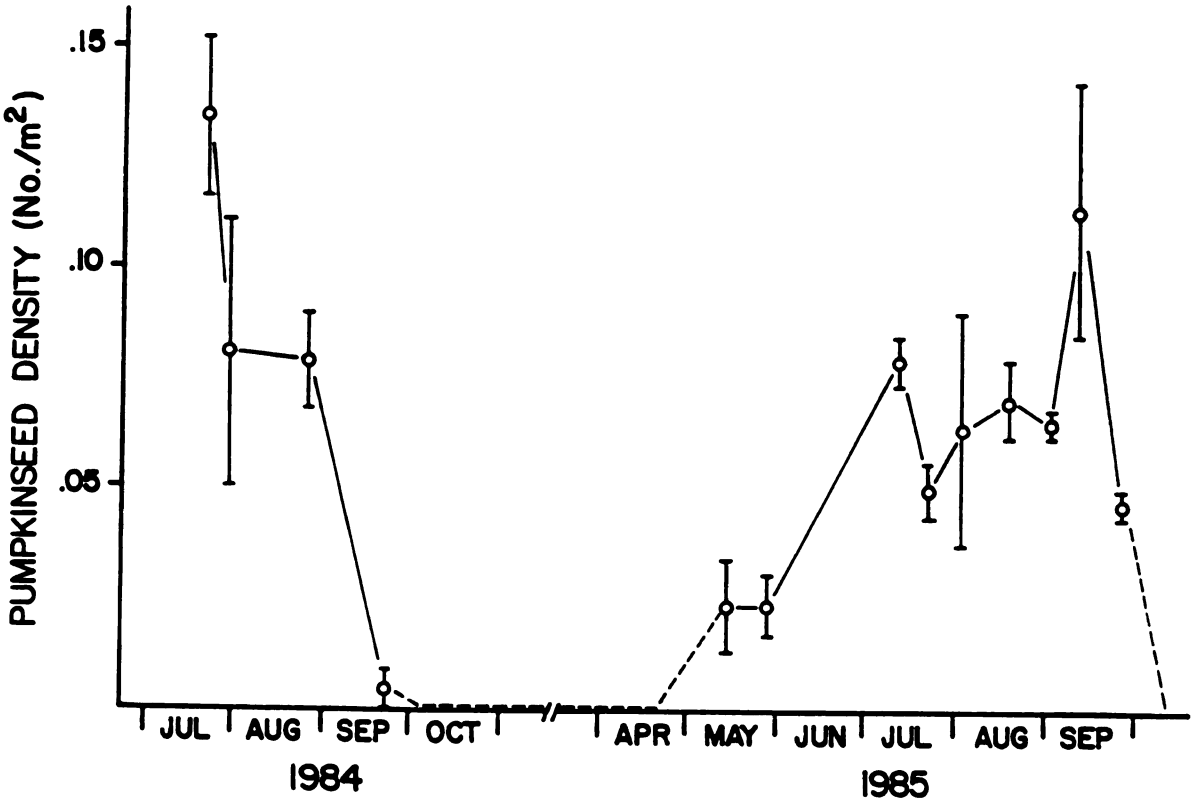
PUMPKINSEED DENSITY (No./m²)
.15
.10
.05
JUL
AUG
SEP
OCT
1984
APR
MAY
JUN
JUL
AUG
SEP
1985

Figure 9

1977). Notice that the peaks in snail sizes in Figure 1 tend to be out of phase with peak littoral abundances of pumpkinseeds (Figure 9). Interestingly, the snail species that recruit latest in the spring (and summer) and are therefore at their greatest risks when fish are most abundant are the three species of small prosobranchs (A. walkeri, A. limosa and M. lustrica), each of which is relatively insensitive to predation (Figure 1; Tables 1, 4). These analyses suggest that the snail community is dominated by relatively predation resistant taxa. The dominant species, A. walkeri, is very small and incurs a very low risk to pumpkinseeds. Even the most vulnerable taxa (e.g. Helisoma and Physa) have life-histories that tend to reduce the potential effects of pumpkinseed predation (Figures 1, 9).

## GENERAL DISCUSSION

There is much debate in the literature concerning the effect of fish on littoral prey communities (e.g. Thorp 1986). Several recent studies have reported apparently contradictory results ranging from the observation that fish have no effect on their prey (Thorp and Bergey 1981a,b; Hanson and Legett 1986) to strong effects on their prey (Crowder and Cooper 1982; Morin 1984a,b). (see also Gilinsky 1984; Hershey 1985; Mittelbach 1988). As Thorp (1986) has pointed out, many of the studies showing strong fish effects (e.g. Hall et al 1970; Crowder and Cooper 1982) are based on introductions of fish into previously fishless communities and therefore do not provide evidence for the effect of fish on their natural prey communities. Mittelbach (1988) has recently offered an additional explanation for many of the results, especially for the variable results that have been observed in natural systems. He argued, as many have for the limnetic systems of

lakes (e.g. Brooks and Dodson 1965; Lynch 1979; Vanni 1987; Turner and Mittelbach 1988), that since fish often prefer larger prey, fish should exert the strongest effects on larger size-classes, thus biasing the prey community in favor of smaller prey. Indeed, in each of the studies that Mittelbach surveyed, fish affected the abundance of large prey and/or the size distribution of the prey community. The studies that did not detect strong fish effects were the studies that did not explicitly examine size-specific responses by the prey community (e.g. Thorp and Bergey 1981a,b). Mittelbach further argued that the total littoral prey density or biomass may not respond strongly to fish manipulations because small organisms are much more abundant than larger organisms (Mittelbach 1981b) and tend to obscure the response by these rarer prey.

The results of this study add further support to the conclusions of Mittelbach (1988). Mortality rates imposed by pumpkinseeds were greatest on large-bodied species (Table 4) due to the predominant role that encounter rates played in determining prey risk (Figure 8). Although snails can eventually reach a size at which predation risk declines (Chapter 1; Osenberg, personal observation), the growth rates in Palmatier Lake were so low that snails rarely attained sizes at which the size refuge became important. In this community, as in many other aquatic communities, increased size translated into increased risk to predators (Figure 8). In addition, the snail species that were most at risk to pumpkinseed predation and incurred the greatest mortality from pumpkinseeds (i.e. the largest species, Helisoma, Physa, and G. deflectus) were the rarest members of the snail community (Tables 1, 4; Figures 3, 10a). Consequently, the overall response of the snail community to the predator manipulation was small. For example, neither mean snail size, nor total density, nor total snail biomass, showed a

Figure 10. Relationships between fish effects and natural prey abundance in six experiments involving fish and their littoral prey communities. a) Results from this study. b) Morin's (1984a,b) study of the effect of fish (mostly bluegill) on larval odonates and other invertebrates. ● = the experiment from Morin (1984a); ■ = the early experiment reported in Morin (1984b); □ = the late experiment reported in Morin (1984b). c) Hershey's (1985) study of the effect of sculpins on chironomids. ● = the experiment performed within a macrophyte bed; ■ = the experiment performed in open sediments. In both Morin's and Hershey's studies, I excluded several extremely rare taxa that did not have mean densities in either treatment greater than 0.5/cage. In addition, a small portion of the data in each of the six experiments come from aggregated prey categories (e.g. Helisoma in this study, which includes two species of snails). Fish effects represent the daily per capital mortality rates on the prey defined per 1 fish/$m^2$.

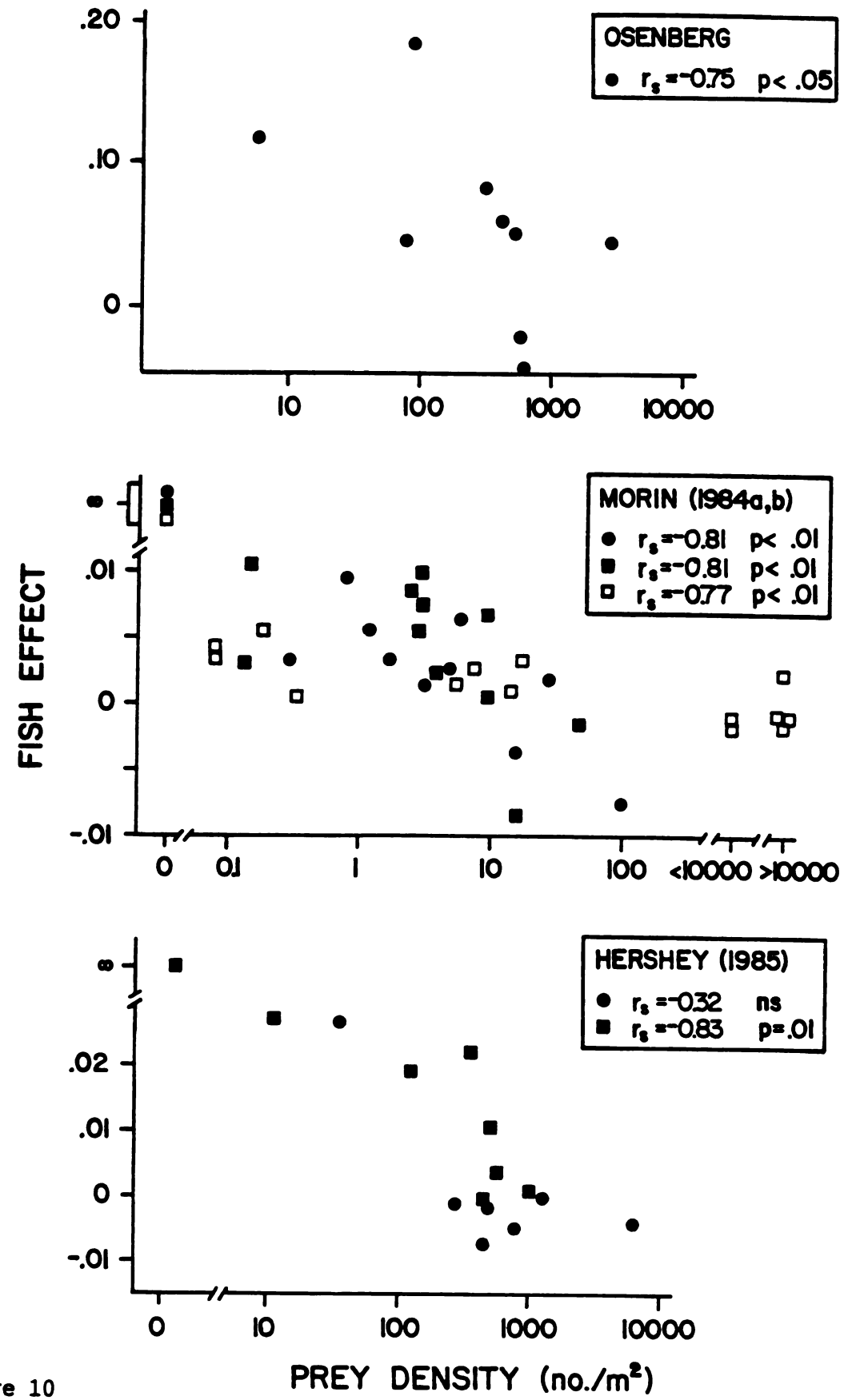
OSENBERG
$r_s$=-0.75 p< .05
MORIN (1984a,b)
$r_s$=-0.81 p< .01
$r_s$=-0.81 p< .01
$r_s$=-0.77 p< .01
HERSHEY (1985)
$r_s$=-0.32 ns
$r_s$=-0.83 p=.01
FISH EFFECT
PREY DENSITY (no./m²)
.20
.10
0
.01
-.01
.02
10
100
1000
10000
0.1
1
<10000
>10000

Figure 10

significant increase with decreased fish density: the relatively safe and abundant species (especially A. walkeri, A. limosa and V. tricarinata) masked the strong reponses by the species that were at greatest risk, albeit at low densities (i.e. Helisoma, Physa, and G. deflectus).

The response of the snail community to the reduction of pumpkinseed density appeared to be limited, in part, as a result of the rarity (or absence) of relatively vulnerable or preferred snail species. Furthermore, because lakes represent discrete habitats and molluscs have extremely limited abilities to migrate among different aquatic habitats, the change in density of these rare species was necessarily mediated through the local populations that had previously coexisted with the predator. Thus, locally rare or extinct species were relatively constrained in their capacities to become abundant following a predator removal, and the refuges provided by shallow ponds that lack fish and harbor large-bodied pulmonates (Eisenberg 1966; Brown 1982) had little effect on the responses observed in Palmatier Lake following the reduction of pumpkinseed density. Interestingly, the adults of aquatic insects are capable of migrating among lakes and ponds, and some of the strongest responses to fish manipulations in natural littoral communities have been observed in dragonflies (Morin 1984a,b); dragonflies are some of the strongest fliers among aquatic insects and are therefore some of the best dispersers among aquatic environments. These data, as well as theoretical work (e.g. Levin 1976; Caswell 1978), suggest that the responsiveness of a prey community to predator exclusion is partly a function of the amount of migration that occurs among different habitat patches because it influences the resilience of rare or locally extinct species.

Other experiments conducted in natural littoral communities also show that fish effects tend to be strongest on the rarest taxa. Morin (1984a,b) used caging experiments to quantify the effect of fish (primarily bluegill) on the densities of larval odonates and other invertebrates. He reported the densities of invertebrate prey at the end of each experiment in a set of fish exclusion cages and in a set of control cages (which natural densities of fish had access to). A measure of the effect of fish can be derived by reference to equation 1 (see previous discussion concerning assumptions of this model). At natural fish densities, $N_{t,F}=N_0e^{-(uF+m)t}$, while in the absence of fish (i.e. F=0) $N_{t,0}=N_0e^{-mt}$. Substitution yields $N_{t,F}/N_{t,0}=e^{-uFt}$, or $u=\ln(N_{t,0}/N_{t,F})/Ft$. Therefore, the per capita effect of fish (u) should be proportional to the logarithm of the ratio of final prey density in the fish exclusion cages to the prey density in the fish cages. I calculated the effect of fish on the density of each species in each of the three experiments reported in Morin (1984a,b). There was a significant rank correlation (Spearman's $r_s$) between the fish effect (u) and the natural density of the prey (i.e. $N_{t,F}$) (Figure 10b) in each of the three experiments. As Morin noted, natural densities and final instar sizes were negatively correlated (i.e. large taxa were rare). Thus, fish effects correlated positively with prey body size and inversely with prey density. Morin (1984a) however rejected this idea because, in part, he defined the effect of fish as an <u>absolute</u> change in final density (i.e. $N_{t,0}-N_{t,F}$), whereas I defined the effect as a relative, or per capita, change in density (i.e. u or $\ln(N_{t,0}/N_{t,F})$). Using the per capita response isolates the effect of fish without confounding it with the effect of prey density in determining total population change. For example, increases from 1 to 2 and from 100 to 200 each represent increases of 100% although the former represents an

increase of only 1 unit while the latter represents an increase of 100 units.

In a similar study, Hershey (1985) excluded sculpins from the benthos of an arctic lake to test for the effect of fish on the densities of chironomids. She conducted two experiments, one in a macrophyte bed and one in an area devoid of macrophytes. In the sites that lacked macrophytes, there was a significant rank correlation between the fish effect (u) and the natural abundance of each species (Figure 10c). In the macrophyte bed, the rarest species showed the greatest fish effect, but the overall correlation was not significant, due in part to the absence of rare taxa and in part to the overall absence of fish effects (Figure 10c; Hershey 1985).

These results from Hershey's and Morin's studies are in agreement with the results from the present study (see also Mittelbach 1981b, 1988) in which fish effects were most severe on the rarest members of the prey community (Figure 10), suggesting that fish directly contributed to the rarity of these prey. Each of these studies also suggest that differential encounter rates are probably largely responsible for the observed patterns of fish effects. In Mittelbach's, Morin's, and my systems, encounter rates have been observed to increase with prey size (Mittelbach 1981a, 1988; Werner et al. 1983; Chapter 1; Figure 8). The rarest prey in these systems tend to be the largest and thus incur the greatest encounter rates with fish. However, in Hershey's system, the rarest species were not the largest, but Hershey argued that fish predation was most intense on smaller taxa because larger prey (especially Stictochironomus) buried deeper into the sediments and were thus relatively unavailable to the fish. This comparison suggests that fish effects are not necessarily greatest on large prey, but does demonstrate that encounter rates play a critical

role in determining which species are most susceptible to fish predation. In many cases, larger littoral prey have greater encounter rates with fish (Chapter 1; Werner et al. 1983); however, other prey characteristics can also determine encounter rates, such as microhabitat use by chironomids in Hershey's study.

Although fish predation clearly increases the mortality of prey that incur high per capita encounter rates, fish might not be the primary reason that these prey are often rare. For example, my results as well as the results from Mittelbach's and Morin's studies, show that the rare members of our prey communities were also the largest; therefore the primary cause of the rarity of these prey might be attributable to other factors associated with large size (e.g. increased energy requirements) and not fish predation. Indeed, in subsequent experiments conducted in another lake, I have shown that Physa and Helisoma were the two species most sensitive to reduced food availability. These were the same two species that incurred the greatest mortality rates due to unexplained sources in the present study (Table 5). In Chapter 4, I argue that the sensitivity to food limitation was greatest for these large-bodied species due in part to their greater energetic requirements. Thus, food limitation might be primarily responsible for the rarity of the large prey, but additional differential mortality mediated by pumpkinseeds further exacerbates the situation. Patterns of abundance in other invertebrate communities, such as those studied by Mittelbach and Morin, might be further influenced by the trophic status of the large and small prey. In many cases, the largest invertebrates are actually predators of the smaller invertebrates, and should therefore tend to be less abundant.

The inverse relationship between prey density and the response of prey to their predators has important consequences for the way we study

the effects of predators on their prey communities. For example, if the effects of fish are greatest on the rarest prey species, then effects of predators will be difficult to document. For example, many studies focus on the responses of the dominant members of the prey community. In these cases, the direct mortality effect of fish will be missed no matter how detailed the analyses if the primary response is concentrated in rare taxa.

Another approach often used to examine the impact of predation on a prey community is direct examination of the predator's diet. However, dietary analyses can also be misleading because diet composition is determined by the abundance of prey in the environment as well as the predator's preference for the prey (Chesson 1983). Prey preference (defined as the standardized ratio of the number of prey in the diet divided by the number in the environment: Manly 1974; Chesson 1978, 1983) is proportional to the per capita mortality rate imposed by the predator on the prey (Vanderploeg and Scavia 1979). If the density of a prey type is high, the diet can be dominated by the prey type even though the predator's preference for that prey type is low, and the predator therefore imposes a small per capita mortality rate on the prey population (relative to other prey). For example, pumpkinseed diets usually consist of well over 50% Amnicola (a very abundant taxa), although the selectivity for Amnicola is generally low (e.g. as indicated by the relatively low risk in Table 4). Therefore, using diets (without reference to prey abundances) as a way to determine which prey species should be most affected by fish predation can often lead to erroneous conclusions because these species may often be non-preferred but extremely abundant prey. On the other hand, if the primary interest of study is energy flow or total prey population change, then predator

diets (or $dN/dt$ or $N_{t,0}-N_{t,F}$) rather than preferences (or $dN/Ndt$ or $\ln(N_{t,0}/N_{t,F})$) will be the more appropriate measure.

One interesting contrast of these two approaches can be illustrated by considering three interacting populations: a predator, an abundant non-preferred prey, and a rare preferred prey. The per capita effect of the predator on the prey populations (i.e. u) will be determined by the predator's preferences, which are directly related to risk: i.e. the predator will impose the greatest per capita mortality rate on the preferred prey's population. However, the effect of the prey populations on the per capita performance of the predator (e.g. feeding rate) will be determined by the total feeding rate of the predator on each prey (which is reflected by the diet). In this case, the non-preferred prey could be the primary source of food for the predator because of its greater abundance in the environment, although the predator imposes a greater effect on the preferred prey (by definition). This sets up an interesting possibility for long-term indirect interactions among the two prey populations (Holt 1977; Vance 1978; see Schmitt 1987 for a related empirical example), where the abundant but non-preferred prey contributes to the mortality of the preferred prey population by sustaining the predator population. Such an interaction might occur in Palmatier Lake between the abundant but relatively non-preferred snail species (e.g. Amnicola) and the rarer preferred species (e.g. Physa and Helisoma), although tests of this idea would necessarily require long-term experimentation lasting for several fish generations.

