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TWO-STAGE LIFE HISTORIES IN FISH: THE INTERACTION BETWEEN JUVENILE COMPETITION AND ADULT PERFORMANCE¹

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Abstract. Pumpkinseed sunfish (*Lepomis gibbosus*) typically exhibit a strong ontogenetic diet shift. Small (juvenile) pumpkinseeds feed primarily on soft-bodied littoral invertebrates and compete with small bluegill (*L. macrochirus*), while large (adult) pumpkinseeds feed extensively on snails. We compared pumpkinseed and snail populations in two Michigan lakes that contain bluegill (Three Lakes II and Three Lakes III) with populations inhabiting Wintergreen Lake, a lake lacking bluegill. In the absence of bluegill, pumpkinseeds were abundant and juveniles grew well; however, snail abundances were low and adult pumpkinseeds grew poorly. Furthermore, no ontogenetic diet shift to snails occurred in Wintergreen Lake, and the pharyngeal muscles and bones used to crush snails were smaller than in fish from Three Lakes II. Pumpkinseeds from Wintergreen Lake also required significantly more time to crush and handle thick-shelled snails, but not thin-shelled snails and nongastropod prey, than did fish from Three Lakes II. In a field caging experiment in Wintergreen Lake snail densities increased fourfold when pumpkinseeds were excluded.

Historical data as well as the among-lake comparisons suggest that the changes in Wintergreen Lake occurred in response to the selective elimination of the pumpkinseed's juvenile-stage competitor, the bluegill, via a winterkill event in the late 1970s. It appears that removal of bluegill released juvenile pumpkinseeds from competition and increased pumpkinseed recruitment into the adult stage, which resulted in the overexploitation of the adults' snail resource. These events then led to changes in adult pumpkinseed diet, growth, morphology, and feeding ability. These data are consistent with predictions from a two-stage life history model developed for the pumpkinseed–bluegill interaction and illustrate some of the important indirect consequences of interactions involving stage-structured populations.

Key words: competition; feeding performance; functional morphology; gastropods; *Lepomis*; ontogenetic diet shift; predation; stage structure.

INTRODUCTION

Most organisms grow substantially in size from birth to death. Associated with this change in body size is often an abrupt shift in diet or habitat use. Such ontogenetic niche shifts are common in size-structured taxa (Werner and Gilliam 1984) and often result in different life stages (e.g., juveniles and adults) interacting with entirely different resources, competitors, and predators. Numerous theoretical studies show that the incorporation of population structure can lead to predicted population dynamics and abundances that contrast strongly with nonstructured models (e.g., Nisbet and Gurney 1982, Tschumy 1982, Prout and

McChesney 1985, Roughgarden et al. 1985, Mittelbach and Chesson 1987, Nisbet and Bence 1989). Despite this rapidly developing theory, there are relatively few field studies that explicitly examine the population and community consequences of interactions among structured populations (but see, for example, Neill and Peacock 1980, Ebenman and Persson 1988, Mittelbach et al. 1988, Persson et al. 1988). Because most populations are stage or size structured and because existing models for stage-structured interactions exhibit such a wide array of complex results, it is important that empirical and theoretical studies in this area develop in concert. Thus, the challenge is to formulate general hypotheses based on a theory for stage-structured interactions, and to test these hypotheses in natural communities.

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Two congeneric sunfishes, the pumpkinseed sunfish (*Lepomis gibbosus*) and the bluegill (*L. macrochirus*) are particularly well suited for the study of interactions within and among stage-structured populations. Both species undergo ontogenetic dietary shifts: small pumpkinseed and small bluegill (approximately <45 mm standard length, SL) feed on a common resource (soft-bodied littoral invertebrates), while large pumpkinseed (approximately >75 mm SL) feed on snails and large bluegill feed primarily on zooplankton (Mittelbach 1981, 1984, Werner and Hall 1988, Osenberg and Mittelbach 1989): the diets of intermediate size classes ($\approx 45\text{--}75$ mm SL) are transitional. Because the shifts of both species to their adult diets are approximately coincident with the onset of maturity, we refer to small and large fish as juveniles and adults. Furthermore, both comparative and experimental studies in natural lakes demonstrate that juvenile pumpkinseed and bluegill compete interspecifically for a limited food resource (Mittelbach 1988, Osenberg et al. 1988). This system motivated the stage-structured model developed by Mittelbach and Chesson (1987). Their model incorporates recruitment from one life stage to another (via maturation and egg production) and interspecific competition between juveniles (which links the dynamics of the two species and their adult resources) (Fig. 1).

Using this model, we previously predicted (Mittelbach and Chesson 1987, Mittelbach et al. 1988, Osenberg et al. 1988) that reduced bluegill density would lead to (1) increased density of juvenile and adult pumpkinseed, (2) increased per capita survival of juvenile pumpkinseed (due to reduced interspecific competition and increased prey availability), and (3) decreased per capita reproduction of adult pumpkinseed (due to increased pumpkinseed density and a consequent decrease in snail abundance). Based on the changes in prey resources (predictions 2 and 3) and data showing that individual growth of sunfish is food limited (Mittelbach 1988, Mittelbach et al. 1988, Osenberg et al. 1988, Osenberg and Mittelbach 1989), we also predicted (4) increased growth rates for juveniles, but (5) decreased growth rates for adults.

The most interesting general result, and the one that arises because the interacting populations are stage structured and resource limited, is that the performance (i.e., survival, fecundity, or growth) of juvenile and adult pumpkinseeds should respond in opposite directions to the removal of the juvenile competitor, bluegill (predictions 2 vs. 3 and 4 vs. 5). This inverse response arises because the benefit obtained during the pumpkinseed's juvenile stage must be balanced by a reduced performance in the adult stage. Thus, the model predicts important indirect effects on adult pumpkinseeds and snails mediated through the release of juvenile pumpkinseed from competition with bluegill.

In this study we exploit a unique opportunity to test this model and examine the consequences of interspe-

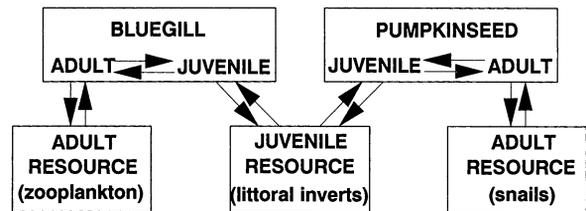


FIG. 1. A graphical representation of the two-stage life history of pumpkinseeds and bluegill and their interactions with their resources. Juvenile and adult components are connected with arrows indicating the effects of growth and maturation of juveniles into the adult stage and the production of larvae by adults. Negative effects of fish on their prey and the positive effect of prey on the predators are based on observational and experimental work showing that fish growth is food limited and that fish decrease food availability (Mittelbach 1988, Osenberg 1988, Osenberg et al. 1988, Leibold 1989, Osenberg and Mittelbach 1989). The elimination of bluegill is predicted to affect adult pumpkinseeds and snails due to an indirect effect mediated through enhanced recruitment of juvenile pumpkinseed into the adult stage.

cific juvenile competition on adult pumpkinseed and their snail resource. We compared pumpkinseeds and snails in lakes where bluegill and pumpkinseed have coexisted for many years, with those in Wintergreen Lake, a lake in which pumpkinseed have existed without bluegill since the late 1970s. Using historical data from Wintergreen as well as the contemporary comparisons between Wintergreen and nearby lakes with bluegill, we show that, as predicted by the model, Wintergreen Lake now has a very abundant pumpkinseed population, a depauperate snail fauna, adult pumpkinseeds that grow poorly, and juveniles that grow quickly. We also show that the high density of pumpkinseeds currently found in Wintergreen Lake contributes to the low snail density, and we document additional consequences to adult pumpkinseeds, including altered diet, morphology, and feeding ability that arise due to the low density of snails in Wintergreen Lake. Finally, we compare several alternative hypotheses with our working hypothesis that the absence of the pumpkinseed's juvenile stage competitor (bluegill) in Wintergreen Lake led to the strong responses observed in the snail and pumpkinseed populations.

