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PERFORMANCE, DIET, AND COMPETITIVE ABILITY
IN MOLLUSCIVOROUS SUNFISH

presented by

Casey J Fisher Huckins

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DOCTOR OF PHILOSOPHY degree in ZOOLOGY


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**FUNCTIONAL RELATIONSHIPS BETWEEN MORPHOLOGY, FEEDING
PERFORMANCE, DIET, AND COMPETITIVE ABILITY IN
MOLLUSCIVOROUS SUNFISH**

By

Casey J Fisher Huckins

A DISSERTATION

**Submitted to
Michigan State University
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for the degree of**

DOCTOR OF PHILOSOPHY

W. K. Kellogg Biological Station and Department of Zoology

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ABSTRACT

FUNCTIONAL RELATIONSHIPS BETWEEN MORPHOLOGY, FEEDING PERFORMANCE, DIET, AND COMPETITIVE ABILITY IN MOLLUSCIVOROUS SUNFISH

By

Casey J Fisher Huckins

Pumpkinseed sunfish (*Lepomis gibbosus*) and redear sunfish (*L. microlophus*), phylogenetic sister-species, are morphologically and behaviorally specialized molluscivores. Except for a small region of natural overlap, their native ranges were allopatric. For purposes of sport fishery enhancement, fisheries managers have introduced redear into lakes of southern Michigan, creating a large zone of artificially sympatric pumpkinseed and redear. Relative to pumpkinseeds, redear display greater specialization than pumpkinseed and were predicted to be better molluscivores and competitively dominant.

I utilize the large scale introduction of redear sunfish into lakes, native to pumpkinseeds, to examine the impacts of this introduced species and also to study the mechanisms of competition between these two size-structured specialists. I performed across lake comparisons, a target-neighbor pond experiment and laboratory feeding trials that highlighted the functional linkages between feeding performance, resource use and competitive abilities.

Redear were found to possess crushing strength that was approximately two times greater than that of pumpkinseed. As a result, redear shifted to a diet of snails significantly earlier in their ontogeny and they were substantially more molluscivorous

than sympatric pumpkinseeds.

Several patterns were evident in the field and experimental data that support the inference of pumpkinseed and redear competition 1) Multiple lake surveys showed that following redear introduction, adult pumpkinseed densities declined by approximately 80%; 2) In Michigan lakes without co-occurring redear, adult pumpkinseed diets were dominated by snails (>80%). Whereas, in lakes with redear, pumpkinseed diets were dominated by soft-bodied invertebrates, and snails contributed only about 30% to their prey biomass; and 3) Snail biomass tended to be lower in lakes with introduced redear and in experimental treatments with redear neighbors. This suggests that redear may reduce resources for pumpkinseeds and drive their reduced molluscivory.

Pumpkinseed growth rates, however, did not differ between lakes with and without redear, yet short-term results from the pond experiment suggest that redear competition limited pumpkinseed growth. A verbal model is proposed that suggests density reductions of pumpkinseed as a compensating mechanism allowing unaffected adult pumpkinseed growth rates in the field.

I dedicate this dissertation to my Mom, Betty Polledo.

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TABLE OF CONTENTS

LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER 1	
COMPETITION BETWEEN ARTIFICIALLY SYMPATRIC MOLLUSCIVORES:	
FIELD AND EXPERIMENTAL EVIDENCE	1
INTRODUCTION	2
METHODS	6
Field Patterns	6
The System	6
Pumpkinsee Density	7
Pumpkinseed and Redear Growth	9
Pumpkinseed Diet Shifts	11
Snail Abundance in Lakes	12
Competition Experiment	13
Experimental Design	13
Resource Dynamics	17
RESULTS	18
Field Patterns	18
Pumpkinseed Density	18
Pumpkinseed and Redear Growth	18
Pumpkinseed and Redear Diets	23
Snail Abundance in Lakes	23
Competition Experiment	30
Target Growth	30
Target Diets	39
Resource Dynamics	46
Target Growth-Resource Abundance Correlations	55
DISCUSSION	58
LITERATURE CITED	68

CHAPTER 2	
INTERPRETING THE FUNCTIONAL RELATIONSHIPS BETWEEN	
MORPHOLOGY, FEEDING PERFORMANCE, AND DIET	73
INTRODUCTION	74
METHODS	77
Study lakes	77
Diet Composition and Ontogenic Shifts	78
Mechanisms Underlying Dietary Patterns	80
Laboratory Analysis of Performance	80
Crushing Strength	82
Prey Handling Time	84
RESULTS	85
Diet Composition and Niche Shift	85
Crushing Strength	92
Prey Handling Time: hard-bodied prey	102
Prey Handling Time: soft-bodied prey	102
DISCUSSION	109
Foraging Tradeoffs	112
Competition	114
LITERATURE CITED	117

LIST OF TABLES

CHAPTER 1

Table 1- Description of the study lakes	8
Table 2 - Target-Neighbor Experimental Design	16
Table 3 - Probabilities from Post-ANOVA contrasts: The mean final mass of large pumpkinseed and redear targets in the no neighbor treatment was contrasted with final target mass in each of the neighbor addition treatments	38

LIST OF FIGURES

CHAPTER 1

Figure 1. Depiction of native ranges of pumpkinseed sunfish (back slashes) and redear sunfish (forward slashes) based upon Lee et al. (1980) and Trautman (1981) 4

Figure 2. Bluegill, pumpkinseed and redear densities (measured as catch-per-unit-effort i.e., fish/trap) from Michigan Department of Natural Resource (MDNR) surveys. Surveys are from eight lakes with introduced redear (Brace, Cub, Duck, Four Mile, Gilead, Gilletts, Grass, and Swains) and seven lakes without introduced redear (Bishop, Craig, East Crooked, Halfmoon, Joslin, Lane, and Prairie). Surveys are from time periods before redear were introduced and also from periods after redear became established in area lakes. The notches on the box plots represent 95% confidence intervals 20

Figure 3. Backcalculated annual change in mass of pumpkinseeds from lakes with introduced redear (Lee Lake, Saubee Lake and Grass Lake) collected 1992-1994, and pumpkinseeds from lakes that have not received redear introductions (Culver, Deep East Crooked, Lawrence, Palmatier, Three Lakes 2 (TL2), Three Lakes Three (TL3), and Warner (Barry Co.)) that were sampled in 1990-1993. Fish are grouped into 10 mm standard length classes for clarity of presentation 22

Figure 4. Size at age relationships for redear and pumpkinseed in lakes with redear (Lee Lake, Saubee Lake and Grass Lake) and without redear (Culver, Deep, East Crooked, Lawrence, Palmatier, Three Lakes 2 (TL2), Three Lakes Three (TL3), and Warner (Barry Co.)). Each data point corresponds to the mean across lakes (± 1 SE) 25

Figure 5. A) Percent snails in diets and B) total prey biomass consumed for redear, and for pumpkinseed in lakes with redear (Lee Lake, Saubee Lake) and pumpkinseed in lakes without redear (Culver, East Crooked, Lawrence, Palmatier, TL2, and TL3). For clarity of presentation fish are grouped into 10 mm SL classes. Data for pumpkinseeds > 100 mm were not collected from Lee and Saubee Lakes and were therefore, not available for analysis 27

Figure 6. Biomass of snails on plastic plants deployed into lakes with redear (Lee, Gilletts and Saubee) and without redear (Lawrence, TL2, TL3, Palmatier and Warner (Calhoun Co.)). June samples were not available for Gilletts Lakes, TL3 and Palmatier. Each dot represents the across lake mean biomass per plant for a lake type (with or without redear) (± 1 SE) 29

Figure 7. Biomass of *Amnicola* (A) and *Physella* (B) collected from plastic plants deployed into lakes with introduced redear (Lee, Gilletts and Saubee) and without redear (Lawrence, TL2, TL3, Palmatier, and Warner (Calhoun Co.)). Each data point represents the mean biomass per plant for a lake 32

Figure 8. Mass of pumpkinseed and redear targets at the three sample dates throughout the pond experiment. For each target class, A) large pumpkinseeds, B) medium pumpkinseeds, C) small pumpkinseeds and D) redear the mean values for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors) are shown. Error bars are ± 1 SE and data are shown on a log10 scale. Initial masses of targets were as follows: redear (19.9 ± 0.2 g), large pumpkinseed (19.7 ± 0.1 g), medium pumpkinseed (2.3 ± 0.1 g) and small pumpkinseed (5.7 ± 0.1 g) 34

Figure 9. Final mass of A) large pumpkinseed and redear targets, and B) small and medium pumpkinseed targets in each of the treatments (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Error bars represent ± 1 SE 36

Figure 10. Total prey biomass from A) large pumpkinseed and redear targets, and B) small and medium pumpkinseed targets in each of the treatments (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Error bars represent ± 1 SE. Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets 41

Figure 11. Prey composition in final target diets displayed as the mean proportion of diet biomass (± 1 SE) for A) large pumpkinseed targets, B) medium pumpkinseed targets, C) small pumpkinseed targets and D) redear targets from the competition experiment. Data are grouped by taxa: macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), small invertebrates (amphipods and dipteran larvae) and snails. Note that the proportions do not necessarily add to one because they are the average proportions for a class of fish. Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets 43

Figure 12. Biomass of snails in the diets of pumpkinseed and redear targets on the final day of the experiment. Bars represent the mean for a target class (± 1 SE) for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets	45
Figure 13. Biomass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) at three sampling dates throughout the experiment. Each point represents the mean (± 1 SE) of two replicates of a treatment. Note different scales on the y-axis	48
Figure 14. Final biomass of A) snails, B) macroinvertebrates and C) small invertebrates in each treatment of the pond experiment. Each data point represents the mean of the two replicates of a treatment (± 1 SE). Note different scales on the y-axis	50
Figure 15. Individual mass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) at three sampling dates throughout the experiment. Each point represents the mean (± 1 SE) of two replicates of each treatment on each date. Note different scales on the y-axis	52
Figure 16. Final individual mass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Each point represents the mean of two replicates (± 1 SE). Note different scales on the y-axis	54
Figure 17. Correlations of target final mass with the mean biomass of snails throughout the experiment. Snail abundance was estimated on three dates throughout the experiment and here snail biomass represents the mean over those three dates. Values of the correlations and significance probabilities are shown for each target class	57
Figure 18. Plots of the percent pumpkinseed and redear in the catch from 7 streams and reservoirs surveyed in North Carolina (data are from Korneygay et al. 1994)	66

CHAPTER 2

Figure 1. Ontogenetic patterns of molluscivory for sympatric pumpkinseed and redear expressed as A) the proportion of snails in the diet (by biomass), and B) the total biomass of snails in the diet. For clarification of presentation the data are grouped into 10-mm size classes and each point represents a mean (± 1 SE). In figure 1A, logistic curves were fit to the complete data set for each species using nonlinear regression: $\text{proportion snails} = Y'_{\text{max}} / [1 + \text{EXP}(A + B \cdot \text{SL})]$, where Y'_{max} , A, and B are constants fitted by the regression. Fitted curves are shown for redear ($Y'_{\text{max}} = 0.916$, $A = 6.463$ and $B = -0.164$) and for sympatric pumpkinseeds ($Y'_{\text{max}} = 0.525$, $A = 3.437$ and $B = -0.044$). 87

Figure 2. Dietary composition of pre- and post-niche shift pumpkinseeds (top panels) and redear (lower panels). The prey categories are amphipods, dipteran larvae, insect nymphs, trichopteran larvae, snails, zooplankton and other (mites, annelids, coleoptera, etc.). The bars represent the mean proportion each prey type contributes to the total diet biomass (mg) (± 1 SE). 91

Figure 3. Composition of the snails in post-niche shift diets of A) pumpkinseeds, and B) redear, represented as the mean proportion each snail type contributed to the total snail biomass (mg). Pumpkinseed were >65 mm SL and redear were >40 mm SL. Error bars are ± 1 SE. 94

Figure 4. Mean crushing resistance (hardness) of A) *Amnicola limosa*, and B) *Physella* sp. in pumpkinseed and redear diets. Analysis of covariance of mean crushing resistance (Newtons) grouped by species along a covariate of SL (*Amnicola* $F_{1,88} = 4.99$, $P \leq 0.028$; and *Physella* $F_{1,69} = 13.327$, $P \leq 0.0005$). 96

Figure 5. Estimated crushing potential (Newtons) of pumpkinseed and redear. Analysis of Covariance shows a significant species effect on the log10 transformed crushing potential when log10 SL is included as a covariate (ANCOVA, $F_{1,22} = 21.71$, $P \leq 0.001$). 98

Figure 6. Upper limit of crushing resistance (hardness) of snails in pumpkinseed and redear diets represented by mean crushing resistance (Newtons) of the upper quartile of A) *Amnicola limosa* and B) *Physella* sp. in the diets plotted against the estimated crushing potential of the fish. The line represents the 1:1 ratio between crushing resistance of snails in the diet and the crushing strength of the fish. For clarification of presentation, fish were grouped into 2 Newton strength classes. Means for these classes ± 1 SE are displayed. 101

Figure 7. A) Handling and B) crushing times of pumpkinseed and redear when feeding on *Physella* sp. with mean crushing resistance of 6.3 Newtons (± 0.91 SD). Analysis shows a significant species*SL interaction for handling time (Figure 7A, ANCOVA, $F_{15,1}=8.607$, $P \leq 0.01$) and no significant difference in crushing time (Figure 7B). 104

Figure 8. Total time pumpkinseed and redear spent handling snails before the snails were rejected uncrushed. Bars represent the mean time (± 1 SE) for all individuals within a species for each of the three snail types offered. 106

Figure 9. Handling time of pumpkinseed and redear when feeding on soft-bodied prey (*Hexagenia*). Two size classes of *Hexagenia* nymphs were offered and analysis of covariance of log10 transformed handling times shows significant differences between pumpkinseed and redear for A) small nymphs ($F_{1,18}=20.726$, $P \leq 0.0001$) and B) large nymphs ($F_{1,10}=8.942$, $P \leq 0.014$,). 108

CHAPTER 1

COMPETITION BETWEEN ARTIFICIALLY SYMPATRIC MOLLUSCIVORES: FIELD AND EXPERIMENTAL EVIDENCE

INTRODUCTION

Competition has been shown to be an important process that shapes the ecology and evolution of freshwater fish communities (for review see Robinson and Wilson 1994). Most fish species also undergo shifts in their diet as they develop and grow (Helfman 1978, Werner 1986) and if these diet shifts are abrupt, the population can be functionally divided into distinct stages. Each functional stage will have unique environmental requirements and ecological roles in the community. Therefore, competition for resources can arise at either stage and can subsequently affect the shift from one functional stage to the other (eg., Bergman and Greenburg 1994, Olson et al. 1995, Olson 1996). In such systems, coexistence can be facilitated by the use of an exclusive resource during at least one stage.

The North American sunfishes (Centrarchidae) are size-structured species and their coexistence in northern lakes is promoted by segregation in diet and habitat use at larger size classes (Werner and Hall 1979, Mittelbach 1984, Mittelbach and Chesson 1987). While smaller size-classes of *Lepomis* compete for soft-bodied prey in the littoral zone of lakes (Mittelbach 1988, Osenberg et al. 1994), each species undergoes an ontogenetic niche shift and feeds on different resources when larger. By switching to snails, large pumpkinseeds (*Lepomis gibbosus*) gain a competitive refuge from the other native *Lepomis* that can not effectively crush and consume snails (Mittelbach 1984).

Within the sunfishes, only pumpkinseed (*Lepomis gibbosus*) and its sister-

species, redear sunfish (*L. microlophus*), are known to be specialist molluscivores as adults (Smith 1981, Mittelbach 1984, Wainwright and Lauder 1992). Both species possess modified pharyngeal jaws and derived muscle activation patterns that allow them to feed effectively on gastropods (Lauder 1983, Wainwright and Lauder 1992). The morphological similarity of pumpkinseed and redear suggests they would compete and may not be able to coexist. Indeed, their native distributions are largely non-overlapping. Pumpkinseed are native to inland lakes throughout the northern midwest, the Great Lakes region and eastern United States, while the native distributions of redear extended southwest from North Carolina to Florida and the Mississippi Basin (Figure 1; Trautman 1981, Lee et al. 1980). However, for purposes of sport fishery enhancement, fisheries managers have introduced redear into lakes throughout the northern midwest states. For example, throughout the last decade redear have been extensively introduced into at least 45 lakes in southern Michigan. As a result, a large zone of artificial sympatry of pumpkinseed and redear populations has been created.

Although fisheries biologists have long recognized that introduced species can have strong impacts on native fish communities (Magnuson 1976, Courtenay and Stauffer 1984, Moyle 1986, Moyle et al. 1986; see also Mills et al. 1994), ecologists have been slow to capitalize on these introductions to test ecological theories (but see Crowder 1984, 1986; Magnan and Fitzgerald 1984, and Herbold and Moyle 1986 for examples). The introduction of redear sunfish into Michigan lakes provides an

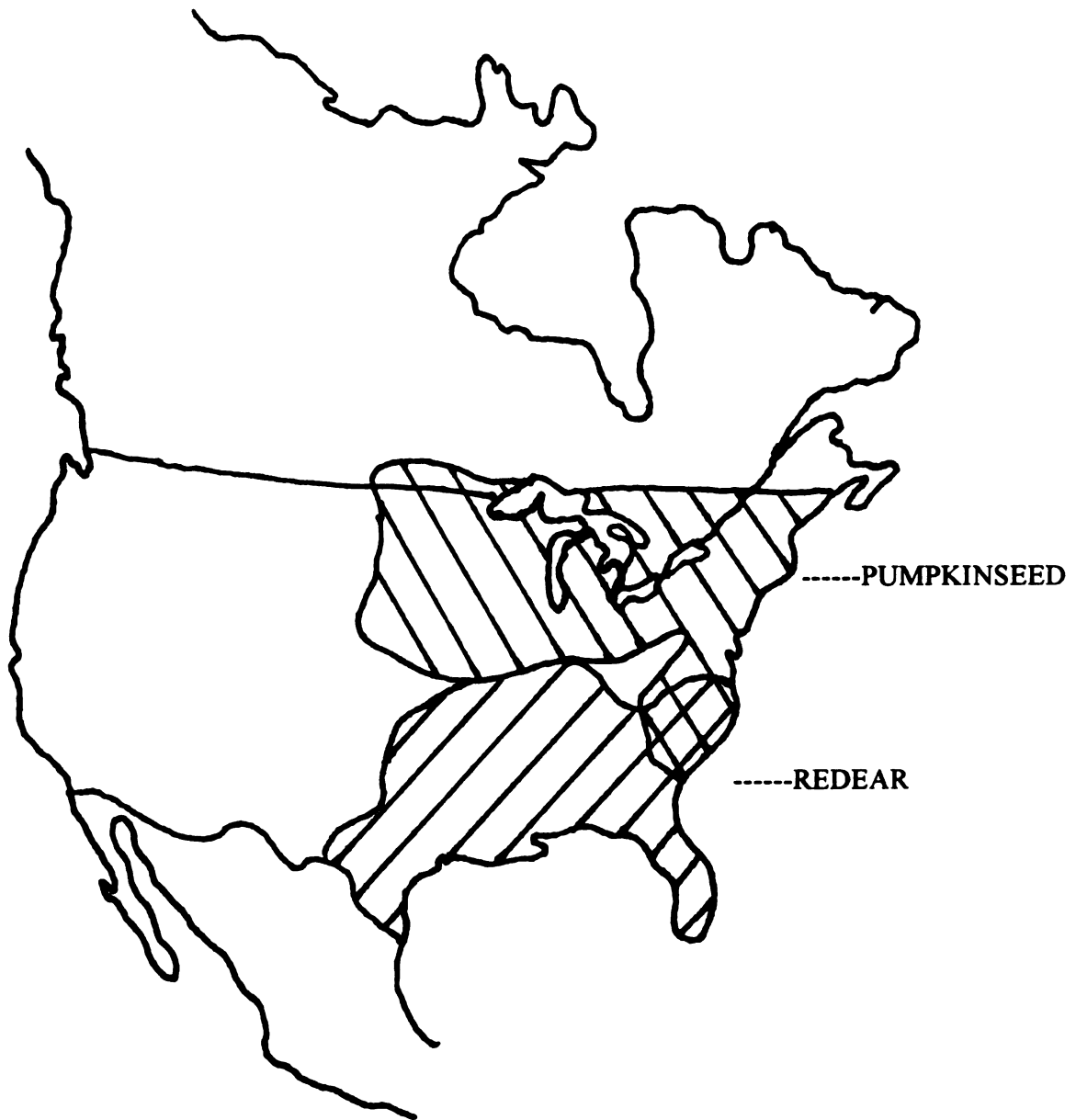


Figure 1. Depiction of native ranges of pumpkinseed sunfish (back slashes) and redear sunfish (forward slashes) based upon Lee et al. (1980) and Trautman (1981).

opportunity to examine competitive interactions between two similarly specialized phylogenetic sister species. Much is known about the ecology of the native sunfishes that provides a background on which to build a mechanistic understanding of pumpkinseed and redear interactions. Also, because the introduction of redear into southern Michigan was planned and extensive, there are good records of the introductions and a level of replication that is generally not available to ecologists studying the impacts of introduced species.

In this study I utilize the large scale introduction of redear sunfish into southern Michigan lakes, in conjunction with a controlled experimental manipulation, to examine the competitive interaction between pumpkinseed and redear. If the local community of sunfishes is functionally saturated with species then the addition of the redear will not be successful without the compensating disappearance or reduction of pumpkinseed or another species (Ricklefs 1987, Wootton 1990). The establishment of this introduced species thus provides a unique opportunity to study the responsive dynamics of the recipient community and the mechanisms driving local species distribution and abundance (Lodge 1993).

Based on feeding performance experiments, redear can generate crushing forces two times greater than similar sized pumpkinseed (Chapter 2). As a result, redear can feed on a greater range of snail sizes and can shift to snails earlier in ontogeny. Therefore, introduced redear are predicted to have strong negative impacts on snail availability and thus, displace pumpkinseed from their competitive refuge. Although pumpkinseeds show considerable morphological and neuromuscular specializations for feeding on snails (Lauder 1983a,b, 1986, Wainwright et al. 1991),

they remain flexible in their diet and habitat choice, which may change in response to resource levels (Werner and Hall 1976,1979; Mittelbach et al. 1992, Osenberg et al. 1992).

Werner (1986) suggested that if interspecific competition is important in a system, one expects a reduction in the density and biomass, and a niche alteration of the resident species when in the presence of an introduced species. Alteration of the niche under sympatry can be in the form of an induced niche shift away from the diet that is normal under allopatry (e.g., Werner and Hall 1979, Persson 1987, Magnan 1988), or it can arise as a disruption of the ontogenetic niche shift of an otherwise size-structured species (e.g., Bergman 1990, Persson and Greenburg 1990). Thus, if pumpkinseed and redear compete for resources, the introduction of redear is predicted to impact pumpkinseeds through a reduction in pumpkinseed population level performance (growth and/or abundance) and/or a shift in the pumpkinseed's niche.

METHODS

Field Patterns

The System

I examined pumpkinseed densities, growth rates, and diets in several southern Michigan lakes to test for negative impacts of redear introductions. Detailed studies were conducted in three lakes with introduced redear sunfish (Lee, Saubee and Grass) and in 8 lakes that have not received redear introductions (East Crooked, Warner, Three Lakes II, Three Lakes III, Palmatier, Culver, Lawrence, and Deep; see Table 1).

All of the study lakes are marl bottomed and are within a 100 kilometer radius of the W. K. Kellogg Biological Station of Michigan State University in southwestern Michigan. Lee Lake, Saubee Lake and Grass Lake were chosen for study based on preliminary surveys that indicated established populations of redeer and pumpkinseeds (Huckins, personal observation) as well as the typical compliment of sunfish and other fish species found in the non-redeer study lakes. Redear were introduced as young-of-year (YOY) at low densities (ca. 100 YOY/acre) by the Michigan Department of Natural Resources (MDNR) into Grass Lake (Jackson County) in 1987 and 1991; Lee Lake (Calhoun County) in 1981, 1991, and 1992; and into Saubee Lake (Eaton County) in 1986. Pumpkinseed diets were studied in a subset of lakes with and without introduced redeer (see Table 1) to document evidence of shifts in their feeding ecology associated with redeer introduction.

