

## Effects of Changes in the Zooplankton Assemblage on Growth of Bloater and Implications for Recruitment Success

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**Abstract.**—Historical variation in the abundance of bloater *Coregonus hoyi* in Lake Michigan may have involved a link between growth rates of juvenile bloaters and the species and size distributions of zooplankton. These distributions have varied dramatically in response to fluctuations in abundance of alewife *Alosa pseudoharengus*. Bloater recruitment was poor from the mid-1960s to the mid-1970s. If bloater growth rates were reduced when large zooplankton were rare, as in the mid-1960s, juvenile bloaters would have been exposed to size-dependent mortality sources longer and, hence, would have experienced poor survival. Two sets of experiments were used to test this hypothesis. First, we investigated changes in prey size selectivity during the ontogeny of bloater. Our experiments showed that the size of prey that elicited significant positive selectivities increased from 0.3 mm in 20-mm bloaters to 2.3 mm in 100-mm bloaters. These results were then used to predict the outcome of 30-d growth experiments involving two controlled zooplankton distributions as food sources. We predicted successfully that fish longer than 40 mm would experience reduced growth when denied access to larger-bodied zooplankton. We suggest that the availability of appropriate sizes of zooplankton may have profound effects on the growth of juvenile fish and subsequent recruitment.

Events in the early life history of fish may determine subsequent recruitment to the adult stock (Cushing 1981; Lasker 1981). Many mechanisms that control recruitment are size dependent (Houde 1987; Pepin et al. 1987; Miller et al. 1988). For example, larger individuals are more resistant to starvation and less vulnerable to predation than are smaller individuals (Miller et al. 1988). Hence, any factor that affects fish growth rates will alter the probabilities that an individual will starve or be eaten. Consequently, recruitment hypotheses based upon single mechanisms cannot be regarded as strictly independent alternative hypotheses (Rice et al. 1987a); rather, the recruitment process will likely result from an interaction of the processes of larval growth and size-dependent mortality.

As with many animals, fish change their diets as they grow (Werner and Gilliam 1984). During development, it is common to find an increase in the size of food particles included in the diet (Siefert 1972; Wankowski 1979; Lemly and Dimmick 1982; Kane 1984; Mills et al. 1984; Peterson and Ausubel 1984; Govoni et al. 1986). The size dis-

tribution of food particles eaten has important energetic consequences. Optimal foraging theory suggests that for any size of fish there exists a restricted range of optimal prey sizes (Werner and Hall 1974; Werner 1977; Mittelbach 1981); those individuals consuming this optimal diet should experience higher growth rates than those fish not foraging optimally. Consequently, any factor that affects the size distribution of available prey may affect fish growth rates and the subsequent pattern of recruitment.

In Lake Michigan, native fishes have undergone dramatic population fluctuations over the last three decades (Crowder et al. 1987). These changes have been linked to the introduction of an exotic planktivore, the alewife *Alosa pseudoharengus* (Eck and Wells 1987). Alewives were first reported in Lake Michigan in 1949 and by 1966 represented more than 80% (by number) of the lake's fish population. In association with this increase in numbers of alewives, which are highly efficient planktivores, the zooplankton community in the lake changed. The taxonomic distribution of the zooplankton community shifted from one dominated by large cladocerans to one dominated by copepods and small cladocerans (Wells 1969; Scavia et al. 1988). Whereas before the introduction of

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alewife, zooplankton larger than 1 mm in size were common, zooplankton of this size subsequently became extremely rare (Wells 1969). In addition, the biomass of zooplankton in the lake declined by, perhaps, two-thirds (Wells 1969). Concurrent with the alewife increase, numbers of bloaters *Coregonus hoyi* declined precipitously (Brown 1970). More recently, as alewife numbers have declined, probably due to the stocking of salmonid predators, the numbers of both larger-sized zooplankton and bloaters have recovered (Kitchell and Crowder 1986; Eck and Wells 1987; Scavia et al. 1988).