METHODS

The system

The pumpkinseed sunfish is widely distributed across the northeastern United States and southern Canada. It possesses highly modified pharyngeal jaws, enlarged molariform teeth, and a novel neuromuscular design, which are used to efficiently crush the shells of gastropods (Lauder 1986, Wainwright et al. 1991). Once crushed, the shell is separated from the body and ejected from the mouth, and the soft body is then swallowed (Lauder 1983a, b, Mittelbach 1984). Most other centrarchids, such as bluegill, lack these morphological adaptations and are typically unable to crush snails

(Wainwright and Lauder, *in press*). Although pumpkinseeds show considerable morphological and neuromuscular specializations for feeding on snails, they remain flexible in their diet and habitat choice, which may change in response to resource levels and the presence/absence of competitors (Werner and Hall 1976, 1979).

Gastropods commonly make up a large fraction of the adult pumpkinseed's diet (often >70% by mass; Sadzikowski and Wallace 1976, Keast 1978, Mittelbach 1984, Osenberg and Mittelbach 1989, Fox and Keast 1991). Small pumpkinseeds, which are unable to efficiently crush snails, typically feed on insect larvae, amphipods, and other littoral-zone invertebrates. Thus, in lakes where snails are common, pumpkinseeds show a pronounced niche shift during their ontogeny. Little is known about the feeding ecology of pumpkinseeds in lakes where snails are rare.

We studied pumpkinseeds and snails in three small (15–22 ha) hardwater lakes, located within 6 km of each other in southwestern Michigan (Kalamazoo County). Two of these lakes, Three Lakes II and Three Lakes III, have bluegill, pumpkinseed, and snail densities that are typical of other lakes in the region (Mittelbach 1984, Osenberg 1988, Osenberg et al. 1988). The third lake, Wintergreen Lake, is unique in that it experienced selective fish kills in 1977 and 1978, due to heavy snow cover and low oxygen concentrations. Three Lakes II and III did not winterkill due to the greater depth of Three Lakes II and the presence of two inlet and one outlet streams in Three Lakes III that provide a refuge from low oxygen conditions (Tonn and Magnuson 1982). The winterkills in Wintergreen Lake eliminated the pumpkinseed's main competitor, bluegill, and one of its major predators, the largemouth bass (*Micropterus salmoides*) (Hall and Ehlinger 1989). Pumpkinseeds, which are better able to tolerate low oxygen levels, came through the winterkill with only minor losses. Unlike most winterkill situations, bluegill have not recolonized Wintergreen because the only potential source of immigrants, a modified drainage creek to Gull Lake, currently prevents immigration by fish. Largemouth bass were reintroduced in 1986.

Pumpkinseed and snail density

Pumpkinseed densities were estimated by seining the littoral habitats in Wintergreen Lake, Three Lakes II, and Three Lakes III. In each lake, two seine sizes were used (a 23 × 1.8 m bag seine with 0.32-mm mesh and a 61 × 2.5 m bag seine with 0.64-mm mesh), and pumpkinseed numbers per seine haul were converted to numbers per unit area of littoral zone by dividing by the total area encircled by the seine. For a subset of the collections in Wintergreen Lake, we also measured the size of each pumpkinseed captured. We operationally defined juveniles and adults based on the approximate midpoint at which the diet shift occurs (see *Results: Pumpkinseed diets and growth patterns*),

i.e., juveniles were ≤60 mm SL, and adults were >60 mm SL.

All collections were made between May and September, with most taken from June–August when fish densities in littoral habitats are relatively constant (Hall and Werner 1977). Most estimates of fish densities were from 1988 to 1990, although a few samples were available from other years (1981–1986). Sampling was distributed similarly across years and seasons for each lake, and data inspection revealed little, if any, variation among years or months. Therefore, we treated each collection as a replicate and used analysis of variance to compare densities among lakes. Fish densities were square root transformed to homogenize variances (Sokal and Rohlf 1969). In these and all similar tests where data were available from Wintergreen Lake and Three Lakes II and III, we decomposed the lake effect into two orthogonal a priori contrasts: we compared Wintergreen Lake with the combined response of Three Lakes II and III and we compared Three Lakes II with Three Lakes III.

Snails were sampled in each of the three study lakes by sweep-netting the littoral-zone vegetation at 4 times; August 1988, May 1989, July 1989, and August 1989. Lakes were sampled within 10 d of each other during each sampling period. During each period, eight samples were typically taken from each lake from locations chosen haphazardly along the entire lake perimeter. Each sample was taken at a depth of 0.5–2.0 m by pushing a sweep net (basal width = 30 cm; mesh = 0.42 mm) through ≈0.5 m of vegetation and then rinsing the contents of the net into a bucket. Live snails were sorted from the vegetation in the laboratory, preserved in 10% neutral formalin, and later counted. Statistical comparisons were made among lakes by conducting a repeated-measures analysis of variance with a priori contrasts. Snail densities were square root transformed to homogenize variances (Sokal and Rohlf 1969).

Because the lakes differ in their littoral-zone vegetation (Three Lakes II is dominated by *Chara*, Wintergreen is dominated by *Ceratophyllum*, and Three Lakes III contains a diverse macrophyte community including both *Chara* and *Ceratophyllum*), it is possible that the differences in snail densities observed among lakes are primarily due to differences in vegetational composition. To examine this, we took eight snail samples from only *Ceratophyllum* in both Wintergreen Lake and Three Lakes III on 23 May 1989. These samples were collected and treated as above.

Pumpkinseed growth rates

Growth rates for pumpkinseeds inhabiting each of the three study lakes were determined by back-calculation from measurements of scale annuli using the Fraser-Lee method (Tesch 1968, Osenberg et al. 1988). Pumpkinseeds were collected from Wintergreen Lake on 6 July and 12 August 1988. Scales were removed

just posterior to the tip of a depressed pectoral fin from nonpreserved fish. Scale impressions were made on cellulose acetate strips, images were projected with a microfiche viewer, and distances from the focus to each annulus and the scale margin were measured. Only nonregenerated scales were used for analysis and only one scale was used per fish. Because length–mass relationships do not differ among the lake populations (C. W. Osenberg et al., unpublished data), back-calculated lengths were converted to wet masses by using a single length–mass regression (given in Osenberg et al. 1988). Annual growth rates were expressed as the change in mass accrued over a year's growth. Pumpkinseed growth rates in Three Lakes II and Three Lakes III were available from a previous study that used methods identical to those described above (Osenberg et al. 1988).