In summary, the effects of fish predation on littoral prey communities are predictable from the predator's prey preferences or from other information about the predator-prey interaction, notably encounter rates. In general, per capita encounter rates are greatest for larger

prey, which therefore incur greater per capita mortality rates from the predator than do smaller prey. However, other factors, such as microhabitat use, can also be influential in determining encounter rates. Additionally, the effects of fish are often greatest on naturally rare prey, and fish predation can therefore exacerbate the rarity of these preferred prey. Indirect interactions between preferred and non-preferred prey species ("apparent competition", Holt 1977) might also contribute to the rarity of preferred prey. If preferred prey are generally rare in prey communities and if the prey communities are relatively closed to migration from other habitats, then the removal of predators will often result in relatively small changes in the prey communities. For the snail community that inhabits Palmatier Lake, predation from pumpkinseed sunfish has documentable effects that can be understood based on the effect of snail size on encounter rates. However, the rarest prey in the community are the most vulnerable to fish predation, and therefore the overall impact of pumpkinseed predation on the snail community is relatively small. It appears that other factors, such as food limitation, determine prey mortality rates to at least as great an extent as does predation from this specialized molluscivore.

# CHAPTER 3

# RESOURCE LIMITATION, COMPETITION AND THE INFLUENCE OF LIFE HISTORY IN A FRESHWATER SNAIL COMMUNITY

# INTRODUCTION

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 the possible effects 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 aquatic systems may have resulted from the strong effects that fish have when introduced into previously fishless communities (Brooks and Dodson 1965; Hall et al. 1970; Hurlbert and Mulla 1981; Crowder and Cooper 1982). However, the effects of fish on their natural prey communities may be much smaller due to the rarity of relatively vulnerable prey (Vanni 1987; Mittelbach 1988; Chapter 2). For example, my work with freshwater snails showed that fish predation significantly decreased snail densities under natural conditions, but that these effects fell disproportionately on rare preferred prey. Thus, the populations of the less preferred 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, resources and predators as limits of population densities (Hairston et al. 1960; Connell 1975; Menge and Sutherland 1976, 1987; Oksanen 1988).

In this chapter, I examine the importance of resource depletion and resource limitation in a littoral snail community. Exploitative competition occurs when the abundance of resources (in this case epiphytic algae) are depressed by natural densities of consumers (i.e. snails) and when the consumers are limited by the abundance of resources. These two components of competition are rarely separated in field experiments, and instead are often aggregated into a general density-dependent relationship (e.g. Eisenberg 1966; Brown 1982; Schmitt 1985; Kerfoot et al. 1985). Separately assessing the roles of resource depletion and resource limitation in natural populations provides general insights into the mechanisms of competition, and also provides greater information about population consequences, for example in cases where competitive effects are small (due to minor resource depletion) but resource-limitation is still severe. Using a series of field experiments, I show that nutrient supply and snail grazing simultaneously limit the biomass of epiphytic algae. In addition, I show that each snail species is limited by the abundance of epiphytic algae, thus demonstrating competition within this group of herbivores. The particular nature of each snail species' response to increased algal biomass depended on the timing of the snails' life histories relative to the dynamics of the epiphytes. Based on the results of another field experiment, I also 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 (Chapter 2). Two species (Physa and G. parvus) produce a second generation during late summer (Chapter 2). All species, except Helisoma, are semelparous: snails produce eggs during a brief period of time and die soon afterward. Helisoma can live up to two years.

Snails feed primarily on the epiphytic community, which is a diverse assemblage of microalgae and bacteria the lie 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 (Moeller et al., unpublished) 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 the snails at each of these sites by sweeping each site with a 0.33 mm net out to a distance of 0.8 m from the center. I combined the snails that I collected from these sweeps into one large sample that I divided into 21 approximately equal subsamples. I returned 1-6 subsamples to each of six sites. I returned no snails to the other 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 cleaning 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$^{o}$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), 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), intercept in the regression was not different from zero); therefore, the 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 that is hypothesized to be food limited. In many systems, this is a difficult task to accomplish, but in Lawrence Lake this was easily accomplished by supplying phosphorus to the epiphytic community. The strong response by epiphytes (see below) confirmed the earlier results of Moeller et al. (unpublished) and conclusively showed that epiphytic algae were phosphorus limited. Therefore, food limitation in the snail community was tested by observing the response of snails to enhanced epiphyte abundances that resulted from phosphorus fertilization.

The test of food limitation was accomplished by using 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).

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. Results from Moeller et al. (unpublished) indicated that fertilization effects would not extend beyond 0.5 m from the edge of fertilized sites. 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 (e.g. on size-structure of the snail community) would not be confounded with the effects of fertilization (e.g. on snail growth) in the caged sites. Open (i.e. uncaged) 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 fertlizer was added three days later. On 11 September I removed half of the fertilizer sticks from each of the fertilized sites because the change in epiphyte biomass had already been 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 were collected and pooled per site. The experiment was run for only a brief time period so that the direct effect 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 (e.g. Chapter 4).

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 vegetation/sediment samples with samples taken from the sides of each cage with a fine-meshed aquarium net. 17% of the netting was sampled per cage, corresponding to an equivalent vegetation area of 0.43 $m^2$ (= 2.5 $m^2$ x 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.

Data from the two vegetation/sediment samples collected at each open site were pooled, and the samples from the caged sites were also pooled, but the vegetation/sediment samples and net samples were weighted to properly combine the collected snails into a single estimate per site (i.e. snails collected on the vegetation and sediments were assigned a relative weight of 1.894 = 0.43/(0.114*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 response was expected to vary depending on when in the snails' life histories the experiment occurred; therefore, snails were classified by generation as well as species when appropriate: e.g. Physa reproduced during the experiment and both adults and newborns were present in the snail samples. G. parvus also reproduced during the experiment; however, I could not distinguish the few adults that

survived to the end of the experiment from the newborn snails due to the overlap in their size distributions. Therefore, I report the data for the entire species. 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). 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 (Figure 1). Epiphyte biomass at the low end of the snail gradient (i.e. 0-1X) was two to four times greater than the biomass at natural (i.e. 2-3X) and greater than natural (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 Figure 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, also showed that epiphyte biomass increased in response to decreased snail densities (Chapter 4). The results of these two experiments demonstrate that snails reduce epiphyte

Figure 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.

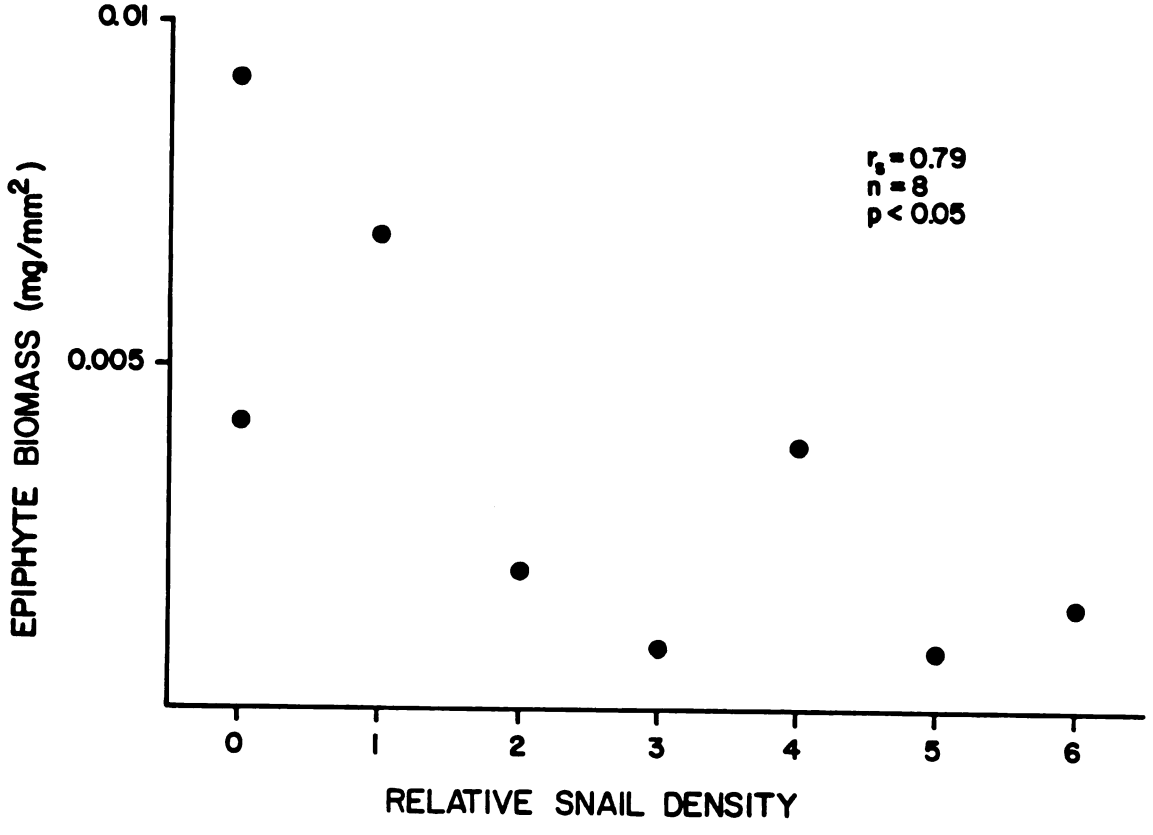
0.01
0.005
EPIPHYTE BIOMASS (mg/mm²)
$r_s = 0.79$
$n = 8$
$p < 0.05$
0
1
2
3
4
5
6
RELATIVE SNAIL DENSITY

Figure 1

biomasses, and suggest that in the absence of snail grazing epiphyte biomass would be from 2-4x more abundant than under natural conditions. 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).

## Food Limitation in the Snail Community

Because natural snail densities significantly depress the biomass of epiphytes (Figure 1), competition among the snails occurs if the depleted resource limits the snail populations. 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 the fertilized sites compared to the controls (Figure 2). Analysis of variance showed that fertilization and caging had significant effects on epiphyte biomass ($F_{fert}$=184.6, $p<.001$; $F_{cage}$=20.5, $p=.01$) as did the interaction between the two factors ($F=31.5$, $p=.005$): caging decreased epiphyte biomass in control sites but increased the biomass in fertilized sites. This 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 (Figure 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, $p=.03$; $F_{cage}$=2.01, $p=.23$; $F_{cage \times fert}$=5.2, $p=.09$). Thus, the depletion effect of snails on epiphyte biomass (Figure 1) coupled with the observation

Figure 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).

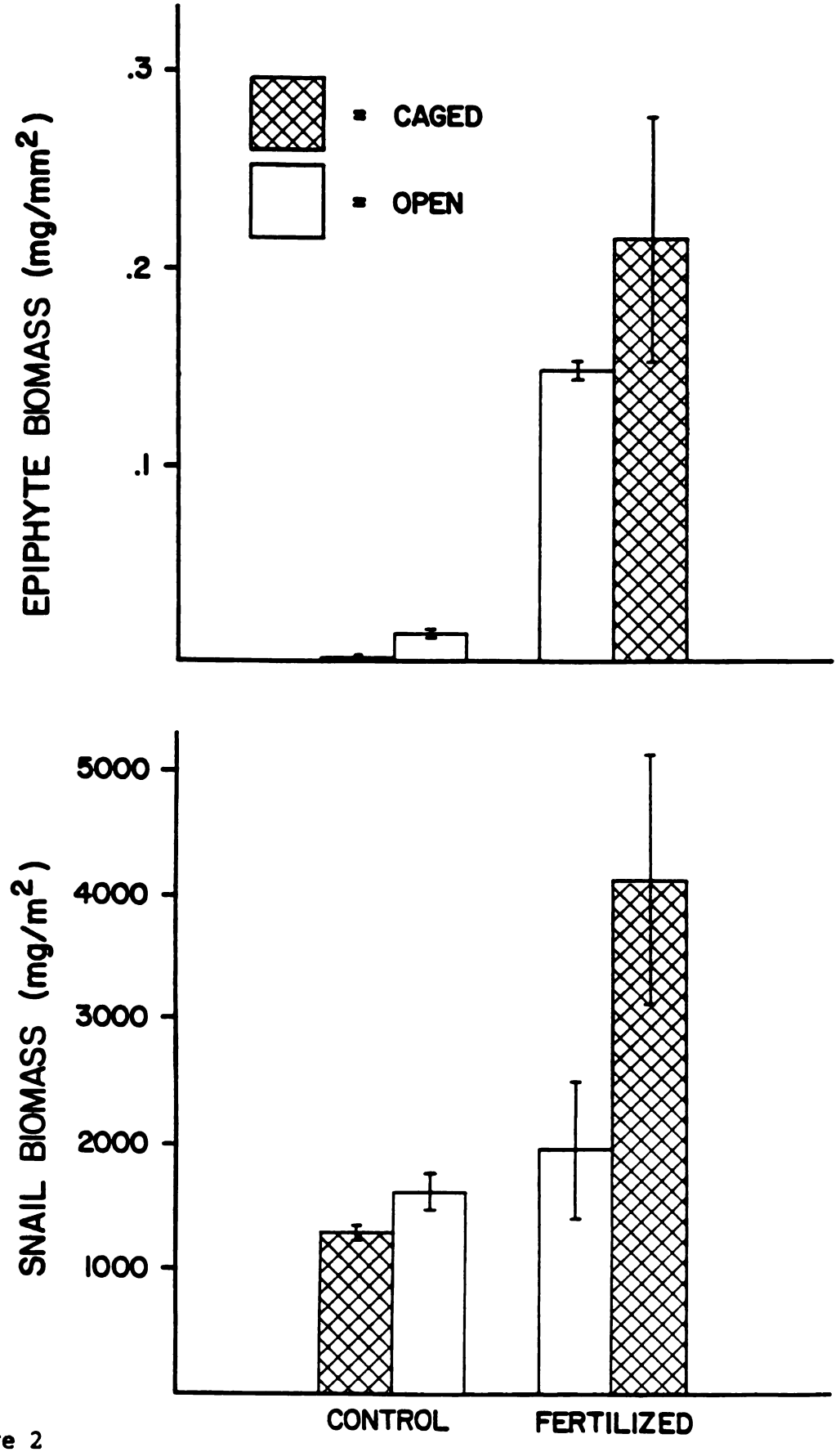
EPIPHYTE BIOMASS (mg/mm²)
.3
.2
.1
= CAGED
= OPEN
SNAIL BIOMASS (mg/m²)
5000
4000
3000
2000
1000
CONTROL
FERTILIZED

Figure 2

that epiphyte biomass limits the production of snail biomass demonstrates that competition occurs within the snail community. I next explore how the survival, recruitment and growth of particular snail species were influenced by the variation in epiphyte biomass.

Snails that had been born prior to the start of the experiment showed no significant variation in density among the treatments (Figure 3), suggesting that their survival was not influenced by the experimental treatments. By contrast, the densities of Physa and G. parvus that were born during the experiment, were approximately 15-fold greater in the sites with the most epiphyte biomass compared to the control sites (Figure 3). The mean individual mass 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 (Figure 4). However, the mean mass for all other species was greater in the fertilized sites (Figure 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), although I could 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 that were born during the experiment 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 the adults (e.g. see adult Physa response in Figure 4), and because fecundity (daily egg production) is strongly related to snail size (Brown 1979; Perron 1985; Chapter 2), the adults would have produced more eggs; 2) additional food

Figure 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: Figure 1). The mean masses from the caged-control sites are shown parenthetically below each species label. Data for different generations of the same species are shown separately. In the figure, generations were distinguished by the timing of their life-histories relatively 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 Figure 1). Means and ranges are indicated (n=2). Asterisks indicate significant effects from analysis of variance (* = $p<0.05$, ** = $p<0.01$, —— not significant).

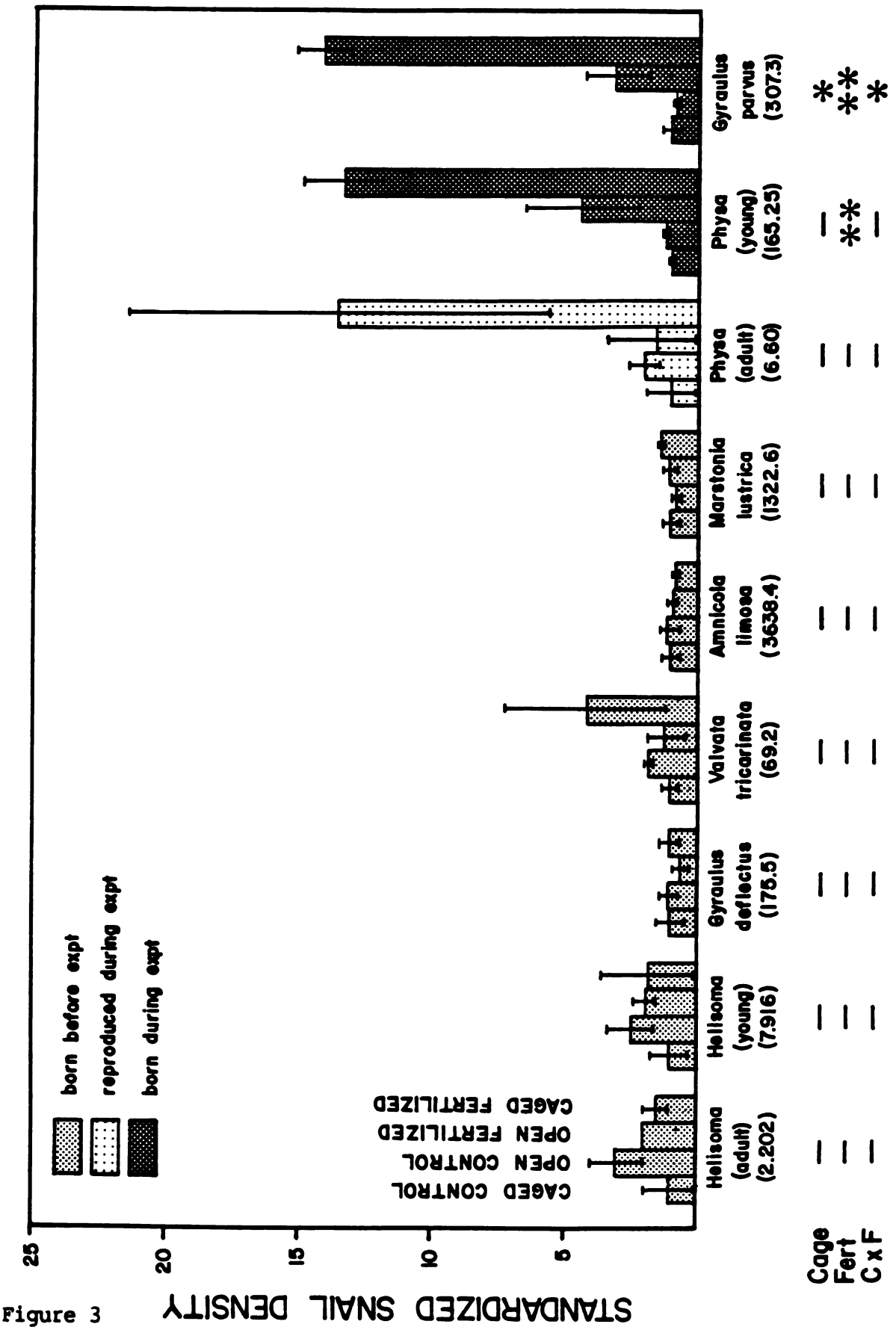
STANDARDIZED SNAIL DENSITY
25
20
15
10
5
CAGED CONTROL
OPEN CONTROL
OPEN FERTILIZED
CAGED FERTILIZED
born before expt
reproduced during expt
born during expt
Helisoma (adult) (2.202)
Helisoma (young) (7.916)
Gyraulus deflectus (178.5)
Valvata tricarinata (69.2)
Amnicola limosa (3638.4)
Marstonia lustrica (1322.6)
Physa (adult) (6.60)
Physa (young) (165.25)
Gyraulus parvus (307.3)
Cage
Fert
C x F
*
**
*

Figure 3

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

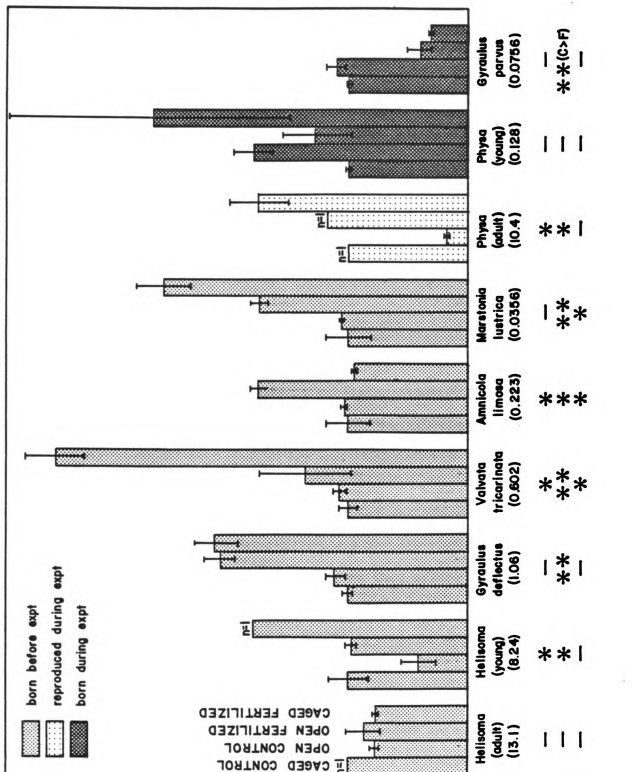
STANDARDIZED SNAIL MASS
3.0
2.0
1.0
0.5
born before expt
reproduced during expt
born during expt
CAGED CONTROL
OPEN CONTROL
OPEN FERTILIZED
CAGED FERTILIZED
n=1
n=1
n=1
Helisoma (adult) (13.1)
Helisoma (young) (8.24)
Gyraulus deflectus (1.06)
Valvata tricarinata (0.602)
Amnicola limosa (0.223)
Marstonia lustrica (0.0356)
Physa (adult) (10.4)
Physa (young) (0.128)
Gyraulus parvus (0.0756)
Cage — — * * — * * * — — —
Fert — — * * * * * * * — —
C x F — — — — * * * — — * * (C>F) —

Figure 4

might have increased the size-specific fecundities of adults: i.e. snails of the same size produced more eggs when there was additional food; 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 with greater food availability.