Pumpkinseed Density

Effects of redeer on pumpkinseed density were examined using data gathered from records of the Michigan Department of Natural Resources (MDNR). As part of the MDNR redeer management plan (Towns 1991) and the overall operation of the MDNR Fisheries Division, surveys are regularly performed to evaluate the quality of the fishery and to assess the status of introduced redeer in area lakes. Surveys provide estimates of species composition and catch-per-unit-effort (CPUE) for the major game fish including pumpkinseed and redeer. The MDNR also surveyed lakes that had not received redeer, which provided a comparison to the introduced systems. Survey techniques employed trap nets that were deployed in the littoral zones at 4-5 sites

Table 1. Description of the study lakes

Lake	Redear introductions (years)	Surface area (ha)	Sample Sizes			
			Growth data		Diet data	
			Pumpkinseed	Redear	Pumpkinseed	Redear
Grass	1987, 1991	139	50	26	---	---
Lee	1981,1991,1992	47	137	100	59	47
Saube	1986	24	49	72	33	34
Culver	N.A.	13	49	N.A.	20	N.A.
Deep	N.A.	13	55	N.A.	---	N.A.
East Crooked	N.A.	25	52	N.A.	14	N.A.
Lawrence	N.A.	5	108	N.A.	43	N.A.
Palmatier	N.A.	6	64	N.A.	21	N.A.
Three Lakes II	N.A.	22	151	N.A.	222	N.A.
Three Lakes III	N.A.	15	157	N.A.	45	N.A.
Warner (Barry Co.)	N.A.	26	106	N.A.	---	N.A.

around the lake. The nets were deployed in the morning and lifted the following morning and the catch recorded on a per trap basis (CPUE). The change in pumpkinseed CPUE in 8 lakes with introduced redeer (Brace, Cub, Duck, Four Mile, Gilead, Gilletts, Grass, and Swains) and 7 lakes without redeer (Bishop, Craig, East Crooked, Halfmoon, Joslin, Lane, and Prairie) was examined to assess the relationship between redeer introduction and the change in pumpkinseed density. I predicted that redeer presence would be associated with reductions in pumpkinseed densities due to competition for a common resource (snails). Observed changes in pumpkinseed densities could alternatively result from other environmental causes associated with, but not caused by redeer introduction. Therefore, I also examined the change in density of bluegill. Bluegill do not feed on snails and were therefore not predicted to respond strongly to the introduction of redeer. Redear, pumpkinseed and bluegill all spend part of their juvenile stage in the littoral zone feeding on soft-bodied prey. Thus pre-niche shift redeer could have a direct effect on the analogous stages of both pumpkinseed and bluegill. Redear shift to a diet of snails very early in their development (Chapter 2), therefore they are not predicted to have strong direct effects on other juvenile sunfish.

Pumpkinseed and Redear Growth

Growth rates of pumpkinseed and redeer sunfish were estimated by back calculations from scale samples collected from Lee Lake, Saubee Lake and Grass Lake throughout the summers of 1992-1994. Scales were also collected between 1990 and 1993 from pumpkinseeds in lakes that have not received redeer introductions (Culver,

Deep East Crooked, Lawrence, Palmatier, Three Lakes 2 (TL2), Three Lakes Three (TL3), and Warner (Barry Co.); see Table 1). Upon collection, standard lengths (SL) were recorded to the nearest millimeter and five scales were removed from the region underneath the tip of the left pectoral fin. Impressions of the scales were made by pressing them between two clear strips of acetate, and the distances from the focus to each annuli and to the scale margin were measured from an image projected on a microfiche viewer. Only one scale was measured per fish and the age estimate from that scale was checked against the remaining four scales from the fish.

The size of the fish at each age was back-calculated using the Fraser-Lee method (Tesch 1986, see Osenberg et al. 1988). Standard lengths were converted to estimates of wet mass using length-mass regressions:

eq. 1.1) **Pumpkinseed: Mass = 0.00001529*(SL^{3.224}) R²= 0.996**
(Osenberg et al, 1988)

eq. 1.2) **Redear:** $\text{Mass} = 0.00001927 * (\text{SL}^{3.162})$ $R^2 = 0.976$
(Huckins unpublished data) mass (grams) and SL (millimeters).

Fish were grouped into 10-mm size-classes (size at the beginning of each growing season), and growth rates were expressed as the mean annual change in mass for each size-class within a lake. Size at age estimates (SL at the end of each growth stanza) were also calculated for each fish and expressed as the mean for each age in a lake.

Pumpkinseed Diet Shift

To examine if introduced redear alter the ontogeny of snail-feeding in pumpkinseeds, pumpkinseed diets in Lee Lake and Saubee Lake were contrasted with existing data on the diets of pumpkinseeds from lakes without introduced redear (Culver, East Crooked, Lawrence, Palmatier, TL2, and TL3). Fish were collected from Lee Lake and Saubee Lake between May and August of 1993 and 1994) by seining. Pumpkinseed feeding peaks between dawn and noon (Hanson and Leggett 1986), therefore fish were collected before 12:30 pm to minimize gut content digestion. Fish were preserved in 10% neutral formalin and later measured for standard length. Stomachs were removed just anterior of the pyloric caeca and posterior of the esophagus, and stomach contents were identified to the lowest possible taxonomic level, (generally to genus). For each fish, all prey items in the gut were enumerated and measured (up to 50 individuals per taxa) for estimation of individual dry mass using length-weight regressions (Huckins, Mittelbach and Osenberg unpublished data). The specific body axis measured for a given prey type depended upon which body part was best preserved. For example, the shells of snails are generally crushed during consumption, so all pulmonate snails were measured along the length of their foot, and all prosobranch snails were measured along the longest axis of their opercula. The resultant biomass calculations for snails excluded their shells. Head capsule widths were measured for most insect larvae and nymphs, and body lengths were measured for Cladocera and most other zooplankton. Fish were excluded from subsequent analysis if their gut contents were in a state of digestion that made identification and measurement of prey uncertain.

Prey items in pumpkinseed diets were grouped into five categories: 1) small invertebrates (amphipods and dipteran larvae); 2) macro-invertebrates (Odonates, Ephemeropterans, Trichopterans, and Coleopterans); 3) snails; 4) zooplankton; and 5) other miscellaneous prey rarely found in the diets, including Homopterans, mites, annelids, Hemipterans, etc. For each fish, I calculated the proportion of the total prey biomass contributed by prey in each of the five categories.

To determine the size at which pumpkinseeds shift diets, I examined the proportion and the biomass of snails eaten in lakes with and without redear. An extensive data set of pumpkinseed diets from seven lakes without redear, (all within 40 km of Lee Lake and Saubee Lake) was used for comparison (Osenberg and Mittelbach, personal communication). These data were compared to pumpkinseed diets in lakes with redear. I restricted the statistical analyses to include only individuals ≥ 65 mm (post diet-shift; see Chapter 2). Proportional data were arcsin square root transformed to meet the assumption of homogeneity of variance and analysis with ANCOVA using SL as the covariate.

Snail Abundance in Lakes

If redear are more proficient at feeding on snails (Chapter 2) and compete with pumpkinseeds, I predicted that redear would be able to reduce snail abundances to lower levels than can pumpkinseeds. To examine this hypothesis, I surveyed snail communities in a subset of lakes with and without introduced redear. To avoid the complications of standardizing snail abundances in samples from lakes with different vegetation, I utilized plastic aquarium plants as uniform artificial substrates to sample

the snail community. In the first week of June 1994, plastic aquarium plants of equal surface area and shape were attached to bricks and placed in the littoral zones of two lakes with introduced reedear (Lee and Saubee) and three lakes without reedear (Lawrence, TL2 and Warner (Calhoun)). Ten plastic plants (12" Cabomba) were laid out in a transect at a depth of approximately 1.5 meters in each lake. The plants were allowed to be colonized for 1 week before retrieval and then rinsed into individual collecting jars. This procedure was repeated in early July 1994 and the number of lakes surveyed was expanded to include TL3 and Palmatier Lake (reedear absent), and Gilletts and Clear Lake (reedear present). The artificial substrates were vandalized in Clear Lake, leaving only three study lakes with introduced reedear for the analysis. Shell lengths of all snails were measured and converted to estimates of tissue dry-mass (not including shell mass) using length-mass regressions (Osenberg unpublished data). For each lake, the mean snail biomass per plant was calculated for all snails combined and for each snail species. Total snail biomass was log₁₀ transformed to stabilize variance and analyzed with repeated measures ANOVA.

Competition Experiment

Experimental Design

To estimate the relative competitive abilities of pumpkinseed and reedear, and to gain a mechanistic understanding of the competitive interaction, I performed a field experiment in collaboration with Gary Mittelbach (W. K. Kellogg Biological Station) and Craig Osenberg (Department of Zoology, University of Florida). The experiment was based on a target-neighbor design (sensu Goldberg and Werner 1983) and

performed at the W. K. Kellogg Biological Station pond facility. The basic design of a target-neighbor experiment utilizes focal individuals (targets) that are exposed to a density gradient of potential competitors (neighbors). There are conspecific neighbor treatments and non-conspecific neighbor treatments, which allows for a comparison of intra- and interspecific competitive effects.

For this experiment, one pond (30 m diameter, 1.8 m deep) was divided into 10 wedge shaped sections (53.8 square meters $\pm$ 2.8 ($x \pm 1$ SD) and blocked into two sets with five sections each, one set in each of the east and west halves of the pond. Divisions were created using 3.2 mm mesh netting that was suspended from cables above the pond. The bottom of the netting was attached to a chain and buried in the sediments. Algae quickly colonized the netting thus limiting the movement of invertebrates between sections. Treatments were assigned using a randomized block design, such that each treatment was represented once in the east half and once in the west half of the pond.

The experimental design included two replicates of one fishless treatment and four treatments in which focal pumpkinseed and redear individuals (targets) were exposed to density gradients of neighbors, either pumpkinseed or redear (see Table 2). Three size classes of pumpkinseed targets were used to examine size specific responses to the competitor treatments.

On June 18, 1994 adult pumpkinseeds (large targets) were collected from Crooked Lake and Three Lakes II. Small and medium pumpkinseed targets and redear targets were seined from monospecific brood ponds located at the W.K. Kellogg Biological Station. The target assemblage (3 redear and 28 pumpkinseed) was

introduced into all but two sections that were left fishless to examine the overall effects of fish on prey composition. Density of large targets was approximately 0.056 individuals of each species per m^2 , which is slightly greater than mean adult densities in Lee and Saubee Lakes (0.044 pumpkinseed/ m^2 and 0.050 redbreast/ m^2 ; based on littoral seines in 1993 and 1994). Combined density of large pumpkinseed and redbreast targets in the experiment (0.11 targets/ m^2) was within the range of molluscivore density typical of southern Michigan lakes without redbreast (Osenberg et al. 1992) and similar to densities used in previous studies on molluscivores (see e.g., Brönmark et al. 1992). Large targets were similar in size to their conspecific neighbors so the left pelvic fin of each large target was clipped for later identification. Small and medium pumpkinseed targets were not fin clipped.

Target and neighbor standard lengths were recorded to the nearest millimeter just prior to their release into the experimental sections (see Table 2). On July 11, targets were collected by seining each pond section two times. The fish were released back into the pond after recording their standard lengths. At the completion of the experiment on August 1, 1994, the pond was drained and all fish were measured for standard length and wet mass. From these values, length-mass relationships for each species were estimated and used to estimate initial and mid-experiment target mass. Stomachs of the target individuals were removed and preserved in 10% formalin for later diet analysis.

Final target mass was used to test for treatment effects on target growth. The mean final mass (hereafter referred to as final mass) of all individuals within a target class was calculated for each pond section, yielding 2 replicates per treatment. Values

Table 2. Target-neighbor experimental design

Treatments	Targets	Neighbors	<u>Total density of fish</u>
			(number/section)
1) NO FISH	0	0	0
2) TARGETS	present	0	31
3) LOW PUMPKINSEED	present	20 pumpkinseed	51
4) LOW REDEAR	present	20 redeer	51
5) HIGH REDEAR	present	40 redeer	71

(Target assemblage = 3 redeer targets + 3 large pumpkinseed targets + 5 medium pumpkinseed targets + 20 small pumpkinseed targets)

		<u>Initial standard length (mean + 1 SE)</u>
redeer targets	-	79.4 $\pm$ 0.25 mm
large pumpkinseed targets	-	79.5 $\pm$ 0.24 mm
medium pumpkinseed targets	-	52.3 $\pm$ 0.36 mm
small pumpkinseed targets	-	38.8 $\pm$ 0.09 mm
pumpkinseed neighbors	-	86.2 $\pm$ 3.15 mm
redeer neighbors	-	81.2 $\pm$ 2.80 mm

of target final mass were log10 transformed prior to analysis to stabilize the variance.

The interspecific and the intraspecific competitive effects were estimated by the difference between the final mass of pumpkinseed and redear target individuals in the target only treatment and the +20 neighbor treatment for each block. For example, by comparing the final mass of pumpkinseeds from the target only treatment with those from the +20 redear treatment and with those from the +20 pumpkinseed treatment, I was able to estimate the interspecific and the intraspecific effects, respectively. Competition coefficients for redear (α_{PR}) and for pumpkinseed (α_{RP}) were defined as the ratio of the inter- and intraspecific effect of neighbors. For each species, I arrived at two estimates of the coefficient (one from each block of replicates).

Resource Dynamics

The invertebrate community was sampled three times over the course of the experiment; one day before the introduction of fish, on day 22 and on day 45 (one day before the experiment was concluded). Samples were taken with a modified Gerking sampler (Mittelbach 1981). In each section, two replicate samples were taken on the first date, three on the second and four samples were collected on the final date. Every prey item was counted and up to 50 individuals per taxa in each replicate sample were haphazardly selected and measured along a taxon specific axis for estimation of dry tissue mass from length weight regressions. Invertebrates were categorized into 5 groups: 1) macro-invertebrates (nymphs of Odonata and Ephemeroptera, Coleoptera larvae, etc); 2) small invertebrates (amphipods and Diptera larvae); 3) snails; 4) zooplankton; and 5) miscellaneous invertebrates such as leeches,

winged insects and other rarely encountered taxa. Total biomass for each prey category was presented on a mg per m² basis.

RESULTS

Field Patterns

Pumpkinseed Density

Comparisons of early and recent CPUE of pumpkinseeds from southern Michigan lakes show a $84 \pm 8.0\%$ ($x \pm 1$ SE) decline in pumpkinseed density following establishment of redeer. In contrast to the strong reductions of pumpkinseed density in all lakes with introduced redeer, pumpkinseed CPUE in nonredeer lakes showed no change (Figure 2). Analogous comparisons of historical and recent bluegill CPUE showed no relationship between the change in bluegill density and the presence or absence of redeer (Figure 2), suggesting that the change in pumpkinseed density was the result of redeer introduction and not a spuriously correlated change in the environment

Pumpkinseed and Redear Growth

The pattern of pumpkinseed growth, characterized by the mean annual change in mass for 10 mm size-classes, was similar in lakes with or without redeer (Figure 3).

Across all size classes, pumpkinseed growth in the two lake types was the same and growth rates tended to plateau between 30 and 40 grams per year. Pumpkinseed size-at-age was also not affected by redeer presence and both species were similar in size

Figure 2. Bluegill, pumpkinseed and redear densities (measured as catch-per-unit-effort i.e., fish/trap) from Michigan Department of Natural Resource (MDNR) surveys. Surveys are from eight lakes with introduced redear (Brace, Cub, Duck, Four Mile, Gilead, Gilletts, Grass, and Swains) and seven lakes without introduced redear (Bishop, Craig, East Crooked, Halfmoon, Joslin, Lane, and Prairie). Surveys are from time periods before redear were introduced and also from periods after redear became established in area lakes. The notches on the box plots represent 95% confidence intervals.

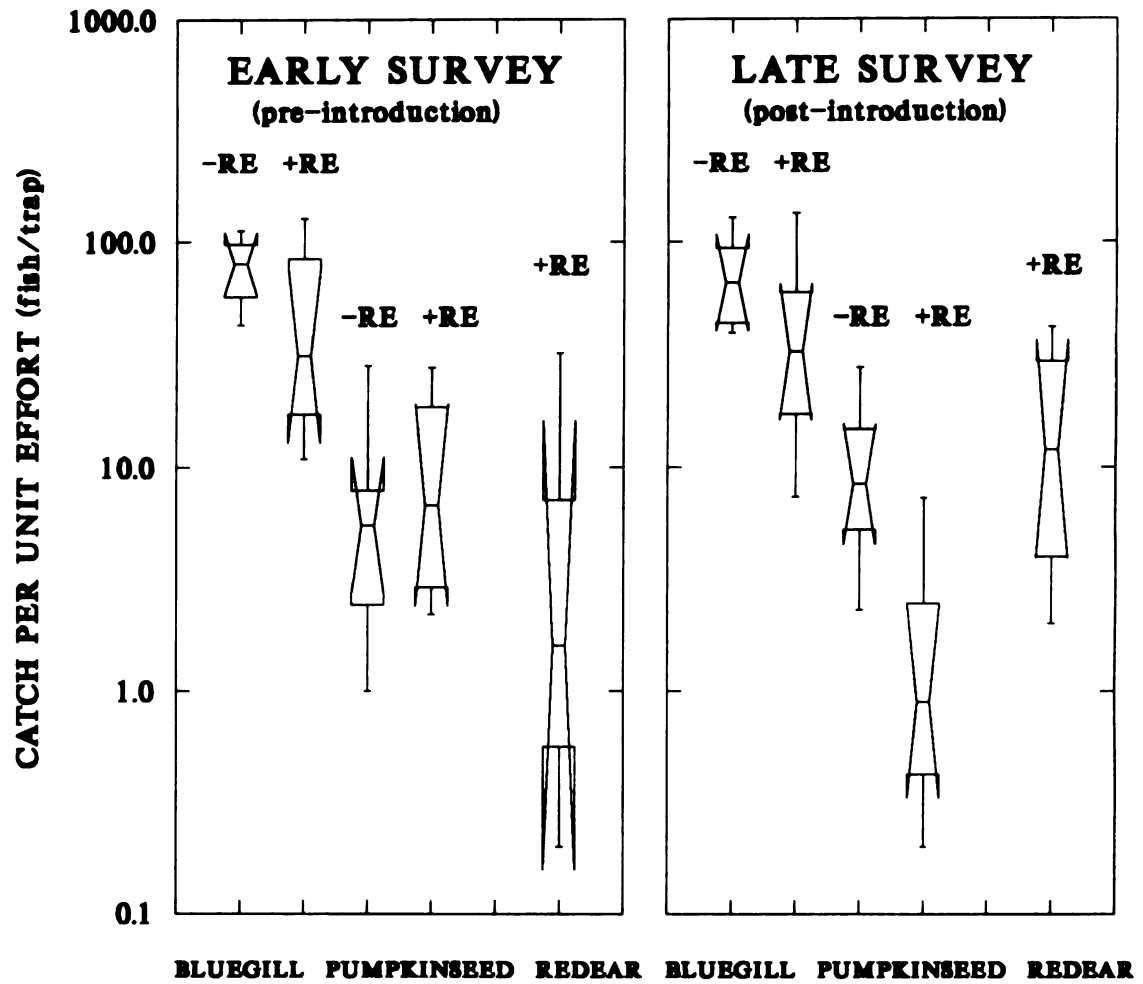


Figure 2

Figure 3: Backcalculated annual change in mass of pumpkinseeds from lakes with introduced redbreast (Lee Lake, Saubee Lake and Grass Lake) collected 1992-1994, and pumpkinseeds from lakes that have not received redbreast introductions (Culver, Deep, East Crooked, Lawrence, Palmatier, Three Lakes 2 (TL2), Three Lakes Three (TL3), and Warner (Barry Co.)) that were sampled in 1990-1993. Fish are grouped into 10 mm standard length classes for clarity of presentation.

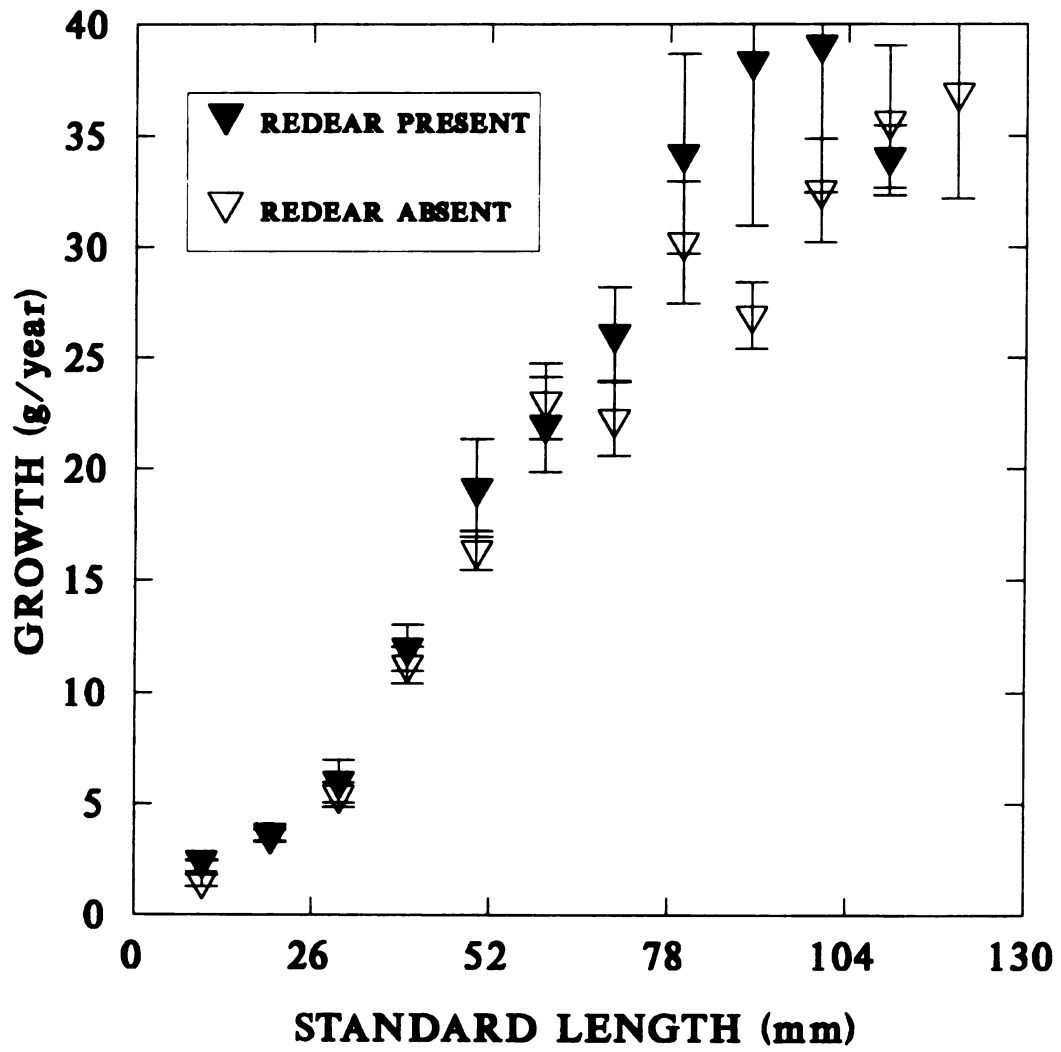


Figure 3

at the end of the first year of growth (Figure 4). However, following the first year, redear were substantially larger than pumpkinseed; two year old redear were similar in size to 3 year old pumpkinseed and by the end of their third year of growth, redear were approximately 60% larger than pumpkinseeds of the same age.

Pumpkinseed and Redear Diets

In lakes without introduced redear, adult pumpkinseeds feed predominantly on gastropod molluscs (generally > 80% gastropods by mass) (Figure 5A, see also: Mittelbach 1984, Osenberg and Mittelbach 1989, Sadizikowski and Wallace 1976, Osenberg et al. 1994). However, in lakes with redear, pumpkinseeds showed a significant reduction in the proportion of snails in their diets (ANCOVA $SL \geq 65$, $F_{1,48}=16.89$, $P \leq 0.0002$), such that snails totaled on average $\leq 30\%$ of the prey biomass of "post niche shift" pumpkinseeds. In these same lakes snails contributed greater than 80% of post-shift redear prey biomass (Figure 5A). Total prey biomass in the stomachs of by pumpkinseeds was, however, unaffected by redear presence (Figure 5B) and was similar to that of sympatric redear.

Snail Abundance in Lakes

For both the June and July surveys, the total biomass of all snail types combined was generally lower in lakes with introduced redear than in lakes without redear. However, repeated measures analysis showed there to be no time by redear interaction and only a marginally significant effect of lake type (eg., with or without redear) ($F_{1,3}=5.05$, $P \leq 0.11$; Figure 6). In July, the mean snail biomass in redear lakes

Figure 4: Size at age relationships for redear and pumpkinseed in lakes with redear (Lee Lake, Saubee Lake and Grass Lake) and without redear (Culver, Deep, East Crooked, Lawrence, Palmatier, Three Lakes 2 (TL2), Three Lakes Three (TL3), and Warner (Barry Co.)). Each data point corresponds to the mean across lakes (± 1 SE).

