Species Introductions and their Ecological Consequences:
An Example with Congeneric Sunfish

By

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ABSTRACT

Pumpkinseed *(Lepomis gibbosus*) and redear sunfish (*L. microlophus*) are sister-species with largely allopatric native ranges. For purposes of sport fishery enhancement, redear have been introduced into lakes of southern Michigan, and as a result, a large zone of artificial sympatry of pumpkinseed and redear has been created. Redear and, to a lesser extent, pumpkinseed are morphologically and behaviorally specialized molluscivores and we hypothesized that introduced redear would have strong negative effects on pumpkinseed due to competition for snails, which are each species' main adult resource. Specifically, we predicted redear would reduce snail availability, alter pumpkinseed diet, and reduce pumpkinseed growth and density. To examine these predictions, we surveyed pumpkinseed diets, growth, and densities, as well as snail availability in lakes with and without introduced redear. We also conducted a controlled field experiment (target-neighbor design) in which relative neighbor densities of each species were manipulated and the effects on target individuals of each species were measured. This experiment was designed to explore mechanisms underlying the competitive interactions suggested by the longer-term field study.

Together, the field patterns and short-term experimental results demonstrate that the introduction of redear negatively affected the native pumpkinseed: 1) in lakes where redear had been introduced, the abundance of pumpkinseed declined an average of 56%, while average pumpkinseed abundance increased 60% in lakes without introduced redear; 2) in the presence of redear, pumpkinseed had fewer snails in their diets and did not undergo a ontogenetic niche shift to feeding on snails; 3) snail biomass was ~69% lower in lakes where redear had been introduced and snail biomass was ~ 50% lower in experimental treatments containing redear instead of pumpkinseed. In the experiment, pumpkinseed growth was reduced in the presence of redear. However, contrary to our predictions, pumpkinseed growth rates did not differ between lakes with redear versus those without redear. We suggest that a reduction in pumpkinseed growth rate is an expected short-term response to redear introduction, whereas the long-term response is a reduction in pumpkinseed density.

Keywords: competition, introduced species, *Lepomis gibbosus*, *L. microlophus*, pumpkinseed, redear, consumer-resource interactions, snails, target-neighbor experiment, time scale

INTRODUCTION

The study of species introduced beyond their native ranges can provide insight into the long-term dynamics of species interactions within ecosystems (Weatherly 1977, Case and Bolger 1991, Lodge 1993a). Freshwater fish can provide particularly good case studies of the effects of species introductions, because fish are often intentionally stocked into new environments by state and federal agencies, and the date, location, and magnitude of these introductions are generally recorded. Also, the discrete nature of lakes can provide a level of replication absent from most other systems, and lakes not receiving introductions can be used as reference systems. For many lake systems, there also exists a rich conceptual background against which we can assess and predict the effects of introduced species. As a result, studies of species introductions in lakes can not only facilitate the testing and development of ecological theory (e.g., Crowder 1986, Herbold and Moyle 1986, Losos et al 1993, Flecker and Townsend 1994), but they may also enhance our efforts to conserve native species and forecast the effects of future invasions (Moyle 1986, Lodge 1993a,b).

In this study, we examine the introduction of redear sunfish (*Lepomis microlophus*) into southern Michigan lakes to investigate its ecological effects on native populations of the pumpkinseed (*L. gibbosus*), its proposed sister-species (Mabee 1993). Pumpkinseed are native to lakes throughout the northern Midwest, the Great Lakes region and the eastern United States through the Carolinas. The native distribution of redear extended southward from Missouri and North Carolina to the Mississippi Basin and into Florida (Trautman 1981, Lee et al. 1980). Thus, except for a small overlap in range in the Carolinas, their native ranges were largely disjunct. Because redear are a desired sport fish, they have been introduced throughout the northern Midwest (Gerking 1950), creating a large zone of artificial sympatry between the species. In Michigan, redear were first introduced in the 1920's (Mills et al. 1994), first collected in 1947 (Fukano et al. 1964) and additional scattered transplants occurred in the 1950’s (Cole 1951). More extensive introductions occurred between 1984 and 1995, when the Michigan Department of Natural Resources (MDNR) introduced redear into approximately 45 southern Michigan lakes.

Pumpkinseed and redear are the only known specialist molluscivores within the sunfish family, Centrarchidae (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 snails (Lauder 1983, Wainwright and Lauder 1992). The ecological and morphological similarities of pumpkinseed and redear suggest they may compete for resources and their disjunct native ranges suggest that they may not coexist.

Compared with sympatric pumpkinseed, redear can more easily crush snails, shift onto snails earlier in their ontogeny (at ~40 mm standard length (SL) vs. ~65 mm for pumpkinseed), and feed more extensively on molluscs (Huckins 1997). To the extent that heightened snail crushing performance and molluscivory allows redear to have greater negative effects on snail availability, we hypothesized that redear would have strong competitive effects on pumpkinseed. We predicted that the introduction of redear would reduce snail biomass in lakes, resulting in a decrease in molluscivory by pumpkinseeds. Because pumpkinseed growth is food limited (Osenberg and Mittelbach 1989), we expected this alteration in pumpkinseed diet to reduce individual growth and to decrease fecundity and population density (Mittelbach and Chesson 1987). We examined these predictions by comparing pumpkinseed populations in lakes where redear have been introduced with those in nearby lakes where redear were absent. In conjunction with the field surveys, we conducted a target-neighbor competition experiment to examine the mechanisms of the interaction between pumpkinseed and redear. This controlled experiment allowed us to manipulate relative densities of both species in order to examine their effects on resource abundances and their effects on growth, survival and diets of each of the two species. We predicted that the intensity of interspecific competition from redear should increase with pumpkinseed size because larger pumpkinseeds consume more snails (Mittelbach 1984, Osenberg et al. 1994). Therefore, in the experiment we looked at the competitive effects of redear on 3 size-classes of pumpkinseed.

METHODS

Field Survey

We examined density, growth and diets of pumpkinseed, and snail abundance in hardwater lakes in southern Michigan (Table 1). The study lakes lie within 120 km of the W. K. Kellogg Biological Station of Michigan State University. Young-of-year (YOY) redear were introduced into some of the study lakes (see Table 1) by the Michigan Department of Natural Resources (MDNR), and stocking generally occurred in the fall at rates of approximately 100 YOY/acre. Nearby lakes that did not receive redear served as reference lakes, and these lakes were similar in basic limnological characteristics to the redear-introduction lakes. We assessed the effects of redear on pumpkinseed and snails by comparing lakes with and without redear. Within lakes containing both sunfish species, we compared the relative performance of pumpkinseed and redear.

Sunfish Density

We examined the relationship between redear introductions and changes in pumpkinseed density (catch-per-unit-effort or CPUE) using data from the MDNR Fisheries Division. As part of the MDNR redear management plan (Towns 1991) and the overall operation of the Fisheries Division, district lakes were surveyed approximately once every three years to evaluate the fishery and to assess the status of introduced redear. Surveys were conducted in May and June using trap nets set overnight usually at 4-5 littoral sites around the lake. These surveys provided estimates of species composition and CPUE for the major game fish including, among others, three *Lepomis* species: redear, pumpkinseed and bluegill (*L. macrochirus*). We compared pumpkinseed and bluegill densities (CPUE) through time in 11 lakes with introduced redear to those in 13 lakes that did not receive redear (Table 1).

There is an expected time lag between the introduction of YOY redear and their predicted effect on pumpkinseed density due to the time required to reduce resources and affect pumpkinseed growth, reproduction and survival. We assumed that four years, which is approximately the time for one generation, was a minimum response time. If redear reduce snail abundance in their first year after introduction, then a decline in pumpkinseed fecundity and subsequent year-class strength could be observed three years later, by which time the young pumpkinseed would be large enough (~75 mm SL) to be captured in the MDNR trap nets . Therefore, for lakes with introduced redear, we included only those lakes with survey data from before redear introduction and with data collected at least four years after introduction. For comparability, we also limited reference lakes to those with initial and final survey data separated by at least four years. If for a given lake, more than one survey was conducted during the analyzed response period following redear introduction, then the mean CPUE was calculated and used in the analysis. Thus, each lake provided only 2 data points to the analysis (e.g., one pre-redear CPUE and one post-redear CPUE). Because densities of sunfish are highly variable across lakes, we analyzed the relative change in fish density by dividing all CPUE estimates by the pre-redear CPUE for each lake with redear, or by dividing by the CPUE in the earliest survey for each lake without redear.

In addition to direct competitive effects on pumpkinseed, redear introductions could also affect pumpkinseed and other native fishes by indirect mechanisms such as inducing a numerical response of anglers (or piscivores) and therefore increased mortality due to fishing pressure (or predation). As a check for this and other alternative hypotheses, we also examined temporal changes in the density of bluegill sunfish in these same lakes. Bluegill rarely feed on snails (Mittelbach 1984) and they are not expected to compete with molluscivorous redear. Redear and bluegill might compete when they are small and feed on soft-bodied littoral prey (Mittelbach 1984, Huckins 1997); however redear generally shift to a diet of snails during or shortly after their first year (Huckins 1997). Therefore, they are not predicted to have a significant effect on bluegill.

Pumpkinseed and Redear Growth.