Factors causing low snail densities in Wintergreen Lake

To test the hypothesis that the observed high pumpkinseed densities in Wintergreen Lake were responsible for the low snail abundances, we conducted a pumpkinseed enclosure/exclosure experiment. The experiment was conducted in 12 3-m² (1.7 × 1.7 m) cages placed in the littoral zone of Wintergreen Lake on 23 May 1989. Cages were constructed of wood frames and enclosed on four sides by 1.0-mm mesh nylon netting buried in the sediment. Vegetation cover was continuous over the cage bottoms and was composed almost entirely of *Ceratophyllum*, the dominant macrophyte in the lake. After installing the cages, we removed resident fish by seining each cage with a net constructed of 0.6-cm mesh seine material attached to a 1.5 × 1.7 m frame, which fit snugly inside a cage. We seined each cage repeatedly until no fish were captured. Fish that were small enough to fit through the seine were removed using minnow traps, which are very effective on small pumpkinseed. No fish were subsequently seen or captured in cages intended to have no fish in them. On average, we captured 5.7 ± 1.2 pumpkinseeds per cage (mean \pm 1 SE), which was very close to our estimate of pumpkinseed density in the lake based on independent seine samples (1.89 pumpkinseeds/m² in the cages vs. 1.77 pumpkinseeds/m² seining).

The experimental design was a 2 × 2 factorial, with pumpkinseed presence/absence crossed with snail addition. Each of the four treatments: fish, no fish, fish + snail addition, and no fish + snail addition, was assigned at random to three replicate cages. We incorporated the snail addition into our design to increase our power to detect an effect of pumpkinseeds, if in fact an effect was present (i.e., over the short time scale of the experiment, limited numerical responses by the few snails initially present in the cages might have limited our power). Five common snail taxa were collected from local lakes and stocked into the snail-addition cages on 26 May 1989 at the following densities

(number/cage): 400 *Amnicola limosa*, 300 *Valvata tricarinata*, 100 *Physa* sp., 50 *Gyraulus* sp., 38 *Helisoma anceps*, and 30 *Marstonia lustrica*. Each species reproduced soon after being added to the cages. Four pumpkinseeds were added to the fish cages on 30 May 1989 (a density equal to 1.33 fish/m²). Because the pumpkinseed population was dominated by the first two age classes, we added two fish from the peak of each distribution (50 mm and 80 mm SL).

Cages were sampled midway through the experiment (22 June) and at the end of the experiment (12 July). On each occasion we collected two types of samples. We sampled the vegetation by lowering a sweep net (basal width = 30 cm, mesh = 0.42 mm) to the base of the vegetation and pushing the sweep net through \approx 0.5 m of vegetation. Contents of the net were put into a bucket, and vegetation was rinsed and returned to the cage. Two sweeps were pooled per cage in June, while in July we collected three sweeps per cage. Three similar samples (each consisting of two or three sweeps) were taken from vegetation outside the cages. We sampled snails on the cage netting by vertically sweeping the inner sides of a cage with a small aquarium net (basal width = 18 cm, mesh < 0.5 mm). Three sweeps were taken and pooled per cage. Three samples (each consisting of three vertical sweeps) were also taken from the outer sides of three cages. In June, live snails from each sample were rinsed through a 0.5-mm sieve, counted, and returned to the cages. In July, snails were rinsed through a 0.5-mm sieve, preserved in 10% neutral formalin, and later counted.

We analyzed snail densities in two ways. First, we analyzed numbers collected in the sweep and side samples separately. Second, for clarity of presentation and to better represent the total response of snails, we estimated snail density (number per cage) by summing the estimated number of snails on the vegetation and netting (based on number of snails collected per sample and the fraction of each habitat sampled).

Pumpkinseed diets

Pumpkinseeds from Wintergreen Lake were collected for diet analyses on four dates: 6 July 1988, 23 August 1988, 9 May 1989, and 24 July 1989. Fish were seined during the morning, put on ice, and preserved in 10% buffered formaldehyde. Pumpkinseeds were also collected from Three Lakes II on 21 and 23 June 1988. This collection, together with the large number of pumpkinseeds (>200 fish) previously collected from Three Lakes II (Mittelbach 1984, Osenberg and Mittelbach 1989), enabled us to examine the temporal consistency of the dietary pattern in this lake. Pumpkinseed diets in Three Lakes III were available from Mittelbach (1984).

Stomach contents were identified, counted, and measured under a dissecting microscope. Nongastropod prey were identified to family or genus, and linear measurements were converted to dry mass using previously

determined length–mass regressions. Gastropods were identified to the lowest possible taxonomic level, typically genus. The shell-crushing behavior of pumpkinseeds required that we determine snail sizes by methods other than shell measurements. For prosobranch snails, we counted and measured opercula because they are swallowed intact and are not digested. For pulmonate snails (which lack opercula), the length of the foot was measured. The foot has greater integrity than other soft parts of a snail and could be clearly identified and measured in the stomach samples. Both opercular diameters and foot lengths were converted to dry mass for each snail taxa using length–mass regressions, and pumpkinseed diets were expressed as proportion of dry mass by prey type. Data were arcsine square root transformed for analysis.

Pumpkinseed feeding ability

In conjunction with dietary analyses of fish collected from Wintergreen and Three Lakes II in June and July 1988, we also performed detailed analyses of pumpkinseed pharyngeal jaw morphology (see Wainwright et al. 1991). Our analyses showed that pharyngeal muscles and bones used to crush snails were significantly larger in fish from Three Lakes II, while muscles and bones not used in snail crushing showed no difference between the two lakes (Wainwright et al. 1991). For example, the main crushing muscle, the levator posterior, was more than twice as massive in the Three Lakes fish as in Wintergreen fish and was calculated to generate slightly more than twice the crushing force in fish from Three Lakes as compared to similar-sized fish from Wintergreen (Wainwright et al. 1991).

Thus, we examined the feeding performance of fish from the two populations to make the important link between variation in snail density, diet, and morphology, and the ability of pumpkinseeds to crush and handle snails. Eight pumpkinseeds (64–110 mm SL) were collected from Wintergreen Lake and 12 pumpkinseeds (49–125 mm SL) were collected from Three Lakes II in August 1988. Fish were housed separately in laboratory aquaria and were fed a diet of earthworms for ≈ 1 wk before starting the feeding trials. Two types of snails were used as prey: *Physa* spp., a relatively thin-shelled pulmonate and *Amnicola limosa*, a thicker shelled prosobranch. Both types of snails are common in the lakes and in the diets of pumpkinseeds collected from those lakes (Osenberg and Mittelbach 1989), with the exception of Wintergreen Lake. *Physa* were collected from Gull Lake (a lake near the study lakes), *Amnicola* were collected from Three Lakes II, and each species was sorted to size by rinsing through a series of sieves. Two size classes of *Physa* and one size of *Amnicola* were used. Snails were offered individually to fish and for each snail that was eaten, we recorded the time required to crush the snail (crushing time) and the total time required to crush and consume the snail (handling time). Crushing and handling time started

when the snail was first drawn into the mouth, and ended either when the shell was first crushed (crushing time) or when the fish oriented to receive another snail after having ejected the shell fragment and swallowed the snail (handling time). Crushing times were easily determined as snail shells make a distinctive “tinkling” sound when crushed by pumpkinseeds, corresponding to the time of first shell failure (Lauder 1986). For each group of snails, we also measured the crushing resistance (the amount of force required to crush a shell) for a random subset of snails using methods described in Osenberg and Mittelbach (1989).