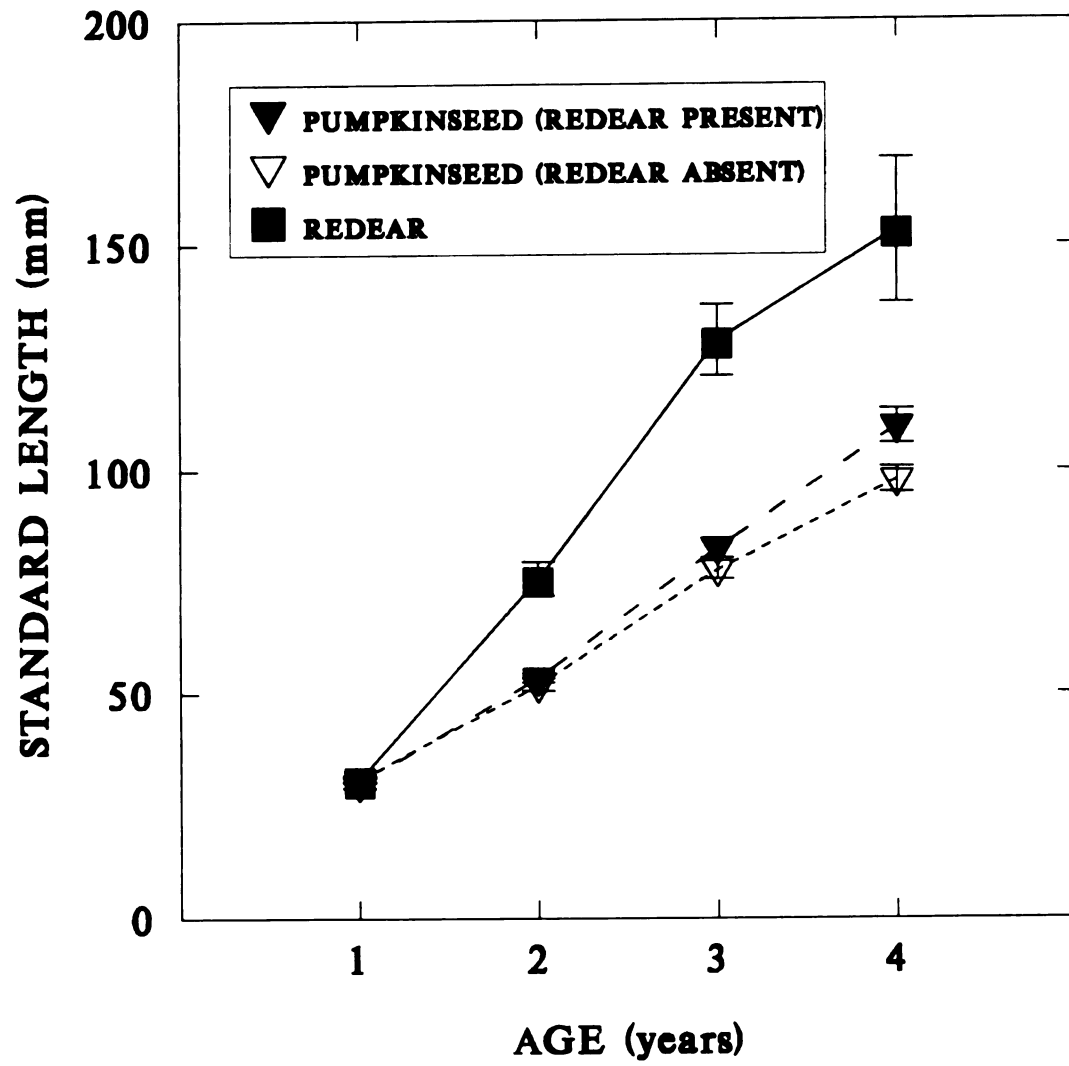


Figure 4

Figure 5: A) Percent snails in diets and B) total prey biomass consumed for redeer, and for pumpkinseed in lakes with redeer (Lee Lake, Saubee Lake) and pumpkinseed in lakes without redeer (Culver, East Crooked, Lawrence, Palmatier, TL2, and TL3). For clarity of presentation fish are grouped into 10 mm SL classes. Data for pumpkinseeds > 100 mm were not collected from Lee and Saubee Lakes and were therefore, not available for analysis.

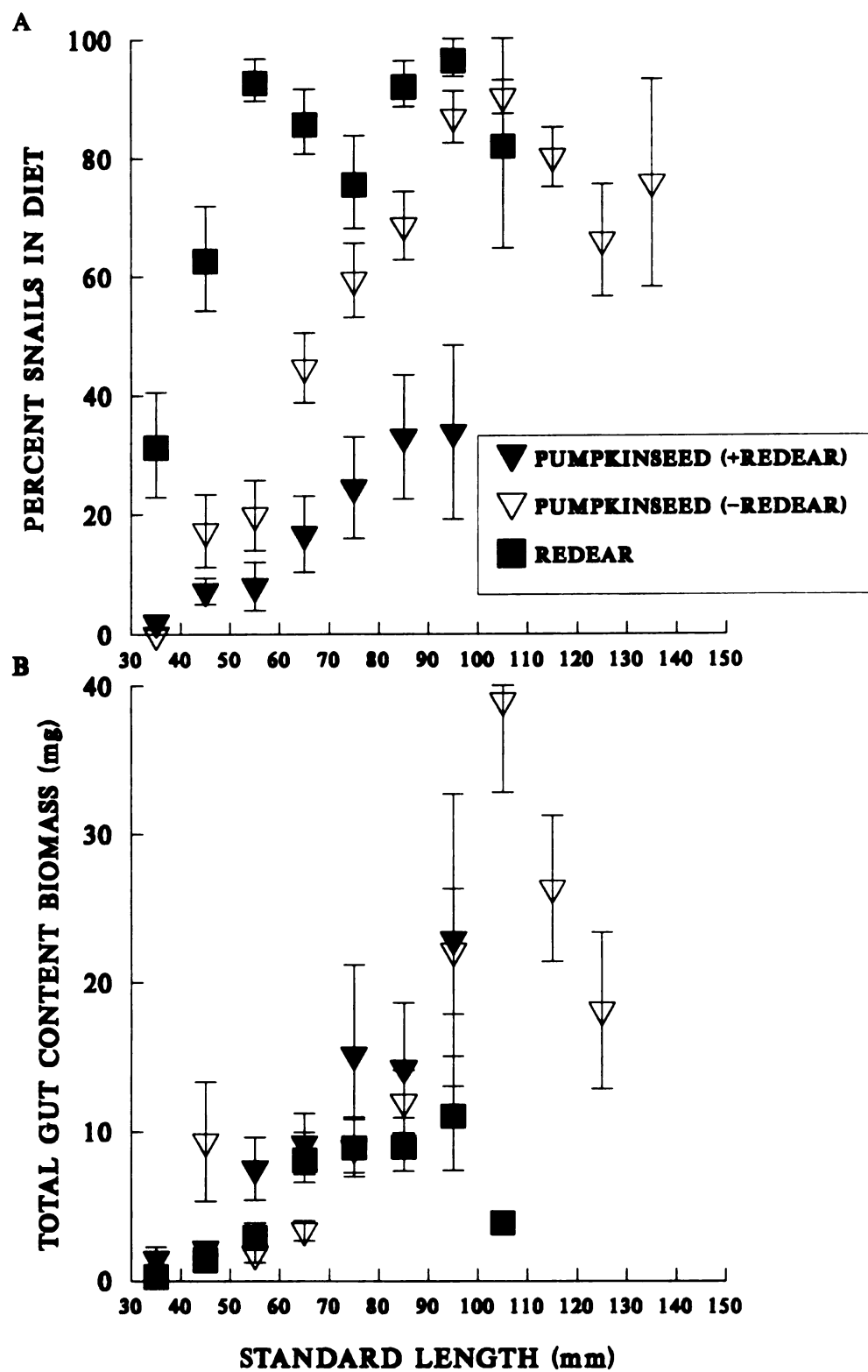


Figure 5

Figure 6: Biomass of snails on plastic plants deployed into lakes with redeer (Lee, Gilletts and Saubee) and without redeer (Lawrence, TL2, TL3, Palmatier and Warner (Calhoun Co.)). June samples were not available for Gilletts Lakes, TL3 and Palmatier. Each dot represents the across lake mean biomass per plant for a lake type (with or without redeer) (± 1 SE).

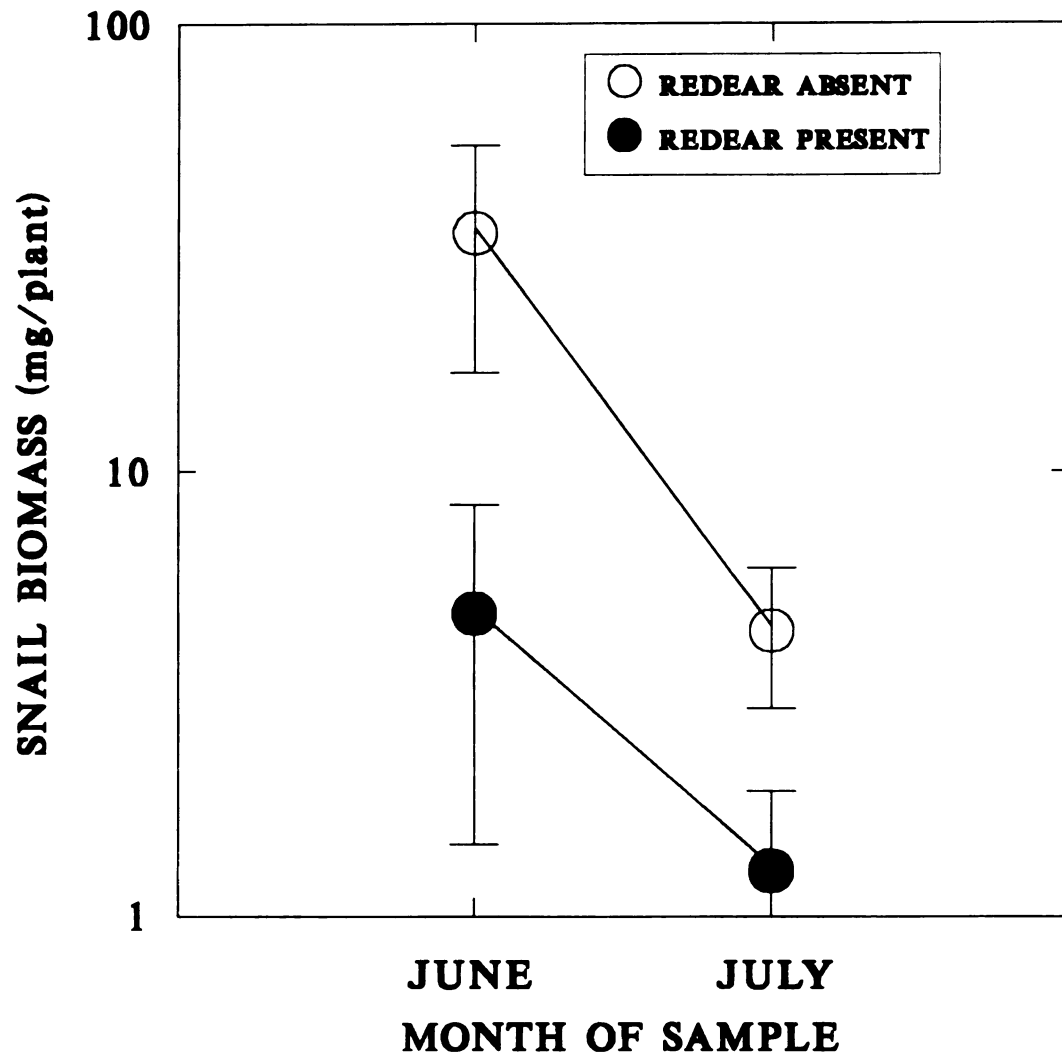


Figure 6

was nearly 4 times that of nonredeer lakes, however the difference between log10 transformed values was not significant (Figure 7; one-tailed $t_6 = 1.377$, $P \leq 0.11$). The same trend existed for the total biomass of individual snail types (e.g., *Amnicola limosa* and *Physella* sp.; Figure 7).

Competition Experiment

Target Growth

Length-mass relationships for each species based on final values of length and mass were:

eq. 1.3)Redear: $\text{mass} = 0.0001242 * (\text{SL}^{2.740})$ $R^2 = 0.90$, $n=141$

eq. 1.4)Pumpkinseed: $\text{mass} = 0.00001927 * (\text{SL}^{2.979})$ $R^2 = 0.99$, $n=244$

where mass is in grams and SL is measured in millimeters. Initial and mid-experiment target mass estimated by the above functions and the final mass (measured directly) showed that large pumpkinseed and redear targets grew significantly during the first half of the experiment and grew very little thereafter. This pattern was most pronounced in the redear neighbor treatments (Figure 8). Small and medium pumpkinseed targets by comparison continued to grow throughout the experiment. Although the final mass of small and medium pumpkinseed targets appeared to be reduced by redear neighbors, the effects were not significant (Figure 9). There were significant overall treatment effects on the final mass of large pumpkinseed and redear targets (Figure 9; ANOVA, $F_{3,3}=9.79$, $P<0.047$ and $F_{3,3}=7.13$, $P<0.044$, respectively).

Figure 7. Biomass of *Amnicola* (A) and *Physella* (B) collected from plastic plants deployed into lakes with introduced reedear (Lee, Gilletts and Saubee) and without reedear (Lawrence, TL2, TL3, Palmatier, and Warner (Calhoun Co.)). Each data point represents the mean biomass per plant for a lake.

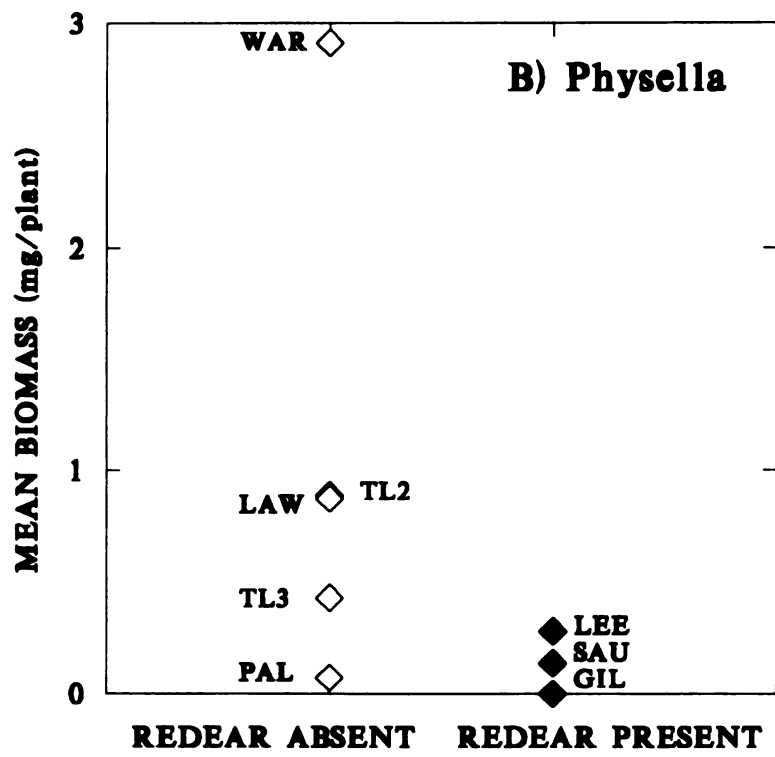
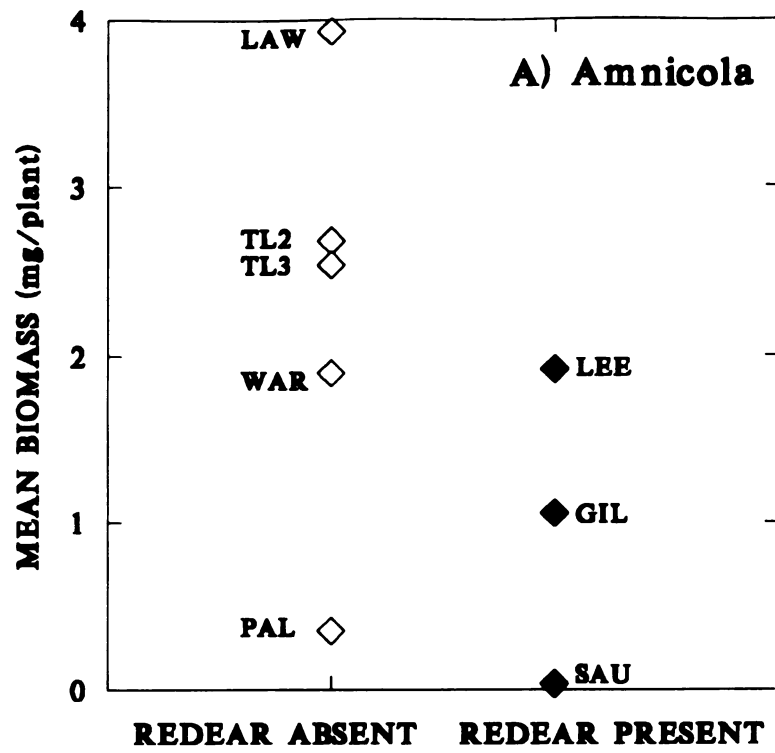


Figure 7

Figure 8. Mass of pumpkinseed and redear targets at the three sample dates throughout the pond experiment. For each target class, A) large pumpkinseeds, B) medium pumpkinseeds, C) small pumpkinseeds and D) redear the mean values for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors) are shown. Error bars are ± 1 SE and data are shown on a log10 scale. Initial masses of targets were as follows: redear (19.9 ± 0.2 g), large pumpkinseed (19.7 ± 0.1 g), medium pumpkinseed (2.3 ± 0.1 g) and small pumpkinseed (5.7 ± 0.1 g).

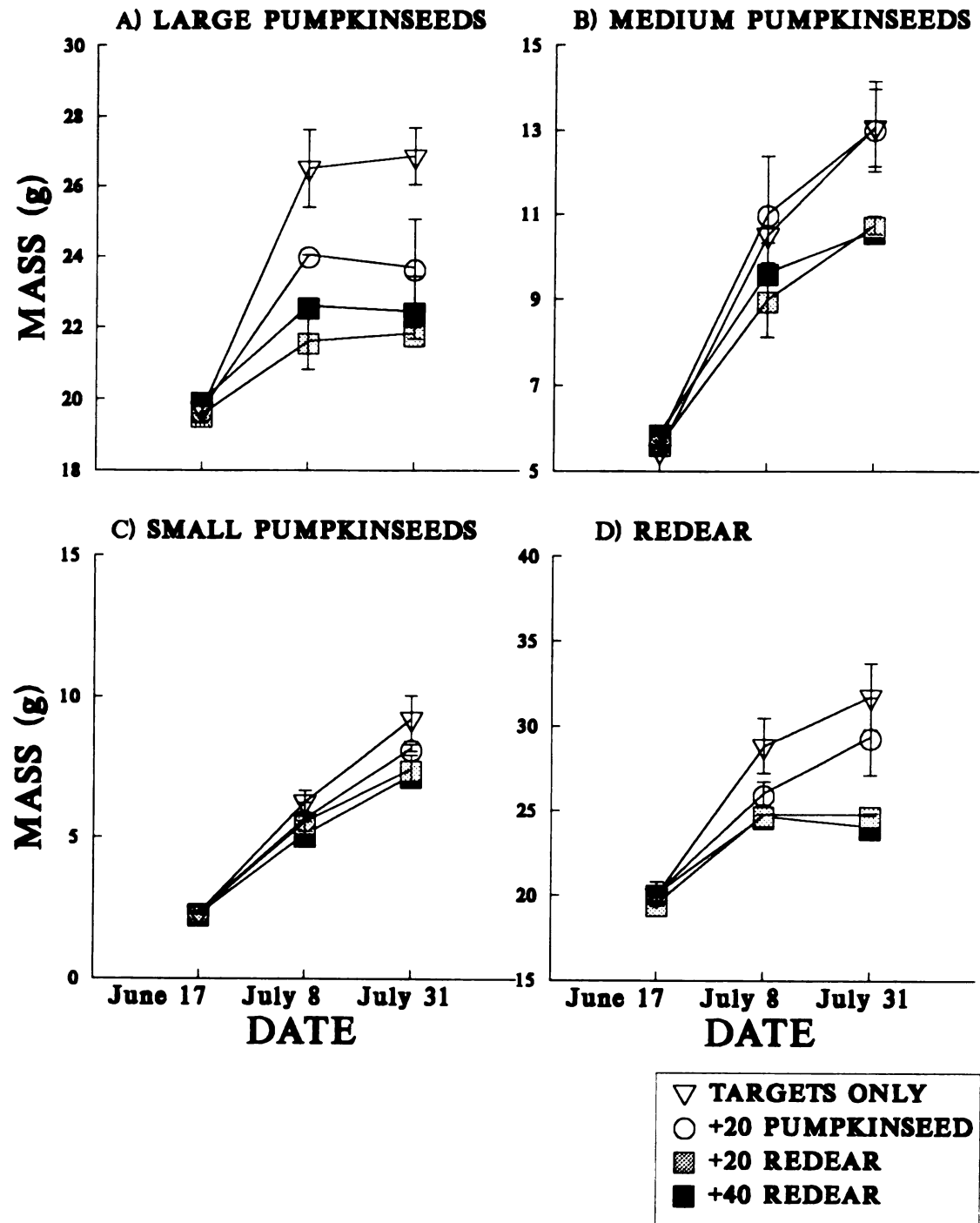


Figure 8

Figure 9. Final mass of A) large pumpkinseed and redear targets, and B) small and medium pumpkinseed targets in each of the treatments (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Error bars represent ± 1 SE.

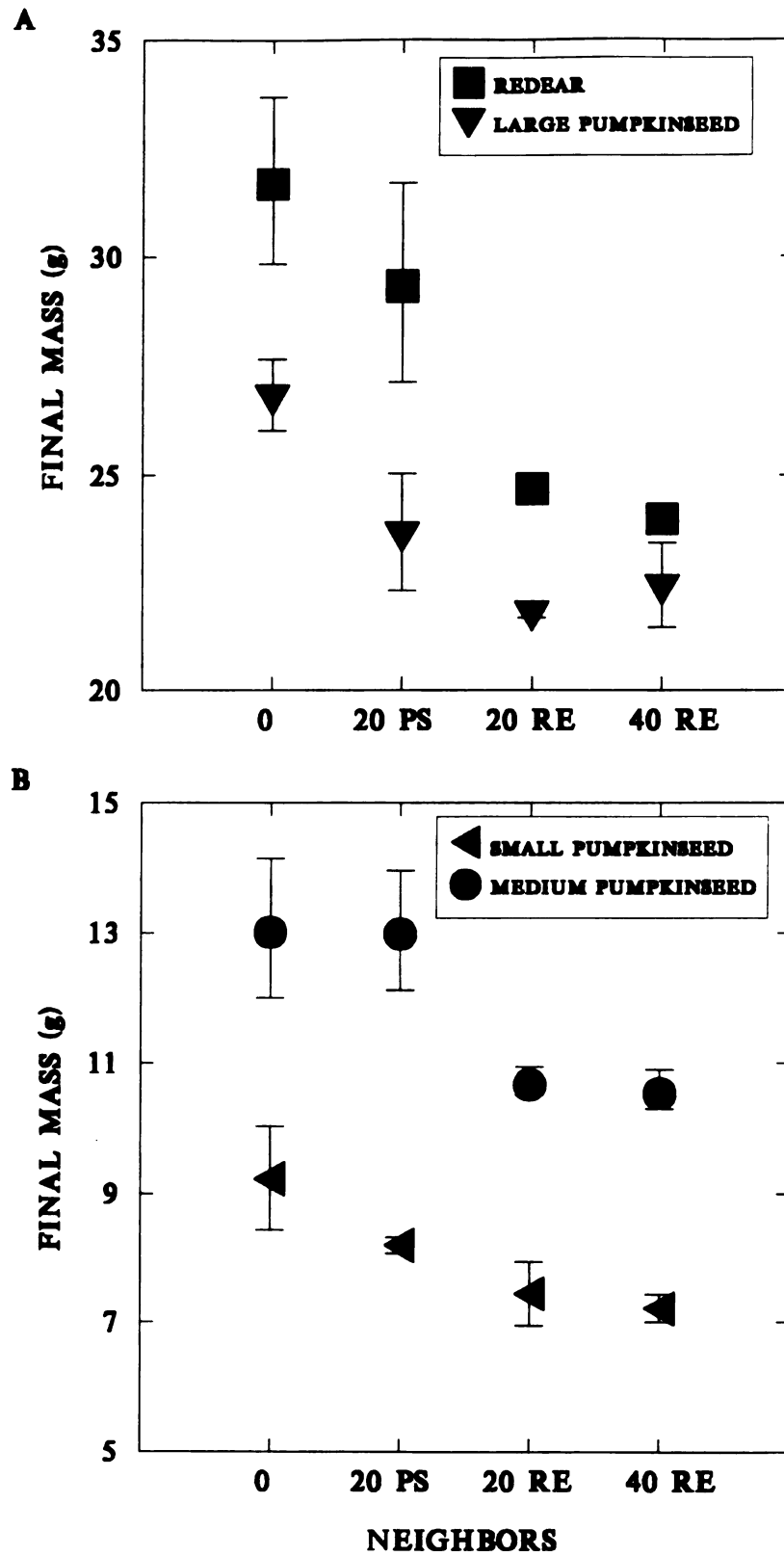


Figure 9

Planned contrasts showed that large pumpkinseed targets grew less in all neighbor treatments relative to the target only treatment (Table 3). Redear target mass was reduced in the presence of redear neighbors, but redear were not significantly affected by pumpkinseed neighbors. Contrasts to detect differences in intra- and interspecific effects on growth were not significant for large pumpkinseed or redear targets.