We measured growth rates of pumpkinseed and redear by back-calculation from scale samples collected from pumpkinseed and redear in 3 lakes with redear throughout the summers of 1992-1994 and from pumpkinseeds in 8 lakes without redear in 1990-1993 (Table 1). Collected fish were measured to the nearest millimeter (standard lengths, SL) and five scales were removed from the region underneath the tip of the depressed 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 analyzed 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, Osenberg et al. 1988). For this calculation we used 11.5 mm and 11.8 mm as the estimates of the initial SL for pumpkinseed and redear, respectively. These estimates were based on the intercepts of regressions of fish length against scale length at time of capture. Estimates of annual change in length were converted to estimates of change in wet mass using length-mass regressions from Osenberg et al. (1988) for pumpkinseed and Huckins (1996) for redear:

Pumpkinseed: $Mass = 0.00001529*(SL^{3.224}); n=116; r^2 = 0.996$ (1)

Redear: $Mass = 0.00001927*(SL^{3.162}); n=105; r^2 = 0.989$ (2)

We then examined whether growth of pumpkinseed that were large enough to be molluscivorous was lower in lakes with redear. For each lake, annual growth rates of pumpkinseed ≥ 65 mm SL (at the start of the year) were characterized by regressing the $\log_{10}$ annual change in mass against the $\log_{10}$ SL at the start of the year. We then used these regressions to estimate the annual growth of a 90-mm SL pumpkinseed for each lake. These estimated growth rates of a typical molluscivorous pumpkinseed were then compared between lakes with and without redear.

Sunfish Diets

Pumpkinseed diets, as well as those of redear where introduced, were studied in two lakes with introduced redear (Lee, and Saubee) and in five lakes without redear (Culver, East Crooked, Lawrence, Palmatier, Three Lakes II, and Three Lakes III; see Table 1). Data for the reference lakes (excluding East Crooked) were taken from Mittelbach (1984) and Osenberg and Mittelbach (1989). Data for Lee, Saubee, and East Crooked Lakes were based on similar methods using fish seined between May and August of 1993 and 1994. Fish were collected in the morning to minimize prey digestion (see Hanson and Leggett 1986), preserved in 10% neutral formalin and later measured for standard length. Stomach contents were identified to the lowest possible taxonomic level, (generally to family, but to genus or species for gastropods). All prey items were enumerated and measured (up to 50 individuals per taxon per fish) for estimation of individual dry mass using length-mass regressions (Mittelbach, Osenberg and Huckins, unpublished data). Mass calculations for snails excluded their shells and opercula.

We categorized prey items into five prey types: 1) small invertebrates (amphipods and dipteran larvae); 2) large invertebrates (odonates, ephemeropterans, trichopterans, and coleopterans); 3) snails; 4) zooplankton; and 5) other miscellaneous prey rarely found in the diets, such as mites, annelids, and hemipterans. For each fish, we calculated the proportion of the total prey biomass contributed by prey in each of the five categories. To quantify the extent to which pumpkinseed were molluscivorous in each lake, we calculated the mean proportion of the diet comprised by snails for all collected pumpkinseed > 75 mm SL, the size at which most pumpkinseed have completed their diet shift to snails (Osenberg et al. 1994).

Snail Abundance

To examine if snail abundances were reduced in lakes with redear, we surveyed snail communities in six lakes with and 10 lakes without introduced redear (Table 1). In August 1996 we collected 10 sweep samples (~1 m long) from each lake using a 30-cm wide D-ring net. All samples were collected from rooted macrophytes in approximately 1-m water depth. Samples were sieved through a 0.5-mm sieve, and all molluscs were then picked from the sample, identified to genus or species, and measured. Lengths were converted to tissue dry-mass using length-mass regressions (Osenberg unpublished data). For each lake, we estimated the mean total snail biomass and number of snails per sweep sample, as well as the mean individual snail mass. We also quantified the mean biomass of amnicolids (*Amnicola limosa, A. walkeri, and Marstonia lustrica*), *Gyraulus* sp. (*G. deflectus and G. parvus)*, *Valvata tricarinata*, *Physella* sp., and *Helisoma* sp. (*H. anceps, H. campanulata and H. trivolvis*). Other taxa (such as *Bythinia tentaculata*, *Viviparus georgianus*) were rare and accounted for <1% of the total biomass. Bivalves such as clams and zebra mussels were rare in the resource samples, always comprising ≤4% of the total biomass, and they never occurred in the diets of redear or pumpkinseed. Therefore, they were excluded from the analyses. To meet assumptions of homogeneity of variance, we log transformed lake means after first adding 0.1 mg to biomass estimates and adding 1 to density estimates for individual taxa due to the presence of zeros. All results were back-transformed for presentation.

Competition Experiment

To examine competitive interactions between pumpkinseed and redear in a controlled setting, we conducted a field experiment at the W. K. Kellogg Biological Station pond facility. The experiment was based on a target-neighbor design (sensu, Goldberg and Werner 1983) in which we measured the growth, survival and diet of target individuals in treatments that varied in the density and the species of neighbors. The target assemblage included three redear (79.4 ± 0.2 mm SL; mean ± 1 SE), three large pumpkinseed (79.5 ± 0.2 mm SL), five medium pumpkinseed (52.3 ± 0.4 mm SL) and 20 small pumpkinseed (38.8 ± 0.1 mm SL). The experimental design included two replicates of each of five treatments: one fishless treatment and four treatments in which target pumpkinseed and redear were exposed to either 0 neighbors (target-only), 20 pumpkinseed (low-pumpkinseed), 20 redear (low-redear), or 40 redear (high-redear) (see Table 2). The target individuals and the neighbor individuals were together within a treatment, however we monitored only the target individuals. This array of treatments, including both pumpkinseed and redear as targets and neighbors, allowed us to compare the relative strength of intra- and interspecific competition.

We established the experimental treatments in a circular pond (30 m diameter, 1.8 m deep) that was divided into 10 wedge-shaped sections (53.8 ± 2.8 m^2; mean ± 1 SD). 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. The highest total density of fish in a section (~1.3 fish/m^2) was within the natural range observed for pumpkinseed (0.04-1.77 pumpkinseed/m^2, Osenberg et al. 1992).

Small and medium pumpkinseed targets and redear were collected from monospecific brood ponds located at the W.K. Kellogg Biological Station. Large pumpkinseed were not available on site and were collected from two nearby lakes. The target assemblage of 3 redear and 28 pumpkinseed was introduced into all but the two fishless sections on June 18, 1994. Prior to release, large targets were fin clipped to distinguish them from the neighbors.

On July 11, 23 days after their release into the pond, target fish were sampled by seining each pond section two times. We measured the standard length of each fish, and released them back into the pond. Individual fish mass at this midpoint in the experiment, as well as at the beginning, was estimated using Equations 1 and 2. On August 1, 44 days after the experiment began, the pond was drained and all fish were collected, measured, and weighed. Mean final target mass from each pond section for each target class was used to test for treatment effects on target growth (means were $\log_{10}$ transformed prior to analysis to homogenize variances). Stomachs of the target fish were removed and preserved in 10% formalin for later diet analysis, following the same procedures used in the lake survey.

We sampled invertebrate prey in the pond on three occasions; June 16 (two days before the introduction of fish), again on July 8, and finally on July 31 (one day before the experiment was concluded). Samples were collected from the vegetation using a modified Gerking sampler (Mittelbach 1981). In each pond section, two replicate samples were taken on the first sampling date, three on the second sampling date, and four on the final date. Samples were rinsed through a 0.5 mm sieve;

invertebrates were picked from the debris and preserved in 10% buffered formalin. All prey were identified and counted, up to 50 individuals per taxon in each replicate were measured, and these measurements were converted to dry tissue masses using length-mass regressions. Invertebrates were categorized into the same five taxonomic groups used in the field survey: 1) small invertebrates, 2) large invertebrates, 3) snails, 4) zooplankton; and 5) miscellaneous invertebrates. Because fish did not feed on the latter two categories, we focused on results for small and large invertebrates and snails. To examine which prey were most closely related to target growth, we calculated the correlation between final target mass and biomass of each invertebrate class, averaged across the three sample dates. We focused on prey biomass because it is a more effective predictor of fish growth than is prey density (Mittelbach and Osenberg 1994).

RESULTS

Field Survey

Sunfish Densities

Redear populations rapidly increased in abundance following their introduction into Michigan lakes. Redear achieved an average abundance of 11.4 (± 3.9 SE) redear/trap 4-6 years after introduction, and 29.6 (± 7.6 SE) redear/trap net after 8-10 years. By comparison, the abundances of pumpkinseed and bluegill in these same lakes prior to redear introduction were 9.3 (± 2.7) pumpkinseed/trap and 55.3 (± 13.6) bluegill/trap. Coincident with the establishment of redear, pumpkinseed CPUE declined in seven of the 11 lakes with introduced redear (Fig. 1a), compared with declines in only two of the 13 lakes without introduced redear, one of which declined by only 4% (Fig. 1b). On average, pumpkinseed CPUE declined by 56% (mean ± 1 SE: 37-69%) in lakes where redear were introduced. This average decline in pumpkinseed abundance contrasted sharply with the 60% average increase (mean ± 1 SE: 32-94%) in pumpkinseed abundance in lakes without introduced redear. Thus, redear were associated with significant reductions in pumpkinseed CPUE (ANOVA, $F_{1, 22}$=11.17, P=0.0029), such that pumpkinseed abundance in lakes with introduced redear was 72.5% lower than expected based on the observed change in lakes without redear. Analogous comparisons of bluegill CPUE in the presence and absence of redear revealed no overall differences (ANOVA, $F_{1,22}$ =0.07, P= 0.788: Fig. 1C, 1D).