We conducted a second set of feeding experiments using six pumpkinseeds (97–115 mm SL) from Wintergreen Lake and six pumpkinseeds (84–112 mm SL) from Three Lakes II. Fish were collected in June 1989. Methods employed in these experiments were identical to those described above. Four different prey types were used in these experiments: two snail species, *Physa* (collected from a pond at the Experimental Pond Facility at Kellogg Biological Station), and *Helisoma anceps* (collected from Gull Lake), plus two soft-bodied prey: damselfly nymphs (*Enallagma*) and mealworm larvae (*Tenebrio*).

For each fish we determined its mean handling time and crushing time (for each prey type) and used these means as replicates in our analyses. Data for each prey type were analyzed by ANCOVA, using lake as the grouping variable and fish standard length as the covariate. We initially used a full model in which separate slopes were fit to each of the treatment groups (i.e., lakes). If the analysis showed no heterogeneity of slopes, we ran the ANCOVA again assuming homogeneous slopes for the two lake groups (and tested again for effects of lake and fish size).

RESULTS

Pumpkinseed and snail density

Pumpkinseed density in Wintergreen Lake was about an order of magnitude greater than densities in Three Lakes II and Three Lakes III (Table 1). A priori contrasts revealed a significant difference between Wintergreen and Three Lakes II and III ($F_{1,88} = 132.2$, $P < .0001$), whereas Three Lakes II and Three Lakes III did not differ ($F_{1,88} = 0.95$, $P > .3$). Hereafter, we indicate the results of these planned contrasts in the form “Wintergreen > (Three Lakes II = Three Lakes III).” Although we have no data on the stage structure of the pumpkinseed populations in Three Lakes II and III, the density of either juvenile or adult pumpkinseeds in Wintergreen Lake was greater than the total density of pumpkinseeds (juveniles plus adults) in Three Lakes II and III (Table 1: $F_{1,66} = 18.6$, $P < .0001$ for juveniles, and $F_{1,66} = 110.8$, $P < .0001$ for adults). Further, pumpkinseed densities in Three Lakes II and III are very similar to those in other nearby lakes containing bluegill (C. W. Osenberg and G. G. Mittelbach, *personal observations*).

TABLE 1. Pumpkinseed and bluegill densities (based on area seined and expressed per unit area of littoral zone) in the three study lakes. Fish ≤ 60 mm SL were designated juveniles, whereas larger fish were designated adults. Separate estimates of juvenile and adult pumpkinseed densities were only available for Wintergreen Lake. n = sample size.

Lake	Pumpkinseed density (no./m ²)			Juvenile bluegill density	
	$\bar{X} \pm 1$ SE	n	Age class	$\bar{X} \pm 1$ SE	n
Without bluegill					
Wintergreen	1.77 \pm 0.26	43	Total	0	43
	1.10 \pm 0.24	21	Adults		
	0.32 \pm 0.08	21	Juveniles		
With bluegill					
Three Lakes II	0.10 \pm 0.03	16	Total	0.52 \pm 0.18	10
Three Lakes III	0.04 \pm 0.01	32	Total	0.13 \pm 0.03	22

Wintergreen Lake also had a depauperate snail fauna, averaging only 10% of the densities in Three Lakes II and III (Fig. 2). A repeated-measures analysis of variance with planned contrasts shows that snails were less abundant in Wintergreen than in Three Lakes II and III ($F_{1,6} = 27.4$, $P < .002$), whereas Three Lakes II and Three Lakes III did not differ ($F_{1,6} = 2.28$, $P > .10$): the effects of sampling date ($F_{3,82} = 5.97$, $P < .01$) and the lake \times sampling date interaction ($F_{6,82} = 2.90$, $P < .05$) were also significant.

The low density of snails in Wintergreen was not simply due to *Ceratophyllum* being the dominant macrophyte in that lake. Samples from *Ceratophyllum* taken in both Wintergreen and Three Lakes III in May 1989 showed that snail densities from the same substrate were also different between the lakes: in Three Lakes III densities were 91.3 ± 21.9 snails/sweep while densities in Wintergreen were 0.3 ± 0.2 snails/sweep (mean \pm SE: $F_{1,14} = 17.2$, $P = .001$, based on square root transformed data). Within Three Lakes III, the snail densities on *Ceratophyllum* were also significantly greater than from macrophytes sampled haphazardly around the lake (31.4 ± 5.4 snails/sweep, $F_{1,14} = 7.04$, $P < .05$, based on square root transformed data), demonstrating that *Ceratophyllum* was a suitable substrate for snails.

Pumpkinseed growth rates

In Wintergreen Lake pumpkinseeds exhibited a very different growth pattern than in Three Lakes II or III (Fig. 3). Juvenile pumpkinseeds inhabiting Wintergreen Lake grew considerably faster than did juveniles inhabiting Three Lakes II and III, whereas adult pumpkinseeds in Wintergreen grew more slowly. This response is consistent with the prediction that removal of bluegill should positively affect juvenile pumpkinseeds but negatively affect adult pumpkinseeds. Accordingly, the slopes of the relationship between annual growth rate and pumpkinseed size at the start of the growing season (shown in Fig. 3) differed significantly among lakes (test for heterogeneity of slopes based on regressions of $\log(\text{annual growth})$ on pumpkinseed size, SL: $F_{2,726} = 337.8$, $P < .0001$). Moreover, there was close correspondence between the size at which the

growth patterns cross, and the size at which pumpkinseeds shift from feeding on soft-bodied prey to feeding on snails. We discuss the correspondence between size-specific growth and diet patterns in detail in *Results: Pumpkinseed diets and growth patterns*.

Factors causing low snail densities in Wintergreen Lake

Our earlier work has shown that pumpkinseeds can have a significant impact on snail abundances in small Michigan lakes (Osenberg 1988). However, this impact is relatively minor at pumpkinseed densities typical of most local lakes ($<0.1/\text{m}^2$; see Table 1 and Osenberg 1988). Pumpkinseed density in Wintergreen Lake, however, is about an order of magnitude greater than the density in Three Lakes II, Three Lakes III, or other lakes we have studied, and our caging experiment in Wintergreen Lake shows that snail density responded strongly to the removal of pumpkinseeds.

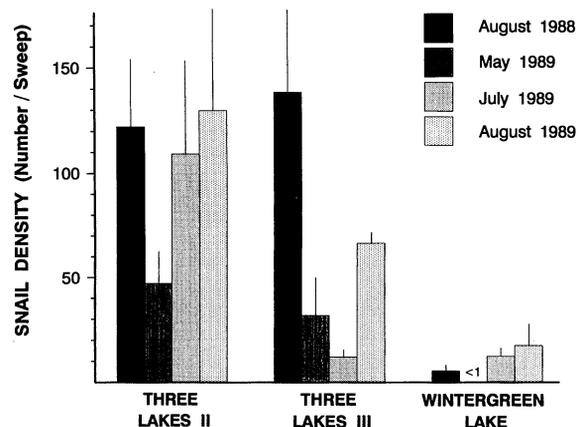


FIG. 2. Snail density in the three study lakes on four different sampling dates. Shown are means and 1 SE (number/sweep sample): $n = 8$ sweeps, except for the August 1988 samples in Three Lakes III and Wintergreen Lake where $n = 3$ and $n = 11$, respectively. Snail densities for each sampling period were lower in Wintergreen than in Three Lakes II and III (planned contrasts, $P < .05$ for each of the four dates), whereas Three Lakes II and III differed on only one of the four dates (July 1989).