Although redear neighbors appeared to have a greater negative effect on pumpkinseed growth than did conspecific neighbors, differences in pumpkinseed final mass in +20 pumpkinseed and +20 redear neighbor treatments were not significant ($P \leq 0.75$). The contrast of redear final mass in the pumpkinseed neighbor treatment with that in the low redear neighbor treatment was marginally significant ($P \leq 0.074$). These results suggest that redear neighbors have a negative effect on pumpkinseed and redear performance, but pumpkinseeds do not strongly impact redear performance.

Estimates of intra- and interspecific competitive effects were calculated as competition coefficients. Calculated competition coefficients (interspecific effect on final mass/intraspecific effect) of pumpkinseed and redear indicate that redear have stronger competitive effects than pumpkinseeds ($\alpha_{PR}=1.69 \pm 0.62$ SE., $\alpha_{RP} = 0.37 \pm 0.17$ SE). An α_{PR} equal to 1.62 implies that each redear competitor is equivalent to 1.62 pumpkinseed competitors, while the $\alpha_{RP}= 0.46$ suggests that the competitive effect of one pumpkinseed on a redear target equals the effect of 0.46 redear (i.e., redear inhibit themselves approximately twice as much as do pumpkinseeds).

Table 3: Probabilities from Post-ANOVA contrasts: The mean final mass of large pumpkinseed and redear targets in the zero neighbor treatment (target only control) was contrasted with final target mass in each of the neighbor addition treatments.

<u>TREATMENT</u>	<u>large pumpkinseed targets</u>	<u>redeer targets</u>
+ 20 pumpkinseed	$P \leq 0.024$	$P \leq 0.329$
+ 20 redear	$P \leq 0.020$	$P \leq 0.025$
+ 40 redear	$P \leq 0.041$	$P \leq 0.017$

Target Diets

There were no significant effects of treatment on the total biomass of prey in target fish stomachs, although for all target groups (except large pumpkinseed), the total biomass of prey in the stomach tended to decline with neighbor density (Figure 10). There were significant differences in diet composition. The diets of target fish at the end of the experiment were dominated by soft-bodied, littoral invertebrates (Figure 11). Zooplankton accounted for a trivial proportion of the diets, never greater than 3% of total prey for any target class. Large pumpkinseed tended to consume small invertebrates (amphipods and dipteran larvae) and macroinvertebrates (predominantly Caenid mayflies) in approximately equal proportions and snails contributed $\leq 2\%$ to their diets. Redear also consumed a mix of soft-bodied invertebrates, however in contrast to pumpkinseeds, they consumed up to $31\% \pm 17\%$ snails in the target only treatment. The percentage of snails in redear diets declined in the presence of neighbors (down to 2% in the high redear neighbor treatment). Variation in extent of molluscivory was the most dramatic result in the diet data. Redear consumed significantly more snails than did co-occurring large pumpkinseeds (Fig. 12; ANOVA, $F_{1,8}=9.881$, $P \leq 0.014$). Snail biomass in both pumpkinseed and redear diets tended to decline across neighbor treatments, however the overall ANOVA model was not significant. There were no treatment effects on the size of snails consumed by large targets, but there was an effect of target species; the average snail in redear diets was larger than in pumpkinseed diets (0.18 ± 0.035 mg) vs. (0.055 ± 0.013 mg) respectively, ($t_{11}=2.768$, $P \leq 0.018$).

Figure 10. Total prey biomass from A) large pumpkinseed and redear targets, and B) small and medium pumpkinseed targets in each of the treatments (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Error bars represent ± 1 SE. Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets.

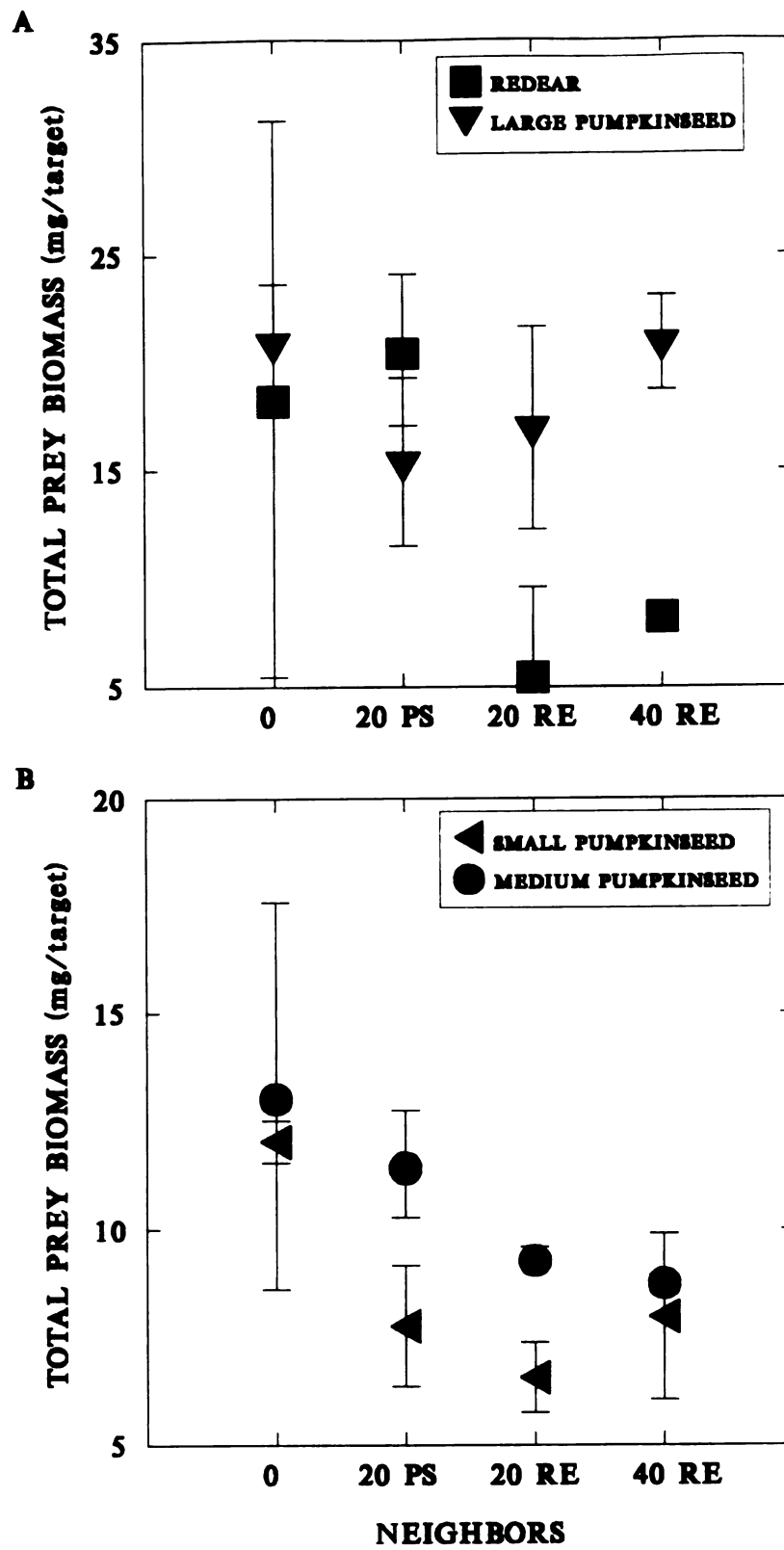


Figure 10

Figure 11. Prey composition in final target diets displayed as the mean proportion of diet biomass (± 1 SE) for A) large pumpkinseed targets, B) medium pumpkinseed targets, C) small pumpkinseed targets and D) redear targets from the competition experiment. Data are grouped by taxa: macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), small invertebrates (amphipods and dipteran larvae) and snails. Note that the proportions do not necessarily add to one because they are the average proportions for a class of fish. Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets.

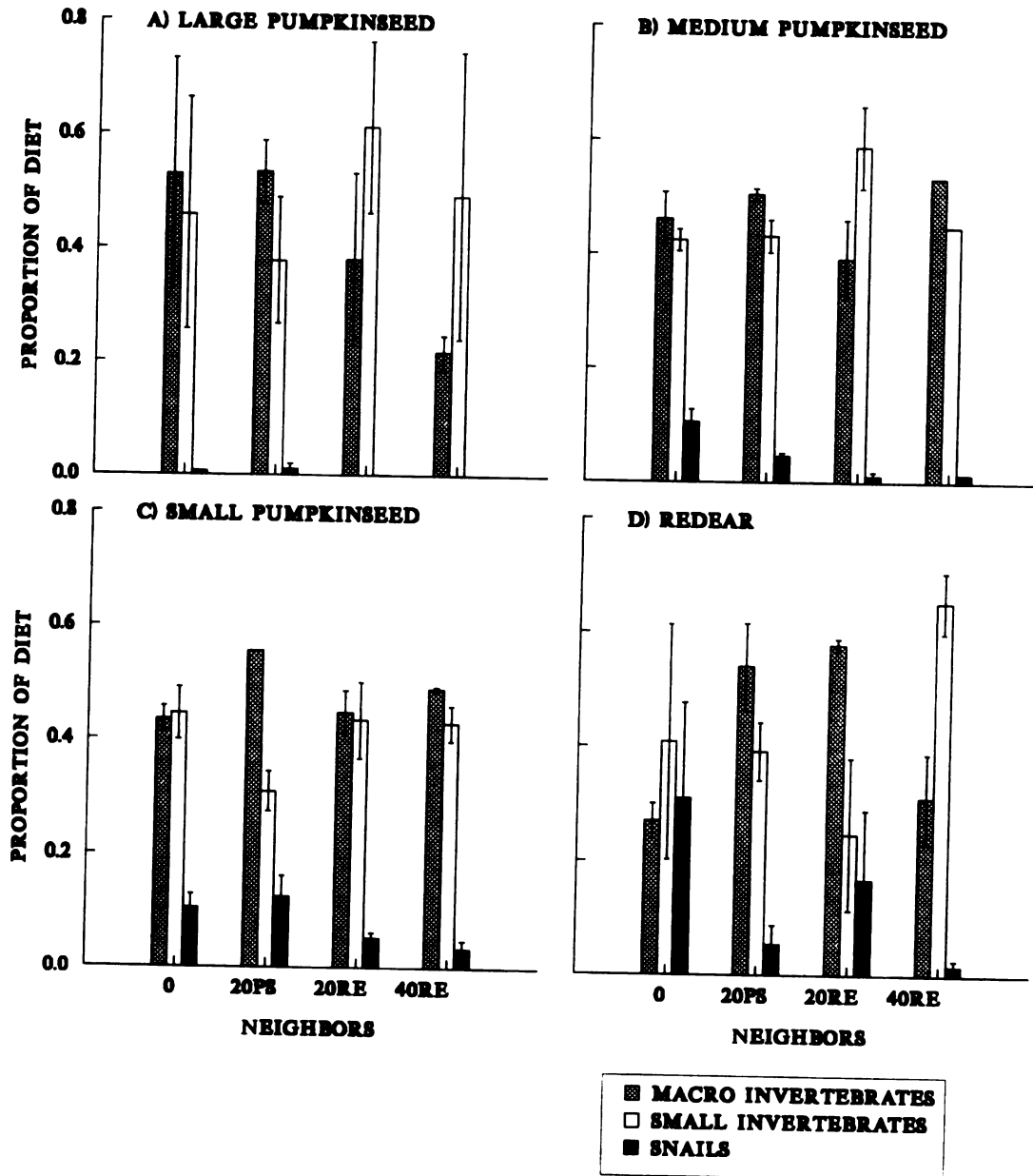


Figure 11

Figure 12. Biomass of snails in the diets of pumpkinseed and redear targets on the final day of the experiment. Bars represent the mean for a target class (± 1 SE) for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Mean standard lengths (SL) of each target class in a section ranged from 82.0-88.0 mm for large pumpkinseed targets, 64.8-71.2 mm for medium pumpkinseed targets, 55.8-62.2 mm for small pumpkinseed targets and 84.3-97.3 mm for redear targets.

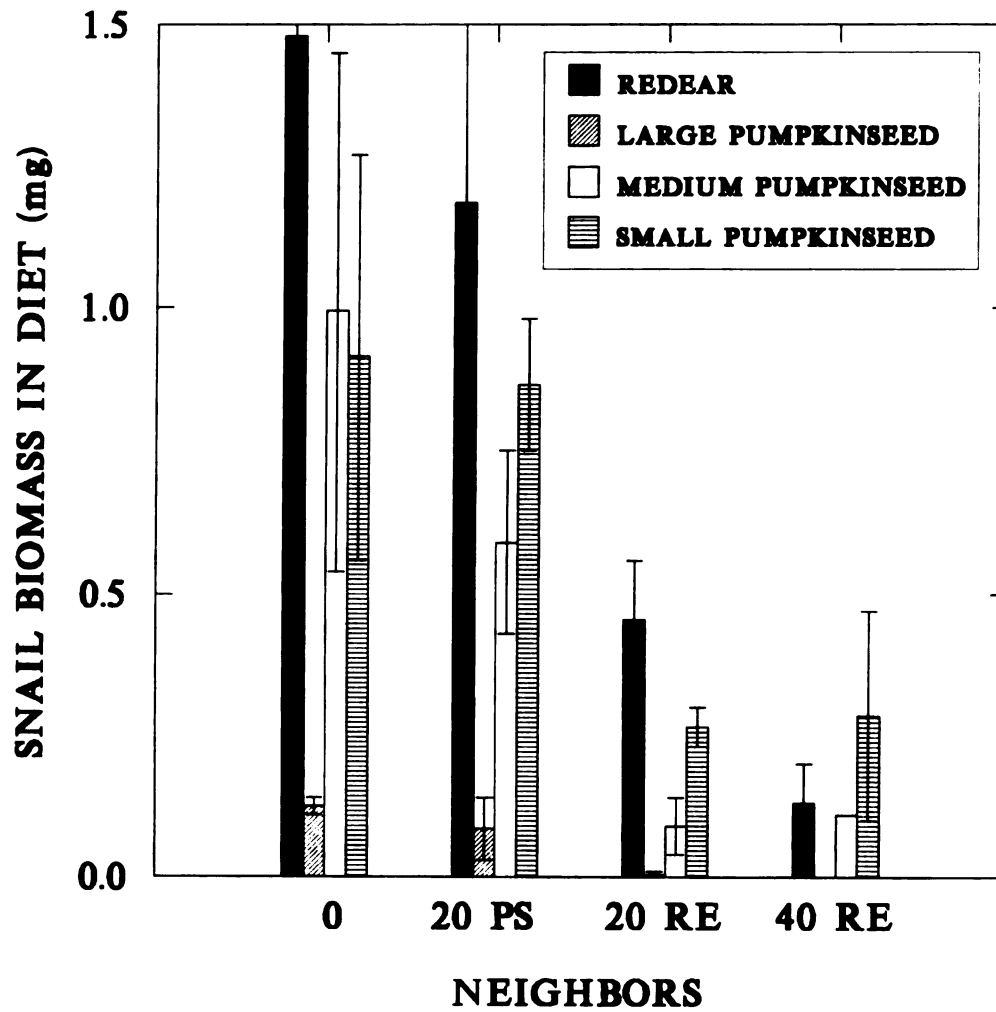


Figure 12

Resource Dynamics

The biomass of invertebrates declined over time in each of the treatments with fish (Figure 13); initially, there were no significant differences in invertebrate biomass among treatments. Because the temporal decline in biomass was nonlinear and there was also a reduction in variance through time, I examined treatment effects by comparing final invertebrate biomass among treatments. Overall fish effects were strong such that final invertebrate biomass was significantly reduced in all the fish treatments relative to the fishless treatment (Figure 14). Pumpkinseed and redear neighbors had similar effects on the biomass of both small invertebrates and macro-invertebrates. However there was a trend for redear to have a greater impact on snail biomass (Figure 14A). Final snail biomass was log 10 transformed to stabilize variance and post ANOVA contrasts showed that final snail biomass was significantly lower in both the low and high redear neighbor treatments than in the zero neighbor treatments ($P \leq 0.058$ and $P \leq 0.013$, respectively). Snail biomass in the pumpkinseed neighbor treatment was not significantly different from the zero neighbor treatment ($P \leq 0.243$).

Because fish are highly size selective, I predicted there would be fish effects on the size-structure of the prey community. The mean size of all prey types generally decreased in all treatments throughout the experiment, especially that of the macro-invertebrates (Figure 15). While there existed an overall treatment effect on the final mean size of macro-invertebrates (Figure 16, ANOVA, $F_{4,5}=23.305$ $P \leq 0.002$), I detected no significant differences in the effects of pumpkinseed and redear neighbors. There were no overall significant effects of treatment on the mean size of either snails

Figure 13. Biomass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) at three sampling dates throughout the experiment. Each point represents the mean (± 1 SE) of two replicates of a treatment. Note different scales on the y-axis.

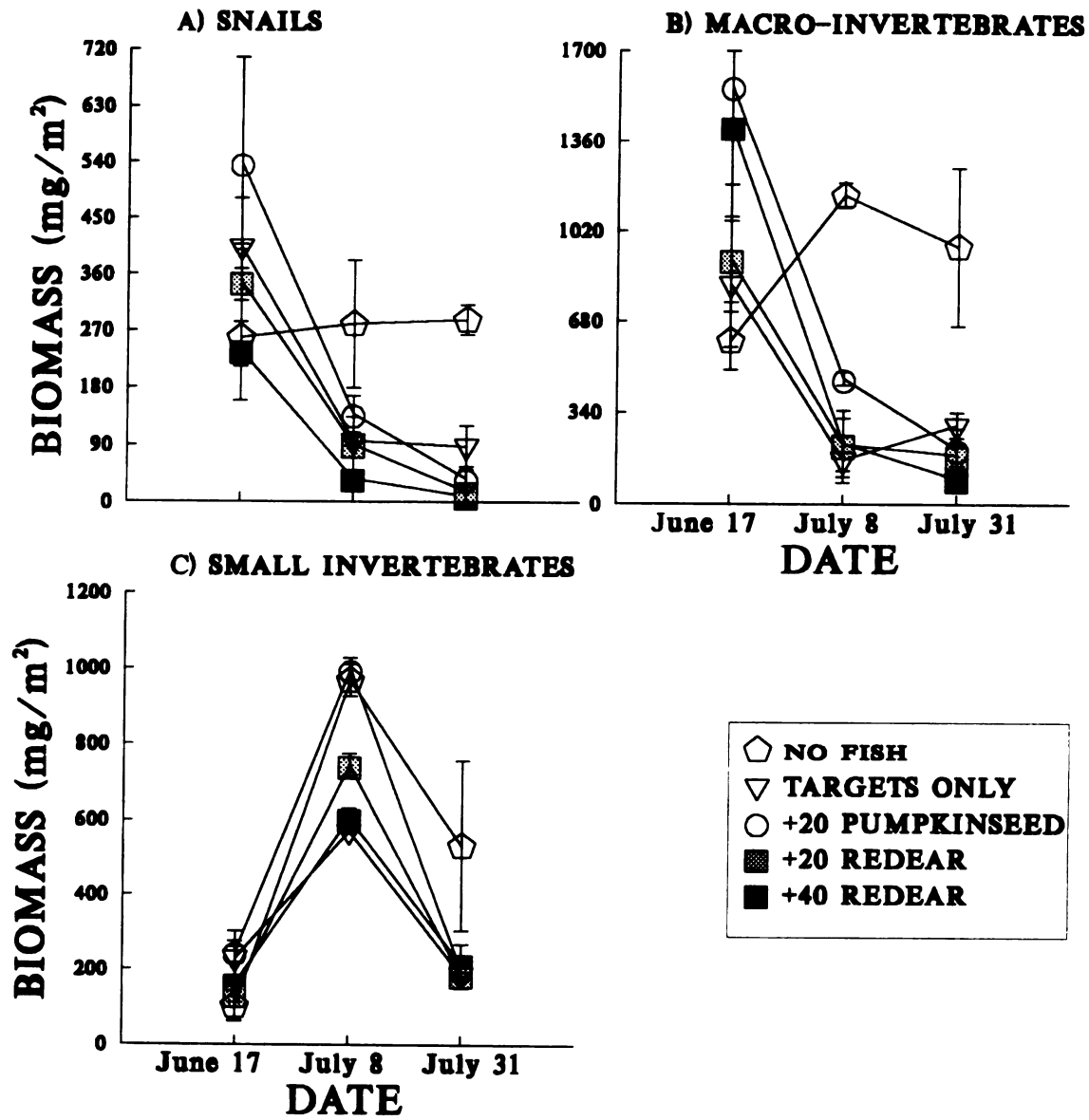


Figure 13

Figure 14. Final biomass of A) snails, B) macroinvertebrates and C) small invertebrates in each treatment of the pond experiment. Each data point represents the mean of the two replicates of a treatment (± 1 SE). Note different scales on the y-axis.

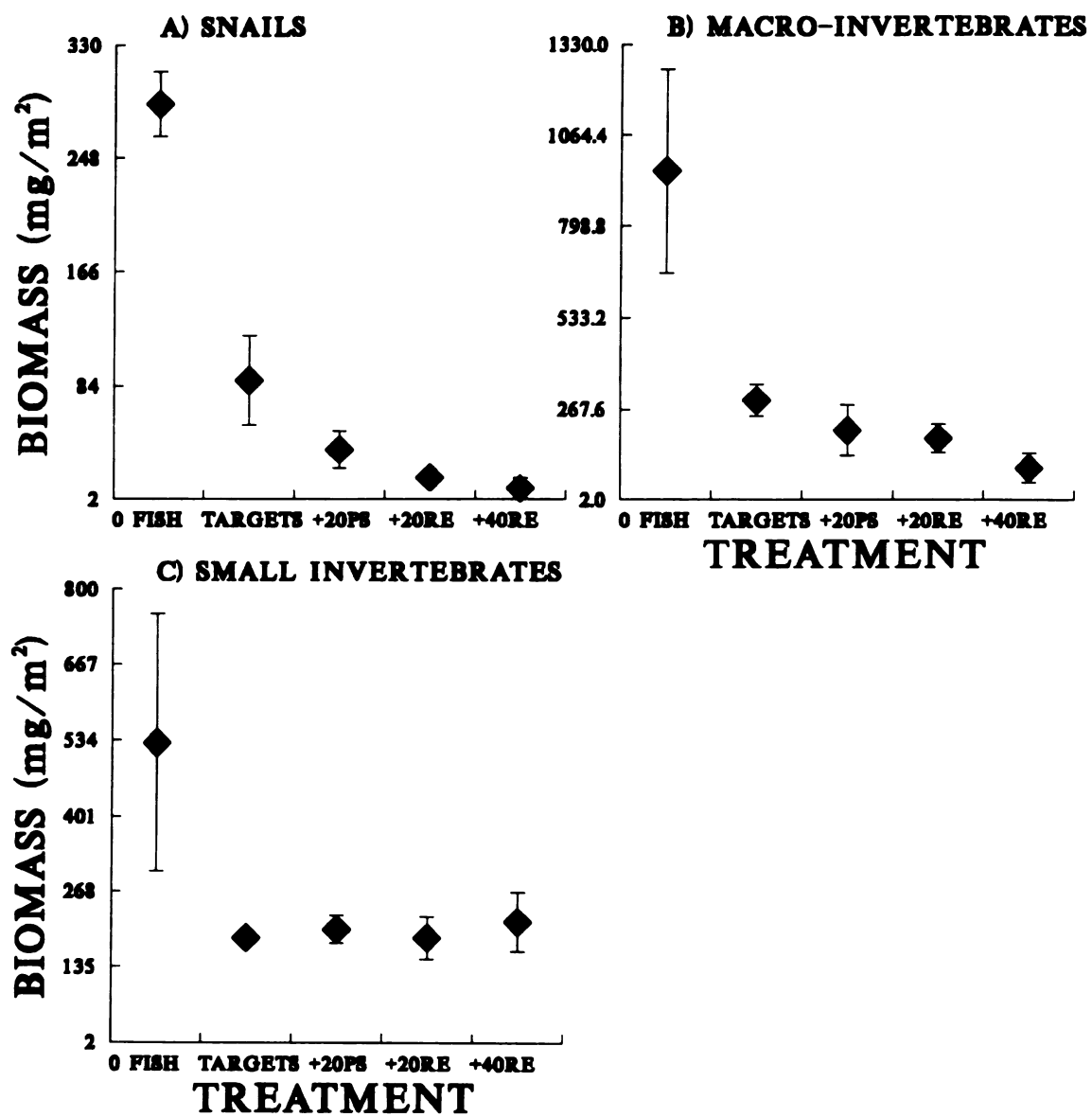


Figure 14

Figure 15. Individual mass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) at three sampling dates throughout the experiment. Each point represents the mean (± 1 SE) of two replicates of each treatment on each date. Note different scales on the y-axis.