Several mechanisms have been suggested to account for the striking, complementary patterns of bloater and alewife abundances (Crowder and Binkowski 1983; Eck and Wells 1987; Rice et al. 1987a; Luecke et al. 1990). The effects of each mechanism are altered by changes in the growth rate of juvenile bloaters such that reductions in bloater growth rates result in reduced recruitment (Rice et al. 1987b). The reduction in zooplankton biomass brought about by alewife planktivory obviously would have reduced the growth rates of juvenile fish in Lake Michigan. A more subtle effect of alewife planktivory on growth rates of juvenile bloaters was proposed by Crowder et al. (1987), whose hypothesis was that the historical truncation of the zooplankton assemblage forced bloaters to exploit smaller, suboptimal sizes of zooplankton. The historical shift forced greater reliance on smaller copepods instead of larger cladocerans. If this shift in the zooplankton assemblage further reduced growth rates of larval or juvenile bloaters, independent of reductions in zooplankton biomass, the likely result would be increased predation and thus reduced recruitment of bloaters (Crowder et al. 1987; Luecke et al. 1990).

The objectives of our research were to test the relationship between zooplankton size-species composition and bloater growth invoked by Crowder et al.'s (1987) hypothesis and thereby test a basic tenet of optimal foraging theory in fish: the existence of a link between food particle size and fish growth. Our approach was to use experiments to determine trends in size selection of zooplankton prey by bloaters during ontogeny. The results of these size-selectivity experiments were then used to forecast the outcome of 30-d growth experiments. In these experiments, fish of different sizes were fed a diet of either the whole, current zooplankton assemblage or a truncated zooplankton assemblage that excluded larger zooplankters. Our intent was to simulate both the truncation

produced during a period of relatively intense planktivory by alewives and the zooplankton assemblage that occurs during a period of less intense planktivory. A range of fish sizes was chosen such that the larger fish would be expected to select prey species larger than those occurring in the truncated zooplankton distribution. If optimal foraging theory is correct, these larger fish should experience slower growth when feeding on a truncated zooplankton assemblage than when they are fed zooplankton including large-size prey. The size of fish at which this restriction first occurs depends upon the truncation applied, but can be predicted a priori from the size-selectivity results. By choosing a suitable truncation, we can apply the results to investigate the effects of the historical truncation of the zooplankton assemblage by alewife in Lake Michigan on bloater growth and possibly on subsequent recruitment.

### Methods

All experiments were conducted from February to November 1987. Bloaters used in the experiments were reared in the laboratory from eggs spawned and fertilized from adults collected in gill nets set in southwestern Lake Michigan. After hatching in early May, larvae were fed a diet of *Artemia* sp. and commercial flake and pellet foods until required for an experiment. All experiments were conducted with a 12-h-light:12-h-dark cycle and at 12–15°C.

Zooplankton used in the experiments were collected from two sites. Lake Michigan zooplankton were collected offshore from Milwaukee in 70 m of water in oblique tows of a 0.5-m-diameter, 163- $\mu$ m-mesh plankton net. To ensure sufficient numbers of zooplankton in larger size-classes, the collections made in Lake Michigan were supplemented with zooplankton collected in a similar way from Lake Nagawicka, Waukesha County, Wisconsin. In the laboratory, zooplankton were kept in 2-m-diameter fiberglass tanks under gentle aeration. Fresh zooplankton were collected every 2 d. All zooplankton size measurements were made with a computer-based imaging system interfaced with a Zeiss DV-4 stereoscope (Sprules et al. 1981). Copepods were measured from the anteriormost point to the end of the caudal rami; cladocerans, from the anteriormost point to the base of the carapace spine.

*Size-selectivity experiments.*—Fish used in the size-selectivity experiments were fed live zooplankton from the current, whole size distribution for 5 d before an experiment. Experiments were conducted on four sizes of fish: 20, 40, 60, and

100 mm (all bloater sizes given as total length). On the day before the experiment with each size-class, 10 fish were transferred to a 125-L static tank and starved for 24 h to standardize hunger.

In preliminary trials, we developed a relationship between the weight of zooplankton added and the concentration of zooplankton in the tank. To begin an experiment, we added the weight of zooplankton predicted to give an initial concentration of 200 zooplankters/L. The size distribution of zooplankton in the tank was immediately sampled by lowering four clean polyvinyl chloride tubes (4 cm in diameter) over randomly placed rubber stoppers on the tank floor. Each enclosed volume of water was measured ( $\approx 750$  mL) and then poured through a 64- $\mu$ m-mesh sieve. The zooplankton retained were preserved (5% formalin) for subsequent enumeration and measurement.