It is very difficult to distinguish these different mechanisms with the available data, and it is likely that each was influential. However, because the experiment lasted only four weeks, and there was a time lag of approximately one week before fertilization influenced epiphyte biomass, the effect of food on snail density had only three weeks to be produced. Furthermore, because eggs require 1.5-2.5 weeks to hatch (Heard 1963; Eisenberg 1966; Osenberg, personal observation), any effect mediated through adults (e.g. explanations 1,2 and 3 above) must have occurred during the second week of the experiment. It is very unlikely that changes in adult fecundity (and/or survivorship) could have accrued in such a short time period. For example, Eisenberg's (1966, 1970) work on food limitation in a pond snail demonstrated that density-dependence in adult fecundities was largely responsible for adjustments of population density. However, this effect, mediated over a longer time period than in the present study, was primarily attributable to changes in the size of adults and not in size-specific fecundities (analysis of Table 2 in Eisenberg (1970)). One week is insufficient time for adult snails to accrue differences in size necessary to produce the observed 15-fold variation in egg production (see Chapter 2). I conclude that the effects of differential adult fecundity were probably small, and I further 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 in the resource-dependent survival of recently hatched snails compared to older snails (e.g. >1 month) given the disparity in the numerical responses of snails born before and during the experiment (Figure 3). However, 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 probably most likely to die due to food limitation during the early phases 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 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. For example, epiphyte biomass was reduced in the caged-control sites (relative to the open-control sites), but their biomass was enhanced in the caged-fertilized sites (Figure 2). In the control sites, phosphorus (and/or other nutrients) may have been relatively depleted within the cages 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 and led to an enhancement of available phosphorus in the caged-fertilized sites relative to the open-fertilized sites. Any other effects of caging (e.g. exclusion of predators--see below (see also Virnstein 1978)) were confounded with this effect of cages on epiphytes. However there were few cage effects in the present study that could not be attributed to the differences in epiphyte densities.

The only species that did not show the same qualitative response to fertilization in the caged and open sites was Amnicola, which did not increase in size in the caged-fertilized sites (Figure 4). Instead, I observed that a number of Amnicola (probably 5-10%) were deformed in the caged-fertilized samples but not in any of the 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 (Chapter 4), 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. I interpret these deformities as indicative that the combination of caging and fertilization created deleterious abiotic conditions that prevented Amnicola from benefitting from what otherwise was a high quality situation.

## 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 the caged/fertilized sites relative to the open/control (i.e. natural) sites. 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 that could not be explained by epiphyte biomass. Additionally, in another lake (Palmatier Lake) I experimentally altered the density of pumpkinseed sunfish (Lepomis gibbosus), the most conspicuous molluscivore in lakes like Lawrence Lake. 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 preferred snail species, which approximately doubled in density (Chapter 2). However, the natural densities of the three most preferred species were only 1/10 of the natural densities of the six least preferred species. Thus, removal of pumpkinseeds had a relatively small effect on the total snail community, and snail biomass was only 50% greater in the absence of pumpkinseeds compared to controls. Since Palmatier and Lawrence Lakes have similar densities of pumpkinseeds (Osenberg et al. 1988), the effects of pumpkinseed predation are probably similar in the two lakes.

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 the control sites on 20 September 1985 (Table 1). Snails of each species were consistently smaller in Palmatier Lake compared with Lawrence Lake, despite the slightly longer period they had available for growth (water temperatures averaged 23.5$^{o}$C

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

| | Mean snail mass (mg) | | | |
|---|---|---|---|---|
| Snail | 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 |

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 food-limitation is much more important than predation (at least by pumpkinseed sunfish) in limiting the biomass of snails in Lawrence and Palmatier Lakes.

These experiments also show that epiphytes in Lawrence Lake were extremely resource limited, based on the 20-fold increase in biomass following additions of phosphorus fertilizer. Thus these results stand in contrast to predictions made by several general models of limitation that have been proposed. For example, Hairston et al. 1960 (see also Slobodkin et al. 1967) proposed that herbivores are maintained at such low densities that biomass of primary producers does not limit the herbivore trophic level; this was clearly not the case for the Lawrence and Palmatier Lake snail communities. 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. Similar observations of resource-limitation have been made in terrestrial systems (Sinclair 1975; White 1978), where it has been argued that much of the prey standing crop (e.g. plants for herbivores) are not suitable food for consumers (see also Murdoch 1966; Ehrlich and Birch 1967). In these sitations, relatively poor quality resources can increase in density until they become resource limited, thus creating

resource-limitation simultaneously at adjacent trophic levels. At present it is difficult to assess how the relative importance of different processes vary with trophic position (or other ecologically important characteristics) within the same ecosystem. Much additional insight is likely to come from studies that simultaneously address different modes of limitation in several trophic levels.

# CHAPTER 4

# FISH, SNAILS AND EPIPHYTIC ALGAE:
# INTERACTIONS IN A FRESHWATER LITTORAL COMMUNITY

# INTRODUCTION

In freshwater lakes, predation and resource limitation (often referred to as top-down and bottom-up processes) are known to influence population abundances and community structure (Brooks and Dodson 1965; Hall et al. 1976; Neill and Peacock 1980; McQueen et al. 1986; Vanni 1986, 1987a,b; Chapter 2,3). Historically, the importance of top-down and bottom-up processes has emerged from separate consideration of the effects of eutrophication, whose effects flow up the food chain, and the effects of fish predation, whose effects cascade down the food chain (see Carpenter et al. 1985; McQueen et al. 1986). Building on early theoretical work by Rosenzweig (Rosenzweig and MacArthur 1963; Rosenzweig 1971, 1973, 1977) and Smith (1969), recent empirical studies have stressed that the final structure of the ecosystem, and the composition of each trophic level, is determined by the simultaneous adjustment of each population to effects that impinge on it from above and below in the food chain (Walters et al. 1987; Mittelbach et al. 1988; Leibold 1988). Some important insights concerning the structure and regulation of lake ecosystems have come from recent field experiments in which nutrient supply and fish densities were simultaneously manipulated (Vanni 1986, 1987a,b; Leibold 1988).

In this study I examine the simultaneous effects of productivity and fish predation on the dynamics and structure of a freshwater snail community. In previous field experiments I showed that natural densities of molluscivorous fish depressed snail densities in a natural lake (Chapter 2) and that the snail community was limited by the abundance of epiphytic algae, the snails' primary food resource (Chapter 3). Although these experiments provided important insights concerning limitation in the snail community, broader interpretations were limited

due to two important drawbacks shared with many other field experiments. First, effects of predation and food limitation were studied in single factor experiments, which precluded the examination of their interaction (see Quinn and Dunham 1983; Sih et al. 1985). Second, as is true in many studies, the experiments were maintained for relatively short time periods in order to isolate the effect of a particular process, while keeping more complex indirect responses to a minimum. For example, in my earlier study of food limitation (Chapter 3), I quantified the short-term responses of snails to enhanced algal biomass in order to isolate the effects of epiphytes on snails without incorporating more complicated dynamics that would have resulted from the subsequent feedback between snails and epiphytes. Although these designs can provide important insights into the strengths of particular processes that impinge on natural populations, they neglect the dynamic linkages among interacting populations. This feedback among populations and its temporal development may have strong influences on population dynamics. The final ecosystem structure that arises following an environmental change can be very different from what might be predicted from the short-term changes (Schaffer 1981; Bender et al. 1984).

Important life-historical and ecological traits can influence the responses of aquatic species to variation in productivity (or resource abundance) and predator density (e.g. Brooks and Dodson 1965; Hall et al. 1976; Zaret 1980; Tessier and Goulden 1987; Chapters 2,3). As environments change, particular species that possess specific suites of traits, become more abundant while other species become rare. Understanding how particular traits influence a species response to changes in its environment provides a powerful way to construct general hypotheses about how the environment shapes the diversity of species existing within a community. Body size, and the way particular traits

vary with body size, can influence a species' response to predators and resources (Werner and Gilliam 1984). For example, fish predation has predictable effects on snail densities based on the ways in which important components of the predator-prey interaction scale with snail body size (Chapters 1 and 2). Responses of aquatic animals to food abundances also scale with body size (Hall et al. 1976; Downing 1981; Peters 1983; Tessier and Goulden 1987), although much controversy still exists concerning the particular role body size plays in determining relative abundances of aquatic organisms (Tillman and Lampert 1984; Persson 1985; Bengtsson 1987). Since most aquatic populations are size-structured (Werner and Gilliam 1984), examining the ecological consequences of body size should provide important insights into the simultaneous roles of predation and productivity in determining community structure in natural systems.

In this study I extend the results of earlier experiments on freshwater snail communities by examining the temporal dynamics of snail and epiphytic algae that result from the simultaneous manipulations of fish densities and limiting algal resources (phosphorus and light). In particular I examine how the interaction between snails and algae is modified by variation in top-down processes (which alter snail mortality rates) and by variation in bottom-up processes (which alter algal production rates). Additionally, I examine species-specific responses of snails during the experiment in order to assess the effects that body size and correlated traits have on population dynamics and the regulation of community structure.

## METHODS

The experiment was conducted in Lawrence Lake, 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). Approximately 20 species of fish occur in Lawrence Lake (Hall and Werner 1977), with the pumpkinseed sunfish (Lepomis gibbosus) being the only species that obtains a majority of its diet from snails (Mittelbach 1984; Chapter 1).

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). From early-May through July (the specific timing depends on the species), snails that were born the previous year lay eggs on vegetation or debris. Hatching occurs within approximately two weeks and substantial somatic growth occurs during the summer and fall (Chapter 2). Two species (Physa and G. parvus) produce a second generation during late summer. All species, except Helisoma, are semelparous; snails produce eggs during a brief period of time and die soon afterward. Helisoma can live up to two years.

Snails feed predominantly on the epiphytic community, which is a diverse assemblage of microalgae and bacteria that lie within a matrix of calcium carbonate crystals and glycocalyx materials (Burkholder 1986). Very small blue-green algae (e.g. Chroococcus and Synechoccus) and small diatoms (e.g. Achnanthes) comprise over 90% of the epiphytic biovolume (Burkholder 1986). The community is severely phosphorus limited, and addition of phosphorus can increase epiphyte biomass to 100

times the biomass in unfertilized sites (Moeller et al. unpublished; Chapter 3).

The experiment was conducted along a 30 m section of shoreline in Lawrence Lake. Cages measured 2.5 m x 1.6 m (4.0 $m^2$) and were built from wooden frames to which fiberglass window screening (1.2 mm mesh) was attached. Ten cages were used in the experimental design and each was placed at a depth of approximately 1-1.25 m. The window screening was buried by pushing it into the sediments, and approximately 25 cm extended above the water surface. A walkway was built among the cages to minimize disturbance to the sediments. All centrarchid fish were removed from the cages by angling or hand netting. Several cyprinids (Notropis heterodon, or N. heterolepis) were present in most of the cages and could not be removed.

The experimental design consisted of five treatments with two replicates each. Four of the treatments comprised a cross-classified design in which I simultaneously manipulated pumpkinseed density and nutrient supply. Four cages received one pumpkinseed (between 85.0 and 86.5 mm SL) while four cages received no fish. A density of one fish/cage is approximately $\geq$5x greater than natural densities in Lawrence Lake and other similar lakes (Osenberg et al. 1988; Chapter 2), although much greater densities can occur in some shallow lakes (Osenberg, personal observation). Thus, results from this experiment overestimate the absolute effect of pumpkinseed predation on the snail community. I have however, previously assessed the impact of pumpkinseeds at natural densities (Chapter 2). I used greater than natural densities in this experiment in order to ensure sufficient predation effects so that I could study the processes of predation and food limitation, as well as their interaction and the role played by snail size.

To each of the four cages assigned to the fertilizer treatments, I added Osmocote 14-14-14 (nitrogen-phosphorus-potassium) fertilizer (manufactured by Sierra Chemical Co., Milpitas, California). 60 g of fertilizer were placed in packets made from window screening and tied to wooden dowels. Four packets were placed in each of the four cages. Phosphorus was in the form of calcium phosphate and the total phosphorus content of the fertilizer was approximately 15 g/cage. Thus the four treatments were control/no-fish, control/fish, fertilized/no-fish, and fertilized/fish, with two replicates per treatment. In the remaining two cages I imposed a fifth treatment in which I reduced light levels by placing a roof over each of the two cages (the roof consisted of two layers of mosquito netting tacked to a wooden frame). Thus, the three treatments without fish constituted a gradient in potential epiphyte productivity ranging from low (the shade treatment) to approximately natural (the control) to very high (the fertilizer treatment).

Cages were installed on 8 May 1986, and first sampled on 17 May (see below). Treatments were imposed on 19 May. On 2 July, I reduced the amount of shading to one layer of mosquito netting, and reduced the number of fertilizer packets to two/cage. On 18 August I returned the second layer of netting to the shade treatments and I removed the two remaining fertilizer packets from the fertilized sites because epiphyte biomass was so great that it was damaging the Scirpus. The experiment was terminated on 29 September 1986.

I observed pumpkinseed feeding behavior in the cages on three dates during the first ten days of the experiment; observations after early June were very difficult to make due to extensive new growth of Scirpus. I made these observations because I was particularly interested in seeing if the fish fed on prey that were associated with the vegetation or with prey that occurred on the sides of the cages. If fish fed

primarily on prey that occurred on the cage, then the effects of fish on the snail community could be greatly biased. Observations showed that caged fish behaved normally and fed primarily on prey that occurred on natural substrates. Of the 61 attacks that I observed, 49 (80%) were directed at prey occurring on natural substrates (primarily Scirpus). 25 of the prey that were attacked were clearly identified as snails, and only three of these (12%) occurred on the cage. Thus, caged pumpkinseeds fed primarily from natural substrates.

Snails and epiphytes were sampled every two weeks (except during the first part of August when one period of three weeks elapsed between sampling dates). Snails were sampled by a combination of sweepnetting the vegetation and by sweeping the sides of the cage. I lowered a sweepnet (basal width = 30 cm; mesh=.425 mm) to the sediment surface, briskly pushed the net approximately 30 cm along the sediments, and then tilted and raised the net through the vegetation. I rinsed the net into a bucket, took one more sweep, and combined it with the first. Scirpus, which is well rooted and very flexible, was not damaged with this sampling procedure, although epiphytes were dislodged. Less than 5% of each cage was sampled per date, so the disturbance to the site as a whole was rather small and by the following week it was difficult to notice where the previous sample had been taken. The location of each sweep was chosen haphazardly. I also used an aquarium net (width=18 cm; mesh < .5 mm) to sample the sides of the cage. I took two vertical sweeps from each cage. Since the samples from the sides and vegetation were each obtained from approximately 4.5% of the available habitat within a cage, I pooled the two types of samples into a single estimate from each cage. I report all densities and biomasses on a per sample basis, but these can be approximated to an areal basis by dividing by 0.18 $m^2$/sample.

After sampling the sides, and once during each week I did not sample, I used the aquarium net to completely remove all snails from the window screening. I returned these snails to the central region of the cage. I also transferred 40 L of lake water to each cage to avoid possible deleterious changes in the water chemistry (Chapter 3).

Snails from the samples wre gently rinsed throught a 0.5 mm sieve, placed in lake water and returned to the lab, where they were picked from the debris, identified to species and measured to the nearest 0.01 mm. Shell sizes were later converted to tissue dry masses using length-mass regressions. The live snails were then returned to their original cage. Due to time constraints, I usually sampled half of the cages (one set of replicates) on one day and the other half on the following day.

Epiphytes were sampled by collecting midsections of Scirpus leaves. Two samples, consisting of a total of approximately 10-20 leaf sections, were collected per site. Epiphytes were removed from the leaf sections by cleaning each leaf with forceps. Lengths and widths of the leaf sections were measured to estimate the surface area sampled. Epiphytes were filtered onto preweighed and precombusted glass fiber filters (Watman, GF/F), dried for 24 hours at 100$^{o}$C, weighed to the nearest 0.01 mg, recombusted at 550$^{o}$C for 1 hour, and reweighed. Epiphyte biomasses were expressed as ash free dry mass per surface area of Scirpus ($mg/mm^2$). A single estimate per site per date was obtained using the mean of the two samples. On two dates during the experiment (2 July and 18 August), an additional sample was collected at each site and preserved in Lugol's solution. Large, loosely-attached filamentous algae were later separated from the finer algal components using forceps, and each of these two components were weighed as explained above.

Data were analyzed as if constituting two separate experiments: a cross classified design involving the effects of fish density and fertilization, and an experiment in which primary productivity was varied at three levels (shade, control, fertilization) in the absence of fish. Each data set was analyzed by repeated measures analysis of variance (Winer 1971). In addition, I performed separate Anovas for each date in order to assess the significance of patterns at each point during the experiment. Data were log-transformed to homogenize variances (data that included zeros were log(x+1) transformed). Proportions were arcsin-squareroot transformed.

## RESULTS

### Epiphyte Response

Treatment effects on epiphyte biomass were manifest very quickly (Figure 1). Repeated measures analysis of variance revealed a variety of significant effects (Table 1). In particular, the main effects of fertilization and fish were significant as was the interaction between date and fertilization (the fish x date interaction was marginally significant). One would expect the treatment effects of fish and fertilization to be manifest as significant interactions with date. However, the very fast response by the epiphytes (and snails, see below) and the single pre-manipulation sample limit the power of detecting significant treatment by date interactions. In this analysis, as well as subsequent ones, it appears that the variation induced by the treatments was primarily partitioned to the main treatment sums of squares. For example, although there were no initial differences in epiphyte biomass among fish and no-fish treatments, differences

Figure 1. Epiphyte biomass through time in each of five treatments. The mean of two replicates per treatment is shown. Complete analyses are given in Table 1. Results from Anovas based on each date are shown at the bottom of the figure for the cross-factored design: -- $p>.05$, * $p<.05$, ** $p<.01$. Separate analyses for the treatment effects of shade, control and fertilization were significant ($p<.05$) only for the date in mid-August.