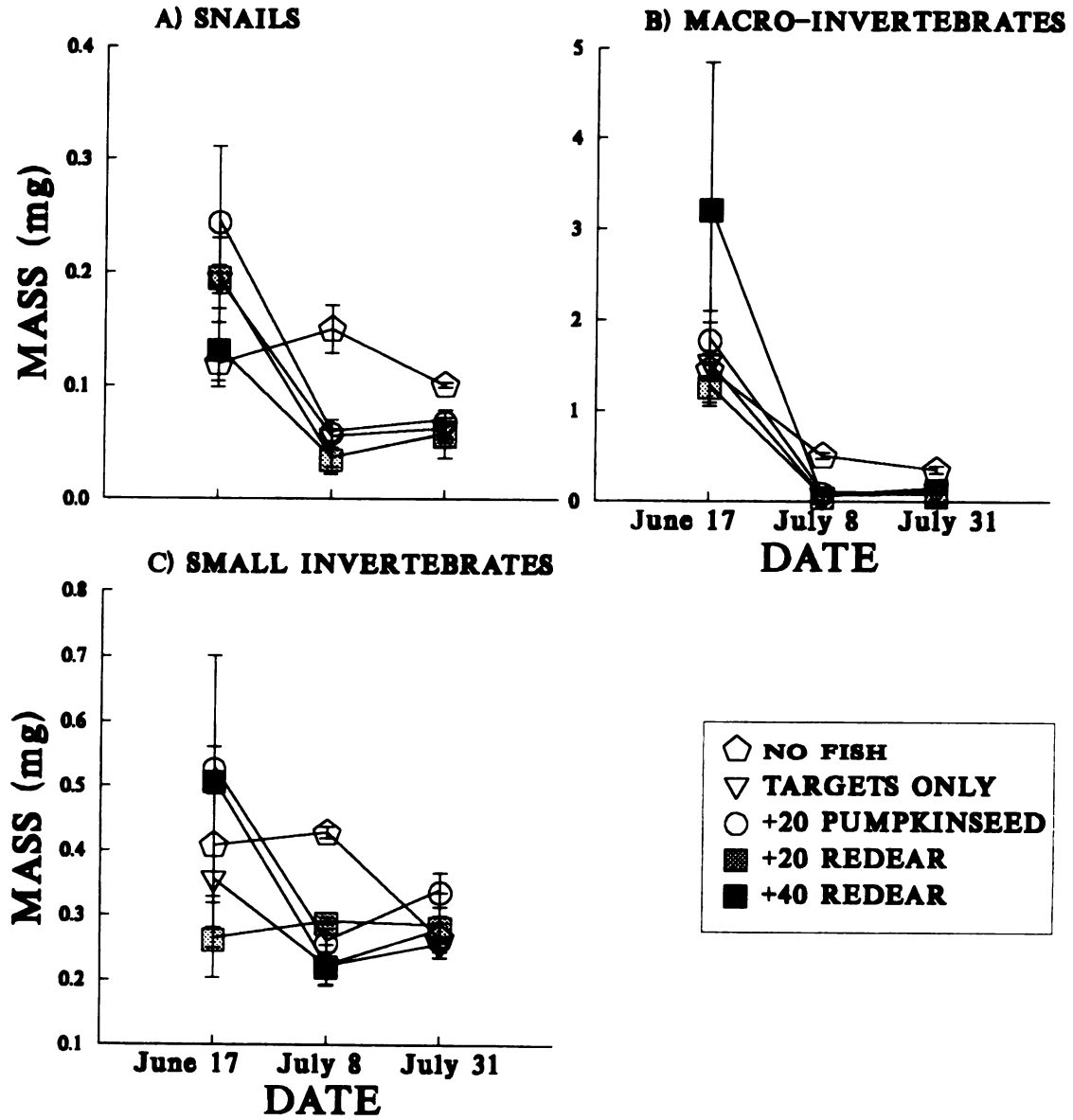


Figure 15

Figure 16. Final individual mass of A) snails, B) macroinvertebrates (primarily: Odonata and Ephemeroptera nymphs), and C) small invertebrates (amphipods and dipteran larvae) for each treatment: (no neighbors, 20 pumpkinseed, 20 redear and 40 redear neighbors). Each point represents the mean of two replicates (± 1 SE). Note different scales on the y-axis.

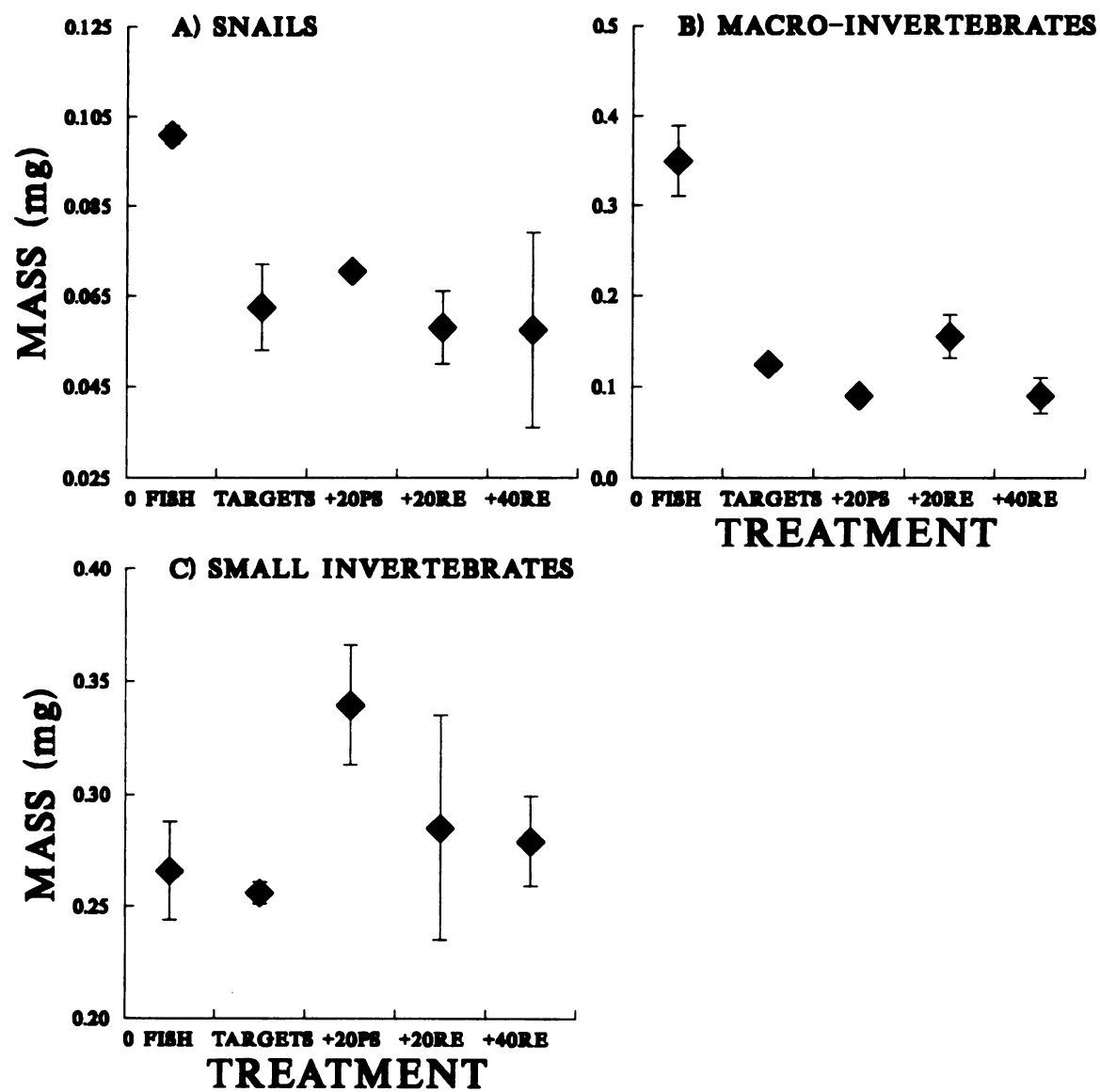


Figure 16

or small invertebrates (amphipods and dipteran larvae).

Target Growth- Resource Abundance Correlations

To identify potential mechanisms responsible for the competitive effect of neighbors on targets I examined relationships between mean invertebrate abundance (averaged across the three sample dates) and the final mass of targets. Growth rates of the target individuals should be related to the availability of the resources that are most limiting and over the course of the experiment the biomass of all prey types was reduced. Neither macroinvertebrate biomass (nymphs and large insect larvae) nor small invertebrate biomass (amphipods and dipteran larvae) was correlated with final size of any target group; at most they explained 9% of the variance. There was, however, a positive correlation between final target size and snail biomass for large pumpkinseed and redear targets and also the medium pumpkinseed targets (Figure 17). The final mass of the small pumpkinseed targets was, more weakly related to the mean biomass of snails (Figure 17), which was expected given that at the start of the experiment they were below the size at which pumpkinseed generally shift to a diet of snails.

Figure 17. Correlations of target final mass with the mean biomass of snails throughout the experiment. Snail abundance was estimated on three dates throughout the experiment and here snail biomass represents the mean over those three dates. Values of the correlations and significance probabilities are shown for each target class.

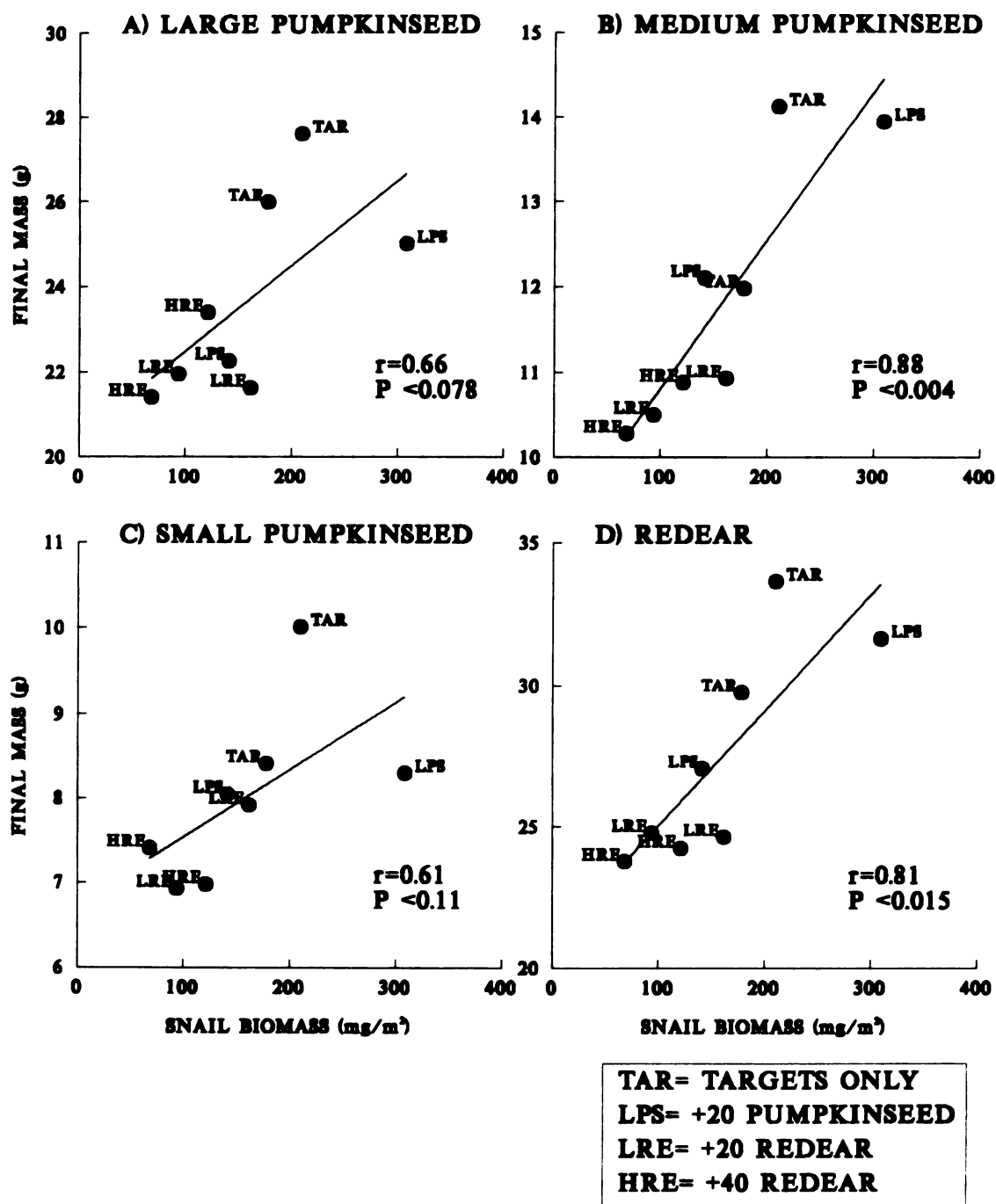


Figure 17

DISCUSSION

Redear and pumpkinseed sunfish are the most specialized molluscivores within the genus *Lepomis* (11 species, Smith 1981) and both species possess modified pharyngeal jaws and derived muscle firing patterns that allow them to feed effectively on gastropods (Wainwright and Lauder 1992). While the native ranges of these sister-species showed little overlap, except for minor regional overlap in the Carolinas (Trautman 1981, Lee et al. 1980), redear have been actively introduced into lakes in southern Michigan where pumpkinseeds are native. In this zone of artificial sympatry, pumpkinseed and redear are predicted to compete for snails. Based on comparative lakes surveys and a field competition experiment, this study provides evidence for resource based competition between redear and pumpkinseed. However, the degree to which redear might exclude pumpkinseeds from their range is unclear.

Interspecific competition is evidenced by altered dietary patterns, reduced density and/or reduced performance (e.g., growth) of a species when sympatric with the proposed competitor, relative to the allopatric condition. In the presence of redear, field populations of pumpkinseeds display two of these three patterns: reductions in density and alteration of their diet. Comparisons of MDNR surveys from before and after redear introduction show that pumpkinseed densities declined following establishment of redear populations (> 80% decline on average). This is the expected result if pumpkinseeds and redear compete for a limited resource (snails) and redear are superior exploiters of the resource. Alternatively, the population reductions may have been driven by factors other than competitive interactions, such as climatic

changes or anthropogenic changes to the environment. However, the lack of a response in bluegill density to the introduction of redeer in the same set of lakes, suggests that redeer introductions are not simply correlated with environmental factors that are ultimately driving the pumpkinseed decline. Rather, pumpkinseed reductions are likely driven by an interaction with introduced redeer, and competition for snails is the most likely mechanism. Although interference competition has also been shown to be an important mechanism driving many examples of resource partitioning in fishes (e.g., Hixon 1982, Langeland et al. 1991), neither aggressive behavior nor habitat segregation between redeer and pumpkinseeds were observed during multiple *in situ* visual observations in the pond experiment and in Lee Lake and Saubee Lake.

Redear are behaviorally and morphologically more specialized for molluscivory than are pumpkinseeds (Lauder 1983b, 1986) and as a result they are more proficient at feeding on snails than are pumpkinseeds (Chapter 2). Given that pumpkinseed diets can be quite flexible (Werner and Hall 1976,1979; Mittelbach et al. 1992, Osenberg et al. 1992), competition with redeer was predicted to induce changes in pumpkinseed diet. Alteration of the diet under sympatry can occur through an induced niche shift away from the diet that is normal under allopatry (e.g., Werner and Hall 1979, Persson 1987, Magnan 1988), or it can arise as a disruption of the ontogenetic niche shift of an otherwise stage-structured species (e.g., Bergman 1990, Persson and Greenburg 1990).

In marl bottomed lakes typical of southern Michigan, adult pumpkinseeds in the absence of redeer feed predominantly on gastropod molluscs (generally > 80% gastropods by mass, Figure 5; see also: Mittelbach 1984, Osenberg and Mittelbach 1989, Sadizikowski and Wallace 1976, Osenberg et al. 1994). However, in lakes

where redeer have been introduced, pumpkinseed diets rarely contain more than 30% snails and the diets of large pumpkinseed tend to resemble those of small pumpkinseed. In these lakes, both large and small pumpkinseed feed on soft-bodied invertebrates (primarily amphipods and chironomid larvae). Results from the pond experiment also show reduced molluscivory by pumpkinseed in the presence of redeer neighbors (see also Hanson and Leggett 1986).

Due to their specializations for crushing and handling snails, and their more extensive *in situ* molluscivory (Chapter 2), redeer are predicted to be able to reduce snail abundances to lower levels than can pumpkinseeds. Associations between redeer presence and low snail availability was seen in both multi-lake comparisons of snail abundances in lakes with and without redeer and also in the target-neighbor experiment. In the July survey of snail abundance, mean snail biomass in lakes without redeer was approximately four times higher than that of lakes with introduced redeer. In addition, results from the pond experiment also suggested that snail biomass tended to be lower with redeer neighbors than with pumpkinseeds at the same density. For example, *Amnicola limosa*, which is the most common snail in redeer diets in lakes, persisted in all experimental treatments in the pond, except in the four sections with redeer neighbors. In the highest redeer density treatment, snail availability was reduced to sufficiently low levels that large pumpkinseeds completely stopped foraging on snails. However, redeer targets of similar size continued to feed on snails. In Chapter 2 I discuss how redeer consume substantially more snails than sympatric pumpkinseeds, even when pumpkinseeds are capable of successfully crushing the majority of the snails found in redeer diets. Thus, large redeer may encounter snails at

a higher rate than large pumpkinseeds. However, this does not explain why small and medium pumpkinseed targets also fed substantially on snails in the high redear treatments. Sampling diets on the final date of the experiment likely does not capture the true patterns of target prey consumption throughout the experiment. Initial and mid-experiment diet data would have been useful to decipher the cause and effect relationships between diets and resource abundance.

The available evidence suggests that the impact of redear introductions is to reduce the abundance of snails, and thereby force pumpkinseeds to include a broader array of prey items in their diet. The generalization of pumpkinseed diets in lakes with introduced redear is likely to have important implications for pumpkinseed resource acquisition because they are then competing with a number of fishes (including the juveniles of all the sunfishes) that feed on littoral soft-bodied prey. Bluegill likely play a major role in mediating these interactions and the extent to which pumpkinseed broaden their diets in response to redear competition is predicted to be negatively related to the density of juvenile bluegill and that of other consumers of soft-bodied prey. An analogous condition has been described for perch (*Perca fluviatilis*) in Swedish lakes. In these lakes, the diet of perch is plastic and depends upon whether the main interaction is with planktivorous competitors (roach) or benthivorous competitors (ruffe), such that perch are "competitively sandwiched" between them (Bergman 1990, Persson and Greenburg 1990, Bergman and Greenburg 1994).

Osenberg et al. (1992) suggests that pumpkinseed growth is constrained when they are unable to shift to snails due to low snail abundances. In addition, the positive

correlations between final target size and overall snail abundance, coupled with the surprising lack of correlation between target mass and the abundance of soft-bodied prey in the target-neighbor experiment also suggests that snail availability may be tightly linked to molluscivore growth. In this study, reductions of pumpkinseed growth in lakes with introduced redbreast were not detected even though redbreast introductions were associated with reduced pumpkinseed molluscivory and a more generalized diet. A potential explanation for this pattern could lie in the relative abundance of competitors for soft-bodied prey and the size structured dynamics of the sunfish. There were no other species of competitors for littoral resources in the system studied by Osenberg et al. (1992), which allowed for good survival and recruitment of juvenile pumpkinseeds to the adult (snail feeding) stage. Subsequently, adult densities were high and per capita performance of adult pumpkinseeds was low. In other systems with more abundant competitors for soft-bodied prey there is potentially a more effective bottleneck at the juvenile stage of pumpkinseed development, which limits adult densities.

A potential outcome of competition is the reduction in growth of the weaker competitor when sympatric with a more proficient competitor. There were no observed differences in pumpkinseed growth in lakes with and without redbreast, yet pumpkinseed growth was reduced in the presence of redbreast in the pond experiment. There may, however, be a temporal component of the effect of redbreast competition on pumpkinseed growth. In the early stages of redbreast establishment before reductions in pumpkinseed densities have occurred, resource abundance is likely reduced by redbreast consumption leading to reduced pumpkinseed per capita intake of prey and therefore

reduced growth rates. Lower growth rates may lead to lower per capita fecundities, lower juvenile densities and lower recruitment to the adult stage (Mittelbach and Chesson 1987). Thus, a reduction in pumpkinseed growth rate is an expected short-term response to redeer introduction, while the long-term response would be a reduction in pumpkinseed density. In the lakes surveyed, the total mass of prey in pumpkinseed diets with and without redeer is similar, suggesting that at reduced densities, pumpkinseeds are able to forage successfully on alternative soft-bodied prey.

Pumpkinseed have persisted, albeit at low densities, with introduced redeer for 40 years in Lake George and Silver Lake (Branch County, Towns personal communication, Huckins personal observation). Thus, the long term dynamics of pumpkinseed and redeer interactions may be a matter of resource partitioning rather than complete competitive exclusion. Alternatively, 50 years may simply not have been sufficiently long for extinction dynamics to occur. As referenced in Ricklefs (1987), simple lab experiments of Miller (1967) suggest that competitive exclusion may require 10 to 100 generations to occur. Assuming 3 years for a generation, this translates into at least 30 to 300 years for pumpkinseed to be competitively displaced by redeer. Since the extent to which pumpkinseed can compensate for redeer competition by feeding on soft-bodied prey depends upon its availability, the time to pumpkinseed exclusion may be predicted to be negatively correlated with bluegill density since bluegill juveniles are effective competitors for soft-bodied resources.

To understand local species diversity and the processes that structure it, ecologists have been urged to broaden the scope of their research to include other disciplines and address questions at the appropriate spatial and temporal scale

(Ricklefs 1987). The interactions of pumpkinseed and redear is a good system for such an approach. In chapter 2, I describe the functional linkages between pumpkinseed and redear feeding performance (the ability to crush snails) and their resource use, and show that redear are more proficient molluscivores than are pumpkinseed. However, the traits which allow redear to feed more effectively on hard-bodied prey may come at a cost in terms of redear ability to feed on soft-bodied prey (Chapter 2). In the hard water lakes of Michigan, where snails are generally abundant, the trade-off may not be ecologically relevant. But, in other systems with lower supply rates of snails, this trade-off may limit redear success. Expanding the scope of examination to a more regional perspective might provide additional insight into these dynamics. For example, in the natural zone of redear and pumpkinseed range overlap in the Carolinas (where the sister-species have presumably interacted on ecological and evolutionary time scales), estimates of catch-per-unit-effort from seven aquatic systems (reservoirs and streams in North Carolina; Kornegay et al. 1994) reveal a virtually mutually exclusive pattern of pumpkinseed and redear presence. In systems dominated by pumpkinseeds, there were few if any redear collected, and as the percent redear in the catch increased the percent of pumpkinseed in the catch decreased to zero (Figure 18). Whether redear competitively dominate in systems with high snail availability and pumpkinseeds are able to numerically dominate where

Figure 18. Percent pumpkinseed and redbreast in the catch from 7 streams and reservoirs surveyed in North Carolina (data are from Kornev et al. 1994).

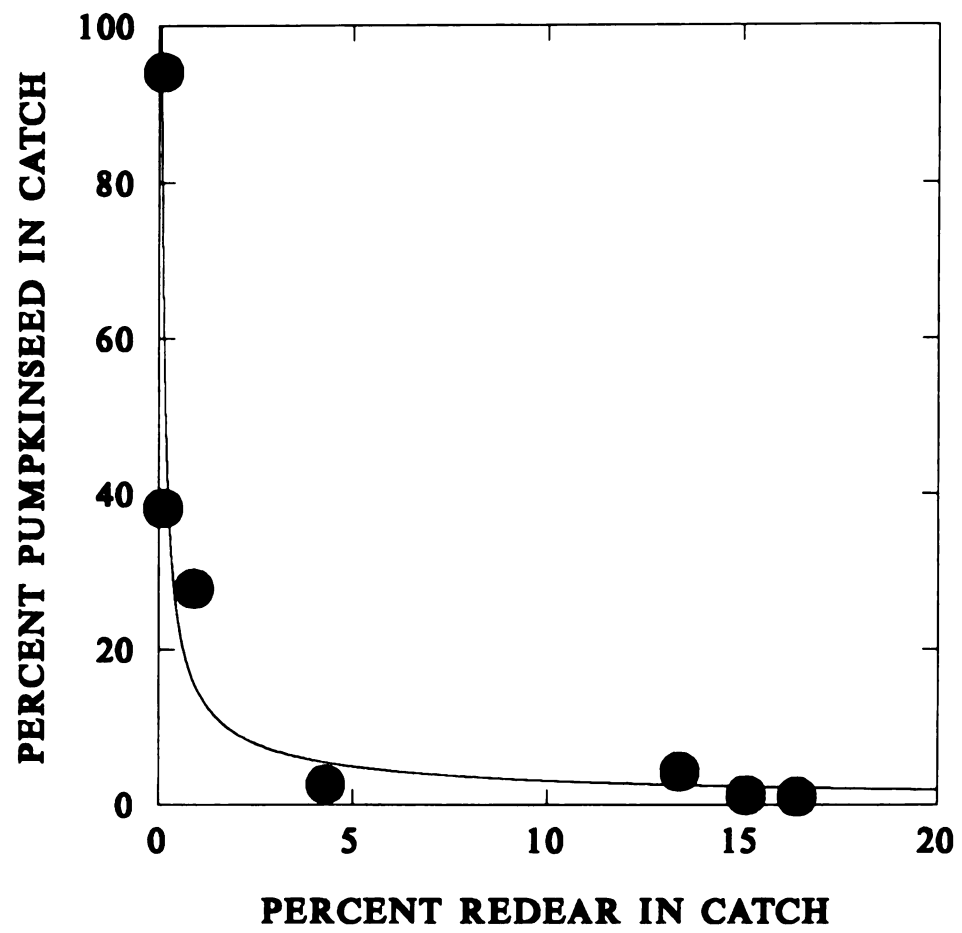


Figure 18

abundant alternative prey exists is a question to be addressed in future research. An alternative explanation could be that pumpkinseed may be able to persist in disturbed habitats (eg., low oxygen availability and/or turbid conditions) that inhibit redear persistence. Thus, where conditions are suitable for redear survival, pumpkinseed populations may not be able to compete.