The feeding period varied from 30 min for fish in the 20-mm size-class to 5 min for fish in the 100-mm size-class. At the end of the experiment, the fish were captured, their mouth gapes measured, and their stomach contents removed and preserved. Additional mouth gape measurements were made on fish ( $N = 192$ ) ranging from 15 to 76 mm. Four zooplankton samples were taken at the end of the feeding period in the same way as the initial zooplankton samples. Samples collected after feeding were used only to check for resource depletion. No more than 20% of the initial zooplankton was consumed in any experiment. We calculated linear selectivity indices (Strauss 1979; Ready et al. 1985) for all sizes of fish based on the zooplankton size distribution before feeding and on gut content samples for those individuals that had fed during the experiment. The index represents the difference between the relative abundances of a prey item in the gut (consumed) and in the habitat (available), and takes values from  $-1$  to  $+1$ . Individual selectivity values were tested with a  $t$ -test for significant difference from zero. Significantly different values are reported at  $P < 0.05$ .

*Growth experiments.*—Two food treatments were tested in a randomized complete block design for each of three sizes of fish. Twelve 250-L round flow-through tanks were used in each experiment. Water flowed into each tank at about 4 L/min along one of two manifolds from a common header tank. All tanks supplied from one manifold constituted a block. Directly above, draining into each tank, was a 20-L feeder tank.

We generated the two food treatments by screening the zooplankton size–species distribution. Tanks in the “whole” treatment received 2

g (fresh weight) of zooplankton per day from the entire or “whole” zooplankton size–species distribution. Tanks in the second or “truncated” treatment received an equal weight of zooplankton only after it had been gently screened through a 1-mm sieve to remove the larger-bodied forms. The screening did not appear to damage the zooplankton passing through the sieve. Consequently, treatments differed in the size distribution and number of zooplankton, not in the total weight of zooplankton provided.

Food lots were made up each morning and immediately added to the appropriate feeder tanks. Water was then added to give 20 L of zooplankton suspension. Fish were fed four times a day by stirring the water in the feeder tanks and then draining 5-L aliquots of the food suspension into the main tanks. Food did not accumulate in the tanks over the course of the experiment. An additional food suspension from each treatment was preserved in 5% formalin for later analysis of zooplankton. To investigate the size distribution of zooplankton provided in each food treatment, we randomly chose five daily samples from each treatment for enumeration and measurement. Differences in the zooplankton distribution in each treatment were analyzed with a chi-square test (Sokal and Rohlf 1981). Each cell value was the total number of zooplankton of that size found in the 15 samples analyzed. To ensure that all cells in the contingency table had values greater than 5, the cells representing zooplankton smaller than 0.4 mm were combined, as were those cells representing zooplankton larger than 1.9 mm.

We conducted experiments with 20-, 40-, and 60-mm fish. The total weight of fish in any tank was approximately constant ( $\approx 10$  g live weight); this required use of different numbers of fish per tank for each size-class. We used sixty 20-mm fish, twenty 40-mm fish, or eight 60-mm fish per tank. We did not conduct experiments with 100-mm fish because an individual fish of this size weighed more than the combined weight of one tank of fish in the other size-classes.

For each experiment, the required number of fish was selected from a stock maintained in the lab. Fish were anesthetized with tricaine (MS-222), measured to the nearest 0.1 mm, and randomly assigned to tanks. During the course of an experiment, any dead fish were replaced with fin-clipped individuals. Data from these individuals were not used in subsequent analyses. Fish were remeasured after 15 and 30 d. Data were analyzed with a one-way analysis of variance (SAS 1985). Because tanks and not fish were the experimental