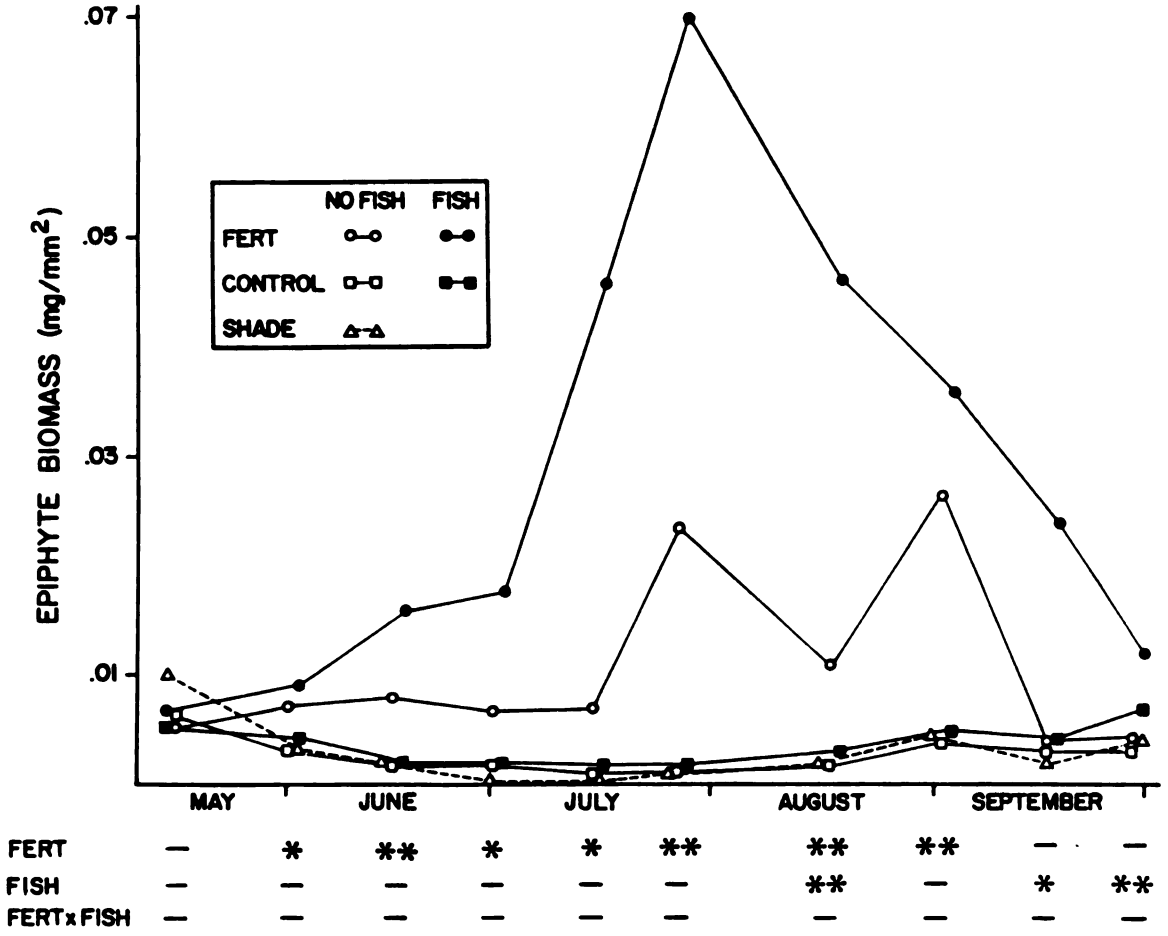
.07
.05
.03
.01
EPIPHYTE BIOMASS (mg/mm²)
NO FISH
FISH
FERT
CONTROL
SHADE
MAY
JUNE
JULY
AUGUST
SEPTEMBER
FERT — * ** * * ** ** ** — —
FISH — — — — — — ** — * **
FERT x FISH — — — — — — — — — —

Figure 1

Table 1. Results of repeated measures Anova for epiphyte biomass. In a preliminary analysis of the cross-factored design, the fish x fertilization x date interaction was not significant ($p>.40$), so the three way interaction was dropped from the model (and pooled with the error term). In both data sets, the main treatment effects (and their interaction in the cross-classified design) were tested using the mean square of the nested component (cage(fish*fert) or cage(treatment)) as the error term. Data were $\log_{10}$ transformed for analysis.

| Source | df | Sums of squares | F | p |
|---|---|---|---|---|
| **FISH x FERTILIZATION:** | | | | |
| fish | 1 | 1.955 | 11.18 | 0.029 |
| fertilization | 1 | 8.573 | 49.03 | 0.002 |
| fish x fert | 1 | 0.462 | 2.64 | 0.179 |
| cage(fish x fert) | 4 | 0.699 | 4.87 | 0.002 |
| date | 9 | 1.287 | 3.98 | 0.001 |
| fish x date | 9 | 0.620 | 1.92 | 0.073 |
| fert x date | 9 | 3.006 | 9.31 | 0.001 |
| error | 45 | 1.615 | | |
| **PRODUCTIVITY:** | | | | |
| treatment | 2 | 3.926 | 4.03 | 0.141 |
| cage(treatment) | 3 | 1.460 | 13.89 | 0.001 |
| date | 9 | 2.793 | 8.85 | 0.001 |
| treatment x date | 18 | 2.154 | 3.42 | 0.002 |
| error | 27 | 0.684 | | |

subsequently arose and persisted throughout the duration of the experiment (Figure 1); however, the repeated measures analysis showed only a marginally significant fish x date interaction (the main fish effect was very significant: Table 1). Analysis of the productivity gradient (shade, control, fertilized, all in the absence of fish) showed a strong interaction between date and treatment (Table 1, Figure 1), due primarily to the greater epiphyte abundances in the fertilized sites relative to the control and shade sites.

On 8 June, only 24 days after the start of the experiment, large filamentous algae began to proliferate in the fertilized/no-fish sites. Samples collected on 2 July showed that these large filamentous algae were only found in fertilized sites and they dominated where fish were absent (Table 2): i.e. where snail biomass (grazing intensity) was greatest (see below). On 18 August, large filaments were only present in samples from the fertilized/no-fish treatment where they comprised between 24 and 28% of the total epiphyte biomass. The filamentous algae consisted primarily of Mougeotia, with lesser amounts of Spirogyra mixed in. A few small diatoms were also epiphytically associated with the entwined filaments. The filaments were only loosely attached to the Scirpus and tended to form stringy, amorphous clouds in the water column. Due to their tough, fibrous morphology and their extension into the water column where snails could not easily feed, these algae appeared to be relatively immune to snail grazing.

## Snail Response

Snail biomass responded very rapidly to fertilization and fish treatments (Figure 2; Table 3). Repeated measures Anova revealed a strong fertilizer x date interaction and a marginally significant fish x

Figure 2. Snail biomass through time in each of five treatments. See Table 3 and legend to Figure 1. Analyses based on the three no-fish treatments showed no significant differences for any of the dates.

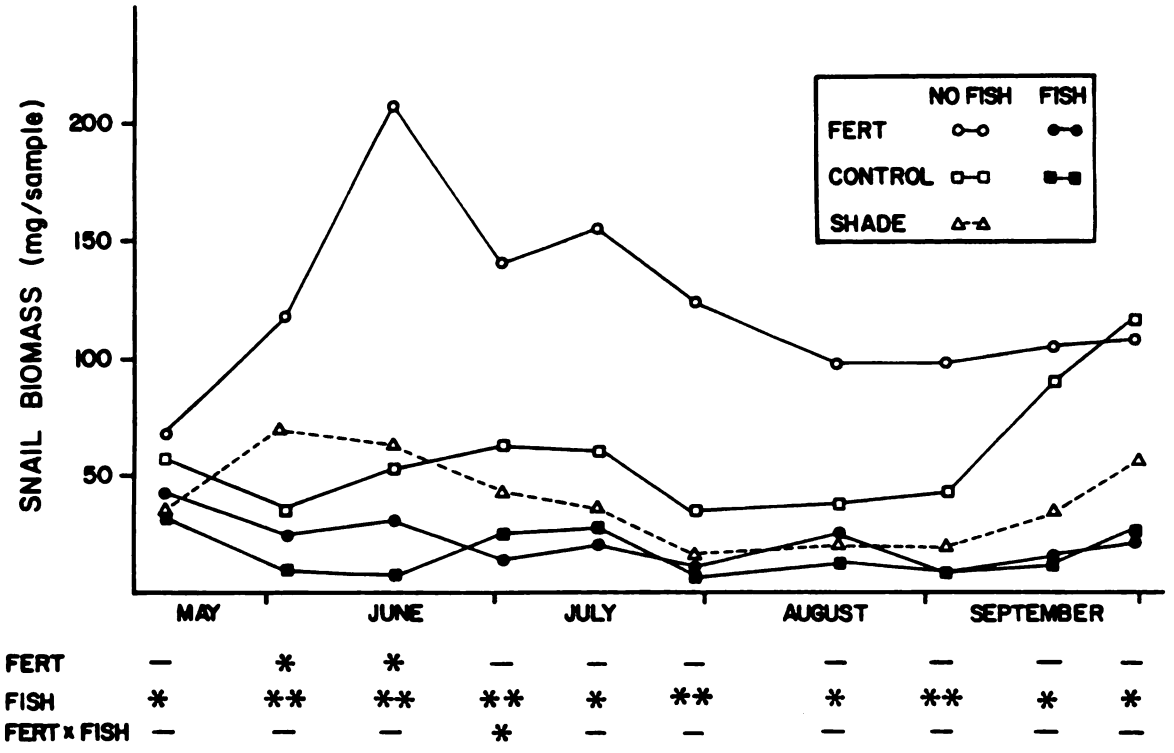
SNAIL BIOMASS (mg/sample)
200
150
100
50
NO FISH
FISH
FERT
CONTROL
SHADE
MAY
JUNE
JULY
AUGUST
SEPTEMBER
FERT — * * — — — — — — —
FISH * ** ** ** * ** * ** * *
FERT x FISH — — — * — — — — — —

Figure 2

Table 2. Contribution of large filamentous algae to the epiphyte community as sampled on 2 July in each of the ten sites. Total epiphyte biomass is based on means (n=2) from each site based on the primary samples. Proportion filaments is based on the extra samples (n=1 per site) in which large filaments were separated and weighed separately from the other epiphyte components.

| Treatment | Total Epiphyte Biomass ($mg/mm^2$) | Proportion filaments |
|---|---|---|
| Fert/no-fish | 0.00660<br>0.00301-0.01020 | 0.87<br>0.87-0.86 |
| Fert/fish | 0.01774<br>0.00749-0.2799 | 0.08<br>0.08-0.07 |
| Control/no-fish | 0.00170<br>0.00088-0.00253 | 0.00<br>0.00-0.00 |
| Control/fish | 0.00198<br>0.00159-0.00237 | 0.00<br>0.00-0.00 |
| Shade/no-fish | 0.00053<br>0.00037-0.00069 | 0.00<br>0.00-0.00 |

Table 3. Results of repeated measures Anova for snail biomass. See legend to Table 1.

| Source | df | Sums of squares | F | p |
|---|---|---|---|---|
| FISH x FERTILIZATION: | | | | |
| fish | 1 | 9.295 | 40.86 | 0.003 |
| fertilization | 1 | 0.850 | 3.74 | 0.125 |
| fish x fert | 1 | 0.331 | 1.46 | 0.294 |
| cage(fish x fert) | 4 | 0.910 | 6.04 | 0.001 |
| date | 9 | 0.804 | 2.37 | 0.027 |
| fish x date | 9 | 0.706 | 2.08 | 0.051 |
| fert x date | 9 | 0.869 | 2.56 | 0.018 |
| error | 45 | 1.694 | | |
| PRODUCTIVITY: | | | | |
| treatment | 2 | 3.316 | 3.14 | 0.184 |
| cage(treatment) | 3 | 1.584 | 20.84 | 0.001 |
| date | 9 | 0.835 | 3.66 | 0.004 |
| treatment x date | 18 | 1.046 | 2.29 | 0.025 |
| error | 27 | 0.684 | | |

date interaction ($p=0.051$); the overall fish effect was strongly significant, due in part to initial differences that existed before treatments were imposed (Figure 2: first sampling date). The fish x date interaction suggests that fish treatments had effects on the dynamics of snail biomass after accounting for the initial differences among treatments. The primary effect of fish was seen in the fertilized cages where, after only one month, snail biomass in the absence of fish was five times the biomass attained in the presence of fish. Following this dramatic increase however, snail biomass in the fertilized/no-fish sites decreased until by the end of the experiment snail biomasses in fertilized and control sites were similar. The peak snail biomass in the fertilized/no-fish sites corresponded with the appearance of large filamentous algae in the same sites, and the decline in snail biomass started when the majority of epiphytic biomass was in the form of large filamentous algae (Table 2).

## Coupled Dynamics of Snail and Epiphyte Biomass

The results from Figures 1 and 2 can be combined in order to examine how the relationships between epiphyte and snail biomasses varied over the course of the experiment. The relationship between epiphytes and snails can be varied in two important ways: by variation imposed at the base of the food chain (e.g. by fertilization or shading) and by variation imposed at the top of the food chain (e.g. by altering fish density). If snail densities influence epiphyte abundances then altering fish density should produce variation in snail densities and a subsequent negative relationship between the abundances of snail and algae (Figure 3). This inverse relationship results from the simple coupling of two predator-prey interactions and is evidence of top-down

Figure 3. Effect of top-down and bottom-up control on the relationship between epiphyte and snail biomasses. Increasing fish density (top-down control) reduces snail biomass and therefore increases epiphyte biomass. Increasing productivity (bottom-up control) moves the inverse relationship between epiphyte and snail biomasses away from the origin.

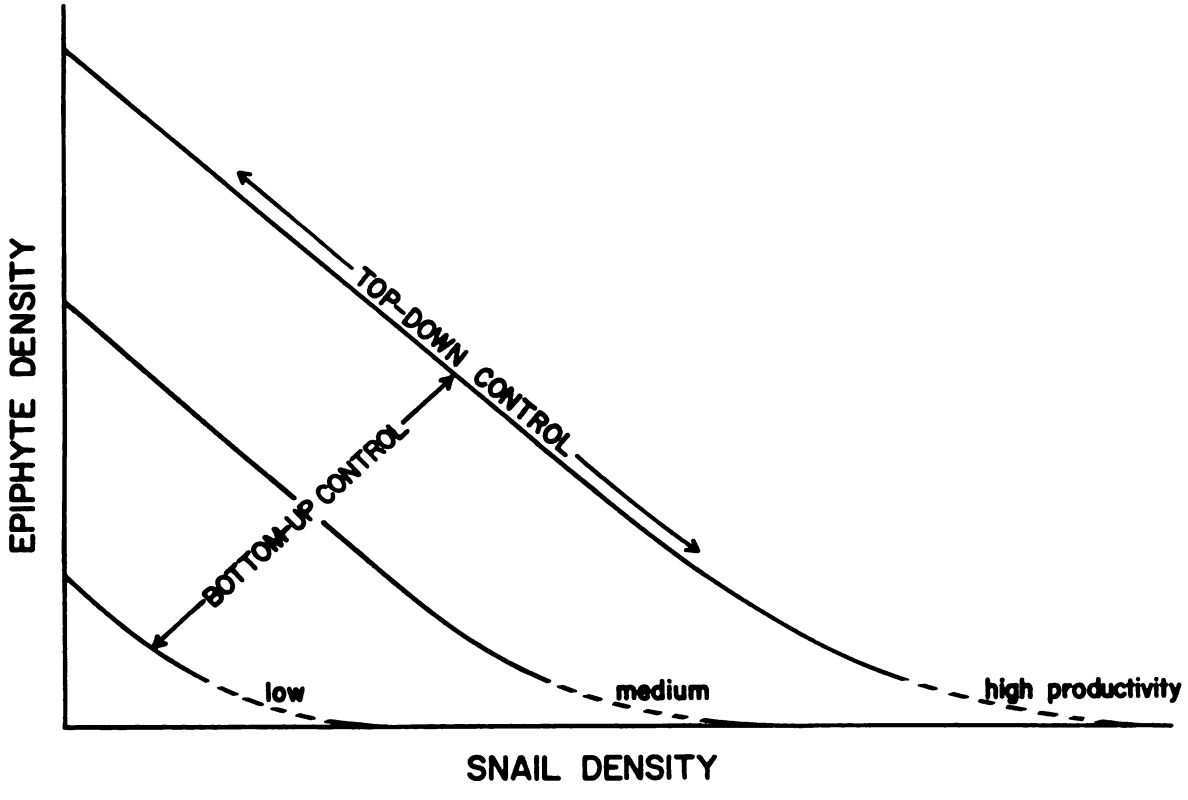
EPIPHYTE DENSITY
TOP-DOWN CONTROL
BOTTOM-UP CONTROL
low
medium
high productivity
SNAIL DENSITY

Figure 3

(or cascading) effects (McQueen et al. 1986; Carpenter et al. 1985). On the other hand, productivity (varied through nutrient and light manipulations) induces changes from the bottom of the food chain. The enhanced production of epiphytes should lead to increased biomasses of organic matter, consisting of epiphytes, snails, fish and detritus (or other components involved in the energy cycle of the ecosystem). If epiphyte and snail biomass are the two major sinks of phosphorus and fixed carbon, then their combined biomasses should be greatest in high productivity treatments, indicating the importance of bottom-up effects (Figure 3). Viewed in another way, the relationships depicted in Figure 3 indicate that a greater biomass of snails is needed to maintain epiphytes at a particular biomass in high productivity environments compared to less productive ones.

The interaction of top-down and bottom-up processes in the algae-snail-fish system, and the temporal changes in the effects, can be seen in Figure 4, where I have plotted the epiphyte biomasses and snail biomasses observed at monthly intervals among the ten experimental sites. At the beginning of the experiment there was little variation among the sites. As the experiment progressed, treatment effects emerged as fish created variation in snail biomass among sites, and fertilization and shading created variation in epiphyte biomass. These effects were then transmitted an additional step: the direct effect of fish on snails was reflected in a change in epiphyte biomass, and the fertilization effect on epiphytes was transmitted to the snail community. In July and August, the data from the three productivity levels (fertilized, control and shade) show very clearly that top-down and bottom-up effects influenced snail-epiphyte relationships (cf. Figure 3). Following the removal of the fertilizer packets on 18 August, the differences between the fertilized and control treatments

Figure 4. Epiphyte biomass in relation to snail biomass among three sets of cages that differed in potential primary productivity. Compare with Figure 3. Productivity was manipulated by shading and by fertilizing. Analysis of covariance detected no significant effects at the start of the experiment (17 May 1985). Snail biomass significantly depressed epiphyte biomass on the last three dates, while productivity significantly affected epiphyte biomass on the middle three dates (the effect on the final date was marginally significant, $p=.09$).