Pimm (1987) suggests that the introduction of specialists into a community is more likely to be benign with respect to their impacts on the local community because generalists can potentially impact a broader array of the community. The results of this study however, suggests that introduced specialists, in this case the sister species of one of the native species, can impact a community depending upon the level of specialization of the host community members, their functional overlap with the introduced species and the specific linkages to the community structure as a whole. Certainly more work is needed in this system to determine the extent of the redear impact on pumpkinseed populations and the community as a whole. The dynamics of these interactions may require decades to play out and longer term and regionally scaled research, in addition to mechanistically focused experiments, are needed to capture these dynamics. The potential value of this type of research is great, as the ability to predict the impacts of species introductions would both demonstrate a working knowledge of the processes structuring communities, and also help guide the efforts to conserve native species (Moyle 1986, Lodge 1993 a,b).

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CHAPTER 2

FUNCTIONAL RELATIONSHIPS BETWEEN MORPHOLOGY, FEEDING PERFORMANCE, AND DIET

INTRODUCTION

Specialization of morphology and prey manipulation may provide some predators with food resources that are unavailable to other closely related species, resulting in niche partitioning, character displacement and evolutionary diversification (Lauder 1983a). Indeed, there is a strong precedent for predicting a relationship between an organism's functional morphology and its potential resource use (see Werner 1977, Werner and Hall 1979, Kiltie 1982, Mittelbach 1984, Wheelwright 1985, Grant 1986, Lavin and McPhail 1986, Wainwright 1987, 1988; Osenberg and Mittelbach 1989, Schluter 1993). However, the argument for causation in this linkage depends ultimately on our ability to link morphology with ecology through performance (Huey and Stevenson 1979, Arnold 1983, Emerson and Arnold 1989, Wainwright 1991). Fishes, by virtue of their great morphological and ecological diversity, have provided some of the best examples of how variation in morphology and behavior of related species may determine species- and habitat-specific foraging performance and resource use (Werner 1977, Lavin and McPhail 1986, Wainwright 1987, 1988; Magnan 1988, Meyer 1989, Osenberg and Mittelbach 1989, Ehlinger 1990, Norton 1991, Sanderson 1991, Malmquist 1992, Mittelbach et al. 1992, Osenberg et al. 1992). Resource use in turn is functionally linked to the abundance and distribution of species (see for example: Keast and Webb 1966, Werner and Hall 1976, 1979; Gatz 1979, Mittelbach 1984, Mittelbach and Osenberg 1994). Thus, knowledge of the mechanistic linkages between phenotype and feeding ability can greatly enhance our ability to predict patterns of species abundance and distribution.

Wainwright (1991) outlined an experimental approach for finding the causal relationships in these linkages. The basis of this approach lies in the corroboration of results and predictions of independent functional analyses. The first step is to determine the effect of morphological variation on the ability of an organism to perform a relevant ecological task. The variation in this metric of potential resource use, which is in many cases an estimate of the organism's maximal capabilities, is then related to the variation in actual resource use. Whether the potential resource use is then realized by the organism in the field is determined by prey availability, foraging behavior, and community composition.

Examination of maximal performance capacities and their role in shaping resource use has only rarely been done (Wainwright 1991; but see e.g., Kiltie 1982, Grant 1986, Wainwright 1987, and Osenberg et al. 1994). Knowledge of both the morphological mechanics of an organism and its basic ecology are required to arrive at the causal role performance plays in the system. Sunfishes (*Centrarchidae*) are an excellent system for such an analysis, and the pumpkinseed sunfish (*Lepomis gibbosus*) and its sister-species the redear sunfish (*L. microlophus*) clearly illustrate the mechanistic linkages between phenotype and ecological interaction. These species are the only sunfishes known to be specialist molluscivores as adults (Lauder 1983b, Mittelbach 1984, Wainwright and Lauder 1992). Both pumpkinseed and redear possess the hypertrophied pharyngeal jaw musculature and bone structure (Lauder 1986), in combination with a specialized neuromuscular motor pattern (Lauder 1983b) that are necessary to feed effectively on gastropod molluscs. However, redear possess a more robust pharyngeal jaw apparatus and more highly specialized muscular activity

(Lauder 1983b, 1986). Variation in the size of pumpkinseed pharyngeal jaw apparatus has been shown to be strongly related to variation in handling efficiency of hard-bodied prey (Osenberg et al. 1992) and positively associated with the abundance of snails in pumpkinseed diets (Mittelbach et al. 1992). Thus, if interspecific variation in the size of the pharyngeal apparatus is similar in its effects on molluscivory to intraspecific variation, then redear are predicted to be more proficient molluscivores relative to pumpkinseed.

The native distributions of redear and pumpkinseeds were largely allopatric such that redear populations extended approximately south from St. Louis, Missouri and east to the coast, while pumpkinseeds were native to the Great Lakes Drainage and throughout the north-east quarter of the United States. These largely disparate ranges, however, included a small region of overlap with redear in the Carolinas (Lee et al. 1980, Trautman 1981). Throughout the last decade, for purposes of sport fishery enhancement, redear sunfish have been introduced into lakes of southern Michigan, thus establishing a large zone of artificial sympatry between pumpkinseed and redear. Surveys of pumpkinseed populations in these systems show significant reductions in the contribution of snails to pumpkinseed diets, and in the density of adult pumpkinseeds following redear introduction (Chapter 1). Data from a field manipulation also demonstrates that competition occurs between pumpkinseed and redear, and suggests that redear are competitively dominant (Chapter 1). From these studies, I predict the relative competitive abilities of these specialized sister-species are strongly linked to morphologically and behaviorally driven variation in molluscivore performance.

In this paper, I explore the patterns of diet ontogeny and resource partitioning in pumpkinseed and redbreel populations in lakes of southern Michigan. I conducted lake surveys of pumpkinseed and redbreel diets to compare species-specific levels of molluscivory. I then use laboratory feeding performance trials to assess how variation in feeding performance determines the diet ontogeny and patterns of resource partitioning between these two specialists. Specialization by an organism, however, may entail a potential cost in the specialist's ability to perform other foraging tasks (Futuyma and Moreno 1988, Schluter 1995, Wilson and Yoshimura 1994, Robinson et al. 1996). Given that redbreel display a heightened level of behavioral and morphological specialization relative to pumpkinseeds (Lauder 1983b), I predicted that redbreel would display heightened proficiency at feeding on hard-bodied prey, which might then result in reduced efficiency when consuming soft-bodied prey. I examine this potential trade-off in foraging ability on hard and soft-bodied prey using laboratory feeding experiments.

METHODS

Study lakes

The diets and feeding ontogeny of redbreel and pumpkinseed sunfish were studied in two southern Michigan lakes: Lee and Saubee. Pumpkinseed are native to these lakes, redbreel are not. Young of year redbreel were introduced at low densities by the Michigan Department of Natural Resources (MDNR) into Lee Lake (Calhoun County) in 1981, 1991, and 1992; and into Saubee Lake (Eaton County) in 1986. Lee Lake and Saubee Lake are marl bottom lakes that are 46 hectares and 23 hectares,

respectively. Lee Lake is ringed with emergent vegetation (bull rush, *Typha* sp. and *Fragmites* sp.) and its bottom is sparsely vegetated (*Chara* sp., *Myriophyllum* and *Potamogeton* sp.). Saubee Lake is ringed with a littoral zone consisting of dense stands of *Potamogeton* sp., assorted emergent vegetation and occasional water lilies (*Nymphaea* sp. and *Nuphar* sp.).

Lee Lake and Saubee Lake were chosen for study based on their proximity (relative to the other lakes with introduced redeer) to the W. K. Kellogg Biological Station of Michigan State University and because preliminary surveys indicated adequate densities of both redeer and pumpkinseeds (Huckins personal observation). Lee and Saubee Lake both support reproductive populations of redeer and pumpkinseed as well as the typical compliment of sunfish and other fish species found in southern Michigan lakes.

Diet Composition and Ontogenetic Shifts

Fish were collected between May and August in 1993 and 1994) by seining. Pumpkinseed feeding peaks between dawn and noon (Hanson and Leggett, 1986), therefore fish were collected before 12:30 pm to minimize gut content digestion. Fish were preserved in 10% neutral formalin and later measured for standard length. Stomachs were removed just anterior of the pyloric caecae and posterior of the esophagus, and stomach contents were identified to the lowest possible taxonomic level (generally to genus). For each fish, all prey items in the gut were enumerated and measured (up to 50 individuals per taxa) for later estimation of individual dry mass using length-weight regressions (Mittelbach and Osenberg unpublished data,

Huckins unpublished data). The specific body axis measured for a given prey type depended upon which body part was best preserved. For example, the shells of snails are generally crushed during consumption, so all pulmonate snails were measured along the length of their foot, and all prosobranch snails were measured along the longest axis of their opercula. Head capsule widths were measured for most insect larvae and nymphs, and body lengths were measured for Cladocera and most other zooplankton. Gut contents of fish were not included in subsequent analysis if they were in a state of digestion that made identification and measurement of prey uncertain.

The composition of pumpkinseed and redear diets was explored by categorizing prey items by type: 1) amphipods, 2) dipteran larvae, 3) nymphs of odonates and ephemeropterans, 4) trichopterans, 5) snails, 6) zooplankton and 7) other miscellaneous prey including coleopterans, mites, annelids, hemipterans, etc. For each fish, I calculated the proportion of the total prey biomass contributed by prey in each of the seven categories (biomass calculations for snails excluded their shells). I then examined the ontogenetic patterns of pumpkinseed and redear molluscivory in particular, in order to categorize the individuals into pre- and post-niche shift stages. The division point between the dietary stages was estimated by fitting logistic regressions relating the proportion of snails in the diet to the standard length (SL) for each species, and then calculating the SL at which the inflection occurred. This calculation was performed on diet data from redear and pumpkinseed collected from Lee Lake and Saubee Lake. I also fit a logistic regression to diet data from pumpkinseeds collected from lakes not containing redear to estimate the SL when

pumpkinseed undergo their niche shift in the absence of redear (Osenberg and Mittelbach, personal communication).

In order to compare redear and pumpkinseed molluscivory under similar environmental conditions (resource levels), I examined the proportion and the biomass of snails in the diets of both species collected from the same set of lakes. I restricted these analyses to include only post diet-shift individuals (>40 mm for redear, >65 mm for pumpkinseeds, see results: Diet Composition and Niche Shift). Proportional data were arcsin square root transformed prior to analysis with ANCOVA to meet the assumptions of homogeneity of variance. Analogous analyses of snail biomass used $\log_{10}(\text{biomass (mg)} + 0.1)$.

Mechanisms Underlying Dietary Patterns

Laboratory Analysis of Performance

To examine if differences in pumpkinseed and redear morphologies and behaviors translated into between species differences in feeding performance, I conducted laboratory feeding trials. I measured maximal crushing strength (capacity) and prey handling times of redear and pumpkinseed sunfish to address if greater specialization by redear allows them to crush harder snails and crush snails more quickly. I also measured prey handling times when feeding on soft-bodied prey to see if a trade-off exists in the abilities to handle soft-bodied and hard-bodied prey. Nine redear (56 mm to 126 mm SL) and 13 pumpkinseed (51 mm to 119 mm SL) were collected in late August, 1993 from Lee Lake. Four pumpkinseeds (58, 65, 68 and 70 mm SL) were also collected from Grass Lake, Jackson County to fill in a small gap in

the pumpkinseed size-range. Grass lake is similar to Lee Lake in terms of its marl bottom, basin size, and presence of introduced redear and more importantly, pumpkinseeds from Grass Lake and Lee Lake have similar diets (Huckins personal observation). In addition, 9 redear (67 to 102 mm SL) were obtained from a MDNR redear brood pond; these fish had the same ancestry as Lee Lake redear. A total of 18 redear and 17 pumpkinseed were used in the performance trials.

The experimental fish were individually housed at 22.2 C (± 0.07 SE) in 33 liter aquaria with a common filtration system. Fish were maintained on a diet of earthworms and snails and were not fed for 24 hours prior to performance trials to standardize hunger and to maintain high levels of motivation. Fish readily fed on snails dropped into the aquaria. After engulfing and manipulating the snails between the pharyngeal jaws, both redear and pumpkinseed crush the snails using simultaneous contractions of the pharyngeal muscles (Lauder 1983a,b, Wainwright and Lauder 1992). The time at which the structural integrity of the snail shell is compromised can be noted by an audible "crinkling" sound. Upon crushing the shell, the fish use their oral and pharyngeal jaws to separate the body of the snail from the shell fragments, which are then ejected indicating the completion of prey handling. I recorded the elapsed time between the snail being engulfed and crushed, and also the total handling time of the prey.

Snails of a single species were sorted into 1 mm shell length classes and ten individuals within a length class were randomly subsampled and preserved in buffered formalin for later estimation of crushing resistance. Crushing resistance of a given snail shell was estimated by placing a one ended acrylic cylinder on top of the snail

and filling the cylinder with sand until the snail shell collapsed (see Osenberg and Mittelbach 1989). The crushing resistance of the shell was defined as the total mass of the cylinder and the sand, which was converted to Newtons by multiplying by $0.009802 \text{ kg m/s}^2$. The mean for the 10 subsampled snails was used as the crushing resistance for the corresponding set of performance trials.

Remaining snails in the length class were offered to the trial fish. Over the course of one month, fish were offered a range of snails (one at a time) from those crushable to those that were rejected uncrushed, presumably due to the upper limit of the crushing ability of the fish. The order in which snails were offered to the fish was haphazard with respect to snail size. To encompass this range of crushing resistance, various sizes of *Physella sp.*, *Helisoma anceps* and *Bithynia tentaculata* were used in the feeding trials. The final outcome of each feeding trial was recorded as ending with one of the following events: 1) successful crushing of the snail (crush time and handling time was measured); 2) consumption of the snail without any audible fractures of the shell; 3) rejection of the snail after it was engulfed (rejection time measured); or 4) rejection of the snail because the fish was gape limited. Ten to 53 performance trials were conducted for each fish. Trials that ended with the occurrence of either event type 2 or 4 were excluded from analysis (<1% of all trials), leaving 1021 trials for analyses.

Crushing Strength

I defined the crushing strength of a fish as being equal to the crushing resistance of snails that have a 0.50 probability of being crushed (see also Wainwright

1987, Arnold 1983). For each fish I estimated the relationship between the probability of being crushed (P) and snail crushing resistance by submitting the data (consisting of a binary response variable: crushed, not crushed) to logistic regression. The fitted equation:

$$\text{eq 2.1} \quad P = 1 / [1 + e^{(a + b \cdot \log(C))}],$$

where a is the intercept and b is an estimated parameter of the function, was then used to estimate crushing strength (C) by setting $P=0.50$ and solving for (C). Crushing strengths were log transformed prior to analysis by ANCOVA with SL included as a covariate. To describe the ontogenetic pattern of crushing strength in each species, I developed models that predict crushing strength as a function of fish length for each species using SYSTAT (Wilkinson 1990). The crushing potential of molluscivorous sunfish is influenced by the mass of the levator posterior (Wainwright and Lauder 1992) and muscle mass increases as a positive power function of body length (Schmidt-Nielson 1975). Therefore, for each species, I fit a linear function to the relationship between the fish's crushing strength and its standard length after log transformation of each variable:

$$\text{eq 2.2} \quad \log C = M \cdot \log SL + B$$

where logC is crushing strength ($\log_{10}$ Newtons), logSL is standard length ($\log_{10}$ mm) and M and B are constants.

While there is no *a priori* reason to assume that organisms will utilize their maximal performance capacities in the field (Wainwright 1991), molluscivores with greater crushing strength have been shown to consume larger and harder molluscs (Wainwright 1988). To examine if: 1) pumpkinseed and redear perform maximally such that their diets are constrained by crushing strength; 2) redear and pumpkinseed partition resources by their crushing resistance; or 3) redear consume larger and thus harder snails than pumpkinseeds, I estimated the crushing resistances of individual *Amnicola* and *Physella* found in individual pumpkinseed and redear diets. I used species-specific relationships between crushing resistance and snail shell length (Osenberg, unpublished data) to estimate the values. The upper end of the distribution of crushing resistance for each pumpkinseed and redear diet was described by the mean of the upper quartile of snail crushing resistances. The relationships between the mean crushing resistance and fish length were compared for pumpkinseed and redear using ANCOVA, such that species was the main effect tested and SL was included as the covariate.

Prey Handling Time

The feeding performance on hard-bodied prey (snails) of pumpkinseed and redear was compared to examine if greater crushing strength confers any advantages that increase the proficiency of molluscivory. The time required to handle a prey item (capture and consume) provides a measure of the efficiency of resource use (Werner 1974, Stein 1977, Mittelbach 1981). Thus, the performance metrics used for the species comparisons were the mean time required for each fish to crush and handle

Physella with crushing resistances between 4.5 and 7.7 Newtons. The mean crushing resistance and shell length were 6.3 ± 0.91 Newtons (mean $\pm$ 1 SD) and 7.9 ± 1.81 Newtons (mean $\pm$ 1 SD), respectively. Handling times were log10 transformed to stabilize variance and the analysis was restricted to the range of SL for which sufficient data were available for both pumpkinseed and redear (SL 75-100 mm).

To address the prediction that redear are less proficient at handling soft-bodied prey than pumpkinseeds, I measured handling times for pumpkinseed and redear feeding on mayfly nymphs, *Hexagenia sp.*, a soft-bodied prey common in marl bottom lakes (Laughlin and Werner 1980). Prior to each series of trials involving one of two nymph size categories, 10 nymphs were subsampled and measured for head width. Nymph headwidths in the small and large size-classes were 2.63 ± 0.04 mm (mean $\pm$ 1 SE) and 3.37 ± 0.05 mm (mean $\pm$ 1 SE), respectively. Fish were offered individual nymphs, handling times were measured and mean handling times per fish for each nymph size were log transformed and compared with ANCOVA using SL as the covariate.

RESULTS

Diet Composition and Niche Shift

No significant differences existed between lakes in the proportion of snails in the diets of either pumpkinseed or redear so fish from Lee and Saubee Lake were pooled by species. Both pumpkinseed and redear shifted from a diet of soft-bodied invertebrates when small, to a diet more inclusive of snails when they were larger. Considering both the proportion of snails in the diet (Figure 1A), and the total snail

Figure 1. Ontogenetic patterns of molluscivory for sympatric pumpkinseed and redear expressed as A) the proportion of snails in the diet (by biomass), and B) the total biomass of snails in the diet. For clarification of presentation the data are grouped into 10-mm size classes and each point represents a mean (± 1 SE). In figure 1A, logistic curves were fit to the complete data set for each species using nonlinear regression: $\text{proportion snails} = Y_{\text{max}} / [1 + \text{EXP}(A + B \cdot \text{SL})]$, where Y_{max} , A , and B are constants fitted by the regression. Fitted curves are shown for redear ($Y_{\text{max}}=0.916$, $A=6.463$ and $B= -0.164$) and for sympatric pumpkinseeds ($Y_{\text{max}}=0.525$, $A=3.437$ and $B=-0.044$).

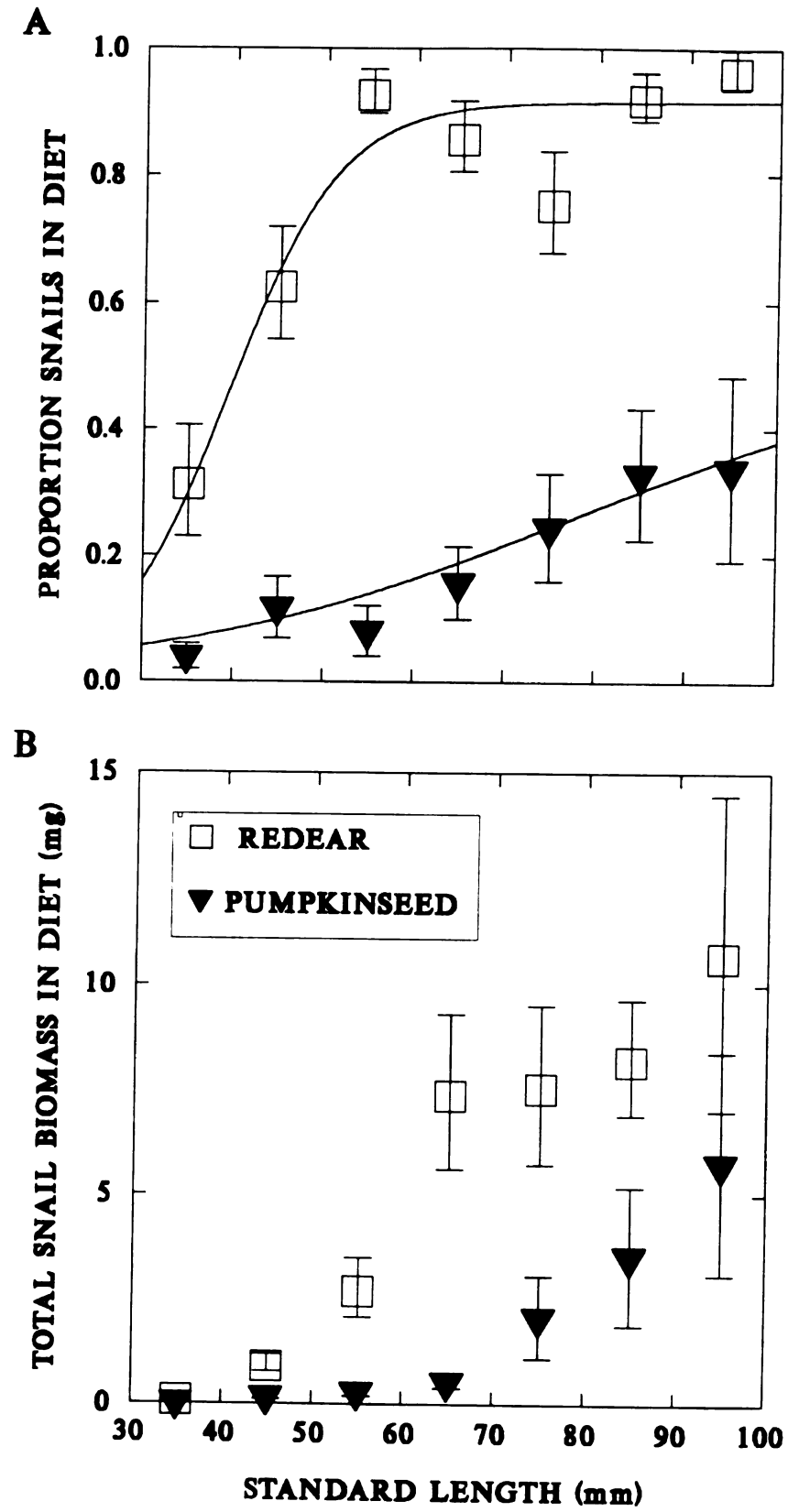


Figure 1

biomass eaten (Figure 1B), redeer are substantially more molluscivorous than sympatric pumpkinseeds. The logistic functions describing the relationship between the proportion of snails (P) in the diet and SL of each species, and the point of inflection (estimated length at niche shift) are:

eq. 2.3) redeer:

$$P=0.916/[1+\text{EXP}(6.463-0.164*SL)], \quad 39.4 \text{ mm}$$

eq. 2.4) pumpkinseeds (redear present):

$$P=0.525/[1+\text{EXP}(3.437-0.044*SL)], \quad 77.9 \text{ mm}$$

eq. 2.5) pumpkinseeds (redear absent):

$$P=0.836/[1+\text{EXP}(7.175-0.110*SL)], \quad 65.0 \text{ mm}$$

In subsequent analyses, pumpkinseed and redeer were divided into ontogenetic stages corresponding to the relative incorporation of snails in the diet (pre- and post-niche shift). Pumpkinseeds collected from Lee and Saubee Lakes (with redeer) showed a very weak shift to snails during their ontogeny compared to the extensive shift of allopatric pumpkinseeds (See Chapter 1, also note y'max values in above functions). Due to the weak diet shift of pumpkinseed when sympatric with redeer, I used the conservative estimate of 65 mm SL as the division between pre- and post-niche shift stages for pumpkinseed. Pre-niche shift redeer are defined as individuals with $SL \leq 40$ mm. Even with this more conservative estimate of when the pumpkinseed niche shift occurs, redeer initiated their diet shift at a much smaller size than do pumpkinseeds (approximately 25 mm). Analysis of covariance using standard

length as a covariate showed that the disparity between the proportion of snails in the diets of molluscivorous pumpkinseed and redear (SL>65 mm) was highly significant (Figure 1A, ANCOVA, $F_{1,39}=64.061$, $P\leq 0.0001$). This result that redear are substantially more molluscivorous than sympatric pumpkinseeds, is also supported by the greater biomass of snails in redear diets (Figure 1B, ANCOVA $F_{1,56}=17.70$ $P\leq 0.0001$).