Pumpkinseed and Redear Growth

The annual growth of pumpkinseed, back-calculated from scale samples, did not vary significantly between lakes with and without redear. Estimated change in mass for a 90 mm SL pumpkinseed averaged 33.0 g/year (mean ± 1 SE: 29.7 - 36.7 g/year) with redear vs. 30.9 g/year (mean ± 1 SE: 29.2 - 33.0 g/year) without redear (ANOVA, $F_{1,9}$=0.21, P = 0.66). Furthermore, the presence of redear had no detectable effect on the size of pumpkinseed at any age (Fig. 2).

Within the same lakes, redear and pumpkinseed exhibited different growth patterns. Although pumpkinseed and redear were similar in size (~ 30 mm SL) at the end of the first year of growth, redear were longer at all subsequent ages (Fig. 2). By the end of their third year of growth, redear were approximately 60% longer than pumpkinseeds of the same age. Because size-at-age comparisons cannot reveal the specific periods in ontogeny where growth rates of redear and pumpkinseed differ (Osenberg et al. 1988), we also examined growth rates as functions of size. Growth rates of redear were 2-3x greater than those estimated for pumpkinseed at all fish sizes (Fig. 3), based on back-calculation from scales of 1+ and older fish.

Pumpkinseed and Redear Diets

Pumpkinseed in non-redear lakes undergo a substantial ontogenetic shift in diet from soft-bodied invertebrates to gastropods (Mittelbach 1984, Osenberg et al. 1994). In contrast, pumpkinseed collected from lakes with redear showed only a weak shift to snails during their ontogeny (Fig. 4a). Snails comprised an average of 69% (mean ± 1 SE: 62 - 76%; n=6) of the prey biomass found in large (>75 mm SL) pumpkinseed in non-redear lakes, but only 33% (mean ± 1 SE: 32-34%; n=2) in lakes with redear (ANOVA, $F_{1,7}$=7.82, P=0.031). In lakes with redear, diets of large pumpkinseed throughout ontogeny were dominated by amphipods and chironomid larvae. In these same lakes, the diets of large redear (>75 mm SL) were dominated by snails: 91% (mean ± 1 SE: 87 - 95%) (Fig. 4a). Redear underwent a diet shift to snails after they were approximately 40 mm SL. In Michigan lakes, this size would be reached by redear in their first year or early in their second year of life (see Fig. 2). While the representation of snails in sympatric pumpkinseed and redear diets was dramatically different, total prey biomass in their stomachs was similar for the two species (Fig. 4b). Thus, in the later stages of redear establishment, pumpkinseed and redear diets differ in their composition but not in total biomass.

Snail Abundance

Total snail biomass was 69% lower in lakes with introduced redear (6.9 mg/sweep) than in lakes without redear (22.0 mg/sweep, Fig. 5, $F_{1, 14}$=10.91, P=0.0052). At a finer taxonomic level, biomass of *Gyraulus* sp. and that of *Physella* sp. were significantly lower in redear lakes (ANOVA, $F_{1,14}$=6.46, P=0.024 and $F_{1,14}$=9.16, P= 0.009; respectively). Biomass of amnicolids and *Helisoma* sp. also tended to be lower with redear, but the differences were not significant (ANOVA, $F_{1,14}$=0.94 and $F_{1, 14}$=1.79, $P \geq$ 0.2). *Valvata* sp. was the rarest group in the absence of redear and showed no significant difference in biomass with or without redear (ANOVA, $F_{1, 14}$=0.15, P = 0.703). The difference in total snail biomass found in lakes with and without redear is the result of both lower snail abundance and smaller snail sizes in lakes with redear. Average total snail density was 47% lower in lakes with redear (71.2 snails/sweep; mean ± 1 SE= 49.1 - 107.3) than in non-redear lakes (134.1 snails/sweep; mean ± 1 SE= 99.3 - 181.8), while mean snail mass differed by 47% (0.12 mg (mean ± 1 SE= 0.10 - 0.15) in lakes with redear compared to 0.23 mg (mean ± 1 SE= 0.19 - 0.29) in nonredear lakes).). Differences in snail density and snail size among lake types, however, are not by themselves significantly different (snail density ANOVA, $F_{1, 14}$=1.61, P=0.23; snail mass ANOVA, $F_{1, 14}$=3.95, P=0.067).

Competition Experiment

Target Survival and Growth

In the competition experiment, survival of target fish was high overall (94.4%) and did not vary across treatments, between species or among size-classes. In contrast, growth varied appreciably across treatments, among target groups and over the course of the experiment (Fig. 6). Growth of large pumpkinseed and redear was high during the first half of the experiment and low during the second half. Small and medium pumpkinseed, on the other hand, continued to grow throughout the experiment. In general, all target classes showed the same qualitative response to treatments, with the greatest growth occurring in the target-only treatment and the lowest growth occurring in the treatments with redear (Fig. 6). The final differences among treatments were statistically significant for redear and marginally significant for large pumpkinseed targets (ANOVA, $F_{3,4}$=7.13, P=0.044 and $F_{3,4}$=5.60, P=0.065, respectively). Differences among treatments were not significant for either the small or medium pumpkinseed targets (ANOVA, $F_{3,4}$=3.679, P= 0.12; $F_{3,4}$=4.107, P= 0.13, respectively).

Resource Dynamics

There were no significant differences among treatments in initial prey biomass (Fig. 7: P>0.3 for small invertebrates, large invertebrates and snails). Following the introduction of fish, the biomass of snails and large invertebrates declined over time in each of the treatments with fish (Fig. 7). By the final sample date (July 31, 43 days after fish were introduced) fish effects on final prey biomass were strong overall, resulting in significant treatment effects on snail biomass (ANOVA, $F_{4,5}$=36.554, P=0.001) and large invertebrate biomass ($F_{4,5}$=6.108, P=0.037), but not on small invertebrate biomass ($F_{4,5}$=1.992, P=0.234). Significant treatment effects largely were due to the dramatic reductions in prey biomass in all treatments with fish (Fig. 7).

At the end of the experiment, the final mean body mass of large invertebrates differed among treatments (ANOVA, $F_{4,5}$=23.305, P= 0.002). The overall significance was driven by the extreme difference between the no fish treatment and the remaining treatments; analysis of only those treatments with fish resulted in no significant treatment effects (ANOVA, $F_{3,4}$=3.80, P=0.12). Mean mass of large invertebrates was 0.350 ± 0.040 mg (mean ± SE) in the fishless treatment and 0.115 ± 0.012 mg pooled across all treatments with fish. A qualitatively similar, albeit weaker, pattern was observed for mean snail mass (0.101 ± 0.002 mg in the fishless treatment and 0.062 ± 0.005 mg pooled across all treatments with fish), although the treatments were not significantly different (ANOVA, $F_{4,5}$=2.65, P=0.15). The final body mass of small invertebrates showed no clear pattern with respect to treatment (ANOVA, $F_{4,5}$=1.28, P=0.38).

Target Growth- Resource Abundance Correlations

Final mass of target fish was not significantly correlated with the biomass of either small or large invertebrates for any of the targets (Table 3). In contrast, all targets exhibited positive correlations between final mass and average snail biomass, although these correlations were statistically significant only for redear and medium pumpkinseed targets (Table 3).

Target Diets

At the end of the experiment (44 days after their initial release into the pond), the diets of all target fish were dominated by soft-bodied prey and treatment effects on snail biomass in pumpkinseed and redear diets were not significant (ANOVA, $F_{3,8}$=2.039, P= 0.187). At this point in the experiment, fish had greatly reduced snail abundance in the pond (see Fig. 7). Despite the low biomass of snails, clear dietary patterns were still evident at the end of the experiment. Snail biomass in pumpkinseed and redear diets increased with increasing snail biomass across the pond sections, although the redear response was substantially greater (Fig. 8). There were no treatment effects on the size of snails consumed by large targets, but there was an effect of target species; the average size of snails in redear diets was larger than in large pumpkinseed diets (0.18 ± 0.035 mg) vs. (0.055 ± 0.013 mg), respectively (F_{11} =7.172, P= 0.018).

DISCUSSION

Fisheries biologists have long recognized that introduced species can have strong effects on native fish communities (Magnuson 1976, Courtenay and Stauffer 1984, Moyle 1986, Moyle et al. 1986; Mills et al. 1994). What is still relatively rare are studies that can predict these effects before hand, measure the magnitude of these effects, and identify the causal mechanisms. In this study, we were able to predict that the introduction of redear would have a negative effect on native pumpkinseed populations, based on prior studies documenting similarities between the species in feeding behavior, functional morphology, and resource use (Huckins 1997). Comparisons of sunfish densities (pumpkinseed, redear, and bluegill) in lakes with and without introduced redear supported this prediction. Further, this conclusion was strengthened by the fact that fish surveys were conducted both before and after the introduction of redear, which enabled us to follow population trends through time. Also, the fact that the bluegill showed no significant response to redear introduction, bolsters the case that it was competition between pumpkinseed and redear that resulted in the 56% decline in pumpkinseed abundance, and not some other unknown factor associated with lakes where redear were introduced. For example, redear were introduced as a game fish and angler effort is positively related to measurements of fishery quality (Johnson and Carpenter 1994). Well stocked lakes attract more anglers, leading to increased fishing mortality of other species in the lake by a mechanism akin to apparent competition (see Holt 1977). Stocked redear could also be prey for piscivorous bass and lead to increased bass densities, which would then result in increased predation on pumpkinseed. However, if this mechanism of apparent competition were operating, either through a numerical response of anglers or of bass, we would have expected to observe similar reductions in the density of bluegill, which we did not. Furthermore, this mechanism alone cannot explain the lack of a pumpkinseed dietary shift to snails or the lower snail abundance in introduced lakes.