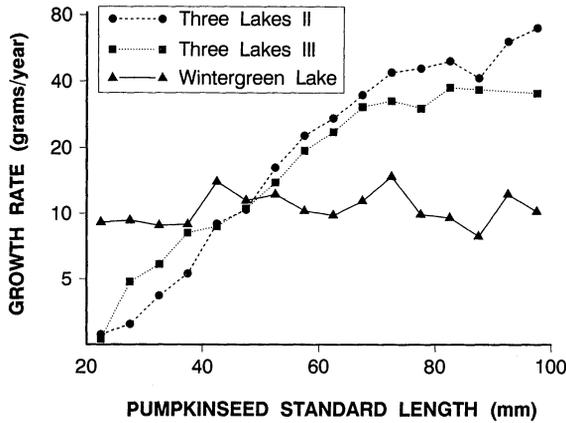


FIG. 3. Size-specific growth rates for pumpkinseeds collected from Three Lakes II and III, lakes where diets of large pumpkinseeds consist mainly of snails, and Wintergreen Lake, where snails are rare in the diets of pumpkinseeds. Means for 5-mm size classes were calculated and are plotted on a logarithmic scale to highlight the relative variation among lakes at all sizes. For clarity, standard errors for each size class are omitted but averaged 19.3% (Three Lakes II), 13.0% (Three Lakes III), and 6.3% (Wintergreen) of the given means. Total sample sizes were 527, 113, and 98 in Three Lakes II, Three Lakes III, and Wintergreen Lake, respectively.

Snail densities in June and July were ≈ 4 times greater in the cages without fish relative to the cages with fish (Fig. 4). Analyses of variance on the original estimates of snail numbers on vegetation and on cage sides show significant fish effects on snail density in June for the side samples ($F_{1,8} = 13.98, P < .01$), but only a marginal difference for the sweep samples ($F_{1,8} = 3.05, P = .12$), and a significant effect in July for both types of samples ($F_{1,8} > 5.5, P < .05$ for each test). In no case were there effects due to snail addition or an interaction between the two treatments ($P > .4$ for each test). Moreover, snail numbers in both sample types did not differ between cages with pumpkinseeds and samples taken from just outside the cages in either June or July (comparison of the fish/no snail addition treatment with the nearby lake area, $P > .40$ for each date and sample type). Thus, for the early- to midsummer period covered by this experiment, pumpkinseeds were capable of maintaining snail densities at levels observed in Wintergreen Lake.

Pumpkinseed diets and growth patterns

Pumpkinseeds in Three Lakes II and III showed a pronounced shift in diet with ontogeny (Fig. 5). Fish smaller than ≈ 45 mm SL had few snails in their guts and were instead feeding on soft-bodied invertebrates (e.g., *Hyalella*, Chironomidae, Caenidae, and Trichoptera). Between 45 and 75 mm SL there was a dramatic increase in the percentage of snails eaten, with pumpkinseeds > 75 mm feeding predominantly on gastropods. Frequency of snails in the diets of pumpkinseeds

collected from Three Lakes II varied only slightly in four different years: $78 \pm 11\%$ in 1988, $95 \pm 2\%$ in 1985, $92 \pm 5\%$ in 1984, and $64 \pm 9\%$ in 1981 (mean ± 1 se). Other studies of pumpkinseed diets in upper midwestern lakes show patterns similar to those exhibited by the Three Lakes fish (Seaburg and Moyle 1964, Sadzikowski and Wallace 1976, Fox and Keast 1991). Diets of Wintergreen pumpkinseeds contrasted strongly with this pattern. Even at large sizes, Wintergreen pumpkinseeds ate few snails, typically $< 3\%$ (Fig. 5). Note that while each pumpkinseed consumed relatively few snails in Wintergreen Lake, the cage experiment demonstrated that the total pumpkinseed population strongly reduced snail density (Fig. 4).

There is good correspondence between the size at which pumpkinseeds began feeding on snails in Three Lakes II and III (≈ 45 mm SL, Fig. 5) and the size at

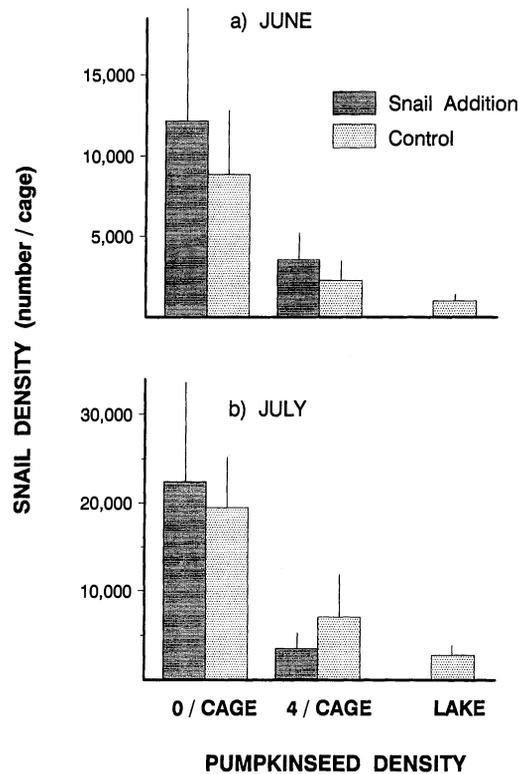


FIG. 4. Snail densities in the pumpkinseed inclusion/exclusion experiment and in adjacent areas of Wintergreen Lake on two sampling dates, 22 June (top panel) and 12 July (bottom panel). Snail densities are number per 3-m² cage or equivalent area (means and 1 se); $n = 3$ cages (or equivalent area) for each group. Analysis of variance for the experimental treatments (based on square root transformed data) shows a marginally significant fish effect on snail density in June ($F_{1,8} = 3.66, P < .10$) and a significant effect in July ($F_{1,8} = 6.82, P < .05$), but no effect of snail addition and no interaction between the two treatments on either date ($P > .50$ for each test). Snail densities in the fish/no snail addition treatment are not different from densities in adjacent lake areas in either June or July (ANOVA, $P > .40$ for each date).

which their growth began to exceed that observed in Wintergreen (Fig. 3). Note that unlike Fig. 5, pumpkinseed size in Fig. 3 is expressed as the size at the start of the growing season (before growth accrues). Pumpkinseeds that were 45 mm in the spring would be expected to reach ≈ 70 mm SL by the end of the summer in Three Lakes II and III and should therefore have fed extensively on snails during much of the year.

For fish that started the year at sufficiently small sizes that they should have rarely fed on snails during their annual growth period (i.e., they started the year at < 30 mm SL), the growth in Wintergreen was more than twice as great as in Three Lakes III and II (9.2 ± 1.8 , 4.6 ± 0.3 , and 3.0 ± 0.1 g/yr, respectively [means ± 1 SE]; planned contrasts based on log-transformed data: Wintergreen $>$ [Three Lakes III $>$ Three Lakes II]). In contrast, for fish that began the year at a size where most of their diet was composed of snails (i.e., they started the year at ≥ 75 mm SL), Wintergreen fish grew substantially slower than did pumpkinseeds in Three Lakes III and II (9.6 ± 0.6 , 34.7 ± 2.6 and 46.5 ± 2.5 g/yr, respectively; planned contrasts based on log-transformed data: Wintergreen $<$ [Three Lakes III $<$ Three Lakes II]).