Pumpkinseeds ≤ 65 mm SL in Lee Lake and Saubee Lake were consuming primarily soft-bodied prey such as insect larvae, the bulk of which were dipteran (e.g., chironomid) larvae (Figure 2A). The diets of larger pumpkinseed (≥ 65 mm SL) in these lakes also tended to be dominated by chironomid larvae, which on average accounted for $36.8 \pm 0.58\%$ (mean ± 1 SE) of the diet biomass (Figure 2B). Snails comprised $29.1 \pm 0.054\%$ (mean ± 1 SE) of the average total prey biomass of large pumpkinseed. Thus, in these lakes where pumpkinseed are sympatric with redear, diets of small and large pumpkinseeds were quite similar and both include a majority of soft-bodied prey. This is in contrast to the dominance of snails in the diets of similarly sized pumpkinseeds in Michigan lakes without redear (Chapter 1). Redear in Lee Lake and Saubee Lake show a striking shift in diet between small (<40 mm SL) and large individuals. Diets of small redear contained approximately 30%-50% each of snails and zooplankton, and the remainder was dominated by dipteran larvae (Figure 2C). Redear larger than 40 mm SL showed an extensive shift to molluscivory; approximately 87% of the average diet was composed of snails (Figure 2D). The composition of the snail biomass in the diet (i.e. the contribution to the total snail biomass provided by each snail genus) was quite similar for pumpkinseed and redear.

Figure 2. Dietary composition of pre- and post-niche shift pumpkinseeds (top panels) and redear (lower panels). The prey categories are amphipods, dipteran larvae, insect nymphs, trichopteran larvae, snails, zooplankton and other (mites, annelids, coleoptera, etc.). The bars represent the mean proportion each prey type contributes to the total diet biomass (mg) (± 1 SE).

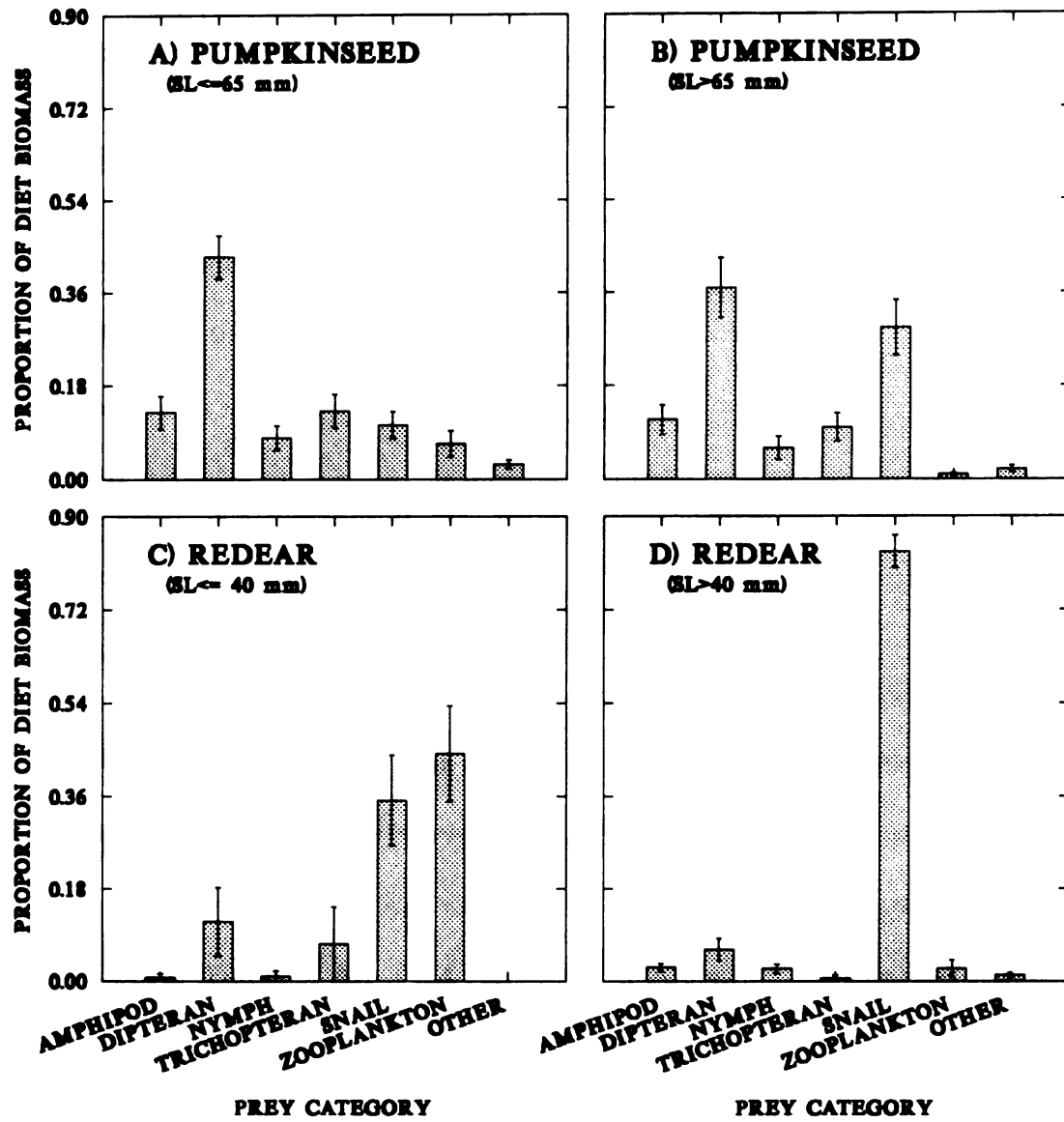


Figure 2

Both species consumed predominantly *Amnicola limosa* and to a slightly lesser extent *Physella* sp. (Figure 3). Post-hoc between species comparisons of the proportions *Amnicola* and *Physella* contributed to the total snail biomass were not significant at a corrected level of significance of $P < 0.025$. Although pumpkinseed and redear fed on a similar array of snail types, analysis of covariance on the mean crushing resistances (hardness) of all the *Physella* and *Amnicola* in redear diets showed that redear consumed significantly harder snails than pumpkinseed (Figure 4, *Amnicola* $F_{1,85}=6.48, P \leq 0.013$, and *Physella* $F_{1,68}=28.908, P \leq 0.001$). Although there is the appearance of a SL*species interaction for *Physella*, it was not significant ($F_{1,67}=2.806, P \leq 0.099$).

Crushing Strength

The feeding performance (estimated crushing strength) of redear collected from Lee Lake and the brood pond were not significantly different (ANCOVA, $F_{1,10}=0.000, P \leq 0.990$) so all redear were pooled. Laboratory estimates clearly showed that for all size-classes examined, redear had significantly greater crushing strength than pumpkinseeds (Figure 5, ANCOVA, $F_{1,22}=21.71, P \leq 0.001$). The estimated between species difference in crushing strength ranged from 2.9 Newtons for 65 mm fish, up to 18.5 Newtons for 120 mm fish (Figure 5), which translates into an estimated redear crushing advantage of 1.7 fold to 2.0 fold over the same size range of fish. Estimated functions that predict crushing strength (C, $\log_{10}$ Newtons) from standard length (SL, $\log_{10}$ mm) for each species are:

Figure 3. Composition of the snails in post-niche shift diets of A) pumpkinseeds, and B) redear, represented as the mean proportion each snail type contributed to the total snail biomass (mg). Pumpkinseed were >65 mm SL and redear were > 40 mm SL. Error bars are ± 1 SE.

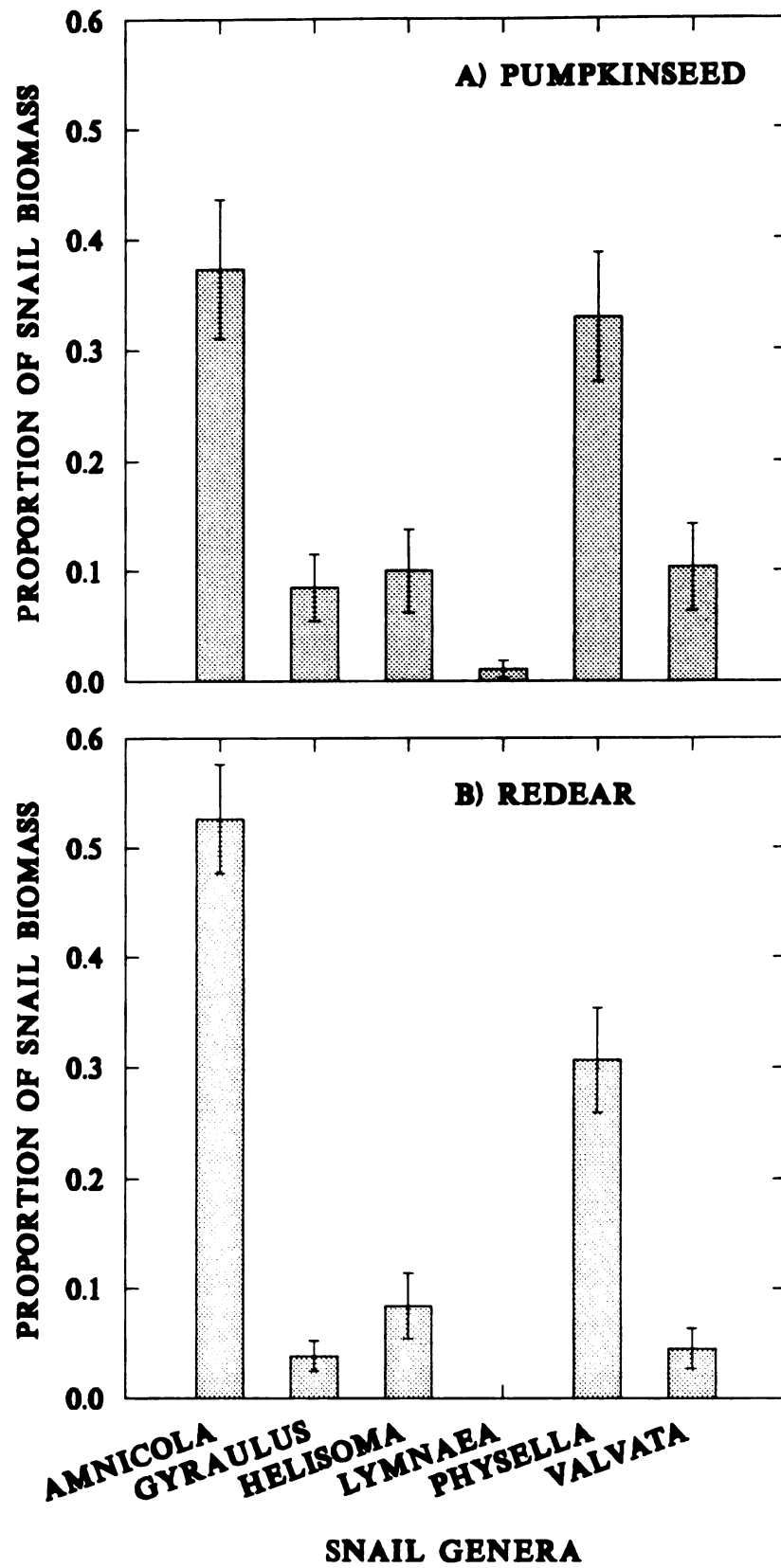


Figure 3

Figure 4. Mean crushing resistance (hardness) of A) *Amnicola limosa*, and B) *Physella* sp. in pumpkinseed and redear diets. Analysis of covariance of mean crushing resistance (Newtons) grouped by species along a covariate of SL (*Amnicola* $F_{1,88}=4.99, P \leq 0.028$; and *Physella* $F_{1,69}=13.327, P \leq 0.0005$).

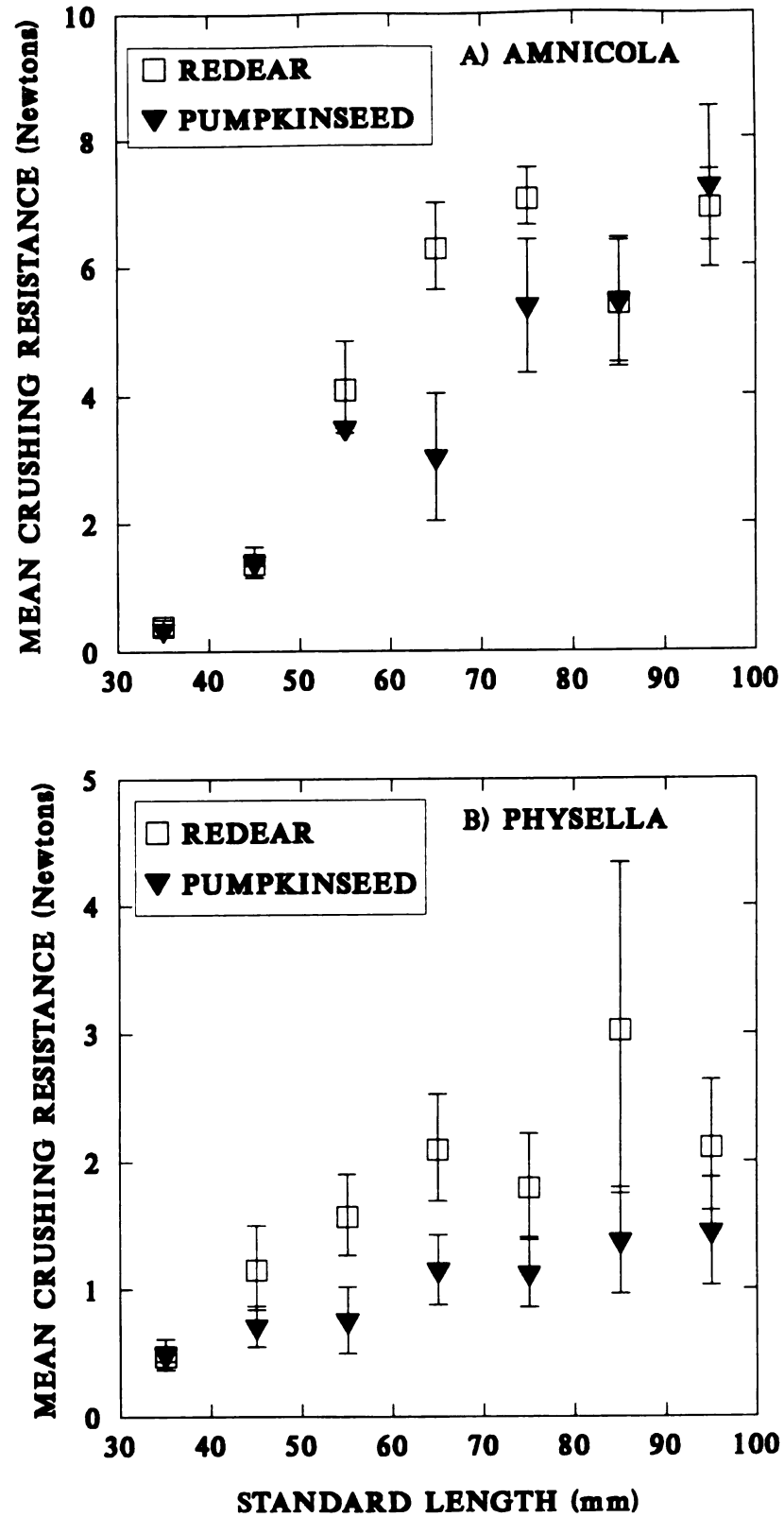


Figure 4

Figure 5. Estimated crushing potential (Newtons) of pumpkinseed and redear.

Analysis of Covariance shows a significant species effect on the log10 transformed crushing potential when log10 SL is included as a covariate (ANCOVA, $F_{1,22}=21.71$, $P \leq 0.001$).

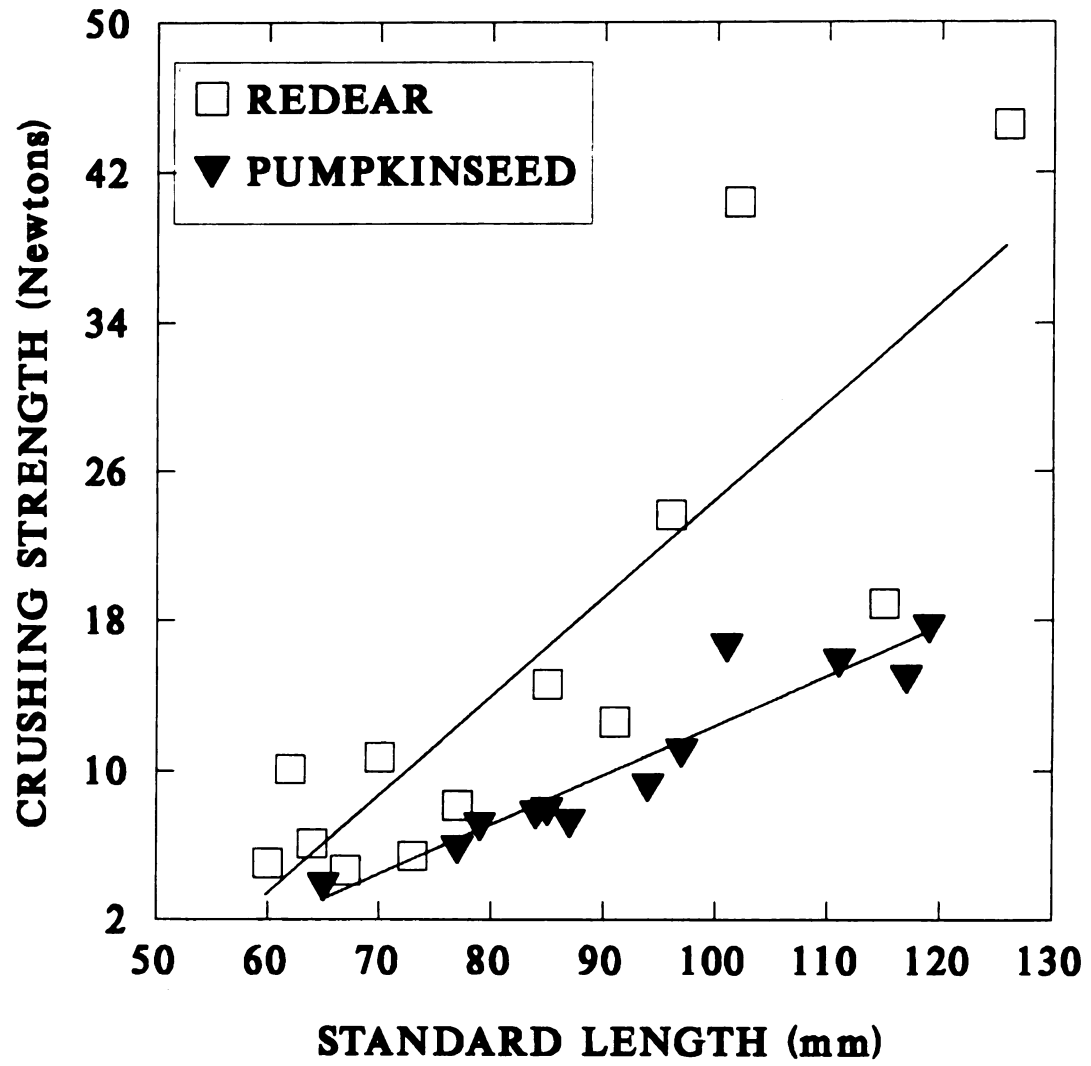


Figure 5

eq 2.6 pumpkinseed: $\log C = 2.480 \cdot \log SL - 3.884$ $R^2 = 0.93$

eq 2.7 redear: $\log C = 2.684 \cdot \log SL - 4.044$ $R^2 = 0.76$.

Given that redear consumed harder snails under field conditions and laboratory analysis showed that they possess greater crushing strength, I expected that crushing strength might limit the maximum size of snail each species can consume. To address if pumpkinseed and redear were utilizing their maximal capabilities while foraging upon snails, I used equations 2.6 and 2.7 to estimate the crushing strength of individual fish used in the diet analysis. If variation in crushing strength drives variation in snail hardness in the diet, plotting the upper quartile of crushing resistance of snails versus the estimated crushing strength of the fish should result in an overlap of the respective relationships for pumpkinseed and redear. Figure 6A shows that this is the case for *Ammnicola*. For both pumpkinseed and redear with crushing strengths less than approximately 10-11 Newtons, the crushing resistance of large *Ammnicola* in the diet and the crushing strength of the fish closely fit a 1:1 ratio. Beyond 10-11 Newtons, the plateau in the relationship suggests that the crushing strength of redear exceeds the crushing resistance of the largest snails commonly available in the environment. The size of each species that corresponds to this threshold crushing strength is estimated to be 96.5 mm SL for pumpkinseed and 75.9 mm SL for redear. The largest *Physella*, which is a larger and more weakly shelled genus than *Ammnicola*, fall well below the estimated crushing capacity of both pumpkinseeds and redear (Figure 6B).

Figure 6. Upper limit of crushing resistance (hardness) of snails in pumpkinseed and redear diets represented by mean crushing resistance (Newtons) of the upper quartile of A) *Amnicola limosa* and B) *Physella sp.* in the diets plotted against the estimated crushing potential of the fish. The line represents the 1:1 ratio between crushing resistance of snails in the diet and the crushing strength of the fish. For clarification of presentation, fish were grouped into 2 Newton strength classes. Means for these classes ± 1 SE are displayed.

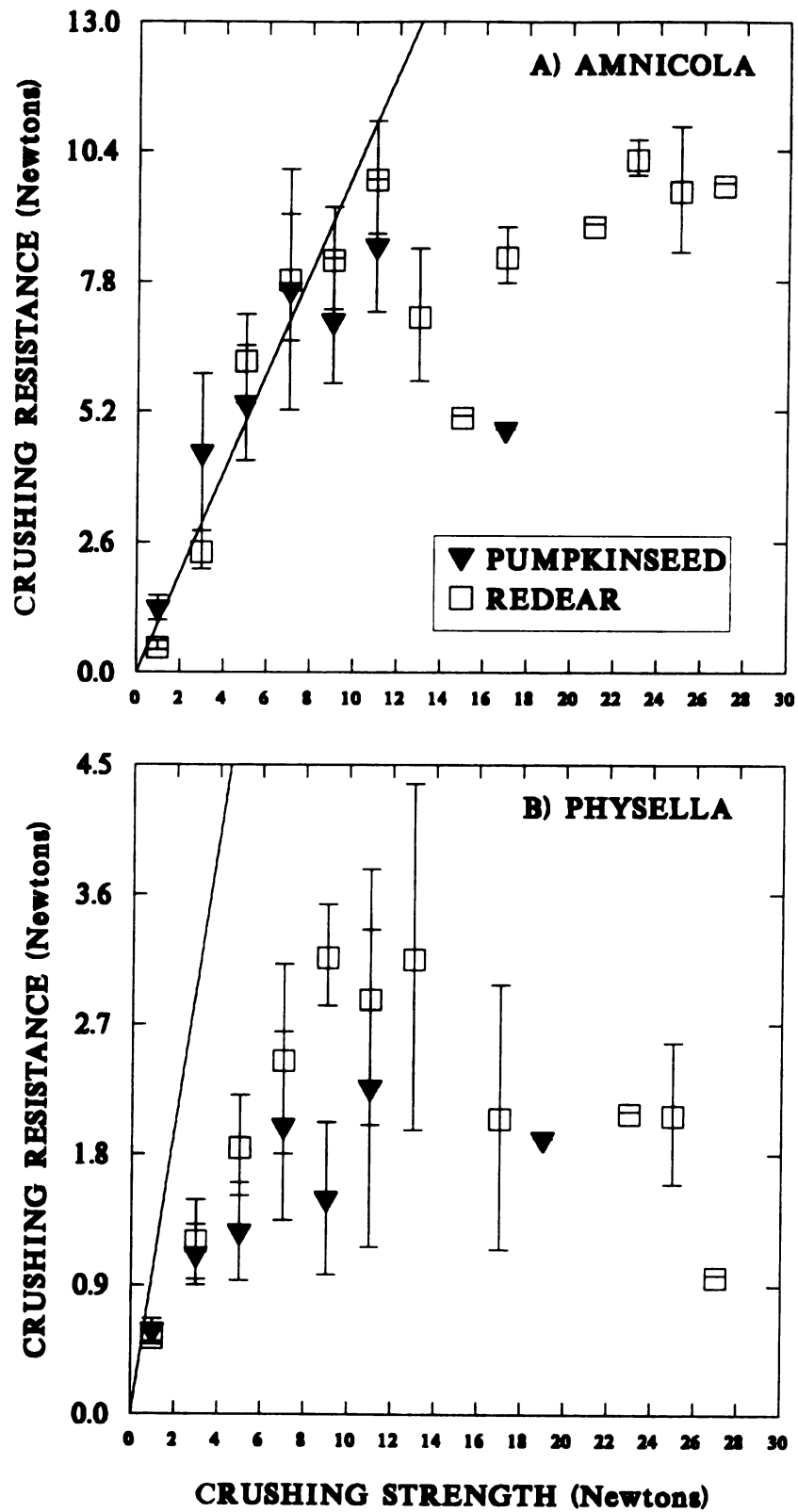


Figure 6

Prey Handling Time: hard-bodied prey

Pumpkinseeds maintained a fairly constant handling time per prey item over a broad range of body sizes; however for redear, larger fish demonstrated significantly shorter handling times relative to small redear when feeding on the same prey (Figure 7A, $P < 0.01$, $F_{1,15} = 8.607$). The time required for each species to crush snails was not significantly different (Figure 7B). However, in feeding trials when the snail was rejected uncrushed, redear displayed significantly longer handling than did pumpkinseeds (Figure 8, $F_{1,51} = 10.2$, $P \leq 0.002$).