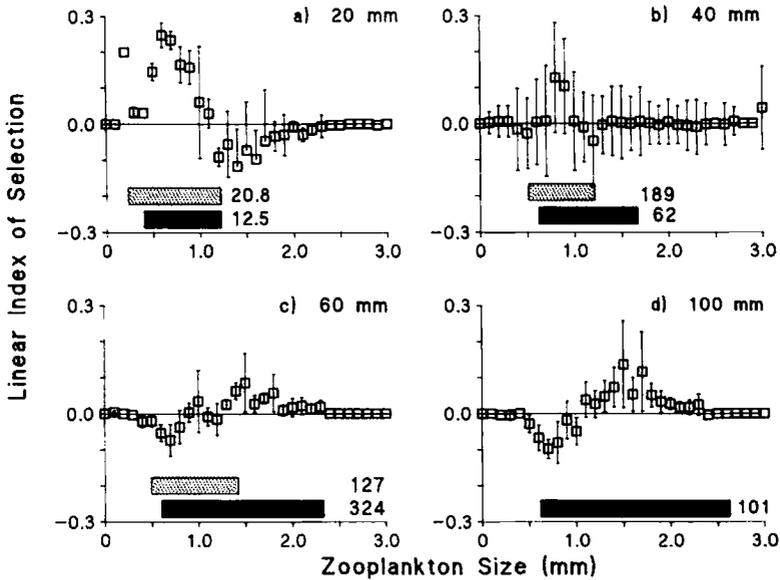


FIGURE 1.—Linear indices of food selection by bloaters as functions of zooplankton prey size. Values of the linear index of selection were calculated only for those fish that had fed during the trial. The numbers of fish whose gut contents were examined were (a) eight 20-mm fish and nine each for the (b) 40-mm, (c) 60-mm, and (d) 100-mm size-classes. Horizontal bars represent the size ranges of copepods (shaded) or cladocerans (solid) consumed. Numbers to the right of each bar are the mean numbers per fish gut for each taxonomic group. Vertical bars represent 95% confidence intervals.

units, mean fish length for each tank was the variable used in the analysis.

## Results

### Size-Selectivity Experiments

Zooplankton used in the experiments ranged in size from 0.2 to 2.9 mm; *Bosmina*, *Daphnia*, *Diaptomus*, *Mesocyclops*, and *Diacyclops* were the dominant genera. The density of zooplankton in the tanks ranged from 126 to 362 organisms/L.

Twenty-millimeter bloaters showed significantly positive selectivities for zooplankton sizes of 0.3–1.0 mm, with a peak selectivity for zooplankton of 0.6 mm (Figure 1a). Copepods were more common in the gut than cladocerans and represented 62% of the gut contents, but both zooplankton groups were utilized. The average mouth gape for 20-mm larvae was 1.2 mm ( $\text{gape} = 0.102 \times \text{length} - 0.84$ ;  $r^2 = 0.96$ ), smaller than the largest size of zooplankton present in the tank. Consequently, prey size for bloaters of this size was restricted by gape size. This was the only size of fish for which gape size was a factor controlling diet.

The selectivity pattern for 40-mm fish was more variable than for 20-mm larvae (Figure 1a, b). In general, although there was a high degree of vari-

ability, the region of positive selectivity shifted toward the right; peak selectivity, although not significantly positive, was for 0.8-mm zooplankton. As with 20-mm larvae, copepods were the dominant item in the gut and represented more than 75% of gut contents. However, both copepods and cladocerans were eaten.

Selectivities of the 60-mm bloaters showed clear differences from those of the smaller fish. The region of positive selectivity was shifted further to the right, and the range of zooplankton sizes eliciting a significantly positive selectivity spanned 1.3–1.8 mm (Figure 1c). Cladocerans were the major diet item, making up more than 70% of gut contents. However, both cladocerans and copepods were eaten. It is this change in diet composition that accounts for the positive selectivities for larger sizes of zooplankton observed for this size-class of fish. In addition, the smaller sizes of prey, 0.3–0.8 mm, were significantly selected against.

The largest size-class of bloaters tested (100 mm) showed a selectivity pattern following the trend observed for the smaller size-classes. The range of significantly positive selectivities, 1.3–2.3 mm, included larger-sized individuals (Figure 1d). The diet was composed almost exclusively of cladoc-

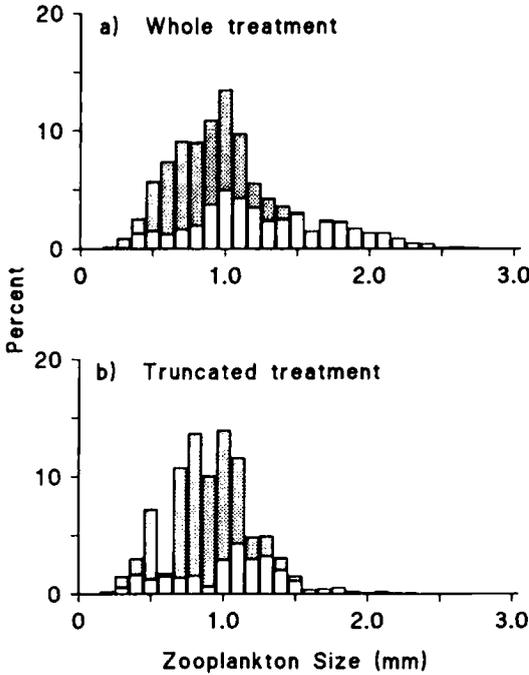


FIGURE 2.—Size distributions of zooplankton in the whole (unscreened) and truncated (screened through a 1-mm sieve) food treatments for 30-d growth experiments with bloaters. Shaded bars represent copepods; clear bars, cladocerans. Food distributions for five dates, chosen at random, for each size-class of bloaters were used to develop the zooplankton size distribution. The two distributions were significantly different ( $\chi^2 = 181.6$ ,  $df = 16$ ,  $P < 0.05$ ).

erans. Smaller sizes of both cladocerans and copepods were significantly selected against.