Competition theory suggests that the introduction of a species that is more efficient at using a shared resource should result in a diet shift by the native species and a broadening of that species' diet (MacArthur and Pianka 1966, Werner 1986). Both pumpkinseeds and redear feed extensively on snails in allopatry (Sadzikowski and Wallace 1976, Mittelbach 1984), and laboratory feeding experiments show that redear are more proficient at crushing snails than are pumpkinseeds (Huckins 1997). Therefore, we predicted that redear would affect the diets of pumpkinseed, causing them to feed less on snails. We found that pumpkinseed in lakes with redear had less than half the biomass of snails in their diet, compared to pumpkinseed in lakes without redear. Also, redear consumed substantially more snails than did pumpkinseeds in lakes where the species co-occurred. Differences in snail availabilities among lake-types were consistent with the pumpkinseed diet response. In lakes with introduced redear, average snail biomass was ~69% lower than in lakes without redear. While these comparisons of pumpkinseed diets and snail biomass in lakes with and without redear support the hypothesized competitive interaction between the species, these data are strictly comparative. Unlike the fish density data, we do not have diet or snail data from lakes before and after redear introduction. Still, the overall pattern of sunfish and snail populations in lakes with and without redear provides a consistent picture of strong, competitive effects of introduced redear on native pumpkinseed populations.

One observation that did not fit initial predictions was that there were no differences in back-calculated pumpkinseed growth rates in lakes with and without redear. Based on previous work (Osenberg and Mittelbach 1989, Mittelbach and Osenberg 1994), we expected that a reduction in snail biomass in the presence of redear would lead to a reduction in pumpkinseed growth (as was observed in the pond experiment). However, in the experiment pumpkinseed density was held constant, whereas in the lake systems pumpkinseed density was free to change. Indeed, the disparity in the results from the lake survey and pond experiment is most easily explained by the differences in their time scales and associated dynamics. In natural lakes, long-term compensatory responses could arise following declines in pumpkinseed and snails. We propose that during the initial stages of redear establishment in Michigan lakes, declines in snail biomass led to lower pumpkinseed feeding rates and lower pumpkinseed growth, which reduced the fecundity or survival of adults, and therefore caused a reduction in population size (see Mittelbach and Chesson 1987). If unchecked, this decline in pumpkinseed population size would continue and lead to the competitive exclusion of pumpkinseed by redear. However, the declining density of pumpkinseed could be counteracted if pumpkinseed compensated for the reduction in snail availability by feeding more on soft-bodied invertebrates. In our field comparisons, we observed that pumpkinseeds in redear lakes increased their feeding on soft-bodied prey. An alternate explanation for the lack of growth differences between pumpkinseeds from lakes with and without redear is that reduced survival of slow-growing individuals may mask any long-term reduction in individual growth rates due to the introduction of a new competitor.

Our field survey and pond experiment document negative effects of introduced redear on pumpkinseed populations over periods ranging from weeks to ~ 20 years. They leave open the question of whether pumpkinseed may coexist with redear over longer time scales. In two Michigan lakes where redear were introduced over 40 years ago, pumpkinseed populations continue to persist, albeit at lower densities (Towns MDNR personal communication 1994, Huckins personal observation). An additional assessment of longer-term dynamics of pumpkinseed and redear interactions can be drawn from literature data collected from streams in North Carolina where both pumpkinseed and redear are native and have potentially interacted over long time scales. Estimates of catch-per-unit-effort taken from Kornegay et al. (1994) suggest the presence of two basic types of streams, those where the molluscivore assemblage is dominated by pumpkinseed and those where the dominant molluscivore is redear (Fig. 9a). All four "redear-dominated” streams contained pumpkinseed, suggesting that the two species may coexist over long periods of time. In the three "pumpkinseed-dominated" streams, redear were completely absent from two streams and represented < 1% of the total CPUE in the third stream. These “pumpkinseed streams” hosted fewer fish species overall, suggesting that these systems may represent refugia for pumpkinseed due to disturbed or otherwise poor conditions that inhibit survival of redear and other sunfish (e.g., due to low oxygen availability: see Evans 1984, Stein et al. 1984).

As seen in the North Carolina systems where redear and pumpkinseed coexist, redear are also relatively more abundant than pumpkinseed in Michigan lakes where redear have been introduced (Fig. 9a). The extent of redear dominance appears to be related to the time that has elapsed since redear introduction (Fig. 9a,b). In the 32 Michigan lakes surveyed, redear accounted for well over 70% of the molluscivore assemblage by the 8th year following introduction (Fig. 9b). Redear were generally introduced into Michigan lakes in which they were expected to do well (i.e., larger lakes with abundant snails: Towns 1991). Thus, these systems may not be as diverse in environmental conditions as the North Carolina systems sampled by Kornegay et al. (1994), and may not include refuge systems hosting larger pumpkinseed populations as we have postulated for some of the North Carolina systems. Thus, while redear dominance of the molluscivorous feeding niche continues to increase in Michigan lakes, the potential for long-term persistence of native pumpkinseed populations in these managed systems is uncertain.

As documented here, the management of fisheries by means of planned introductions of exotics may have negative long-range consequences (i.e., Moyle et al. 1986). Although the introduction of species probably has a legitimate place in the management of aquatic systems (Dill and Cordone 1997), introductions should be based on sound management of all aquatic resources rather than management designed to benefit one user group (Courtenay and Kohler 1986). Ultimately, this requires assessment of potential ecological risks prior to species introductions (e.g., Arthington 1991). In at least one case, such assessment has successfully averted a potential environmental tragedy (e.g., Townsend and Winterbourn, 1992). However, assessments are not easy to make and may often prove to be incorrect in part because assessments must rely on existing information, which is often inadequate for forecasting long-term ecological dynamics (Ambrose et al. 1996). The continued study of the ecological effects of introduced species will provide an empirical and theoretical base that can facilitate future assessments of species introductions (Hilborn and Walters 1981, Ambrose et al. 1996), and thus improve the management of our natural resources.

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Table 1. Description of study lakes used in the analyses of pumpkinseed and bluegill density, growth and diets of pumpkinseed and redear, and snail availability. Lakes used in the analysis of fish and snail density are indicated by a "+" in the respective column. Numbers in the growth and diets headings give the number of fish (pumpkinseed and redear, respectively) used in the analyses. "---" indicated that data were not obtained, and "N.A." indicates cases where redear could not be collected because redear were not yet present in the lake.

Lake (County)	Redear Introduced (years)	Surface Area (ha)	Fish Density	Fish Growth	Fish Diets	Snail Abundance
Lakes with Redear						
Brace Lakes (Calhoun)	1984, '86	75	+	---	---	+
Bruin (Washtenaw)	1990, '91, '93	55	+	---	---	---
Clark (Jackson)	1984	235	+	---	---	---
Clear (Jackson)	1987	55	+	---	---	---
Cub (Hillsdale)	1985, '89	46	+	---	---	---
Fourmile (Washtenaw)	1987, '91, '92, '93	104	+	---	---	+
Gilletts (Jackson)	1986, '87, '91, '92	142	+	---	---	+
Grass (Jackson)	1987, '91, '92	141	+	50, 26	---	+
Lee (Calhoun)	1984, '91, '92	47	---	137, 100	59, 47	+
Mill (Washtenaw)	1990, '91, '93	57	+	---	---	---
Portage (Jackson)	1985, '87, '91	146	+	---	---	---
Round (Jackson)	1985, '91, '92	63	+	---	---	---
Saubee (Eaton)	1986	24	---	49, 72	33, 34	+
Reference Lakes						

Big Portage (Washtenaw)	---	261	+	---	---	---
Big Wolf (Jackson)	---	152	+	---	---	---
Bishop (Livingston)*	1993, ‘94	48	+	---	---	---
Cedar (Washtenaw)	---	30	---	---	---	+
Crispell (Jackson)	---	33	+	---	---	---
Craig (Branch)	---	49	+	---	---	---
Culver (Barry)	---	13	---	49, N.A.	20, N.A	---
Deep (Barry)	---	13	---	55, N.A.	---	+
East Crooked (Livingston)*	1995	102	+	52, N.A.	14, N.A.	---
Fine (Barry)	---	130	---	---	---	+
Goguac (Calhoun)	---	142	+	---	---	---
Halfmoon (Washtenaw)**	1987	96	+	---	---	---
Joslin (Washtenaw)*	1995	76	+	---	---	---
Lake of the Woods (Calhoun)	---	20	+	---	---	---
Lane (Calhoun)	---	10	+	---	---	---
Lawrence (Barry)	---	5	---	108, N.A.	43, N.A.	+
Palmatier (Barry)	---	6	---	64, N.A.	21, N.A.	+
Prairie (Calhoun)	---	32	+	---	---	+
Three Lakes II (Kalamazoo)	---	22	---	151, N.A.	222, N.A.	+
Three Lakes III (Kalamazoo)	---	15	---	157, N.A.	45, N.A.	+
Vineyard (Jackson)*	1997	204	+	---	---	+
Warner (Barry)	---	26	---	106, N.A.	---	---
Warners (Calhoun)	---	23	---	---	---	+

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* Analyzed as a reference (non-redear) lake because redear were stocked after the surveys and sampling for growth and diets.

** Analyzed as a reference (non-redear) lake because stocked redear were in poor condition and did not establish in the lake.