Prey Handling Time: soft-bodied prey

Performance trials involving soft-bodied prey, *Hexagenia* sp, were analyzed to address if redear display reduced proficiency at handling soft-bodied prey; i.e., a functional trade-off. Redear required significantly longer time to handle both small and large size-classes of *Hexagenia* nymphs (Figure 9). Although the slopes of handling time relationships for small nymphs appear to be nonparallel, the species*SL interaction was only marginally significant ($F_{1,17} = 3.428$, $P \leq 0.082$) and the majority of redear handling times were well above those of pumpkinseeds. *Hexagenia* were never rejected by pumpkinseed nor by redear. Therefore, longer handling times of redear are not the result of redear being more persistent than pumpkinseeds with difficult prey, as observed in feeding trials involving snails. Rather, greater behavioral and morphological specialization of redear for molluscivory (consumption of hard-bodied prey) may result in a trade-off in their proficiency at handling soft-bodied prey.

Figure 7. A) Handling and B) crushing times of pumpkinseed and redear when feeding on *Physella* sp. with mean crushing resistance of 6.3 Newtons (± 0.91 SD). Analysis shows a significant species*SL interaction for handling time (Figure 7A, ANCOVA, $F_{15,1}=8.607$, $P \leq 0.01$) and no significant difference in crushing time (Figure 7B).

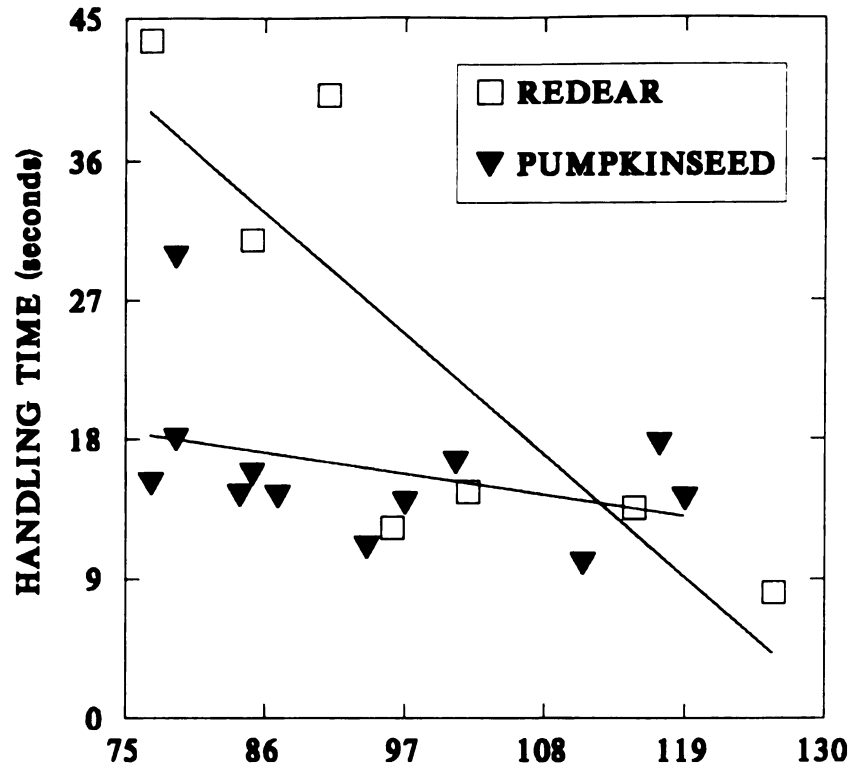
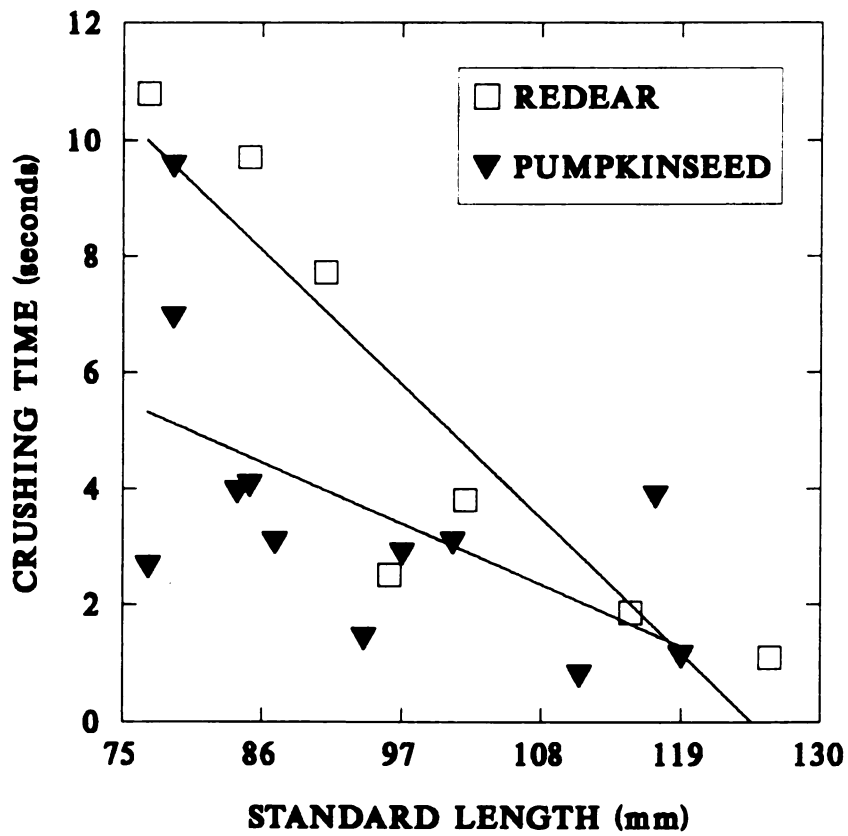
A**B**

Figure 7

Figure 8. Total time pumpkinseed and redear spent handling snails before the snails were rejected uncrushed. Bars represent the mean time (± 1 SE) for all individuals within a species for each of the three snail types offered.

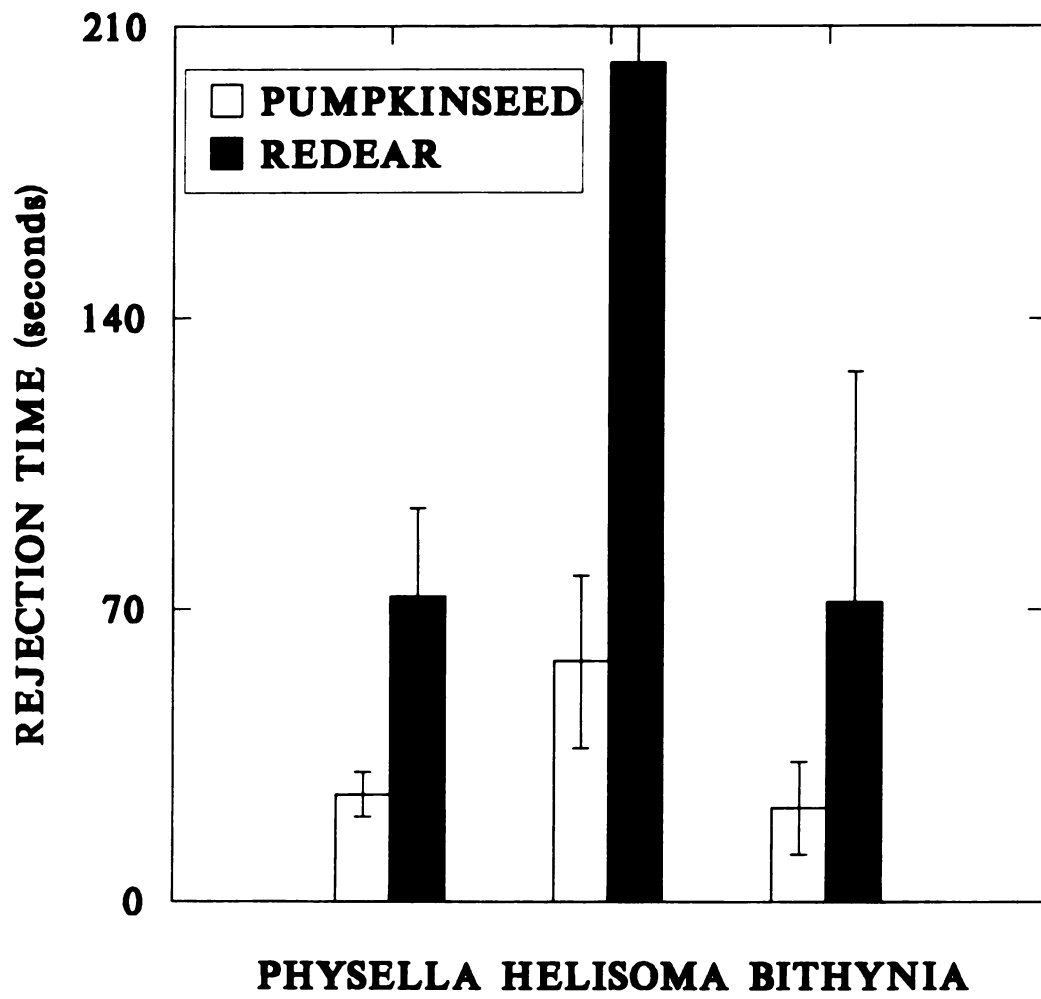


Figure 8

Figure 9. Handling time of pumpkinseed and redear when feeding on soft-bodied prey (*Hexagenia*). Two size classes of *Hexagenia* nymphs were offered and analysis of covariance of log10 transformed handling times shows significant differences between pumpkinseed and redear for A) small nymphs ($F_{1,18}=20.726$, $P\leq 0.0001$) and B) large nymphs ($F_{1,10}=8.942$, $P\leq 0.014$).

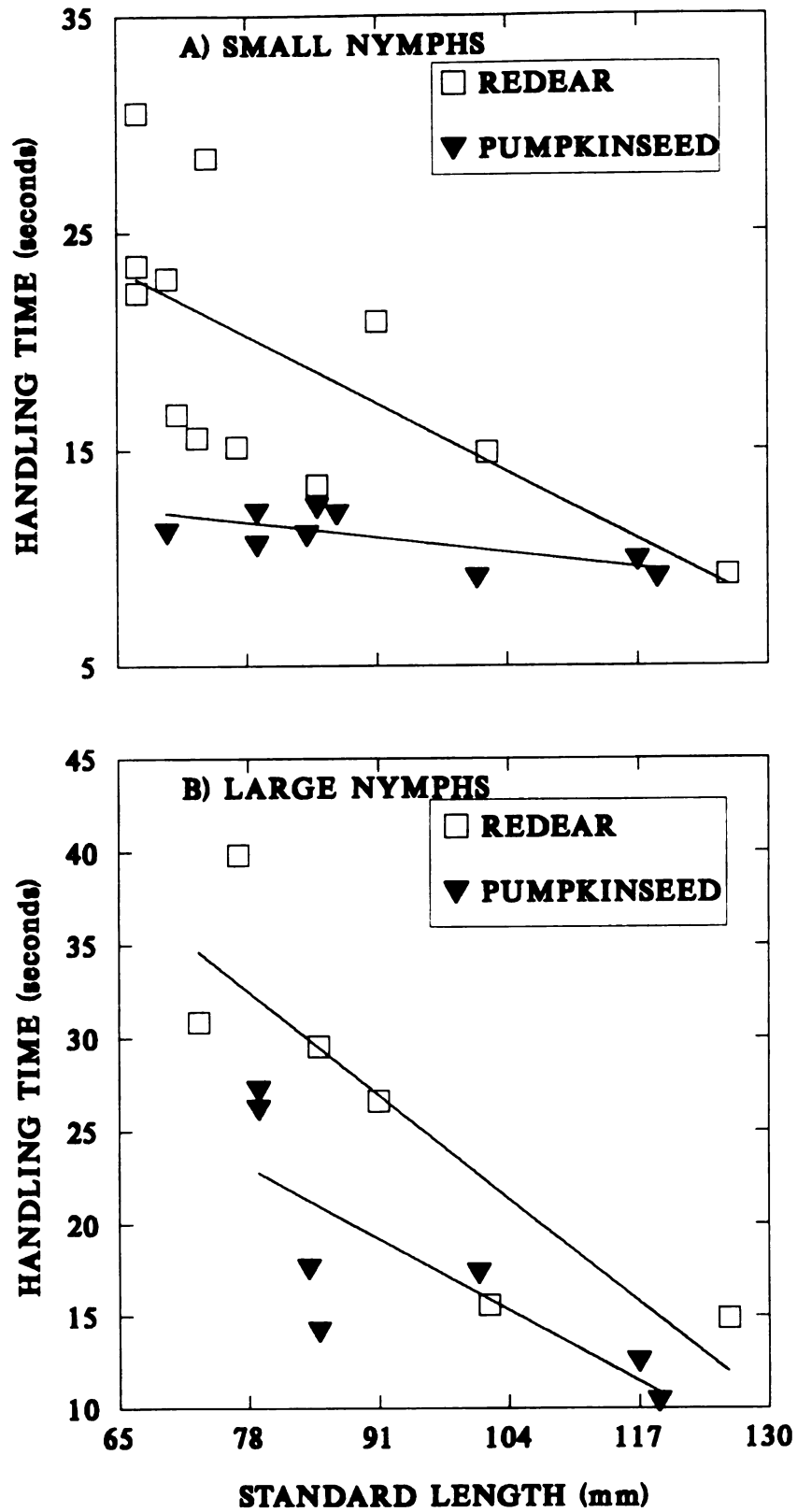


Figure 9

DISCUSSION

It is axiomatic in biology that phenotypic differences among individuals within or between species are related to differences in their ecology (Wainwright 1994). For example, within the sunfishes, only the redear and the pumpkinseed possess hypertrophied pharyngeal jaw musculature and bone structure (Lauder 1986) in conjunction with the ability to activate simultaneously a subset of the pharyngeal muscles, thus generating forces sufficient to crush gastropod shells (Lauder 1983a). It follows that they are also the only sunfish that commonly crush and consume snails.

Both pumpkinseed and redear that were artificially sympatric in Lee Lake and Saubee Lake underwent an ontogenetic shift from a diet of mostly soft-bodied invertebrates to a diet more inclusive of snails, but redear became extensively more molluscivorous compared to pumpkinseeds of similar size. Pre-shift diets of pumpkinseed (<65 mm) were dominated by dipteran larvae such as chironomids (see also: Sadizikowski and Wallace 1976, Keast 1978, Mittelbach 1988). The diets of larger pumpkinseed (≥ 65 mm SL), which are generally highly molluscivorous in the absence of redear (Chapter 1, Mittelbach 1984, 1988; Osenberg and Mittelbach 1989), also tended to be dominated by chironomid larvae (see also Osenberg et al. 1992), and the proportional representation of snails was only approximately 30%. In contrast to pumpkinseeds, redear $> \sim 40$ mm SL in Lee and Saubee Lakes generally shifted from a diet of very small snails and microcrustaceans to greater than 87% molluscivory.

Compared to pumpkinseeds, redear possess more robust pharyngeal jaw apparatus and more highly specialized muscular activity patterns (Lauder 1986); and

these phenotypic differences give rise to a much greater crushing strength of redear. It is tempting to assume that for molluscivorous organisms, possession of greater crushing strength, as displayed by redear, would directly translate into superior exploitative ability. However, greater crushing strength would only yield a functional benefit if the performance advantage allowed redear access to resources that were unavailable to, or less efficiently obtained by, weaker molluscivores (pumpkinseed). For example, Osenberg and Mittelbach (1989) and Osenberg et al. (1994) argued that large pumpkinseed are usually not constrained by their crushing strength and can instead crush most of the snails that occur in southwestern Michigan lakes. Few snails in these lakes exceed 10 Newtons of crushing resistance. Indeed, observations in this study support this inference; pumpkinseed and redear with crushing strengths > 10 Newtons showed little change in diet with increasing size (Figure 6).

That both pumpkinseed and redear diets contained the largest snails commonly available in the environment, demonstrates that the large snails are functionally available to both species at some point in their ontogeny. However, redear are able to capitalize on these snails (eg., with crushing resistance of 10 Newtons) once they reach approximately 76 mm SL, whereas pumpkinseeds do not develop the necessary strength until they are approximately 97 mm SL. This critical point of development is reached much earlier in their ontogeny by redear, sometime in their second year, whereas pumpkinseeds require at least 3-4 years of growth (Chapter 1). This discrepancy is further augmented by the greater absolute growth rates of redear relative to pumpkinseeds (Chapter 1). Thus redear are able to consume larger snails than can similarly sized pumpkinseeds, and in addition, redear begin shifting to a diet

dominated by snails at ~40 mm SL, whereas pumpkinseeds only weakly shifted between approximately 65-80 mm SL. In these lakes, many redear would make the transition to snails during their first summer of life, while pumpkinseeds would not shift their diet until late in their second or their third summer. Early diet shift to snails in ontogeny and then access to the majority of snails in the environment, is expected to provide valuable energetic rewards to the consumer, assuming that soft-bodied prey are not extremely abundant. .

Wootton (1990) suggests that the study of such ontogenetic niche shifts is central to developing an understanding of the ecology of fishes (see for example: Mittelbach 1984, Werner and Gilliam 1984, Mittelbach and Chesson 1987, Mittelbach et al. 1988, Werner and Hall 1988, Osenberg et al. 1988, 1992,1994) and the timing of the niche shifts may play an important role in determining the population dynamics and the strengths of species interactions. For example, Olson (1996) has demonstrated the importance of an early niche shift for increasing growth in largemouth bass (*Micropterus salmoides*). Observational evidence of bass growth and diets in the field showed significant increases in growth trajectories that occurred when young-of-year (YOY) bass shifted to piscivory. Similarly, in this study, pumpkinseed and redear were similar in size at the end of their first year of growth when both species were feeding extensively on soft-bodied prey. However, growth rates of redear then exceeded those of pumpkinseed soon after redear switched to snails and size-at-age advantages were maintained by redear throughout their development (Chapter 1). Thus, advantages incurred early in life may tend to provide redear with benefits throughout life.

Foraging Tradeoffs:

When feeding on snails, pumpkinseeds display the typical crushing behavior of simultaneous activation of pharyngeal muscles, but when feeding on soft-bodied prey they can simply transport the prey to the esophagus (Lauder 1983b). Redear, however, lack the ability to modulate their pharyngeal activity patterns such that they use the "crushing pattern" of pharyngeal movement for both hard and soft-bodied prey.

Redear also show an alternating pattern of pharyngeal jaw movement during pharyngeal transport that is suggested to be a specialization for effectively separating the snail body from shell fragments (Lauder 1983b and references therein). Thus redear display two salient specializations for molluscivory that are not displayed by pumpkinseed, and specializations often entail trade-offs. While trade-offs can not be assumed a priori, they are a fundamental component of models of evolutionary specialization (Futuyma and Moreno 1988).

When I measured the time required for redear and pumpkinseeds to consume nymphs of *Hexagenia*, I found that redear spent significantly more time handling these soft-bodied prey than did pumpkinseeds. This suggests greater specialization for consumption of hard-bodied prey may limit redear handling efficiency of soft-bodied prey (see also Wainwright 1988). In other systems, trade-offs in foraging efficiency have been shown for within-species comparisons of morphotypes (Malmquist 1992, Ehlinger 1990, Robinson et al. 1996) and also for between species comparisons of consumers (Werner 1977, Mittelbach 1984, Sanderson 1991). In the latter category, Lavin and McPhail (1986) and Schluter (1993, 1995) have shown that two stickleback species with different habitat-specific specializations incur steep trade-offs in foraging

efficiency that translate into fitness costs when they are maintained in reciprocal habitats. For molluscivores, the trade-off in feeding efficiency on soft-bodied prey versus hard-bodied prey will become important as snail availability decreases. At reduced availability of snails, pumpkinseed may be able to more efficiently switch to soft-bodied prey due to their ability to modulate their prey handling mode.

Small redear also tended to display longer handling times than pumpkinseeds when feeding on snails (*Physella*). The performance of an organism is due to the often complex interaction between morphology and behavior (Lauder 1983b, Emerson and Koehl 1990) and in this case longer handling times may in fact result in redear being more successful molluscivores. When attempting to crush difficult snails, pumpkinseed and redear often reposition the snail in between attempts to crush it, and the orientation of the snail with respect to an applied force does affect the shell's crushing resistance (Huckins, personal observation). Since redear are more persistent in their attempts to crush snails, this persistence may allow them to eventually properly position and crush a shell that would be beyond the limits of the fish's crushing capacity if only short bouts of handling were attempted. This inference is supported by electromyographical analysis of redear pharyngeal jaw movements during snail crushing that reveal the crushing pattern of muscle activity displayed by redear is repeated several times (up to 20 for large shells) with periods of either no activity or of buccal and pharyngeal manipulations between crushing phases (Lauder 1983b).

Although redear appear to pay a trade-off cost in handling times of individual prey under lab conditions, it is not clear that the costs will be incurred under field conditions. When fish consume larger numbers of individual prey (e.g., zooplankton),

prey handling times can be critically important to their energetic returns (Mittelbach and Osenberg 1994). However, for piscivorous fish which may consume only one or few large prey daily, handling time of the prey is unimportant relative to encounter rate (Christensen 1996, see also Osenberg and Mittelbach 1989). Furthermore, the foraging opportunity that redear may lose due to longer handling times may be countered by them encountering snails at a greater rate. Redear were substantially more molluscivorous than sympatric pumpkinseeds and although redear diets contained large snails not crushable by pumpkinseeds, the majority of the snails in redear diets were within the crushing potential of pumpkinseeds. High redear encounter rates could therefore be an important component driving redear molluscivory and the low abundance of snails in lakes with introduced redear. A careful analysis of the relative importance of species specific encounter rates and handling times is warranted, and their incorporation into foraging models would help resolve this issue.

Competition

Results of laboratory feeding performance trials, in corroboration with field surveys of diet ontogenies of pumpkinseed and redear sunfish, clearly demonstrate that variation in feeding performance of these species is linked to their feeding performance (Chapter 1). Observations from a pond competition experiment and from lake surveys also suggest that pumpkinseed and redear do compete and that superior exploitation of snails by redear is involved in the mechanism of the interaction (Chapter 1). The coexistence of native sunfishes (*Centrarchidae*) in northern lakes is promoted by segregation in diet and habitat use at the adult stage (Werner and Hall

1979, Mittelbach 1984, 1988, Mittelbach and Chesson 1987). By eating snails as adults, pumpkinseeds gain a competitive refuge from the other native *Lepomis* that can not crush and consume snails effectively (Mittelbach 1984). However, the introduction of redear may have reduced the value of this foraging refuge for pumpkinseed.

That redear display high levels of molluscivory while pumpkinseeds show reductions when the species are sympatric is predicted by the extensive morphological and behavioral specializations and therefore, the greater capacity of redear to crush snails. Extrapolating the earlier niche shift by redear to the population and community level adds to our understanding of the mechanisms driving the reduction in pumpkinseed molluscivory by redear. An earlier niche shift allows young-of-year redear access to a limiting resource that pumpkinseed juveniles will not be able to consume until their second or third year of life. The earlier shift also translates into a greater proportion of the redear population being molluscivorous. All else being equal, a redear population will therefore, have a greater impact on snail abundances than will a same-size pumpkinseed population. This greater per-capita effect of redear on gastropod abundance, in conjunction with greater individual foraging capacity, is likely the driving mechanism behind the observed competitive interactions of pumpkinseed and redear.

Snail-crushing ability has a functional basis in the design of the feeding system possessed by molluscivorous fishes (Wainwright 1994). In this study variation in the crushing ability of pumpkinseed and redear, estimated from performance analysis, has been shown to constrain actual resource usage. Thus, crushing strength, in conjunction

with prey availability, determines the upper limit of prey-hardness in pumpkinseed and redear diets, and therefore, determines the timing and the extent of pumpkinseed and redear niche shifts. In this case, interspecific variation in morphologically and behaviorally driven feeding performance of artificially sympatric sister-species has been shown to be functionally linked to their patterns of resource use and competitive interactions. The continued synthesis of functional morphology and ecology promises to be an important avenue for insight and advancement of our understanding of community structure and patterns of species distribution and abundance.

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