It thus appears that the low abundance of snails in Wintergreen Lake caused a severe growth reduction in adults. This interpretation is supported by the fact that the total biomass of prey in the stomachs of pumpkinseeds ≥ 75 mm SL was also less in Wintergreen Lake than in either Three Lakes II or III (based on analysis of covariance with a priori contrasts using log[biomass in stomach] as the response variable, lakes as the grouping variable, and log[fish size, SL] as the covariate). The back-transformed adjusted mean prey biomasses (\bar{X} and $[\bar{X} \pm 1$ SE]) were: Wintergreen (3.14 [2.50–3.96] mg) $<$ (Three Lakes III (7.59 [6.11–9.43] mg) $<$ Three Lakes II (14.64 [12.98–16.50] mg)). (Because the SE limits were not symmetrical around the mean after back transformation, we have presented the range of values obtained after calculating the back-transformed $\bar{X} + 1$ SE and $\bar{X} - 1$ SE.) Thus, in Wintergreen Lake, where snails were rare (both in the environment and in pumpkinseed diets), adult pumpkinseed grew slower and their stomachs contained less total prey, which suggests that their feeding rates were lower than in lakes with abundant snails.

Pumpkinseed feeding ability

Pumpkinseeds from Three Lakes II and Wintergreen Lake, which exhibit strong divergence in pharyngeal jaw morphology (Wainwright et al. 1991), also show distinct differences in their abilities to crush and handle snails, especially for stronger shelled taxa (Fig. 6). Analyses of covariance (Table 2) show a highly significant lake effect on the times required to crush and handle *Ammnicola*, the hardest shelled species. Crushing and handling times for pumpkinseeds feeding on *Ammnicola* were ≈ 3 times longer for fish from Wintergreen than

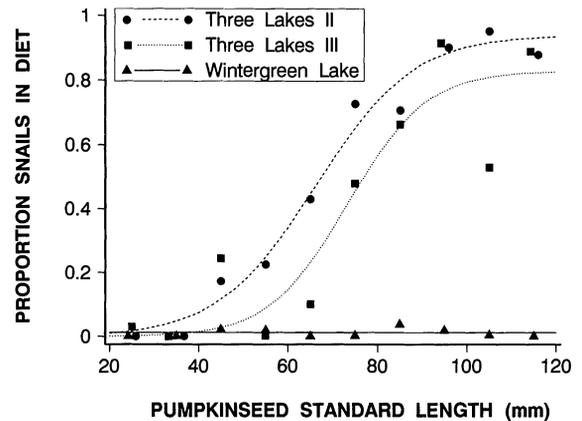


FIG. 5. Pumpkinseed diets, expressed as percent of dry mass composed by snails, in Three Lakes II and III, which have typical snail densities, and Wintergreen Lake, which has very low snail densities. Means for 10-mm size classes are shown, and standard errors (not shown) averaged 0.05 (Three Lakes II), 0.11 (Three Lakes III), and 0.01 (Wintergreen). Logistic curves were fit to the complete data set (using individual fish) using nonlinear regression: percent snails = $Y_{\max}/[1 + \exp(a + b \cdot \text{SL})]$, where Y_{\max} , a , and b are the constants fit by regression. Fitted regressions are shown for Three Lakes II ($Y_{\max} = 91.5$, $a = 6.877$, $b = -0.105$) and Three Lakes III ($Y_{\max} = 84.7$, $a = 5.399$, $b = -0.0748$), but because there was no significant effect of fish size for Wintergreen, only the overall mean is shown (0.01). Numbers of fish sampled were 193, 43, and 82 in Three Lakes II, Three Lakes III, and Wintergreen Lake, respectively.

for fish from Three Lakes II (5.5 ± 1.8 vs. 1.9 ± 0.1 s for crushing time, and 23.6 ± 1.8 vs. 8.5 ± 0.9 s for handling time [means ± 1 SE]; see also Fig. 6a). For snails of intermediate crushing resistances, *Physa* from 1988 and *Helisoma* from 1989, pumpkinseed populations had significantly different slopes for the relationship between handling time (or crushing time) and fish length in two of the three comparisons (Table 2). In each case, the slope for fish from Wintergreen was steeper and more negative than for fish from Three Lakes II, with handling and crushing times being most different between the lake groups at the smallest fish sizes. Although slopes were heterogeneous, feeding abilities only converged at larger fish sizes (e.g., Fig. 6b): there was never an indication that fish from Wintergreen outperformed fish from Three Lakes. For the most easily crushed snail (*Physa* in 1989) and for the soft-bodied damselfies and mealworms, feeding performance did not differ between Wintergreen and Three Lakes fish (Table 2 and Fig. 6c). Thus, the more robust pharyngeal jaws of pumpkinseeds from snail-rich Three Lakes II relative to snail-poor Wintergreen Lake (Wainwright et al. 1991) were associated with an increased efficiency at crushing and handling hard-shelled species. This enhanced feeding ability did not appear to come at a cost of reduced efficiency when feeding on soft-bodied prey.

TABLE 2. Results of analysis of covariance on times required by pumpkinseeds from Wintergreen and Three Lakes II to crush and handle seven different prey types. Sizes and crushing resistances are reported as means \pm 1 SE. Prey types are ranked by their crushing resistances.

Prey	Year	Prey size (mm)†	Prey crushing resistance (N)	ANCOVA results					
				Prey handling time			Prey crushing time		
				Fish SL	Lake	Lake \times fish SL	Fish SL	Lake	Lake \times fish SL
<i>Ammnicola</i>	1988	3.1 \pm 0.1	10.1 \pm 0.6	NS	***	NS	NS	**	NS
<i>Physa</i> (small)	1988	4.8 \pm 0.1	6.1 \pm 0.6	***	**	*	***	***	***
<i>Physa</i> (large)	1988	8.1 \pm 0.1	6.0 \pm 0.8	*	NS	NS	**	**	**
<i>Helisoma</i>	1989	6.1 \pm 0.1	4.5 \pm 0.4	**	*	*	**	NS	NS
<i>Physa</i>	1989	9.1 \pm 0.2	2.7 \pm 0.3	***	NS	NS	***	NS	NS
Damselfly nymphs	1989	18.0 \pm 0.5	NA	NS	NS	NS	NA	NA	NA
Mealworm larvae	1989	19.8 \pm 0.5	NA	NS	NS	NS	NA	NA	NA

† Size refers to shell height for *Ammnicola* and *Physa*, shell diameter for *Helisoma*, and body length for damselflies and mealworms.

*** = $P < .001$; ** = $P < .01$; * = $P < .05$; NS = $P > .05$; NA = not applicable to prey type.

Historical comparisons within Wintergreen Lake

While the contemporary comparisons between Wintergreen and Three Lakes II and III are compelling, these analyses do not control for differences between Wintergreen and Three Lakes II and III that may be correlated with, but not caused by, the absence of bluegill and/or the low density of snails. Therefore, we also compared our postwinterkill data with data from Wintergreen Lake that were collected before the winterkills of 1977 and 1978 when bluegill were the dominant fish in Wintergreen.

Prior to these winterkills, bluegill was the most abundant fish species in Wintergreen Lake, outnumbering pumpkinseeds by 4 to 1 (Cooper 1935, Fetterolf 1952, Hall and Ehlinger 1989). This ratio of bluegill to pumpkinseed abundances is within the range observed in Three Lakes II and III (Mittelbach 1984). The data also show that pumpkinseed densities before winterkill were only 25–50% of their densities today (Cooper 1935, Fetterolf 1952, Hall and Ehlinger 1989).