Table 2. Design of the target-neighbor experiment conducted in a 30 m diameter circular pond divided into 10 wedge-shaped sections. The target assemblage consisted of three large redear, three large pumpkinseed, five medium pumpkinseed and 20 small pumpkinseed. Each of the five treatments were randomly assigned to one of the five sections in each half of the pond, yielding two replicates of each treatment.

Treatments	Targets	Neighbors	Total density of fish (number/section)
1) NO FISH	0	0	0
2) TARGET-ONLY	present	0	31
3) LOW-PUMPKINSEED	present	20 pumpkinseed	51
4) LOW-REDEAR	present	20 redear	51
5) HIGH-REDEAR	present	40 redear	71

Table 3 Correlations between the mean final mass (g) of four target classes of fish and the mean biomass of three prey categories (large invertebrates, small invertebrates and snails) across sections. The correlation coefficient and the associated *P*-value of each correlation are given. *n*=8 for all comparisons.

	large invertebrates	small invertebrates	snails
redear	-0.13, 0.76	0.17, 0.68	0.81, 0.015
large pumpkinseed	-0.22, 0.60	-0.20, 0.64	0.66, 0.078
medium pumpkinseed	0.06, 0.89	0.30, 0.47	0.88 0.004
small pumpkinseed	-0.23, 0.58	0.10, 0.82	0.61, 0.11

Figure 1. Pumpkinseed and bluegill abundance in 11 lakes with introduced redear and 13 lakes that did not have redear. Values are catch-per-unit-effort (CPUE, fish/trap) from the Michigan Department of Natural Resource surveys that were standardized to initial CPUE values within each lake to show relative changes in abundance within lakes (i.e., initial surveys all have standardized CPUE = 1). Values <1 indicate a decrease in CPUE and those >1 indicate an increase in CPUE. Each line represents survey data from one lake and each dot represents a survey. In some cases the lines for multiple lakes overlap. Data shown within shaded regions of each figure were not included in statistical analyses of change in CPUE, which were based on lake means obtained by averaging all estimates within a lake over the period to the right of the shaded region.

Figure 2: Standard length (mm) of redear, pumpkinseed from lakes without redear, and pumpkinseed from lakes with introduced redear as a function of age of fish (years). Means (± SE) for redear and pumpkinseed in lakes with redear are based on three lakes; those for pumpkinseed in the absence of redear are based on eight lakes.

Figure 3. Back-calculated growth rates (annual change in mass, grams/year) for redear, pumpkinseed from lakes with introduced redear, and pumpkinseed from lakes without redear. For clarity of presentation, data are shown grouped into 10 mm standard length classes (e.g., length-class of 75 includes fish between 70-80 mm SL). Length classes are based upon the size of the fish at the start of the growth season. Means (± SE) for redear and pumpkinseed with redear are based on 3 lakes, those for pumpkinseed in the absence of redear are based on 8 lakes.

Figure 4. Percent snails in diets (a) and total biomass of prey in the stomach (b) for redear and 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 and means (± SE) are shown . Means for redear and pumpkinseed in lakes with redear are based on three lakes, and those for pumpkinseed in the absence of redear are based on six lakes. Pumpkinseeds > 100 mm were not collected from Lee and Saubee Lakes. Curves shown in (a) are from a logistic function: $P=Y_{max}/(1+e^{(a-bL)})$, where P is the mean percent snails in the diet of fish in length-class, L, and Y_{max}, a and b are estimated constants. Estimated parameters were Y_{max}=92.292, a=6.413, b= 0.161 for redear, Y_{max}= 70.373, a=6.136, b=0.105 for pumpkinseed in the absence of redear, and Y_{max}=62.894, a=3.208, b=0.032 for pumpkinseed living with redear.

Figure 5. Snail biomass in 10 lakes with no redear (open bars) and six lakes with introduced redear (grey bars). Results are given for all snails combined (total) as well as the five major taxonomic groups: amnicolids (*Amnicola* sp. and *Marstonia* sp.), *Gyraulus* sp., *Valvata tricarinata*, *Physella* sp., and *Helisoma* sp. Means ± 1 SE are shown.

Figure 6. Mass of pumpkinseed and redear targets at the three sample dates in the pond experiment. The mean values for each treatment (target only, low (20) pumpkinseed, low (20) redear, and high (40) redear neighbors) are shown for each target class: (a) small pumpkinseeds, (b) medium pumpkinseeds, (c) large pumpkinseeds, and (d) redear. Means ± 1 SE are shown.

Planned contrasts showed that the size of large pumpkinseed targets was smaller in all treatments with neighbors relative to the target-only treatment ($P<0.05$ for all comparisons), but that redear target mass was reduced only in the presence of redear neighbors ($P=0.33$ for low-pumpkinseed vs. target-only treatments, $P<0.05$ for both redear treatments vs. the target-only treatment).

Figure 7. Biomass of (a) snails, (b) large invertebrates (primarily Odonata and Ephemeropteran nymphs), and (c) small invertebrates (amphipods and dipteran larvae) on three sampling dates during the experiment. Each point represents the mean (± 1 SE) of two replicates of a treatment. Note different scales on the y-axes. Final snail biomass was significantly lower in both the low and high-redear neighbor treatments than in the target only treatments (planned contrasts, P = 0.048 and P = 0.035, respectively), whereas snail biomass in the pumpkinseed neighbor treatment was not significantly different from the target-only treatment (P = 0.126).

Figure 8. Snail biomass in the diets of pumpkinseed and redear at the end of the experiment shown as a function of snail biomass in each of the sections of the pond. The mean snail biomass in the diet (± SE) for each pond section is based on two or three target fish per species. There is a significant interaction between the covariate (final snail biomass in a section) and fish species in an analysis of covariance (ANOVA, $F_{1,12}=8.14$, $P=0.015$), indicating that under these conditions, redear diet composition changes more in response to changes in snail availability than does pumpkinseed diet composition.

Figure 9. Composition of the molluscivorous sunfish assemblage in 32 Michigan lakes and seven North Carolina streams. a) Frequency of Michigan lakes (light bars) and North Carolina streams (dark bars) with different compositions (expressed as the percentage of redear out of all molluscivous species (i.e., pumpkinseed + redear)). North Carolina data are from Kornegay et al. 1994) and Michigan data are from the Michigan Department of Natural Resource Fisheries Surveys. Numbers above each Michigan bar give the average number of years elapsed since redear were first introduced into the lakes. b) Composition of the molluscivores (expressed as % redear) in Michigan lakes as a function of years since redear were introduced. For presentation, lakes were categorized based on time since redear introduction: 1-3, 4-6, 7-9, 10-15 and >15 years. Means ± SE are shown. Samples sizes range from 3 to 10 lakes.

Fig.1

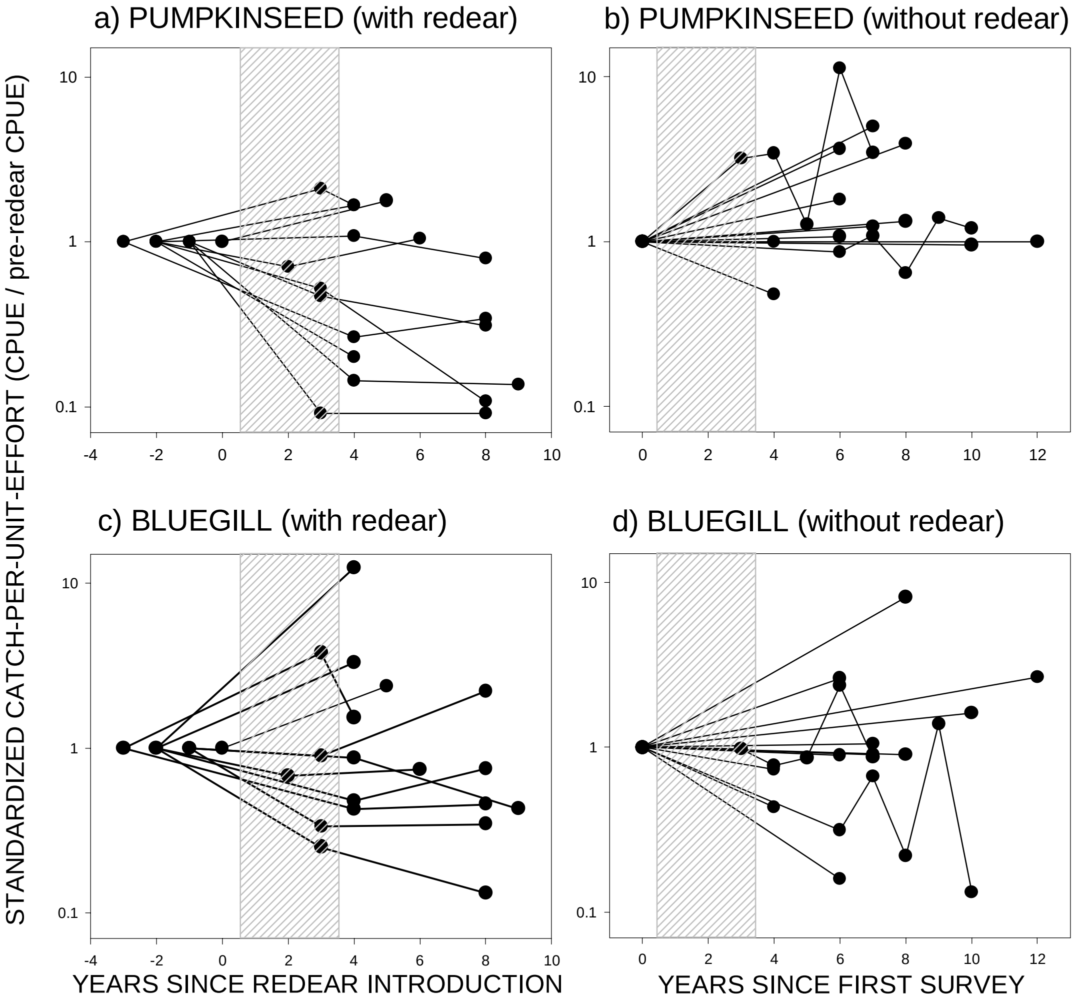

a) PUMPKINSEED (with redear)
b) PUMPKINSEED (without redear)
c) BLUEGILL (with redear)
d) BLUEGILL (without redear)
STANDARDIZED CATCH-PER-UNIT-EFFORT (CPUE / pre-redear CPUE)
10
1
0.1
-4
-2
0
2
4
6
8
10
12
YEARS SINCE REDEAR INTRODUCTION
YEARS SINCE FIRST SURVEY