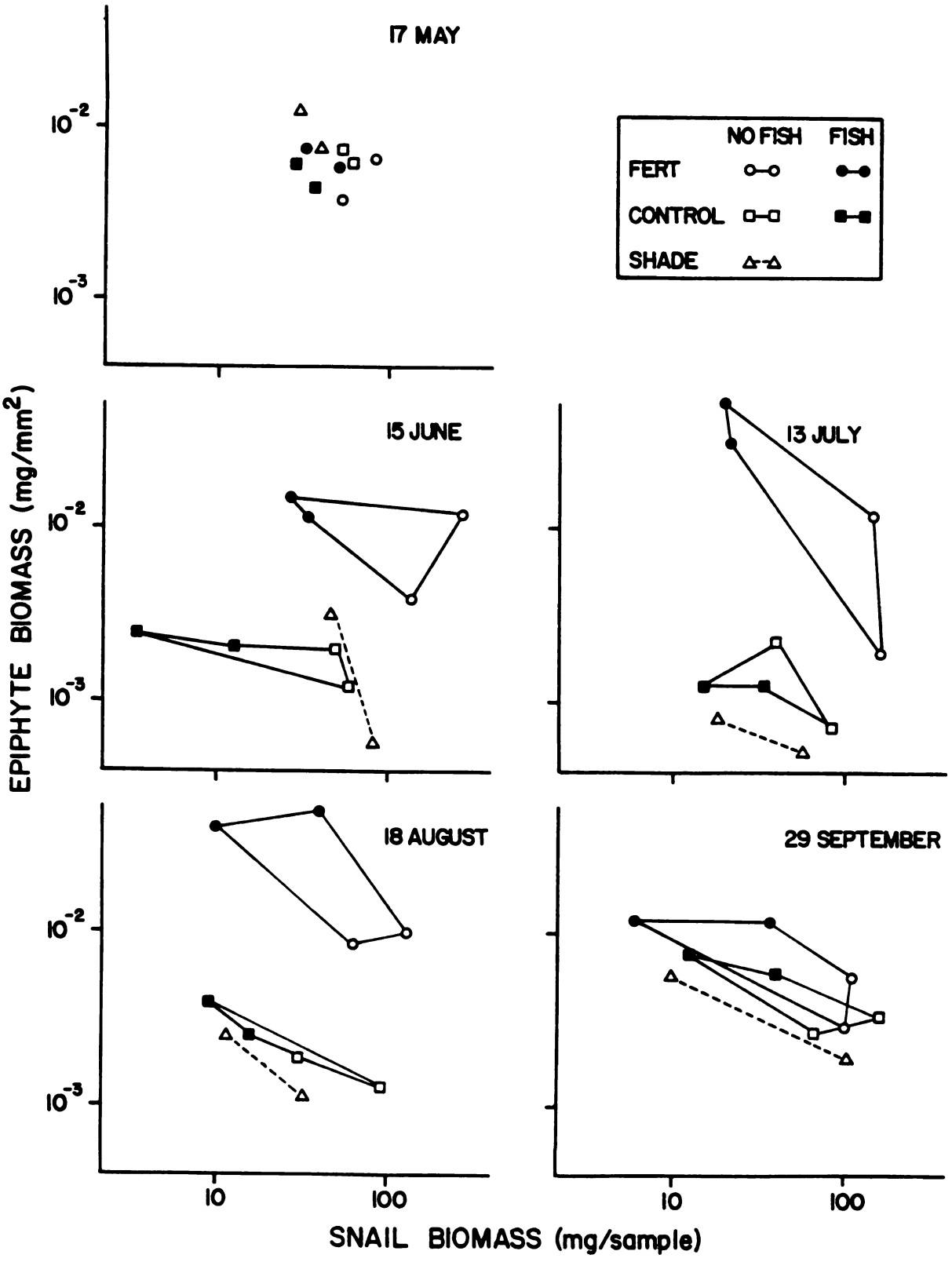
17 MAY
15 JUNE
13 JULY
18 AUGUST
29 SEPTEMBER
NO FISH
FISH
FERT
CONTROL
SHADE
EPIPHYTE BIOMASS (mg/mm²)
SNAIL BIOMASS (mg/sample)
10⁻²
10⁻³
10
100

Figure 4

were greatly reduced (Figure 4, 29 September). These patterns demonstrate the simultaneous effects of the treatments on the production and loss rates incurred by each trophic level (e.g. Brocksen et al. 1970).

## Species-Specific Responses in the Snail Community

I assessed species-specific snail responses by analyzing snail biomasses at two important points in the experiment. I examined the short-term responses by species by analyzing their biomasses on 15-30 June, which corresponded to the end of the period of highest food quality in the fertilized sites (i.e. before and just up to the filamentous algae bloom (Table 2)). I assumed that these data gave the best measure of the short-term response of snails to fish predation and epiphyte productivity, without incorporating the subsequent effects of snails on the epiphyte community. I also examined the final responses defined by biomasses on 15-29 September, which I assumed was the best available indication of the cumulative long-term effects of the manipulations (including feedback between the snail and epiphyte communities). At the end of the initial phase of the experiment, the biomass of each species was greatest in the fertilized/no-fish sites and least in the sites with fish or roofs (Figure 5). Physa and Helisoma showed the most extreme responses. The biomasses of Physa and Helisoma in the fertilized/no-fish sites were 55 and 144 times greater than in the shaded sites, while their biomasses in the fertilized/no-fish sites were 33 and 48 times greater than in the fertilized/fish sites. The responses by other species in these comparisons averaged only 6.3X (range: 1-16x). Thus, Physa and Helisoma were most responsive to variation in both fish and productivity levels at the start of the

Figure 5. Biomasses for each snail taxa in the five treatments during 15-30 June 1986. The mean biomass in two replicates per treatment is shown. Anova results are shown for the cross-factored design (— $p>.05$, * $p<.05$, ** $p<.01$). The analysis of treatment effects among the three non-fish treatments showed no significant effects. Data were log(x+1) transformed for analysis. Since young Marstonia and Amnicola had not yet recruited, their data are based on adults, while data for the other species are based almost exclusively on young snails (adults had died since reproducing). Data for Helisoma exclude adults, which generally represented a minor (although quite variable) part of the biomass. Lines connect means with the same fish densities and represent increasing productivities from left to right within a line segment.

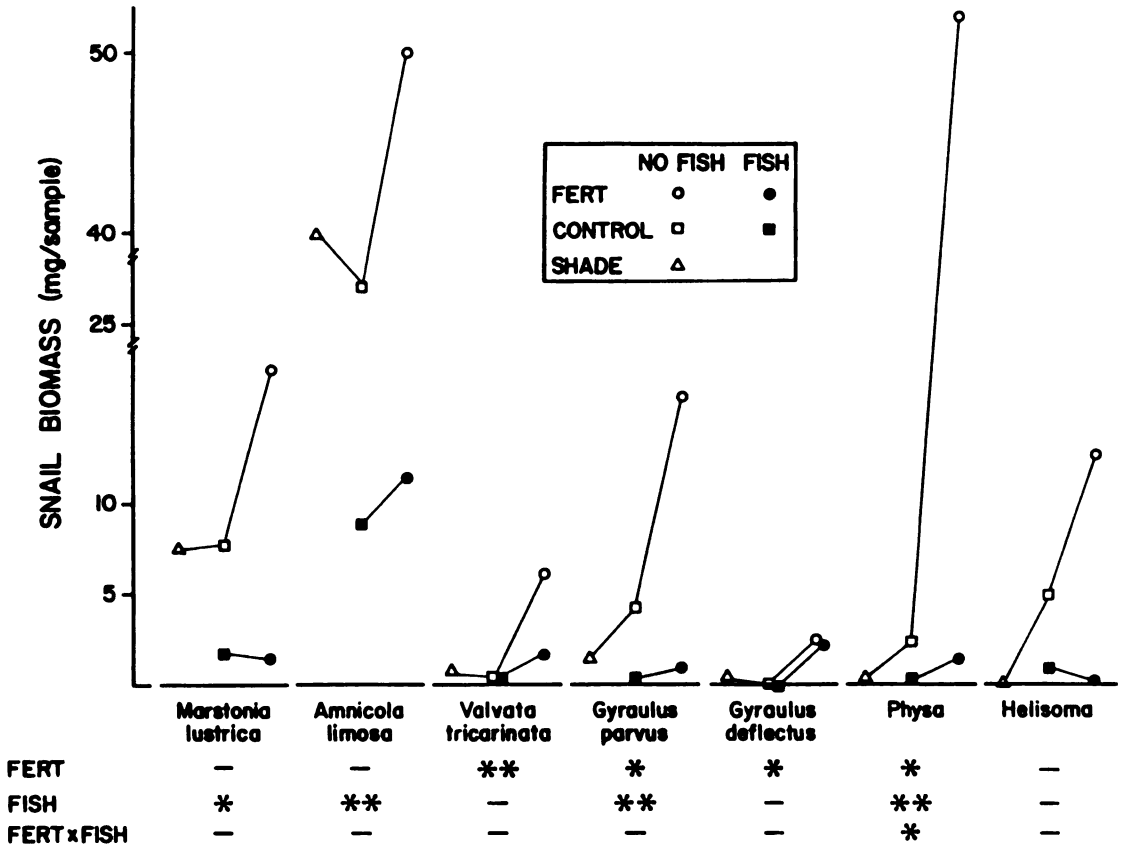
SNAIL BIOMASS (mg/sample)
50
40
25
10
5
NO FISH FISH
FERT
CONTROL
SHADE
Marstonia lustrica
Amnicola limosa
Valvata tricarinata
Gyraulus parvus
Gyraulus deflectus
Physa
Helisoma
FERT — — ** * * * —
FISH * ** — ** — ** —
FERT x FISH — — — — — * —

Figure 5

Figure 6. Biomasses for each snail taxa in the five treatments at the end of the experiment (14-29 September 1986). See legend to Figure 5. The analysis of treatment effects among the three non-fish treatments showed significant differences for G. parvus and for Physa. Data for Marstonia and Amnicola include young (cf. Figure 5) since recruitment occurred prior to these samples.

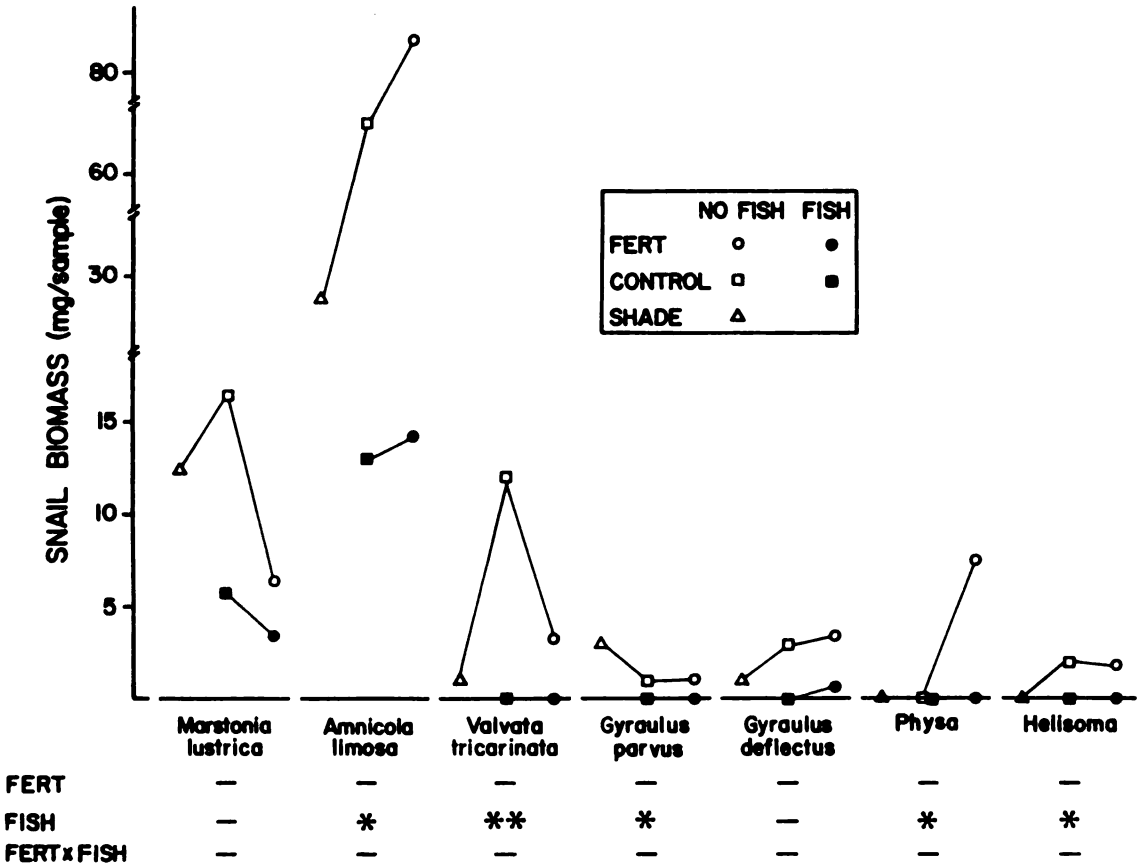
SNAIL BIOMASS (mg/sample)
80
60
30
15
10
5
NO FISH FISH
FERT
CONTROL
SHADE
Marstonia lustrica
Amnicola limosa
Valvata tricarinata
Gyraulus parvus
Gyraulus deflectus
Physa
Helisoma
FERT — — — — — — —
FISH — * ** * — * *
FERT x FISH — — — — — — —

Figure 6

experiment. By the end of the experiment, the effect of fish was still apparent for most of the snail taxa; however, the effect of epiphyte productivity had greatly diminished (Figure 6). All species except Amnicola and Marstonia were extinct (or close to extinction) in the fish treatments. Physa and Helisoma were also close to extinction in the shaded sites.

These data suggested that the responses by Amnicola and Marstonia were very different from the responses by Physa and Helisoma. Therefore I examined the temporal dynamics of these two important groups during the entire experiment (Figure 7). Despite showing reduced biomass in fish treatments and in the shaded and control sites, the biomass of Amnicola and Marstonia tended to increase through time in all treatments (Figure 7a: the decline between 15 and 31 June was related to the decline in adult densities due to reproduction associated mortality). Physa and Helisoma on the other hand were rapidly driven to extinction (or near extinction) in the fish treatments and the shade treatment (Figure 7b). Even the large biomass initially produced in response to fertilization (in the absence of fish) dissipated rapidly midway through the experiment. This peak biomass and the dramatic decline were correlated in time with the appearance and dominance by filamentous algae in the fertilized/no-fish sites (Table 2). The rather stable biomasses of Amnicola and Marstonia and the dynamic changes in Physa and Helisoma led to dramatic shifts in the relative contributions of Physa and Helisoma to the total snail community biomass (Figure 7c).

As a consequence of the differential responses by snail taxa (Figures 5, 6 and 7) the species diversity of the snail community varied through time among the treatments (Figure 8; Table 5). Early in the experiment (through July), species diversity was greatest in sites with enhanced productivity and/or without fish. After August, species

Figure 7. Temporal dynamics of biomass of a) Amnicola and Marstonia and b) Physa and young Helisoma in five experimental treatments. c) Proportion of total snail biomass comprised by Physa and young Helisoma. Means of two replicates per treatment are shown. Results of repeated measures Anova are given in Table 4.

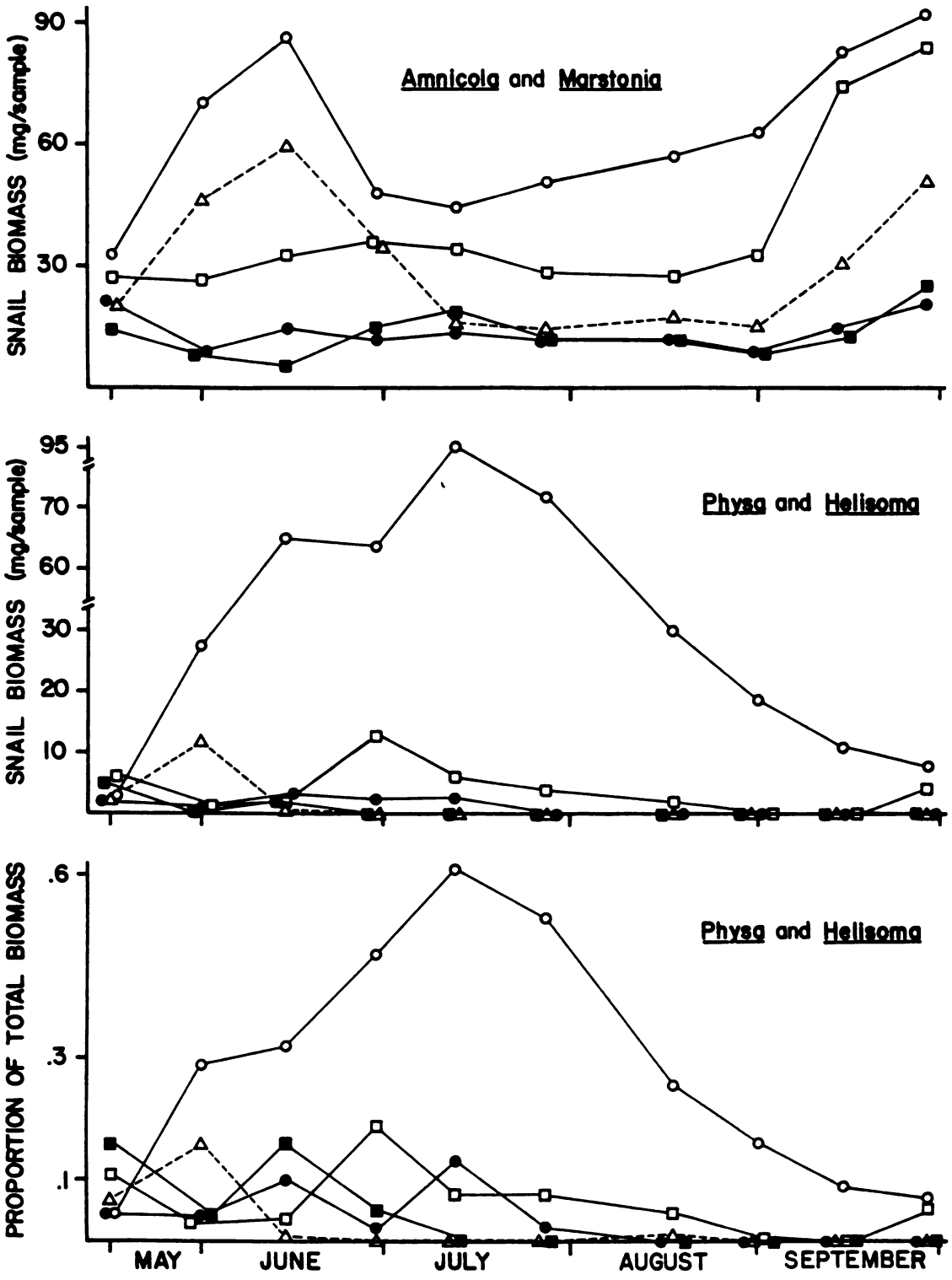
SNAIL BIOMASS (mg/sample)
90
60
30
Amnicola and Marstonia
SNAIL BIOMASS (mg/sample)
95
70
60
30
20
10
Physa and Helisoma
PROPORTION OF TOTAL BIOMASS
.6
.3
.1
Physa and Helisoma
MAY
JUNE
JULY
AUGUST
SEPTEMBER

Figure 7

Figure 8. Species diversity through time in each of five treatments. Species diversity was defined using the Shannon-Weaver index: $H' = -\sum p_i \ln(p_i)$, where $p_i$ is the proportion of the total snail density comprise by species i. Means of two replicates per treatment are shown. Complete analyses are given in Table 5. Results from Anovas based on each date are shown at the bottom of the figure for the cross-factored design: -- $p>.05$, * $p<.05$, ** $p<.01$. Analyses based on the three no-fish treatments showed significant differences only for the mid-June sample.