Although there are no historical data on snail densities, snails did occur more frequently in pumpkinseed diets before the winterkill: 90 and 58% of the pumpkinseeds collected in 1935 and 1936 had fed on snails (Funk 1942), whereas only 9 and 10% of the pumpkinseeds we collected in 1988 and 1989 had eaten snails. Similarly, molluscs comprised an average of 62 and 32% of the diet (by volume) of pumpkinseed collected in 1936 and 1937, but <2% (by dry mass) in 1988 and 1989.

To examine how the growth of small and large pumpkinseeds has changed, we compared data from Cooper (1935), which gives size-at-age data for fish collected in May 1935, with our own collections made in May 1988. One-year-old pumpkinseeds collected in 1988 were twice as large as the same age pumpkinseeds collected in 1935 (4.4 \pm 0.2 vs. 2.2 g, respectively; means \pm 1 SE, $n = 82$ in 1988 and $n = 48$ in 1935). Older fish, however, grew much more slowly following the winterkill than before the winterkill: 4- and 5-yr-old

pumpkinseeds used to reach 204 and 229 g, but they now reach only 50.7 \pm 1.9 and 58.2 \pm 2.9 g ($n = 19$ and 16 in 1935, $n = 4$ and 7 in 1988).

While a more complete time series of quantitative data are not available from before 1977, unpublished data and qualitative monitoring of Wintergreen Lake from 1960s through the 1980s also suggest that pumpkinseed density has increased and average adult size has decreased substantially following the winterkill (W. C. Johnson, Resident Biologist at Wintergreen Lake, *personal communication*). Thus, both the among-lake comparisons and available historical data suggest that since the winterkill in Wintergreen Lake, pumpkinseed abundances have increased, snail abundances have decreased, and growth rates of small pumpkinseeds have increased while growth rates of large pumpkinseeds have decreased.

DISCUSSION

Stage structure in sunfish populations

Because juvenile bluegill and pumpkinseed compete for littoral prey (Mittelbach 1988), we predicted that the elimination of bluegill from Wintergreen Lake would have important effects on the pumpkinseed population and its adult resource, snails. Among these predicted effects were an increase in pumpkinseed density, a decrease in snail density, a decrease in growth of adult pumpkinseeds, but an increase in growth of juveniles. The observed responses of snails and pumpkinseeds in Wintergreen are consistent with these predictions.

The essential feature of the system that drives the above predictions is the two-stage life history of the pumpkinseed. Due to the population's stage structure, any net benefit accrued by one life stage must be balanced by a corresponding decrease in the performance (e.g., growth) of the other life stage (Mittelbach and Chesson 1987, Mittelbach et al. 1988, Osenberg et al. 1988). In this particular case, where bluegill winterkill increased the share of littoral production that was available to juvenile pumpkinseeds, the advantage de-

rived by juveniles was balanced by decreased adult performance. Thus, the benefit to juveniles had indirect negative consequences on the adult life history stage and was mediated by an increase in pumpkinseed density and a subsequent decline in snail availability.

These results complement our previous research in which we compared the density and growth patterns of bluegill and pumpkinseed across a series of lakes in which both species coexist (Mittelbach et al. 1988, Osenberg et al. 1988). We found that in lakes with high bluegill densities, juvenile bluegill and pumpkinseed growth rates were low, but adult bluegill growth rates were high. Using the stage-structured model, we determined that much of this observed variation could be explained if lakes varied in the production of the adult bluegill's resource, zooplankton. Thus, in lakes with bluegill, it appeared that increased production of zooplankton caused increased growth and reproduction of adult bluegill, and that this increased input of bluegill larvae into the littoral zone increased competition among juvenile bluegill and pumpkinseed. This indirect effect between zooplankton and juvenile pumpkinseed (mediated through the bluegill life history) was also predicted to cascade to adult pumpkinseeds and their resource, snails. Whereas adult pumpkinseed growth was positively correlated with juvenile bluegill density (Mittelbach et al. 1988, Osenberg et al. 1988), the correlation was weak, probably due to a diminution of the signal (i.e., zooplankton productivity) as it was transmitted through the system (Carpenter 1988a; Fig. 1) and to the relatively low variation in bluegill density among the lakes. On the other hand, the complete removal of bluegill in Wintergreen Lake created a much stronger signal that required fewer steps before impacting adult pumpkinseeds.

*Consequences of low snail density in
Wintergreen Lake on adult
pumpkinseeds*

In addition to the effects discussed above, which were predicted by the stage-structured model, bluegill removal had other effects on adult pumpkinseed that were not explicit in the model. The most fundamental of these was the effect of low snail abundances on pumpkinseed dietary patterns: pumpkinseeds in Wintergreen Lake did not exhibit the typical ontogenetic diet shift to snails. Instead, fish of all sizes fed mostly on soft-bodied littoral invertebrates. As a result of the low density of their preferred prey resource (snails), adult pumpkinseeds incurred a considerable depression in the total prey biomass in their diets, and this appears to have caused the exceptionally low growth rate of adult pumpkinseeds in Wintergreen Lake. The rarity of snails in the diets of fish from Wintergreen Lake also appears to have caused a decrease in the mass of muscles and bones used to crush snails (Wainwright et al. 1991). This interpretation is strengthened by a comparative study we conducted in six lakes in

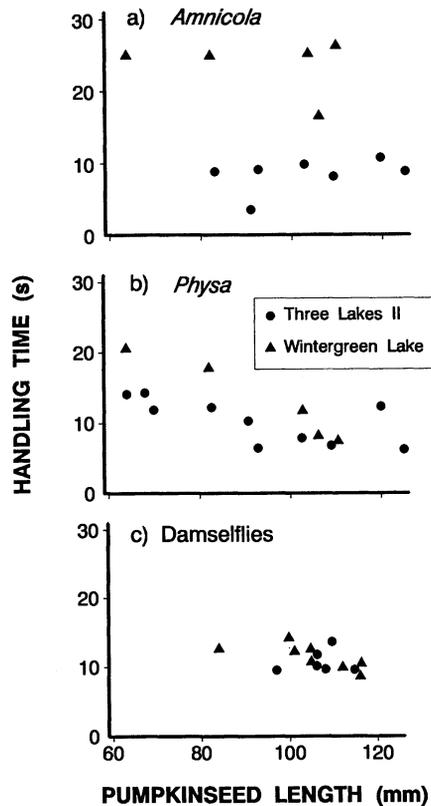


FIG. 6. Prey handling times for fish collected from Three Lakes II and Wintergreen Lake. Shown are mean handling times for each fish determined in laboratory feeding trials. Prey sizes, crushing resistances and statistical results are given in Table 4. (a) *Amnicola* were the hardest to crush of all the snails used. (b) Small *Physa* (used in 1988) were of intermediate crushing resistance. (c) Damselfly nymphs were a soft-bodied prey that did not require crushing. Each plotted mean (one for each fish) is based on an average of 11 (for *Amnicola* and damselfly nymphs) or 16 (for *Physa*) observations.

northern Wisconsin, where differences in water hardness provide a greater range of snail densities than in the Michigan lakes (Lodge et al. 1987). In the survey, we found that the mass of the levator posterior muscle (the principal shell-crushing muscle) was positively correlated with the frequency of molluscs in the diets of pumpkinseeds (G. G. Mittelbach et al., unpublished data). Studies of molluscivorous cichlids have also suggested a cause-effect relationship between diet and subsequent morphological development (Hoogerhoud 1986, Meyer 1990). As has been suggested for these cichlids (Hoogerhoud 1986, Meyer 1987), it is likely that the morphological polymorphism in pumpkinseeds was induced by the interaction between diet and subsequent morphological development (see Wainwright et al. 1991).