Fig. 2

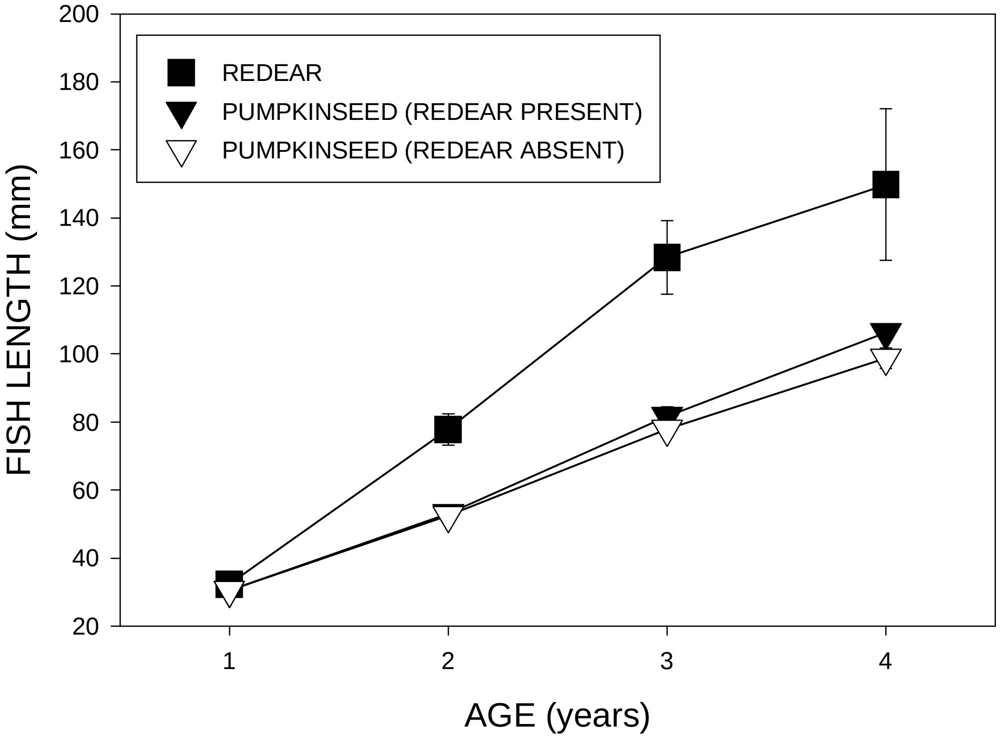

■ REDEAR
▼ PUMPKINSEED (REDEAR PRESENT)
▽ PUMPKINSEED (REDEAR ABSENT)
FISH LENGTH (mm)
AGE (years)
200
180
160
140
120
100
80
60
40
20
1
2
3
4

Fig. 3

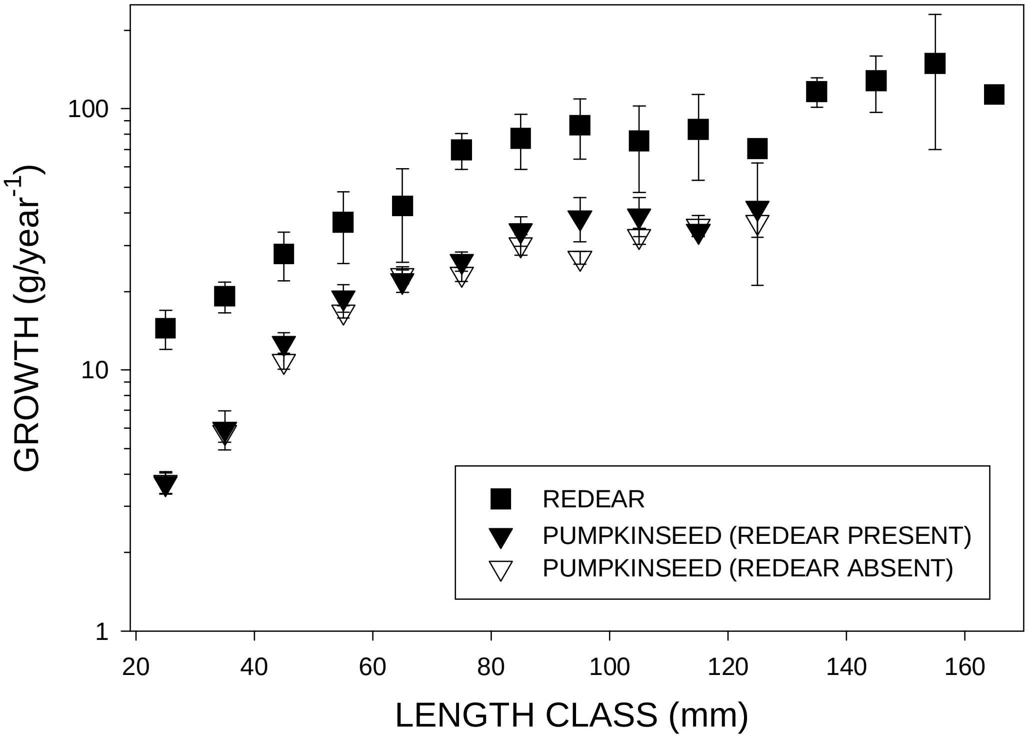

GROWTH (g/year^{-1})
1
10
100
20
40
60
80
100
120
140
160
LENGTH CLASS (mm)
■ REDEAR
▼ PUMPKINSEED (REDEAR PRESENT)
▽ PUMPKINSEED (REDEAR ABSENT)

Fig. 4

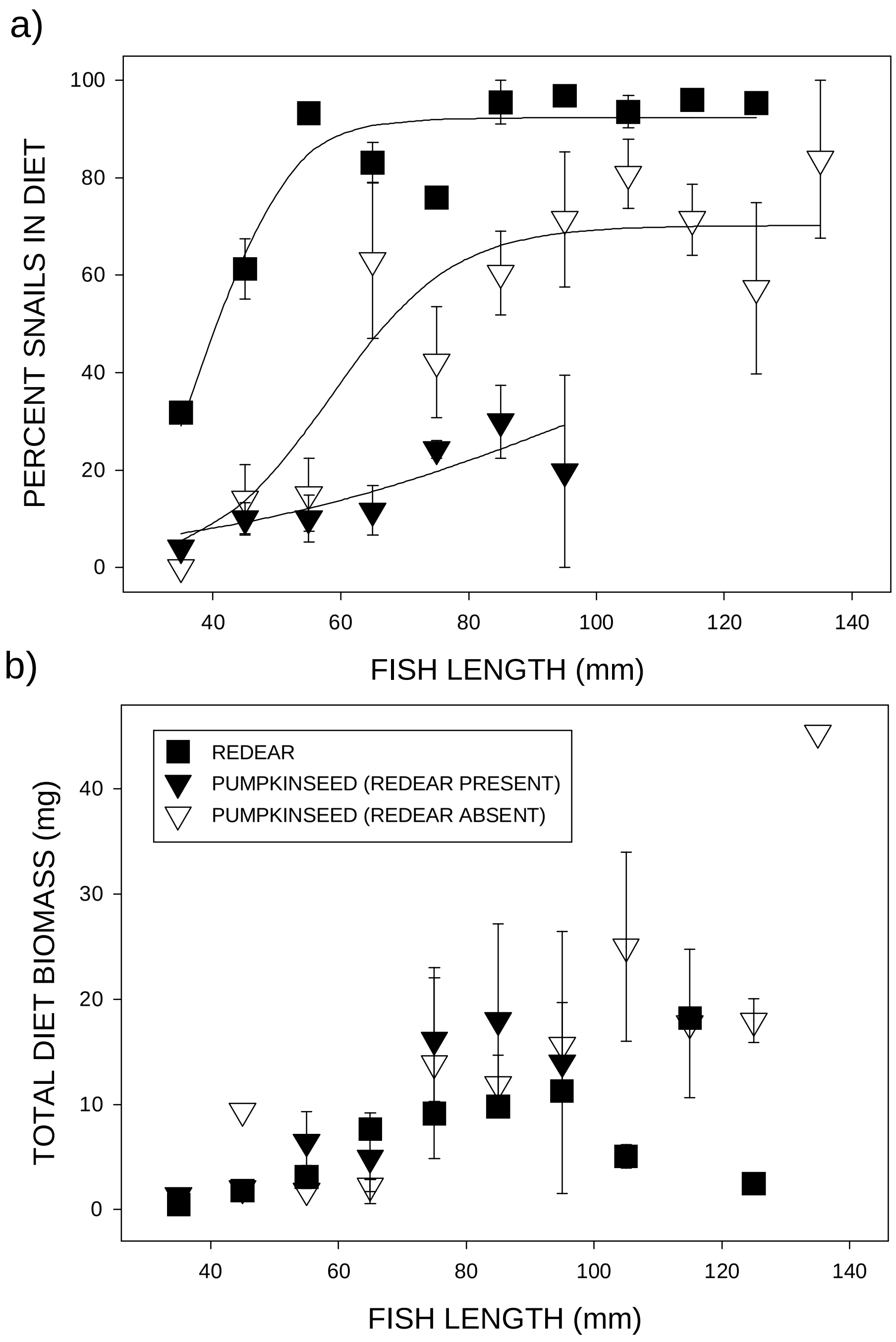

a)
PERCENT SNAILS IN DIET
0
20
40
60
80
100
40
60
80
100
120
140
FISH LENGTH (mm)
b)
TOTAL DIET BIOMASS (mg)
0
10
20
30
40
REDEAR
PUMPKINSEED (REDEAR PRESENT)
PUMPKINSEED (REDEAR ABSENT)
40
60
80
100
120
140
FISH LENGTH (mm)