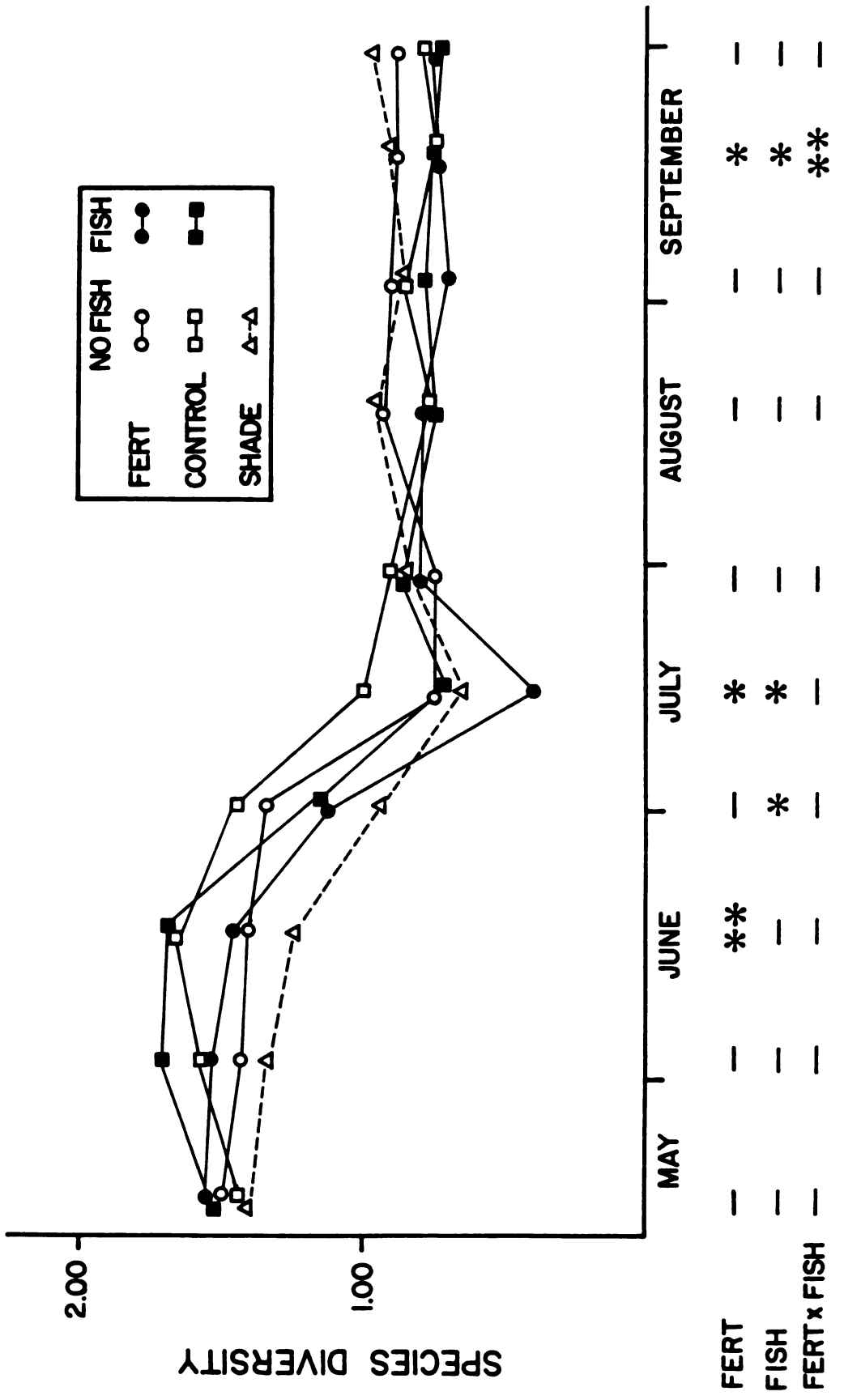
NO FISH FISH
FERT
CONTROL
SHADE
SPECIES DIVERSITY
2.00
1.00
MAY
JUNE
JULY
AUGUST
SEPTEMBER
FERT
FISH
FERT x FISH
**
*
*
*
*
**

Figure 8

Table 4. Summarized results of repeated measures Anova for biomass of Amnicola and Marstonia, Physa and Helisoma, and proportion of total snail biomass comprised by Physa and Helisoma (see Figure 7). See legend to Table 1 for description of analyses. Data for Amnicola and Marstonia were log tranformed. Data for Physa and Helisoma were log(x+1) transformed. Proportions were arcsin-squareroot transformed. This table provides F ratios for tests associated with the listed effects.
* $p<0.05$, ** $p<0.01$, *** $p<0.001$.

| Source | Amnicola and Marstonia | Physa and Helisoma | Proportion |
|---|---|---|---|
| FISH x FERTILIZATION: | | | |
| fish | 28.45 ** | 55.96 ** | 45.25 ** |
| fertilization | 0.67 | 21.94 ** | 23.27 ** |
| fish x fert | 0.75 | 17.75 * | 20.32 * |
| cage(fish x fert) | 6.61 *** | 2.67 * | 1.55 |
| date | 2.11 * | 4.82 *** | 7.18 *** |
| fish x date | 1.80 | 3.03 ** | 3.17 ** |
| fert x date | 1.26 | 3.59 ** | 3.66 ** |
| PRODUCTIVITY: | | | |
| treatment | 1.44 | 25.84 * | 38.22 ** |
| cage(treatment) | 14.59 *** | 3.29 * | 1.44 |
| date | 3.46 ** | 3.61 ** | 4.16 ** |
| treatment x date | 1.44 | 3.37 ** | 3.02 ** |

Table 5. Results of repeated measures Anova for snail species diversity (see Figure 8). See legend to Table 1.

| Source | df | Sums of squares | F | p |
|---|---|---|---|---|
| FISH x FERTILIZATION: | | | | |
| fish | 1 | 0.105 | 3.79 | 0.124 |
| fertilization | 1 | 0.070 | 2.53 | 0.187 |
| fish x fert | 1 | 0.009 | 0.33 | 0.599 |
| cage(fish x fert) | 4 | 0.111 | 2.43 | 0.061 |
| date | 9 | 9.386 | 91.78 | 0.001 |
| fish x date | 9 | 0.361 | 3.53 | 0.002 |
| fert x date | 9 | 0.329 | 3.22 | 0.004 |
| error | 45 | 0.511 | | |
| PRODUCTIVITY: | | | | |
| treatment | 2 | 0.110 | 2.11 | 0.268 |
| cage(treatment) | 3 | 0.078 | 1.23 | 0.318 |
| date | 9 | 4.418 | 23.27 | 0.001 |
| treatment x date | 18 | 0.696 | 1.83 | 0.075 |
| error | 27 | 0.570 | | |

diversity in all treatments stabilized to similar and relatively low levels, due to the dominance by Amnicola and Marstonia in all treatments.

The previous analyses demonstrate that resource productivity and fish density were influential in determining snail dynamics during the experiment. However, these analyses provide very little understanding of how these dynamics were produced. In the following section I examine the available data in more detail, attempting to determine how the treatments influenced three important demographic components: recruitment, survivorship, and the growth of individual snails.

To examine patterns of recruitment, I estimated the density of each species' cohort in each cage by counting the number of young on the earliest possible date following reproduction (i.e. when the snails comprising the cohort were large enough to be retained on the 0.5 mm sieve). Recruitment was greatest in the sites without fish and in sites that were fertilized (Figure 9). Due to large variability, many of the effects were not statistically significant; however, each of the species exhibited similar qualitative responses. These patterns in recruitment were probably produced by several mechanisms, including differential survival of adults, differential growth and therefore fecundity of adults (Eisenberg 1970; Brown 1985; Chapter 2), and differential survival of eggs and very young snails (Chapter 3). It is very difficult to assess the influence of each of these processes without detailed demographic data, but some of these can possibly be ruled out for some species. For example, Valvata, Helisoma, Physa and G. parvus all reproduced during the beginning of May and into the earliest part of the experiment. Thus, effects mediated through the adults were probably small, suggesting that the primary differences in recruitment were

Figure 9. Densities of recruits for each species in the five treatments. Data derived from different dates depending on the recruitment and growth patterns of the species (see text). Means from two replicates are shown. The scale on the left is for the prosobranchs and the scale on the right is for pulmonates. Symbols as in Figure 1. Anova detected significant effects of fertilization for G. deflectus and Helisoma ($p=.02$), significant effects of fish for Physa ($p=.04$) and marginally significant effects of fish for Amnicola, Valvata, G. deflectus and Helisoma ($p<.09$). None of interactions (based on log transformed data) were significant. Comparison of the three no-fish treatments showed significant effects for Helisoma ($p=.01$) and Physa ($p=.08$).

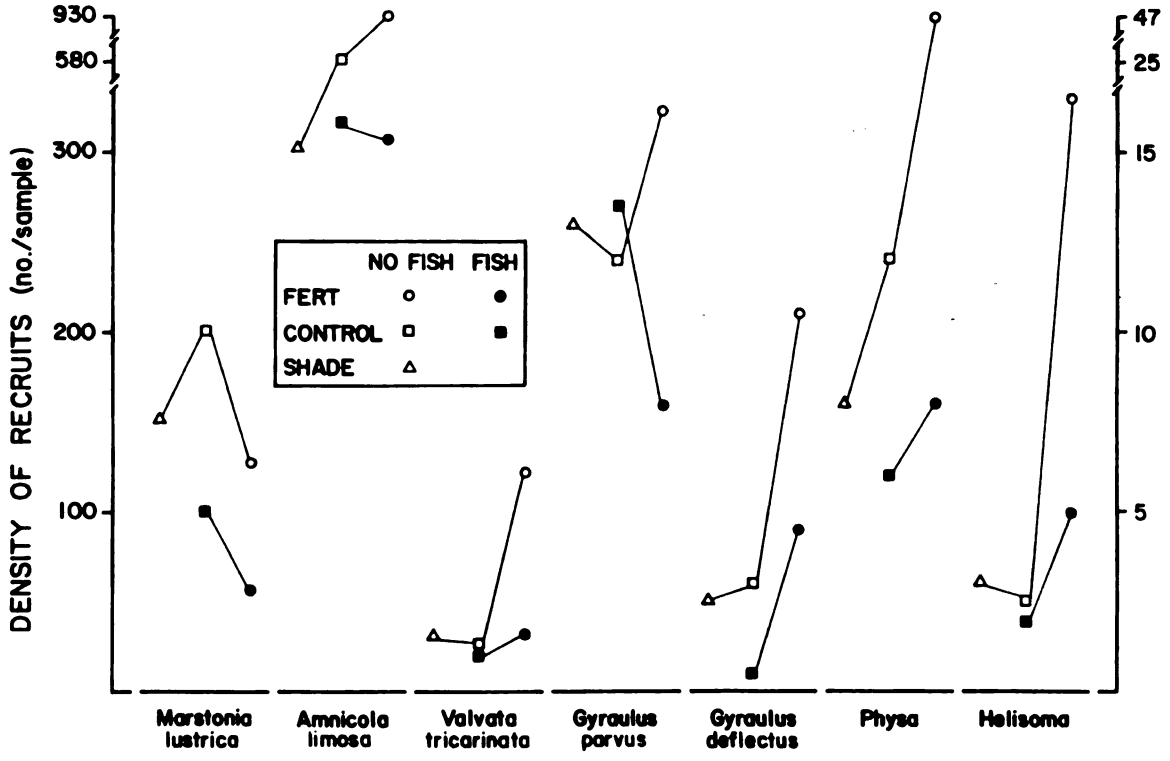
DENSITY OF RECRUITS (no./sample)
930
580
300
200
100
47
25
15
10
5
NO FISH FISH
FERT
CONTROL
SHADE
Marstonia lustrica
Amnicola limosa
Valvata tricarinata
Gyraulus parvus
Gyraulus deflectus
Physa
Helisoma

Figure 9

largely attributable to differential survival of eggs and young snails (see also Chapter 3).

It is more difficult to evaluate the importance of the various processes for Amnicola, Marstonia and G. deflectus, which reproduced later than the other species. However, adult densities and mean masses for adult Amnicola and Marstonia during the approximate time that they were reproducing show that the effects of treatments on the adult populations could explain the recruitment patterns without invoking differential survival of young (Table 6). Adults were more abundant in the absence of fish, and they were larger in fertilized sites, which together led to a significant correlation between the biomass of adults and the number of recruits observed in a cage ($r=0.65$, $n=10$, $p<0.05$ for Amnicola and also for Marstonia).

Growth rates of new recruits were also calculated. In particular, I was interested in determining if growth rates were enhanced by fertilization, and if the enhancement disappeared following the bloom of large filamentous algae, as expected if the filamentous algae were inedible or of low nutritional quality. Growth rates depend not only on environmental conditions (the factor of interest in this analysis), but they also depend on the size of the animal (Calder 1984; Osenberg et al. 1988). Since environmental conditions and snail sizes varied among treatments (and through time within a treatment), the effects of size and the environment could not be simultaneously assessed. Therefore, I assumed that growth could be modeled according to a power function $\Delta m/\Delta t = am^b$, where m is the observed change in mass, t is the time period over which the growth occurred, m is the mass at the beginning of the time period, a is the growth constant, and b is the allometric scaling parameter. Many studies have shown that the scaling parameter, b, varies around 0.75 (Peters 1983; Calder 1984). Therefore I corrected

Table 6. Densities and mean masses of adult A. limosa and M. lustrica. Data are based on samples collected 15 June for A. limosa and 30 June for M. lustrica. Means (and ranges) from the two replicates per treatment are given. Densities are expressed as numbers per sample. Masses are expressed as mg dry mass per snail.

| | Fish | No-fish |
|---|---|---|
| A. limosa | | |
| Density: | | |
| Fertilized | 18.5 (12- 25) | 97.5 (58-137) |
| Control | 9.5 ( 5- 13) | 60.5 (60- 61) |
| Shaded | --- | 110.0 (83-137) |
| Mass: | | |
| Fertilized | 0.67 (0.64-0.70) | 0.66 (0.60-0.71) |
| Control | 0.39 (0.37-0.42) | 0.41 (0.39-0.43) |
| Shaded | --- | 0.44 (0.41-0.48) |
| M. lustrica | | |
| Density: | | |
| Fertilized | 3.0 (2-4) | 23.5 (17-40) |
| Control | 3.5 (3-4) | 20.0 (14-26) |
| Shaded | --- | 15.0 (11-19) |
| Mass: | | |
| Fertilized | 0.44 (0.43-0.45) | 0.46 (0.45-0.48) |
| Control | 0.44 (0.42-0.46) | 0.37 (0.34-0.41) |
| Shaded | --- | 0.37 (0.35-0.38) |

for the influence of snail size and estimated the growth constant, a (the estimate of environmental quality) by dividing the observed growth rate by $m^{0.75}$: $a = m^{-0.75}(\Delta m/\Delta t)$

Snail size distributions were used to determine the mean mass of snails occurring in peaks of the size distributions in order to calculate changes in mass between successive sampling dates. Size-specific mortality can bias these estimates; therefore I did not use data from the sites with fish (although mortality may have still imposed a bias in the three no-fish treatments). For many species, there were few estimates of growth available from the experiment, therefore I combined the data for each species into categories based on two broad distinctions: 1) I combined data from the shade and control sites into an "unfertilized" category (epiphyte biomasses were relatively similar among these treatments (Figure 1)), and 2) I aggregated the data from the ten different dates into three time periods: 2 May - 15 June (early), 15 June - 18 August (mid) and 18 August - 29 September (late). The early period preceded the bloom of filamentous algae in the fertilized/no-fish sites. Adjusted growth rates were highest during the early period in the fertilized sites, but dropped dramatically during the mid and late periods to levels close to (or below) the growth rates in the unfertilized sites (Figure 10). Thus fertilization reduced food limitation and led to increased growth rates of snails during the initial phase of the experiment. However, growth rates in these fertilized sites subsequently decreased, and the precipitous decline was correlated with the dramatic shift in the epiphyte community towards large filamentous algae that appear to have been resistant to grazing (Table 2).

In the final analysis, I compared the survivorships of snails among the different treatments by following the numbers of snails in each

Figure 10. Relative growth rate for young cohorts of each taxa during three periods of the experiment in fertilized and unfertilized sites (without fish). See text for explanation. Plotted are the means $\pm$ 1 s.e., based on backtransformations from log tranformed data (standard errors smaller than the symbols are not shown). Sample sizes range from 2 to 20 and average 6.5.

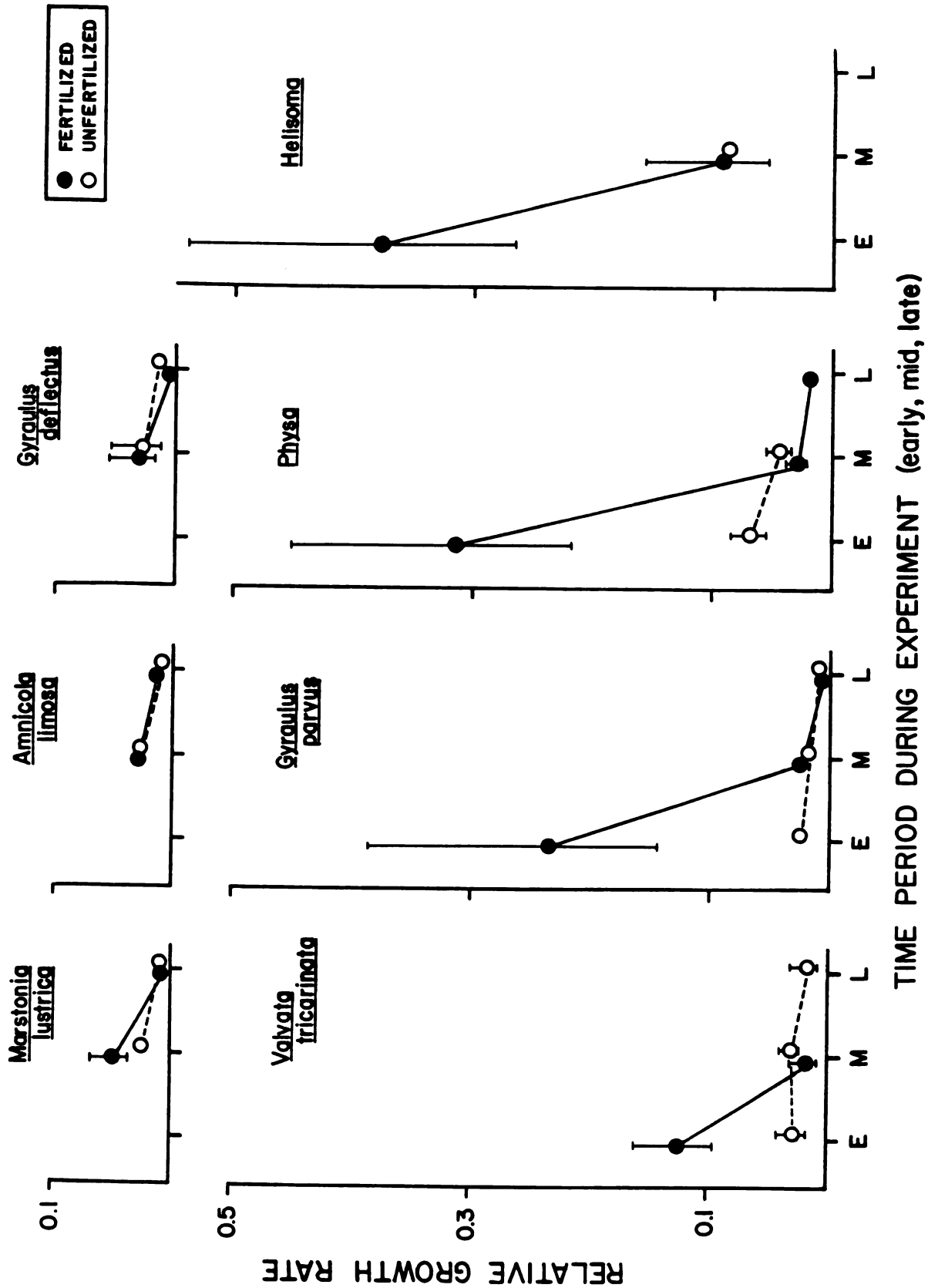
FERTILIZED
UNFERTILIZED
Marstonia lustrica
Amnicola limosa
Gyraulus deflectus
Helisoma
Valvata tricarinata
Gyraulus parvus
Physa
0.1
0.5
0.3
0.1
E M L
E M L
E M L
E M L
RELATIVE GROWTH RATE
TIME PERIOD DURING EXPERIMENT (early, mid, late)

Figure 10

definable cohort through time in each treatment (due to sampling variation and low sample sizes for some species, I combined the densities observed in two replicates into one measure per treatment). I used the initial density of the cohort (defined on the first date on which the entire cohort was clearly retained on a 0.5 mm sieve) to adjust all subsequent densities in order to obtain a percentage surviving through time. Cohorts of Physa and G. parvus could not be clearly defined (beyond single sampling intervals) and many other species and treatment combinations did not have sufficient densities to permit reliable calculation of survivorhip curves. Data that were obtained are shown in Figure 11. The principal pattern evident from Figure 11 is that fish increased the mortality rates of all cohorts, except for young Marstonia, which were still very small (<0.17 mg) and probably not encountered by fish (Chapter 1). Effects of food levels could not be evaluated due to the absence of reliable estimates of cohort densities (and therefore survival) during the early part of the experiment (prior to the bloom of filamentous algae).