Pumpkinseeds from Wintergreen Lake, which have reduced crushing muscles and bones, also were less able to efficiently crush and handle snails. This effect was

strongest when the snails were relatively difficult to crush and/or when the fish were relatively small. Under other conditions (e.g., for the weakest shelled snails), the variation in crushing strength between fish from Three Lakes II and Wintergreen Lake was apparently less important because the snails were easy to crush for even the weakest of the fish we used (see Osenberg and Mittelbach 1989 for a related discussion concerning prey selection). The similarity in performance of fish from the two lakes when the fish were large or the prey were easy to crush suggests that the development of robust pharyngeal structures in fish from Three Lakes II does not carry a cost of reduced efficiency when feeding on softer bodied prey. To the extent that this system can be viewed as a model for how feeding mechanisms change during evolution, this result implies that ecologically significant innovations in feeding systems need not result in the compromise of primitive roles. Though in some cases it seems that trophic specialization may only come with a loss in potential diet breadth (e.g., Ehlinger and Wilson 1988, Meyer 1989), this does not appear to be the case with the pumpkinseed polymorphism.

Alternate hypotheses

An alternative explanation for the low snail densities in Wintergreen Lake (and therefore the effects on adult pumpkinseeds) is that the abiotic changes associated with winterkill of fish (e.g., low oxygen concentrations) also had direct negative effects on snails. This explanation has at least two shortcomings. First, it is unable to explain the increased pumpkinseed density that has resulted since winterkill because the direct negative impact on snails should have led to a decrease in pumpkinseed density (all else being equal). Second, snails, like many invertebrates, are probably more tolerant of low oxygen than are fish, which are more active. In fact, in her study of snail-macrophyte interactions, Sheldon (1987) relied extensively on winterkill lakes to obtain systems with exceptionally *high* snail densities. Thus, it seems unlikely that the low density of snails in Wintergreen Lake can be attributed to direct effects of winterkill. Furthermore, our pumpkinseed enclosure/exclosure experiment shows that the high density of pumpkinseeds in Wintergreen Lake plays a role in maintaining snails at their low levels.

It is also possible, however, that the high density of pumpkinseeds in Wintergreen Lake (and therefore the relatively low snail densities) is not due to the absence of bluegill. One of the pumpkinseed's primary predators, the largemouth bass, was also eliminated from Wintergreen Lake during the winterkill, although other piscivorous fish, such as bowfin (*Amia calva*), grass pickerel (*Esox americanus*), and yellow bullhead (*Ictalurus natalis*) remained common. Tonn and Paszkowski (1986) and Hall and Ehlinger (1989) have shown that winterkill can cause large population increases in

forage fish, due probably to their release from piscivory. However, several lines of evidence suggest that an effect on pumpkinseeds mediated through bass is unlikely to be the sole explanation of the changes we observed in Wintergreen Lake. First, bass are no longer absent from Wintergreen Lake: they were reintroduced in 1986 and reproduced in 1988 and 1989, and yet pumpkinseed densities continue to be high. Second, several pond experiments (Werner et al. 1983, Werner and Hall 1988, Turner and Mittelbach 1990) suggest that bass impose only small levels of mortality on sunfish when vegetation is abundant, as it is in Wintergreen Lake. Third, and most compelling, if the removal of a predator (i.e., bass) caused the increase in pumpkinseed density in Wintergreen, then we would predict that growth of all size classes of pumpkinseeds should be lower now than they were before winterkill (due to increased intraspecific competition within all size classes). This prediction is refuted by both the historical data and the among-lake comparison, which show that while large pumpkinseeds grow more slowly in post-winterkill Wintergreen, small pumpkinseeds grow considerably better. Therefore, removal of bass is unlikely to account for the effects we see (although they might contribute).

The patterns we document in snail abundance, and pumpkinseed density, diet, growth, morphology, and feeding ability are obviously based on comparisons involving only a single lake that lacks bluegill, Wintergreen Lake. In any such unreplicated comparison, one must be cautious in assigning causality to an observed pattern (Hurlbert 1984). In this study, however, there are several important points that give us confidence in interpreting (1) the pumpkinseed's responses as being caused by variation in snail density among lakes and (2) the cause of low snail density and high pumpkinseed density being related to removal of bluegill from Wintergreen.

First, we know a great deal about the actual mechanisms of pumpkinseed feeding and diet selection (e.g., Lauder 1983a, b, Osenberg and Mittelbach 1989, Wainwright et al. 1991). For example, we can predict which jaw muscles and bones should be affected by a lack of snails in the diet, and which muscles and bones should show no effect. Also, because we know when pumpkinseeds normally shift to feeding on snails (Mittelbach 1984, Osenberg and Mittelbach 1989), we can predict at which body sizes growth rates in the two lake types should begin to diverge. Further, our studies of prey selection and growth in sunfish have shown that variation in growth of any life history stage of sunfish can be understood with regard to variation in the density of that stage's primary prey resource (Mittelbach 1988, Mittelbach et al. 1988, Osenberg et al. 1988, Osenberg and Mittelbach 1989).

Second, in this study we were able to look at the pumpkinseed's response to resources at a number of different levels. In particular, we examined size-specific

diets, growth rates, morphology, and feeding ability and showed that each of these responses changed in a manner consistent with a change in snail abundance. Therefore, the consistency of variation at these diverse levels and the mechanistic links among the levels suggest that changes in the adult pumpkinseeds were caused by low snail densities in Wintergreen Lake. Thus, regardless of the mechanism responsible for the low snail density, our study demonstrates how altered resource availability can affect consumer diet, growth, morphology, and feeding ability.

Third, we have previously demonstrated that assumptions made in Mittelbach and Chesson's stage-structured model are justified in this system (e.g., juvenile pumpkinseed and bluegill compete, adult pumpkinseed limit their food supply, and sunfish growth is food limited). Therefore, the ability of the model to correctly predict the changes we have observed in Wintergreen Lake suggests that the low snail density and the associated changes in pumpkinseed were ultimately caused by the removal of bluegill. Although other processes may play a role, they seem unable to explain important observations, such as the inverse growth response of juvenile and adult pumpkinseed.

While definitive statements regarding the exact role of bluegill must await completion of our long-term study of Wintergreen Lake, including a planned reintroduction of bluegill, our working hypothesis is consistent with the available data, which includes both contemporary among-lake comparisons as well as historical data from Wintergreen Lake. Thus, it appears that the removal of bluegill, a species that does not interact directly with snails, may have had serious consequences for both the pumpkinseed, a "snail specialist," and its snail resource. Such complex or indirect interactions (Kerfoot and Sih 1987, Carpenter 1988b) are likely to be common in ecological systems that are dominated by size- and stage-structured populations. By explicitly incorporating population structure into our conceptual approaches, it is possible to generate testable predictions about how a system should respond to an environmental change. Due to the ubiquitous occurrence of complex life histories (Werner and Gilliam 1984), it is important that ecologists develop and test structured population models if we are to go beyond the simple description of such apparently "complex" results.

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