Fig. 5

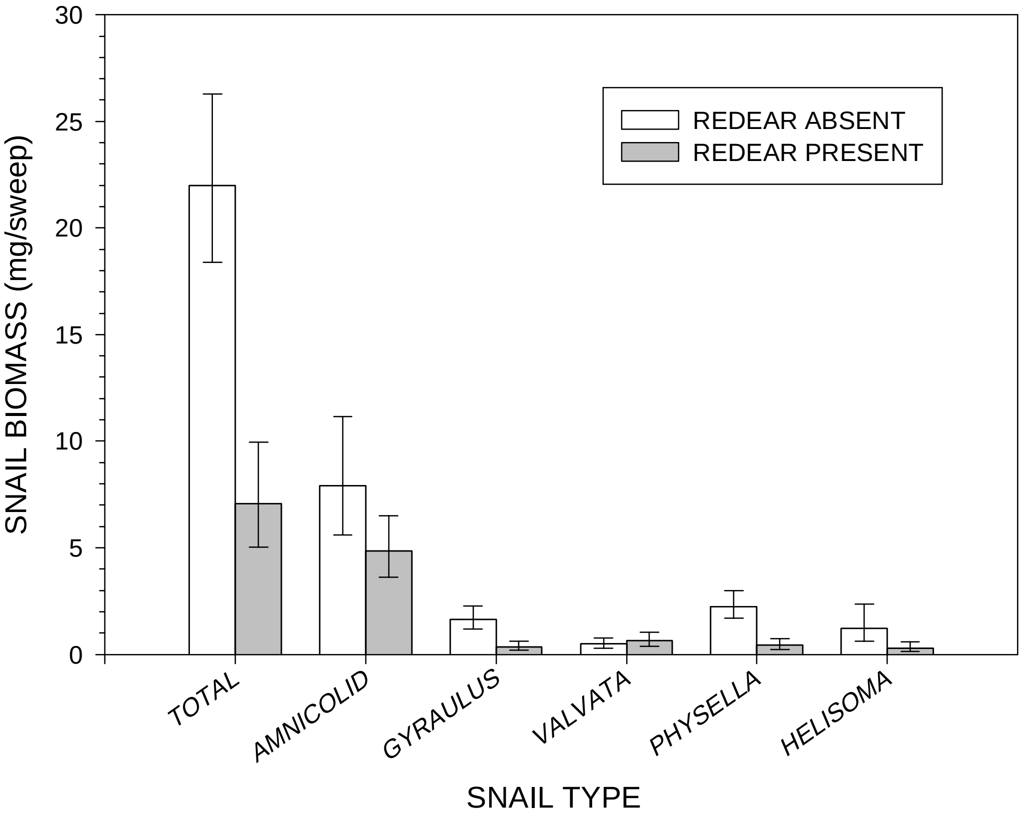

30
25
20
15
10
5
0
SNAIL BIOMASS (mg/sweep)
REDEAR ABSENT
REDEAR PRESENT
TOTAL
AMNICOLID
GYRAULUS
VALVATA
PHYSELLA
HELISOMA
SNAIL TYPE

Fig. 6

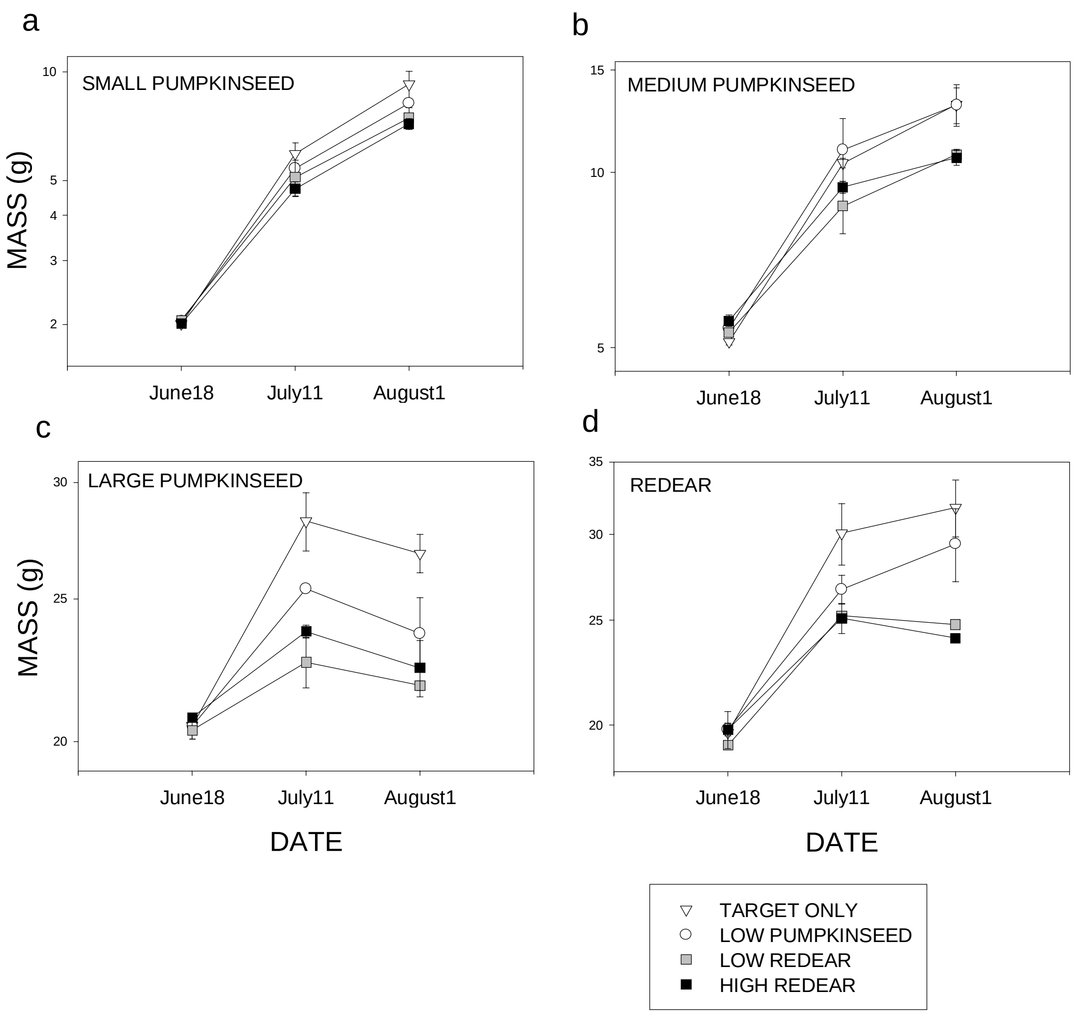

a
SMALL PUMPKINSEED
MASS (g)
10
5
4
3
2
June18
July11
August1
b
MEDIUM PUMPKINSEED
15
10
5
June18
July11
August1
c
LARGE PUMPKINSEED
MASS (g)
30
25
20
June18
July11
August1
DATE
d
REDEAR
35
30
25
20
June18
July11
August1
DATE
▽ TARGET ONLY
○ LOW PUMPKINSEED
▨ LOW REDEAR
■ HIGH REDEAR