## DISCUSSION

The results of this experiment demonstrate that there were strong linkages among all three trophic levels in this simple community consisting of fish, snails and algae. Manipulations of fish and productivity simultaneously influenced snail and algal biomass. Indeed, this experiment clearly showed that top-down and bottom-up processes interact to determine patterns of abundance in the snail-epiphyte system. The effects of fish on snail biomass were transmitted an additional step to the algae, resulting in inverse correlations between the abundances of fish and snails and between the abundances of snails

Figure 11. Survivorship curves for snails in five experimental treatments. See text for explanation. Curves for Helisoma and G. deflectus are indicated by H or G. Curves were terminated after densities declined below 5% of the initial cohort densities.

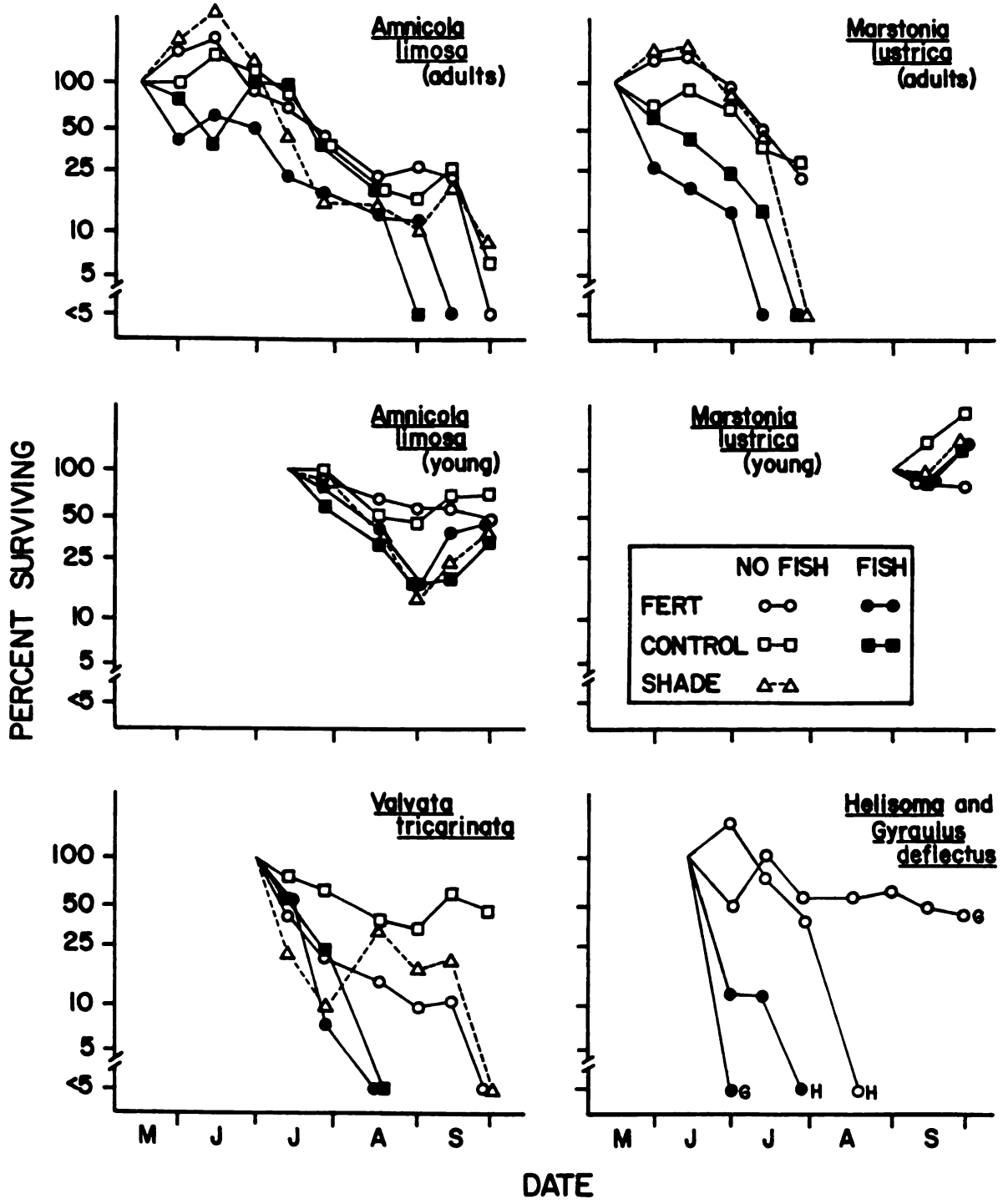
Amnicola limosa (adults)
Marstonia lustrica (adults)
Amnicola limosa (young)
Marstonia lustrica (young)
NO FISH FISH
FERT
CONTROL
SHADE
PERCENT SURVIVING
100
50
25
10
5
<5
Valvata tricarinata
Helisoma and Gyraulus deflectus
G
H
H
M J J A S
DATE

Figure 11

and epiphytes (within a productivity level). Productivity effects were first manifest in increased biomass of algae and then transmitted an additional step upward to the snail community. These patterns were produced by the simultaneous effects of the treatments on the production and loss rates incurred by each trophic level (Brocksen et al. 1970), and provides an important example of the different patterns produced by variation in the densities of top predators and by variation in nutrient supply or potential primary production (McQueen et al. 1986; Mittelbach et al. 1988; Leibold 1988).

In presenting my interpretations of the indirect effect of fish on epiphytes, I have assumed that the positive effect of fish was attributable to the combined negative effect of fish on snails and the subsequent release of the algae from snail grazing. It is also possible that the effect of fish was mediated by their role in recycling nutrients. For example, fish might have excreted phosphorus and thereby increased the growth and biomass of epiphytes. However, work by Kitchell et al. (1975) and Nakashima and Leggett (1980) suggest that the amount of phophorus released by fish is rather small compared to other sources. In particular, Nakashima and Leggett suggested that phosphorus released by the prey of fish (zooplankton in their study) is much greater than the amount released by fish. Therefore, fish may actually reduce nutrient recycling by reducing prey densities. Additionally, phosphorus might be lost from the system through sedimentation of fish fecal pellets (Nakashima and Leggett 1980). These arguments suggest that fish did not significantly increase nutrient recycling in the community, but suggest instead that the indirect effect of fish on epiphytes was mediated primarily through the reduction of snail biomass.

The feedback between snails and epiphytes was more complicated than a simple reduction in epiphyte biomass at high snail densities. Grazing

also contributed to a shift in the composition of the epiphyte community (Table 2), which probably had subsequent effects on the dynamics of the entire system. High biomasses of snails (which were produced by fertilization in the absence of fish) led to an epiphyte community dominated by filamentous green algae, primarily Mougeotia. This shift toward grazing-resistant algae probably resulted from a combination of the high grazer densities and the altered nutrient status within these cages. Similar changes have been noted in plankton communities under high nutrient loadings and high grazer densities (e.g. Lynch and Shapiro 1981; Vanni 1987b; Leibold 1988). The increased biomass of resistant algae buffers the primary producers from further losses imposed by the grazer trophic level. For example, in this study, the bloom of filamentous algae brought a rapid halt to the dramatic increase in snail biomass that had been developing in the fertilized/no-fish sites. Snail growth rates and biomasses decreased for many species during the second half of the experiment in these sites (Figures 6 and 10). If the epiphyte community had not shifted toward greater dominance by grazing-resistant algae, then energy would have continued to flow quickly through the relatively edible components of the epiphyte community and into snail biomass. Instead, the filamentous algae in the fertilized/no-fish sites acted as a sink for phosphorus and prevented further increases in snail biomass (see Phillips 1974; Leibold 1988).

The effect of algae on snail performance (e.g. growth) can be influenced by two general characteristics of the epiphyte community: its quantity (e.g. biomass) and its quality (e.g. availability and digestability). The early phase of the experiment provided comparisons in which epiphyte quantity, but not quality varied among the treatments, while the early and late phases within the fertilized/no-fish sites provided a comparison of the effects of food quality (due to the

presence of the filamentous algae). In the following section, I compare the responses of different snail species to variation in the quantity and quality of food and I suggest several explanations for this variation in response.

Physa and Helisoma showed the most dramatic short-term responses to variation in epiphyte biomass (Figures 5 and 7). The biomass of each of these species increased by over 50 fold in the fertilized/no-fish sites compared to the shaded sites. No other species' biomass varied by more than 10 fold between these sites (Figure 5). Physa and Helisoma are the largest species in the community: adult Helisoma are typically larger than 10 mg dry mass, and adult Physa commonly reach 3-5 mg (rare individuals can attain masses exceeding 20 mg). No other snails in this community get larger than 3 mg. Because these two species achieve adult size in the same (or less) time than other species in the snail community, Physa and Helisoma have the greatest potential individual growth rates of any of the species. In addition, both species appear to have relatively high activity levels based on their movement rates in laboratory aquaria (Osenberg, personal oberservation). Indeed, metabolic rates reported by Berg and Ockelmann (1959) show that Physa and other related pulmonates have metabolic rates that are approximately double those of prosobranchs, after correcting for body size differences. These differences in metabolic rates appear to be more related to activity level and potential growth rate than to adult size per se. For example, Bythinia tentaculata was the largest prosobranch studied by Berg and Ockelmann, and although it often reaches sizes comparable to many of the large pulmonates studied by Berg and Ockelmann, it still had a much lower mass-specific metabolic rate. However, Bythinia takes several years to reach this large size whereas the large pulmonates reach their large sizes in less than one year.

Interestingly, Berg and Ockelmann also report data for two small ancylids (freshwater limpets that are in the pulmonate group) that are annuals with small body size and therefore have growth rates similar to small prosobranchs (e.g. Amnicola). These snails had mass-specific metabolic rates that were similar to the prosobranchs studied by Berg and Ockelmann. Thus it appears that the snail species that exhibited the greatest variation in biomass accumulation in the Lawrence Lake experiment (i.e. Physa and Helisoma) were also the species with the greatest potential growth rates and relatively high mass-specific metabolic rates.

Laboratory work on herbivorous zooplankton also show that species with the greatest maximal growth rates (in general those species with large adult body mass) exhibit the greatest variation in production (individual growth or fecundity) under a range of food densities (e.g. Tillman and Lampert 1984; Tessier and Goulden 1987). For example Tessier and Goulden (1987) raised three species of cladocera at four food levels. The largest species exhibited the greatest growth rate at high food levels, but exhibited the poorest growth at low food levels. The smallest species on the other hand did better than the other two species at low food levels and worst at high food levels.

These data for zooplankton and snails suggest that there is a trade-off between metabolic efficiency and ingestion rates. That is, the largest species have high ingestion rates due to their high activity levels, but these active animals incur greater mass-specific energy losses due to their increased metabolism. At high food concentrations, the gain in ingestion far outweighs the metabolic loss, and the large active species fair proportionately better than smaller species. At low food abundances, ingestions rates are reduced and metabolic efficiency becomes more important in determining relative growth. The larger

species expend energy more quickly than the smaller species (even after correcting for body size) and therefore perform relatively poorly. Thus at low food, the more conservative strategy is advantageous (see also Persson 1985, Bengtsson 1987).

The advantages of metabolic efficiency can also be important during periods when food quality is low, for example, following the bloom of Mougeotia in the fertilized/no-fish sites. Despite the high biomass of algae during this period (Figure 1), Physa and Helisoma performed exceptionally poorly (Figure 7), while other species, in particular Amnicola and Marstonia, performed comparatively well (Figure 7). Another factor, acting in concert with the poor metabolic efficiency of the two large pulmonates, probably helps explain these extreme differences among snails in their reponse to the proliferation of filamentous algae. Calow and Calow (1975) showed that green algae were relatively difficult for snails to assimilate due to the resistance of the cellulose wall to degradation. However, some snail taxa could assimilate green algae with high efficiencies because they possessed high cellulase activities. Of the thirteen species studied by Calow and Calow, the four prosobranchs had greater cellulase activities and assimilation efficiencies than the nine pulmonate species. For example, the assimilation efficiencies of the prosobranchs averaged 89%, while the assimilation efficiency for Physa was only 39% and averaged only 27% for three species of Planorbis (which is in the same family as Helisoma). Kesler and Tulou (1980) found cellulase activities for A. limosa that were very similar to those found for the prosobranchs studied by Calow and Calow.

Based on these studies of cellulase activity and metabolic rates, I suggest that the initially large response of Physa and Helisoma to variation in epiphyte biomass was mediated primarily through their

greater activity levels (metabolic rates) and potential for high secondary production. The subsequent decline in their biomasses following the bloom of grazing-resistant green algae was probably mediated by both their higher metabolic costs and their relatively poor ability to digest the green algae. However, because the algal filaments extended as clouds into the water column and were largely inaccessible to snails, the role of differential digestibility might be rather small. The primary explanation for the decline in biomass of Physa and Helisoma might be that available food levels were very low relative to the high maintenance costs associated with these snail species.

In addition to showing the most exteme responses to epiphyte biomass and composition, Physa and Helisoma also exhibited the most extreme responses to predator density. During the first part of the experiment, their biomasses in fertilized/no-fish sites were more than 30 times greater than in the fertilized/fish sites. No other species showed a response greater than 16 fold (Figure 5). The absolute magnitudes of these responses were very large compared to the results from a previous experiment conducted in a nearby lake (Palmatier Lake) using natural densities of pumpkinseeds (approximately 1/4 the density used in this experiment: Chapter 2). However, the relative effects on the snail species were fairly similar in both of these experiments. In particular, Physa and Helisoma incurred greater mortality rates due to pumpkinseed predation in Palmatier Lake than 6 of the 7 other snail species. The only species incurring a greater mortality rate was G. deflectus, which showed the smallest biomass response to fish in this experiment. However, the effects of fish were measured at different times during the life-history of G. deflectus in these two experiments. The Palmatier Lake experiment was conducted in late summer after young G. deflectus had already grown to large sizes and were very vulnerable

to fish predation. In Lawrence Lake, adults were exposed to fish for only a brief period at the beginning of the experiment, and newborns had only hatched recently when the samples shown in Figure 5 were collected (see also Figure 11). Thus, encounter rates between G. deflectus and fish were very low in Lawrence Lake, but much larger in Palmatier Lake, leading to the differences in the rankings of the effect of fish.

Encounter rates, which increase with snail size, play a central role in determining fish-mediated mortality rates (Chapters 1 and 2). Physa and Helisoma show the greatest negative responses to fish because they spend more time than the other species at larger sizes, due to their large adult size. Thus, adult body size plays an important role in determining both the effects of food and the effects of predators. Snails from species with large adults spend more time at larger sizes and therefore are encountered by predators more often than are smaller species. In addition, the large adult body size requires that activity levels be high in order to achieve the large adult size in the same time as smaller species. Thus the two largest species were most affected by both food and fish and the particular explanations of these effects depend on the ways body size influences different aspects of the snails' ecologies (Chapters 1, 2 and 3).

Over short periods of time, Physa and Helisoma can do exceptionally well when food is abundant and predators are rare. In these situations, the diversity of the snail community increases owing largely to the greater representation of these two naturally rare species (Figures 5-8). However this community structure is unstable over the long term owing to the strong response by the epiphytic community. Therefore, the conditions required by Physa and Helisoma in order to achieve biomasses comparable to Amnicola and Marstonia, high nutrient levels and low fish densities, are the same conditions that favor grazing-resistant algae.

Thus Physa and Helisoma incur strong limitation mediated through bottom-up and top-down processes. Given these results, it is rather suprising that these two large pulmonates co-exist in the lake community at all, rather than being completely restricted to temporary or shallow ponds that lack fish and prosobranch snails (Osenberg, personal observation). Their maintenance in the lake ecosystem could be produced by a number of mechanisms. For example, theoretical work by Levins (1979), Armstrong and McGhee (1976, 1980) and Abrams (1984) have shown that temporal fluctuations in resouce abundances can lead to coexistence of consumers that all use a single resource. Epiphyte biomass is known to be temporally (and spatially) variable in many lake systems (e.g. Castenholz 1960; Cattaneo and Kalff 1978; Burkholder 1986; Meulemans 1988). These pulses (or patches) of high epiphyte biomass might be short-lived but probably provide Physa and Helisoma with resources that they can quickly convert into snail biomass (i.e. these snails are "variance specialists", sensu Levins 1979). The gains made during these favorable conditions are balanced by the losses incurred to predators and losses incurred during periods of low food availability. Physa and Helisoma do relatively poorly during these bad times, but their populations appear to be maintained by the inertia provided during the good conditions (Warner and Chesson 1985). On the other hand, I suggest that Amnicola and Marstonia have lower activity levels and are less responsive to fluctuations in food abundance: they exhibit a more conservative energetic strategy. As with Physa and Helisoma, they do better when food is abundant, but their performances are increased relatively slightly compared to the responses by the large pulmonates.

The theoretical studies cited above are all based on fluctuations that occur among generations and are therefore concerned with changes in population density. Much of the data for epiphyte dynamics shows that

the most extreme fluctuations in algal biomass occur seasonally and therefore within single snail generations. Therefore, the results from these theoretical studies are not strictly applicable to the snail-epiphyte community. However, in size-structured populations, I suggest that individual growth (or biomass accumulation) can probably influence coexistence under fluctuating resource levels in a manner similar to the situations modeled in the theoretical studies. Additional work on this question is needed given the ubiquitous occurrence of size-structured populations (Werner and Gilliam 1984) and the sensitivity of individual growth to short-term variation in resource levels (e.g. Chapter 3; Figure 10).

Physa and Helisoma might also be protected from extinction by a possible refuge from predation at low densities. Previous work on prey selection by pumpkinseeds suggested that additional resolution of prey selection by pumpkinseeds might be provided by consideration of patch selection (Chapter 1). If pumpkinseeds feed preferentially in patches that offer relatively high feeding returns, then preferred prey (e.g. Physa) could coexist at low densities with pumpkinseeds if less preferred prey (e.g. Amnicola) were abundant and the preferred prey occurred outside of the high-density patches (Murdoch and Oaten 1975; Murdoch 1977).

In summary, these experiments demonstrate strong connections among algal resources, epiphytes, snails and fish. The epiphyte and snail communities can be dramatically affected by environmental changes that cascade down through the food chain (e.g. by variation in fish density) or that flow up through the food chain (e.g. by variation in nutrient supply). Contrary to the common dogma in ecological literature, there is not a trade-off between traits that adapt a snail species to low resource availability and traits that adapt a snail species to high

predator densities (e.g. Paine 1966; Lubchenco 1978). Instead, the results of this experiment suggest that a correlated set of traits appears to provide protection from both types of adverse environments: small body size protects a species from predation by visually feeding pumpkinseeds, and metabolic efficiency (which is correlated with small adult size) buffers a species against poor food conditions. Thus the snail species that dominate under high food, high predator conditions are the same species that dominate under low food, low predator conditions (e.g. Amnicola and Marstonia). Other species (e.g. those with large adult body size) are favored primarily during the transient nonequilibrial phases following extreme perturbations to the system (e.g. when nutrients are abundant and fish are rare) and are subsequently a minor component of this littoral community.

# CHAPTER 5

# THE RELATIVE IMPORTANCE OF RESOURCE LIMITATION AND PREDATOR LIMITATION

# INTRODUCTION

A major challenge of community ecology remains the elucidation of the relative importance of different processes in limiting populations. A general theory must include how the importance of the processes vary spatially and temporally, and among species that differ in their morphologies, life-histories or positions in the food web. Several attempts have been made to synthesize existing data into general models that predict the relative importance of various processes: e.g. resource limitation, competition, predation, disturbance, and recruitment success (Hairston et al. 1960; Slobodkin et al. 1967; Connell 1975, 1978; Menge and Sutherland 1976, 1987; Oksanen et al. 1981). For example, Hairston et al. (1960) and Slobodkin et al. (1967) proposed that resource limitation and predator limitation alternated in importance among different trophic levels: i.e. primary producers and carnivores were resource limited while herbivores were predator limited. Although originally developed for terrestrial food chains, their ideas have been recently applied to other systems (Schoener 1983, 1985; Connell 1983; Sih et al. 1985; Persson et al. 1988).