*Growth*

The truncation produced different zooplankton size distributions in the two treatments. Although the mesh size of the sieve used to develop the truncation was 1.0 mm, the actual zooplankton distribution appeared to be truncated at, conservatively, 1.5 mm (Figure 2). The truncated distribution included both copepods and cladocerans. The additional individuals contained in the whole distribution, but screened out of the truncated distribution, were primarily large cladocerans, but included large copepods.

The size-selectivity results suggested that if zooplankton size were truncated at 1.5 mm, only the diets of bloaters longer than 40 mm would be restricted, whether due to size or taxonomic preferences (Figure 3a). Thus, we predicted that the growth rate of 60-mm bloaters would be reduced

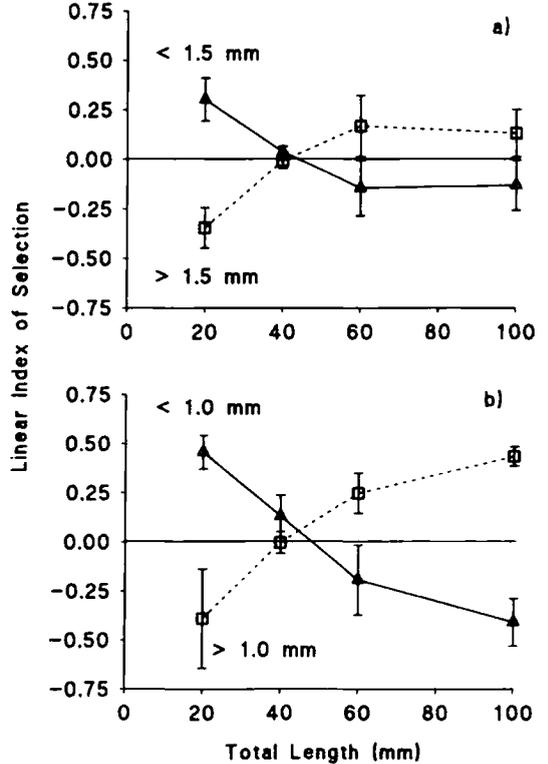


FIGURE 3.—Linear indices of food selection by different sizes (total lengths) of bloaters. The zooplankton size distributions were partitioned into two size-classes: (a) larger (dashed line) or smaller (solid line) than 1.5 mm, the size at which the zooplankton size distribution was truncated in a 30-d growth experiment, and (b) larger (dashed line) or smaller (solid line) than 1.0 mm, the size at which the zooplankton size distribution was truncated by alewives in Lake Michigan during the 1960s. Vertical bars represent 95% confidence intervals.

in the truncated treatment, whereas that of smaller bloaters would not.

We initially planned to conduct all experiments over 30-d periods. However, in the experiment with 20-mm bloaters, an unacceptably high level of mortality occurred and the experiment was stopped after 15 d. A second trial was attempted, but we again experienced high bloater mortality. Initially, both trials had 60 fish per tank. After 15 d, the mean number of live fish per tank in the first trial was  $21.16 \pm 6.5$  (mean  $\pm$  SD; range, 11–31) and in the second trial was  $33.92 \pm 4.62$  (range, 27–42). In the first trial, significantly more fish died in the whole treatment tanks than in the truncated treatment ( $\chi^2 = 8.248$ ,  $df = 1$ ,  $P < 0.005$ ). This pattern of mortality was not repeated in the second trial, where there was no significant differ-

ence in the numbers of deaths between treatments ( $\chi^2 = 2.25$ ,  $df = 1$ , NS). The mortality level in the trial with 40-mm fish was much lower than with 20-mm fish. Out of an initial twenty 40-mm fish per tank, only an average of 1.75 fish (SD, 1.81; range, 0–5) died per tank, and there was no significant difference in mortalities between treatments ( $\chi^2 = 0.428$ ,  $df = 1$ , NS). There was no appreciable mortality in the trial with 60-mm fish: only one fish died (total, 96) over the course of the experiment.