Fig. 7

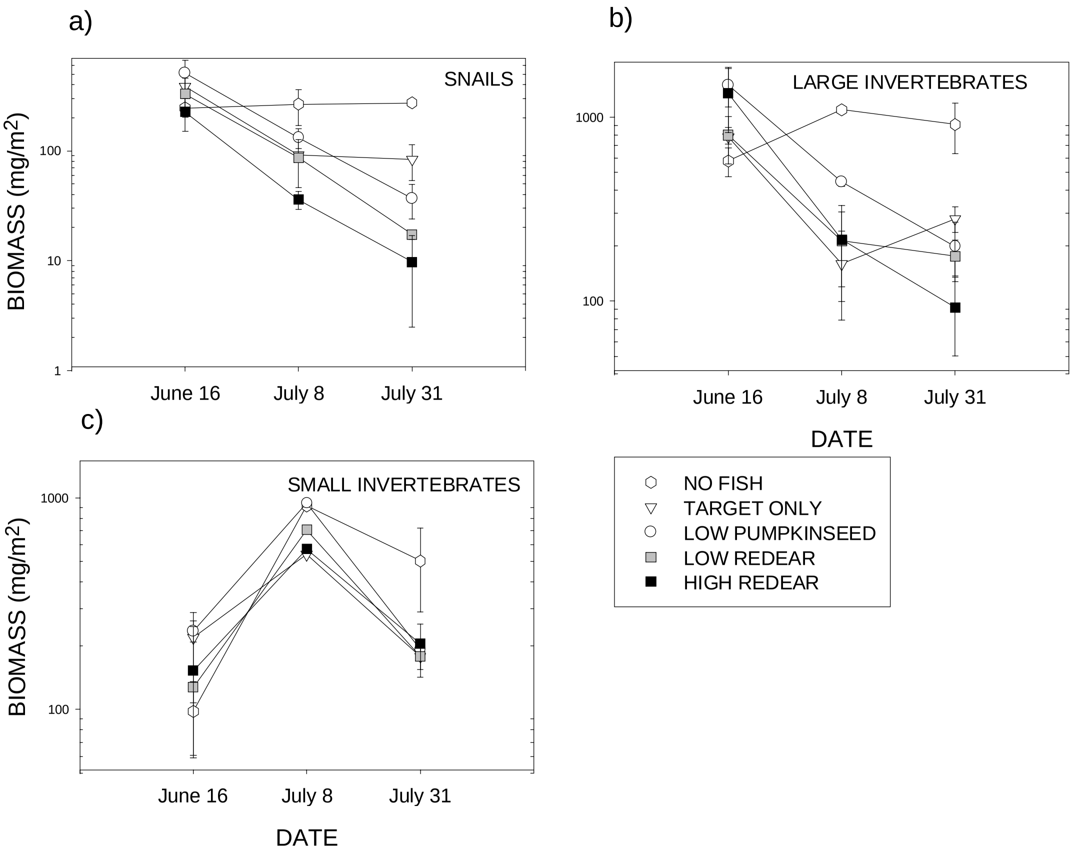

a)
SNAILS
BIOMASS (mg/m^2)
1
10
100
June 16
July 8
July 31
b)
LARGE INVERTEBRATES
100
1000
June 16
July 8
July 31
DATE
c)
SMALL INVERTEBRATES
BIOMASS (mg/m^2)
100
1000
June 16
July 8
July 31
DATE
⬡ NO FISH
▽ TARGET ONLY
○ LOW PUMPKINSEED
▨ LOW REDEAR
■ HIGH REDEAR

Fig. 8

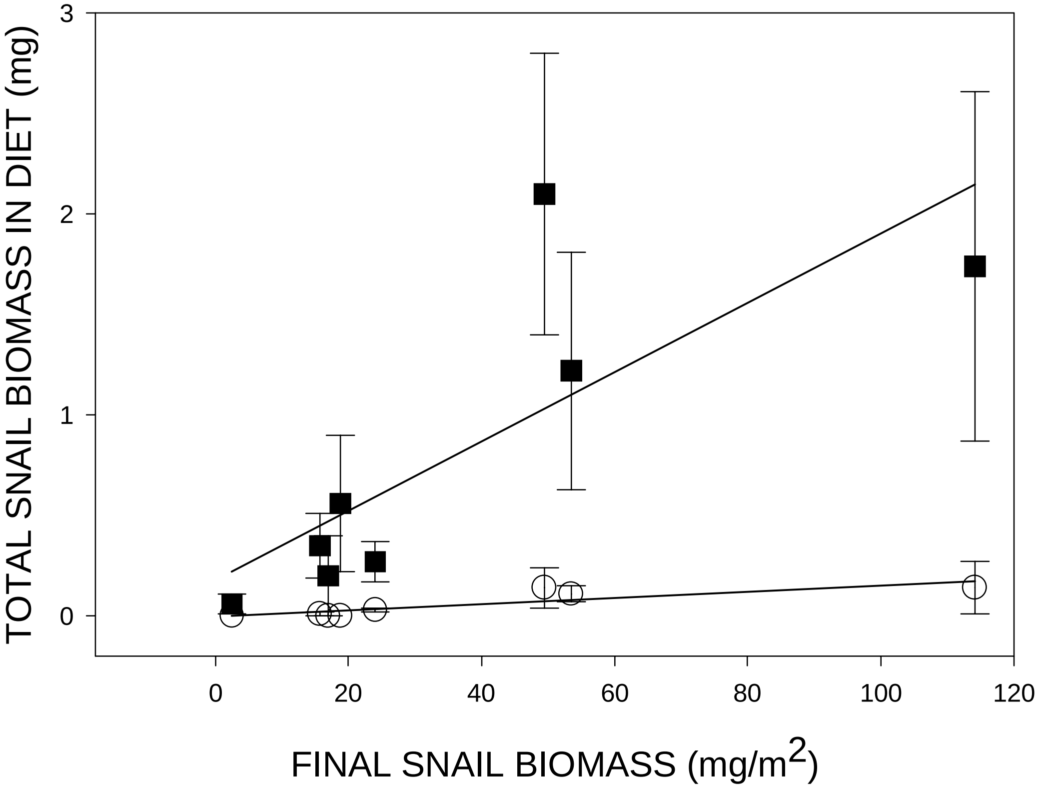
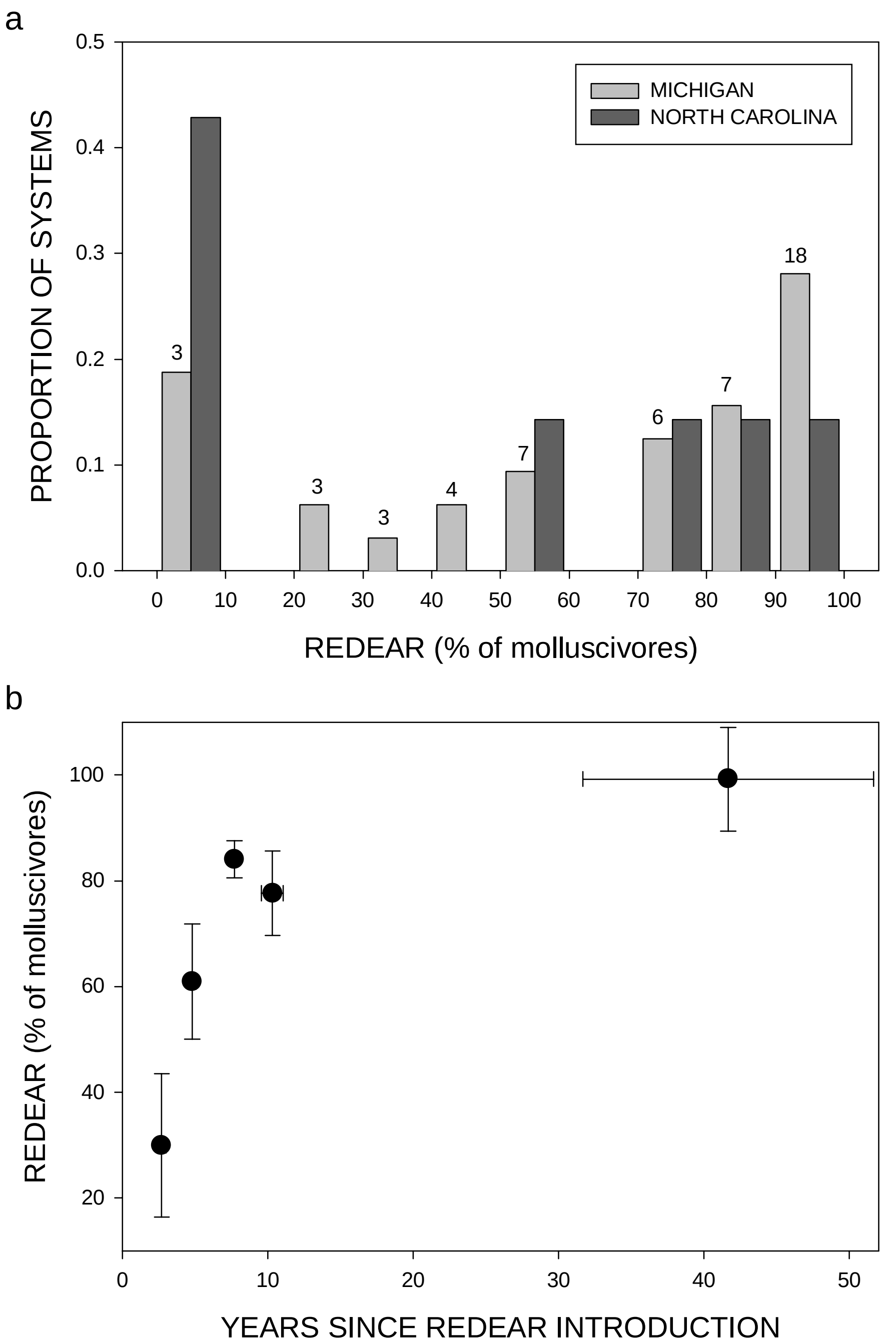

TOTAL SNAIL BIOMASS IN DIET (mg)
3
2
1
0
0
20
40
60
80
100
120
FINAL SNAIL BIOMASS (mg/m2)

Fig. 9


a
PROPORTION OF SYSTEMS
0.0
0.1
0.2
0.3
0.4
0.5
MICHIGAN
NORTH CAROLINA
3
3
3
4
7
6
7
18
0
10
20
30
40
50
60
70
80
90
100
REDEAR (% of molluscivores)
b
REDEAR (% of molluscivores)
20
40
60
80
100
0
10
20
30
40
50
YEARS SINCE REDEAR INTRODUCTION