Several recent reviews of competition and predation (Connell 1983; Schoener 1983; Sih et al. 1985) attempted to test the predictions of Hairston et al. (1960; Slobodkin et al. 1967) by surveying the literature and comparing the frequency of experiments in which competition (or predation) were detected. The tests consisted of compiling the proportion of all studies (or experiments or total comparisons) that showed <u>significant</u> effects of competition (for the reviews by Connell and Schoener) or predation (for the review by Sih et al.) on a target species. Thus these tests used statistical significance as an index of relative importance. However, a significant

result in a univariate test does not exclude the importance of other processes, nor does it indicate the primacy of the single process that was studied. Indeed, it is likely that many processes simultaneously limit populations (e.g. Quinn and Dunham 1983). The relative importance of a factor can only be ascertained by comparing the effect of a particular process (which is a quantitative measure of magnitude, not statistical significance) relative to the effect of other processes. Furthermore, as Oksanen (1988) has recently pointed out, combining the results from different systems can lead to erroneous conclusions about the importance of particular factors because differences among the systems (e.g. due to the number of trophic levels, or productivity) can alter the relative importance of factors (Smith 1969; Oksanen et al. 1981; Fretwell 1977, 1987).

Perhaps one of the best ways to explore the validity of these models would be to conduct several sets of experiments within a single ecosystem, each oriented at determining the relative importance of resource limitation and predator limitation at differential trophic levels. The comparison of results from these types of experiments in different ecosystems could lead to the development of more explicit models of the relative importance of factors that limit population growth. Tests of the predictions of Hairston et al.'s model within a single natural community do not exist; however, in the absence of an ideal data set, I use data from a single aquatic system (Lawrence Lake) to address the importance of food limitation and predation in a freshwater littoral community consisting of algae, herbivores, microcarnivorous fish and piscivorous fish. This work was largely motivated by my previous work on freshwater snails, which demonstrated that both resource limitation and predation were important in determining the dynamics of the snail community (Chapter 2, 3 and 4).

Additional data from these studies also provide information on the effects of nutrient limitation and grazing on epiphytic algae, and there are similar data for the effects of piscivorous fish and prey availability on predator and resource limitation in sunfish (Werner et al. 1983; Werner and Hall 1988; Mittelbach 1986; Osenberg et al. 1988; Turner and Mittelbach 1988). Few of these experiments were originally intended to be used to compare the relative importance of resource limitation and predator limitation, and therefore this synthesis is necessarily preliminary. Given the importance of this question however, and the lack of more appropriate data, this analysis should provide interesting insights into the simultaneous limitations imposed by resources and predators on several trophic levels.

## DEFINITIONS, METHODS AND RESULTS

Historically, "limitation", "regulation" and "control" have been used interchangeably in discussions of the relative effects of resources (or competition) and predation on population dynamics and community structure: this usage has led to some confusion (e.g. Ehrlich and Birch 1967; Slobodkin et al. 1967; Persson et al. 1988). Regulation and control refer to processes that maintain a population or community near a particular state, and therefore necessarily involve the action of negatively density-dependent processes that result from direct and indirect effects mediated throughout the community. Limitation, on the other hand, is a simpler concept and can be defined without reference to the potential complexities inherent in regulation: limitation is the extent to which a population's growth rate would increase following the removal of a limiting factor (e.g. predators). The difference between the growth rate in the natural system and the growth rate following the

removal of various limiting factors provides an estimate of the relative importance of each factor. For example, if the removal of predators produces a 100% increase in the growth rate of a population (compared to the natural growth), while the addition of surplus, high quality, food leads to a 500% increase, then I would argue that food limitation is 5 times more severe than predator limitation. It would also be possible to assess the importance of the interaction between two (or more) factors by simultaneously removing both sources of limitation and comparing the response with that predicted from the additive responses following removal of each factor separately. However, although interactions between resources and predators probably exist within this system (Werner et al. 1983; Mittelbach 1986), the available data only allow me to address their separate effects.

Under ideal situations, population growth rates should be measured immediately following removal of the limiting factor, or by preventing other populations from changing abundances (i.e. indirect effects should be excluded from the results); however, this is rarely possible due to time lags in the responses of populations, or due to inherent difficulties in performing appropriate manipulations or in measuring very small short term responses. Thus, estimates of limitation will often include indirect effects in addition to the direct effects of removing the factor. Furthermore, because few populations reproduce continuously, measures of predator effects are often inferred from observed changes in survival (e.g. following the removal of predators) while measures of resource limitation typically involve changes in individual growth (e.g. following the addition of food). Thus, comparisons of limitation imposed by different factors are often difficult due to the use of various response parameters. In some cases, these responses can all be expressed in terms of changes in population

biomass (e.g. resulting from mortality or growth of individuals), thus permitting a comparison of the responses in a common currency.

In order to derive estimates of instantaneous rates of change in biomass production (or loss) following the removal of a limiting factor, I assume that population biomass changes exponentially according to:

$$B_t = B_0 e^{rt} \tag{1}$$

in the natural system, and

$$B_t^* = B_0 e^{(r+x)t} \tag{2}$$

in sites where the limiting factor has been removed. $B_0$ is the biomass of the focal population (or trophic level) at the start of the experiment (and is assumed equal in the two treatments), $B_t$ is the biomass of the control (i.e. natural) population after t days, r is the net instantaneous per capita growth (in terms of biomass) of the control population, $B_t^*$ is the biomass of the population in the absence of the limiting factor after t days, and x is the additional population growth resulting from the removal of the limiting factor. Therefore, x is a quantitative estimate of limitation caused by the factor. In cases where t is the same in each treatment, x can be estimated by as:

$$x = \ln(B_t^*) - \ln (B_t) \; / \; t \tag{3}$$

In other conditions,

$$x = \ln(B_t^*/B_0)/t^* - \ln(B_t/B_0)/t \tag{4}$$

where $t^*$ is the length of time during which the limiting factor was removed.

Before presenting the estimates of resource and predator limitation, let me briefly describe the composition of the Lawrence Lake littoral community and the types of experiments used to estimate limitation. The epiphyte assemblage forms the base of the littoral food chain and consists primarily of small closely adhering microalgae (Burkholder 1986). Resource limitation in these algae was demonstrated by supplying large amounts of phosphorus fertilizer to sections of the littoral habitat (Chapters 3 and 4). Biomass accumulation in fertilized and control sites was used to assess limitation imposed by phosphorus availability. Estimates were restricted to the first month of any experiment in order to minimize the subsequent effect of snail biomass, which increased following the increase in epiphyte biomass (Chapter 4).

The littoral grazer community in Lawrence Lake is dominated by gastropods (Mittelbach 1981b; Osenberg, personal observation). A gradient in gastropod densities was used to assess the extent to which snail grazing limited net production of epiphytes (Chapter 3). In another experiment, high densities of molluscivorous fish were confined to cages and reduced snail densities below natural densities. These changes in snail biomass were also used to estimate the response of epiphytes to the complete removal of snails (data were extrapolated from reduced snail biomasses to complete removals).

The snail assemblage consists of eight species, most of which graze on epiphytic algae during their entire life histories. Food limitation in these herbivores was assessed by quantifying the change in biomass following greatly increased epiphyte biomasses (which followed fertilization). Again, biomass was measured at the end of the first month, so that feedback between snails and epiphytes (e.g. a shift

towards grazing-resistant algae) would be small (Chapter 4).

Effects of large snail predators appear to be relatively small in Lawrence Lake (Chapter 3), although direct tests have not been conducted. However, a field test was made of the effect of pumpkinseed sunfish (Lepomis gibbosus) on snail abundances in a nearby system, Palmatier Lake. Because Palmatier Lake and Lawrence Lake have similar densities of pumpkinseeds (Osenberg et al. 1988), the effects of pumpkinseeds are probably similar in the two lakes. Pumpkinseeds were chosen for manipulation in the study because they are the most conspicuous molluscivore in these lakes: fish >50 mm standard length obtain over 80% of their diet from snails (Mittelbach 1984; Chapter 1). The change in total snail biomass over a gradient in pumpkinseed densities was used to estimate the response of the snails to a complete removal of pumpkinseeds.

Estimates of food and predator effects are not available for molluscivorous sizes of pumpkinseeds in Lawrence Lake. There are however data for food and predator effects on juvenile pumpkinseeds, which feed on soft bodied littoral invertebrates (Mittelbach 1984). In addition, there are data for bluegill sunfish (L. macrochirus) which is the most abundant fish species in Lawrence Lake (Werner et al. 1977). The bluegill is also an important predator on non-molluscan littoral invertebrates (Mittelbach 1981a, 1984). Because bluegills and pumpkinseeds are very similar morphologically, the effects of piscivores on their mortality rates are probably similar (Mittelbach 1986; Werner and Hall 1988). In addition, because of the joint use of the littoral habitat by juveniles of both species, the patterns of growth of small and large fish of the two species are similar (Mittelbach and Chesson 1987; Osenberg et al. 1988; Mittelbach et al. 1988). For all of these reasons, I include data on bluegills and pumpkinseeds into the analysis

of resource and predator limitation of the third trophic level.

Resource limitation was assessed in experiments by Mittelbach (1986) and Werner and Hall (1988) in which they introduced small bluegills and pumpkinseeds into ponds that had been previously devoid of fish and thus had high densities of invertebrate prey. I compared these growth rates with growth rates taken from similar dates in Lawrence Lake (Mittelbach, personal communication; Osenberg et al. unpublished).

The primary predator on these sunfish are largemouth bass, Micropterus salmoides (Werner et al. 1977; Mittelbach 1981a; Gilliam 1982; Werner and Hall 1988; Turner and Mittelbach 1988). The effects of bass were assessed in several studies in which densities of bass (comparable to Lawrence Lake) were established in experimental ponds at the Kellogg Biological Station. Changes in bluegill biomass (or numbers) were then monitored in ponds (or sections of ponds) with and without bass.

In each of these experiments predator densities and resource densities were altered in particular ways. It is possible that different alterations in resources (i.e. food) might have produced even better growth responses. It is also possible that removal of additional predator taxa might have increased the responses in the predation experiments. Without extensive data on the nutritional requirements of consumers and the relative impact of different predators, ideal experiments testing for food and predator limitation cannot be achieved. Therefore the estimates of limitation for trophic levels in Lawrence Lake might be somewhat biased; however, in all cases, food limitation was assessed by creating what appeared to be close to ideal food conditions for the consumers, and in each predation experiment, the most obvious and putatively important predator was manipulated.

The results of each of these analyses are given in Tables 1 and 2,

Table 1. Estimates of food limitation in three trophic levels in Lawrence Lake. The estimates of limitation are based on equations 3 or 4 and represent changes in the instantaneous daily rate of biomass production.

| Trophic level | Limitation | Comments |
|---|---|---|
| Sunfish | 0.0139 | based on growth rates in ponds (high food) compared with growth during a comparable time period in another year in Lawrence Lake (based on raw data for bluegills summarized in Mittelbach 1986). |
| | 0.0410 | using same pond data as above but compared with annual growth of similar sized bluegills in Lawrence Lake during the same year, 1984. Annual growth was taken from raw data used by Osenberg et al. (1988) assuming a growth season of 150 days. |
| | 0.0408 | using data from the same pond experiment (based on growth of pumpkinseeds) compared with average annual growth of pumpkinseeds of similar size in Lawrence Lake (see above). |
| Snails | 0.0322 | based on accumulation of snail biomass during first month of fertilization experiment (Chapter 3). |
| | 0.0525 | based on accumulation of snail biomass during first month of fertilization experiment (Chapter 4). |
| Epiphytes | 0.1070 | based on accumulation of epiphyte biomass during first month of fertilization experiment (Chapter 3). |
| | 0.0878 | based on accumulation of epiphyte biomass during first month of fertilization experiment (Chapter 4). |

Table 2. Estimates of predator limitation in three trophic levels in Lawrence Lake. The estimates of limitation are based on equations 3 or 4 and represent changes in the instantaneous daily rate of biomass growth.

| Trophic level | Limitation | Comments |
|---|---|---|
| Sunfish | 0.0031 | based on mortality of juvenile bluegills and pumpkinseeds in a pond partitioned in half with and without bass (Werner and Hall 1988). |
| | 0.0010 | based on change in total bluegill biomass in a pond partitioned in half with and without bass. Bluegills of several size classes were used although mortality only occurred in the smaller sizes (Werner and Hall 1988). |
| | 0.0001 | based on change in total bluegill biomass in a pond partitioned in half with and without bass. Bluegills of several size classes were used and the result includes effects of survival and growth. Because some small fish were continually added to the pond half with bass, the estimate shown is the midpoint of the possible range: -0.0003 - +0.0005 (see Werner et al. 1983). |
| | 0.0002 | based on change in total bluegill biomass in ponds that were partitioned. Three sections had bass, while three did not. Bluegills were small to medium in size and the result includes effects of both growth and survival (Turner and Mittelbach 1988). |
| Snails | 0.0035 | based on the predicted differences in snail biomass at natural pumpkinseed densities and complete removal: generated from regression of snail biomass on pumpkinseed density established in an experiment in Palmatier Lake (Chapter 2). |
| Epiphytes | 0.0519 | based on the change in epiphyte biomass following the reduction in snail biomass (Chapter 3). |
| | 0.0098 | based on the change in epiphyte biomass one month after the addition of high pumpkinseed densities to cages in Lawrence Lake. The fish reduced snail biomass to 15% of the natural biomass (Chapter 4). The estimate was corrected to a correspond to a complete removal of snails. |

Table 3. Average values of food limitation and predator limitation in three trophic levels in Lawrence Lake. The relative importance of food limitation is the ratio of food limitation to predator limitation. See Tables 1 and 2.

| Trophic Level | Food Limitation | Predator Limitation | Relative Importance of Food Limitation |
|---|---|---|---|
| Sunfish | 0.032 | 0.001 | 29.0 |
| Snails | 0.042 | 0.003 | 12.1 |
| Epiphytes | 0.097 | 0.031 | 3.2 |

and the final summary is given in Table 3. Several patterns emerge from these data. First of all, as indicated in many of the original studies, resources and predators impose important constraints on each of the populations/trophic levels, and removal of either source of limitation causes increased performance of each population/trophic level, as indicated by limitation estimates greater than zero. Therefore, resources and predators simultaneously limit the production of all three trophic levels. However, these factors to not operate to similar degrees. Each trophic level showed a greater percent change in biomass in response to food addition than they did in response to the removal of predators. Therefore, resource limitation is more severe than predator limitation. However, the relative importance of resource limitation was greatest at the high levels in the food chain. Addition of food led to a 29-fold greater increase in rates of biomass production for sunfish than did the removal of predators. Similar comparisons for snails and epiphytes showed 12-fold and 3-fold variation, respectively. Finally, the change in biomass production due to release from limitation by either food or predators was strongest at the lowest trophic levels. This pattern is probably a simple consequence of the expression of limitation in terms of biomass specific production rates. Because smaller organisms have greater production to biomass ratios (Peters 1983), they should probably exhibit the greatest measures of limitation (at least as defined here).

## DISCUSSION

Although these comparisons are admittedly crude, they suggest that food limitation is consistently strong among epiphytes, herbivorous snails and microcarnivorous fish that coexist within the same lake

ecosystem (Gilliam 1982 also shows that the fourth trophic level, bass, is resource limited, but there are no available data on predation effects at that level). These data suggest that although predation (including herbivory) has documentable negative effects on prey biomasses, the effects of predation appear to be less than food-limitation in reducing the potential growth of each trophic level. These patterns are not predicted by the model of Hairston et al. (1960), nor are they suggested in the recent papers by Oksanen (Oksanen et al. 1981; Oksanen 1988), although Oksanen et al.'s model clearly includes the simultaneous effects of resource and predator limitation. The dominant role of food limitation has been suggested by Sinclair (1975; Sinclair et al. 1985) and White (1978) who argued that most plants are not suitable food for most herbivores (see also Murdoch 1966, Ehrlich and Birch 1967 and Rhoades 1985), and that similar forms of limitation might occur at higher trophic levels. The idea that trophic levels can be comprised by relatively unsuitable prey might explain the patterns of limitation in the Lawrence Lake system.

In freshwater systems predators are known to be able to restrict the types of prey that coexist with them. For example, strong effects of fish on invertebrate densities have been documented when fish are introduced into previously fishless situations (e.g. Brooks and Dodson 1965; Hall et. al. 1970; Crowder and Cooper 1982). The strongest effects of fish are often seen on the prey that do not naturally co-exist with the predator. Therefore, the prey that coexist with fish are relatively immune to predation, and recent studies have suggested that even within the natural prey community relative abundances are often biased toward the least susceptible prey (Mittelbach 1988; Vanni 1987a; Chapter 2). Thus, although predators can have large effects on some prey species, the most abundant taxa are relatively insensitive to

predation. For example, removal of pumpkinseeds from sections of Palmatier Lake led to a doubling of the densities of the three most vulnerable snail species (Chapter 2); however, effects on the six least preferred species were much less. Furthermore, natural densities of the six least preferred species were 10-fold greater than the natural densities of the three preferred species. Thus, removal of pumpkinseeds had relatively small effects on the total snail community, increasing snail biomass by less than 50% over a 93 day period. Manipulations of herbivores have also resulted in differential effects on algal taxa resulting in grazer-resistant communities in the presence of herbivores (e.g. Lynch and Shapiro 1981; Cattaneo and Kalff 1986; Vanni 1987b; Chapter 4).

Thus, the activity of predators tends to create prey communities in which the co-occurring prey are relatively immune to predation. These prey might then be able to build up large populations (because predators impose low mortality rates) until food limitation prevents further increases in their population size. If prey overlap in resource use, then food limitation should be transmitted to all prey, including those that are most susceptible to predation. Because these shifts in community composition can occur at each of the trophic levels, the relative importance of predation and food-limitation does not necessarily "flip-flop" (Hairston et al. 1960; Fretwell 1977; Persson et al. 1988; see also Connell 1983; Schoener 1983; Sih et al. 1985). Instead, the development of predation-resistant taxa at each trophic level causes food limitation to remain relatively strong throughout the ecosystem.

For example, in Lawrence Lake, the epiphyte community is strongly limited by phosphorus and is dominated by moderately grazer-resistant taxa: e.g. Melosira and other chain forming diatoms, which are

selectively grazed by gastropods, are extremely rare in Lawrence Lake, but very small adnate blue-green algae and small attached diatoms (e.g. Achnanthes), which are less selectively grazed (Nicotri 1977; Hunter 1980; Sumner and McIntire 1982), are very abundant (Burkholder 1986). The snail community is also strongly resource limited and is dominated by small snails (e.g. Amnicola and Marstonia), which are less preferred by pumpkinseeds compared to larger species (e.g. Physa) (Chapter 2), due primarily to the reduced encounter rates between fish and the smaller snails. Fish in this ecosystem are also resource limited and the fish community is dominated by spiny-rayed fishes (Werner et al. 1977), which are least preferred by piscivores, compared to soft-rayed fishes (Hoogland et al. 1957; Lewis et al. 1961; see also Tonn and Magnuson 1982). Although predation might influence the historical development of lake ecosystems (Thorp 1986), predators appear to impose only minor limitation on populations that co-exist with the predators (Table 3). Instead, food-limitation appears to be far more important, and if relaxed can produce large increases in biomass at all trophic levels.

Previous theoretical work on trophic exploitation have necessarily simplified real ecosystems into abstracted entities. One critical simplification has been that trophic levels are generally assumed to be comprised by only one type of organism (Rosenzweig 1973; Wollkind 1976; Oksanen et al. 1981). However all trophic levels are known to consist of diverse species that vary in many important aspects of their ecologies, and therefore differ in their responses to predators, resources and other environmental factors. An important advance in these models should be incorporation of the occurrence of alternate species at each of the trophic levels. Theoretical work by Phillips (1974), Lane and Levins (1977) and Leibold (1988) represent important first steps that need to be further elaborated to include diversity at

more than one trophic level. These types of models also need to be explored more rigorously for predictions that can be tested in field situations (e.g. how limitation should vary among trophic levels). Importantly, field experiments are needed in which responses to predator removals and responses to food addition are systematically assessed for different species and trophic levels within the same ecosystem.

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