Fish in all tanks showed significant growth in each experiment. However, fish of different size-classes responded differently to the two food treatments. There was no significant difference in growth between the two treatments in either of the trials with 20-mm fish (Table 1). In the trial with 40-mm fish, analysis of variance indicated a significant difference in growth between treatments. Fish in the truncated treatment tanks grew significantly more than their counterparts in the whole treatment tanks (Table 1). There was also a significant difference in growth between treatments in the trial with 60-mm fish. Unlike 40-mm fish, 60-mm fish in the whole treatment tanks grew significantly more than those in the truncated treatment tanks (Table 1).

### Discussion

As with other species (Siefert 1972; Wankowski 1979; Lemly and Dimmick 1982; Kane 1984; Mills et al. 1984; Peterson and Ausubel 1984; Govoni et al. 1986), the size of prey eaten increases as bloaters grow in size. In our experiments, the size of prey that elicited significantly positive selectivities increased from 0.3 mm for 20-mm bloaters to 2.3 mm for 100-mm bloaters. However, this increase also involved a shift in taxonomic preference from a diet dominated by copepods to one dominated by cladocerans. Because zooplankton size and taxon composition are correlated in lakes (e.g., the largest zooplankton tend to be cladocerans), this size-species shift may be common. If

we had been able to provide the larger fish with copepods longer than 1.5 mm, the bloaters may indeed have shown positive selectivities for copepods. However, this pattern of selection for small copepods by small bloaters and for larger copepods and cladocerans by larger bloaters is similar to results of diet studies in the field, thus suggesting a robust relationship (Crowder and Crawford 1984; Crowder, unpublished data).

One objective of our study was to investigate the link between prey size and fish growth predicted by optimal foraging theory. The 30-d growth experiments suggest such a link: equal biomasses of food were not necessarily of equal utility to bloaters. The size distribution of the food must be taken into account when investigating diet and growth patterns. However, because of the taxonomic differences introduced by the truncation process, we were not able to show definitively that the differences observed in the growth experiments were due solely to a size effect independent of a taxonomic effect. Shifts in size selectivity cannot be distinguished as completely independent of shifts in taxon selectivity. The reduced growth of 60-mm fish in our truncated treatment may have resulted from reduced availability of favored prey taxa rather than favored prey sizes. Yet, in the truncation, no species of zooplankton was removed completely; rather, the size distribution was altered.

In other studies, food particle size has been shown to affect fish growth. Mills et al. (1989b) demonstrated the existence of a link between *Daphnia pulex* size and growth of yellow perch *Perca flavescens* in the field. This link has also been demonstrated for yellow perch in the laboratory by Mills et al. (1989a), who fed age-0 fish equal weights of three different size-classes of *Daphnia pulex* and found significant growth differences among food treatments. In similar experiments, small yellow perch (24–40 mm) grew better on small copepods (*Diaptomus sicilis*; mean size, 1.08 mm) than on either mixed Oneida Lake

TABLE 1.—Growth of bloaters fed zooplankton of two different size distributions, either whole (unscreened) or truncated (screened through a 1-mm sieve). Significant treatment differences are indicated by *F*-test values ( $df = 1, 9$ ) for which  $P \leq 0.05$ .

Fish size (mm)	Month (1987)	Duration of experiment (d)	Mean bloater growth (mm)		<i>F</i>	<i>P</i>
			Whole	Truncated		
20	May	15	1.09	0.84	1.37	NS
	Jun	15	2.32	2.52	0.65	NS
40	Aug	30	6.34	7.13	6.25	0.034
	Oct	30	6.81	6.29	9.27	0.014

zooplankton (1.29 mm) or large *Daphnia magna* (2.48 mm) (Confer and Lake 1987). Wankowski and Thorpe (1979) showed that growth rates of juvenile Atlantic salmon *Salmo salar* were influenced by food size. They offered equal volumes of one of six sizes of commercial pelleted food to groups of fish in 10 separate experiments (first-feeding alevins to second-year smolts). The results indicated that maximum growth for each age-class was shown with only one size of particle; larger or smaller particles resulted in reduced growth. Tabachek (1988) showed that different sizes of Arctic char *Salvelinus alpinus* experienced greatest growth on different food particle sizes.

A second objective of our study was to test Crowder et al.'s (1987) hypothesis that the historical truncation of the Lake Michigan zooplankton community during the peak of alewife abundance may have contributed to reduced bloater growth rates. Our experimental truncation produced a bias in the taxonomic composition of the zooplankton size distribution provided in the experiments. This compromised our ability to clearly distinguish size selectivity from taxon selectivity in the diet. However, the confounding of size and taxonomic composition is unimportant in the growth experiments because the historical truncation of the Lake Michigan zooplankton community involved both size and taxonomic shifts. When planktivores "truncate" the size distribution of zooplankton, they shift the taxon distribution as well.

We used our size-selectivity results to predict outcome of the growth experiments. A priori, we expected to find results that supported the hypothesis with 60-mm fish, but not with fish 40 mm and smaller. Additionally, because we provided equal weights of food in both treatments, there were increased numbers of prey smaller than 1.5 mm in the truncated treatment. Therefore, bloaters that select prey smaller than 1.5 mm might be expected to show enhanced growth when exposed to the truncated zooplankton distribution.

The results of the growth experiments were in agreement with the hypothesis. When exposed to larger prey, 60-mm fish grew faster than those that were denied access to such prey. This difference was apparent, but not significant, after 15 d. The results for 40-mm fish showed an advantage in growth for fish in the truncated treatment consistent with our expectation: 40-mm bloaters which selected prey smaller than 1.5 mm (especially copepods), grew better in the truncated treatment than in the whole treatment. This pattern was not

evident in the results for 20-mm fish, probably due to the shorter duration of these experiments.

In Lake Michigan, the truncation of the zooplankton size distribution occurred at about 1.0 mm (Wells 1969). Our experimental truncation occurred at 1.5 mm. Because historically the truncation was more severe than our experimental conditions, the taxonomic dominance of copepods was even more pronounced (Wells 1969). Hence, based on both size and taxon, our test of the historical situation in the lake was extremely conservative. Our treatment involved removing only the largest 18% of the size distribution and substituting an equal weight of smaller individuals. The fact that we could demonstrate a growth effect with such a small change suggests that the reduction in zooplankton caused by alewives would have had an even stronger effect on the growth of native fishes than that seen in this study. Further, if we had achieved a truncation at 1 mm, our size-selectivity results suggest that the growth reduction might well have been apparent in bloaters as small as 30 mm (Figure 3b). The size-based effects we have documented here would cause the overall reduced growth due to the 50–75% decline in zooplankton biomass that accompanied the truncation induced by alewives (Wells 1969). As Mills et al. (1989a) suggested, under reduced food availability, food-size-based growth effects would have been even more marked.

Although we have documented a link between food size and growth rate, we have yet to address the question of how growth rate differences are reflected in survival and subsequent recruitment. Houde (1987) suggested that growth rate variation has a strong effect on recruitment. It seems intuitively obvious that larger fish should be hardier than smaller ones, but it is not clear how only small differences might have important effects on survival and recruitment. Miller et al. (1988) showed that size differences of only tenths of millimeters can confer considerable advantages in resistance to starvation. Certainly, slight size differences may have important consequences to a fish's vulnerability to predators (Mittelbach and Chesson 1987; Miller et al. 1988). Luecke et al. (1990) used a simulation approach to investigate the role of growth-rate variation and size-dependent predation in determining recruitment of age-0 bloaters. Their work strongly supports the importance of small growth-rate differences in regulating survival. From their results, the growth-rate difference observed in our study (10%) could alter survival over 30 d by up to 10 times, depending on

predation intensity. Given that our zooplankton truncation was extremely conservative, we argue that the indirect effect of size-selective consumption of zooplankton by alewives may have been an important factor reducing growth rates of juvenile fish, thus influencing the recruitment of native fishes.

However, the changes in the zooplankton community in Lake Michigan brought about by alewives were not solely responsible for the decline in bloaters and other native fishes. There is clear evidence that alewives are efficient predators of larval fish and may have depressed bloater numbers in this way (Luecke et al. 1990). Adult alewives are also more efficient planktivores than are bloaters (Crowder and Binkowski 1983) and so may have outcompeted bloaters. We do, however, suggest that changes in both the abundance and size of zooplankton may have reduced bloater growth rates and made bloaters even more susceptible to multiple size-dependent sources of mortality.

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