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Theodore R. Gray[1]* **, James E. Breck**[2,1]**, and Paul W. Webb**[1]

[1] *The University of Michigan*
School of Natural Resources and Environment
Ann Arbor, Michigan 48109-1115

[2] *Michigan Department of Natural Resources*
Institute for Fisheries Research
212 Museums Annex Building
Ann Arbor, Michigan 48109-1084

Abstract.–We investigated whether age-1 (25-50 mm total length) bluegill *Lepomis macrochirus* reduced the abundance of large cladocerans (0.81 mm and larger) and thereby reduced growth of age-0 bluegill and their survival to the following spring. Adult bluegill successfully produced age-0 fish in six 0.25-ha ponds stocked with age-1 bluegill at 0 and 5.6 kg/ha, but not in three ponds stocked with age 1s at 16.8 or 23.5 kg/ha. For zooplankton sampled weekly from May to early June, before age 0s began exogenous feeding, mean density of medium (0.41 to 0.80 mm) zooplankton was lower in ponds with higher stocking densities of age-1 bluegills; this trend was not significant for large cladocerans. Most age-0 growth occurred from exogenous feeding in early June until early July. Even though the density of large zooplankton was depleted to an average of 6 L^{-1} by 18 June, fast growth of age-0 bluegill continued for an additional 11 to 21 d. Fast growth of age-0 bluegill ended when foraging reduced the densities of medium and small (0.40 mm or less) zooplankton to less than 50 L^{-1}. In ponds containing age-0 bluegill, the average density of large and medium zooplankton during the period of rapid age-0 growth was not significantly lower in ponds with age 1s than in ponds without age 1s. If age-0 bluegill were present in seine samples in early June, then they were found in seine samples throughout the summer, and substantial numbers (at least 140,000 ha^{-1}) were present at pond draining the following spring. The negative correlation found by Clark and Lockwood between the spring density of age-1 bluegill and the strength of the next year class could not be attributed to competition for food, including that for large zooplankton. Year-class failure in this experiment was only seen in ponds receiving the highest densities of age 1s (16.8 and 23.5 kg/ha), and was most likely due to predation by age 1s on eggs and larvae. Bluegill may be prone to stunting in part because age-0 fish can maintain fast growth even with total zooplankton densities as low as approximately 50 L^{-1}.

* *Ted Gray & Associates, 1024 Laurie Lane, Burr Ridge, IL 60521*

Several fish species are prone to stunting. A stunted fish population contains similar-sized adults of different ages whose growth rates are below the regional average for the species (Linfield 1979). Stunting can greatly reduce the value of commercial and recreational fisheries. Therefore, an understanding of stunting and development of techniques to renovate stunted populations are of significant ecological and practical importance.

The bluegill *Lepomis macrochirus* is a species in which stunting is especially common. Stunted bluegill populations may result from a low food availability per individual, combined with foraging advantages favoring smaller fish when large prey are rare (Mittelbach 1983). Stunting can be maintained because of relatively high rates of reproduction and survival in spite of low food levels (Beard 1971; Beyerle 1977). Therefore, understanding mechanisms that can reduce recruitment may be essential to the development of management techniques to influence bluegill population dynamics and renovate stunted populations.

One factor known to affect bluegill recruitment is the density of juvenile bluegills (especially age 1s, 25-50 mm total length, TL). The density of juvenile bluegill stocked in April in experimental ponds was negatively correlated with the abundance of the successive age-0 year class (Clark and Lockwood, 1990). Indeed, the expected new recruits were frequently not found when the age-1 stocking densities exceeded 12 kg/ha. In nine ponds followed over 5 years, new recruits were absent at the annual spring pond draining on 22 of the 45 occasions (Clark and Lockwood 1990). Such an intraspecific interaction may explain why many bluegill populations are characterized by large variations in year-class strength and recruitment of young fish, resulting in dominant year classes (Anderson 1973). For instance, in a small Michigan lake that was treated with rotenone and then stocked with adult bluegill, a very large year class was produced which evidently completely inhibited reproduction or survival of age-0 bluegill for the next 3 years (Beyerle 1971). The mechanism producing this strong negative effect on recruitment has not been determined.

Insufficient food for larval fish has been proposed as a cause of poor recruitment. According to the match-mismatch hypothesis of Cushing (1975; Rothschild 1986), a match in the timing of marine fish spawning relative to the annual bloom in plankton can lead to a strong year class, whereas a mismatch leads to a poor year class due to inadequate food for the larval fish. DeVries and Stein (1990; DeVries et al. 1991; Stein et al. 1995) make it clear that age 0s of threadfin shad *Dorosoma petenense* and gizzard shad *Dorosoma cepedianum* can reduce the density of zooplankton to a level that causes reduced survival of other age-0 fishes, including bluegill. Bluegill larvae may starve within just a few days of leaving the nest if appropriate food is not available. Toetz (1966) held bluegill larvae in aquaria at 23.5°C, and observed that the starvation time to 50% mortality was between 2.1 and 2.6 d after becoming free-swimming, which occurred at 6.4 d after fertilization.

The negative effect of age 1 and older juvenile bluegill on age-0 bluegill may be due to competition for food. Juvenile bluegill selectively consume larger zooplankton (Werner et al. 1974; Mittelbach 1983), which also constitute an important food source for age-0 growth and survival of several other fishes (e.g., yellow perch *Perca flavescens*, Noble 1975; Mills and Forney 1981; Mills et al. 1989; bloater *Coregonus hoyi*, Miller et al. 1990). We tested the hypothesis that selective foraging by age-1 bluegill would deplete the abundance of large zooplankton, reducing age-0 growth and survival to the following spring.

Our expected results were based in part on studies on the effects of foraging by size-selective planktivores on the size structure of the zooplankton community (Brooks and Dodson 1965; Hall et al. 1970; Lynch 1979; Zaret 1980). In the absence of size-selective planktivores such as age-1 bluegill, large-sized zooplankton frequently become abundant. In the presence of size-selective planktivores, large zooplankton can be replaced by a relatively higher density of smaller zooplankton (Hall et al. 1970). This is because size-selective planktivores directly deplete the larger zooplankton (both herbivores and invertebrate predators), in turn releasing populations of smaller-sized zooplankton from

competition and invertebrate predation (Zaret 1980). Smaller-sized zooplankton may be an inadequate food source for producing a strong year class of bluegills.

The purpose of our study was to evaluate the effects of different stocking levels of age-1 bluegill on the density of large zooplankton and the growth and survival of age-0 bluegills. We expected that, in the absence of age-1 bluegills, the zooplankton community would have more larger-sized zooplankton, allowing faster growth of age-0 bluegill and higher survival to the following spring. We hypothesized that, when present, age-1 bluegills would decrease the abundance of larger zooplankton, which would negatively affect age-0 growth and survival to the following spring. We further hypothesized that high levels of age-1 bluegill would reduce zooplankton densities to such low levels that age-0 bluegills would not have sufficient food to survive, causing year-class failure.

Methods

Pond treatments.–Nine ponds (approximately 0.25 ha, mean depth, 1.5 m) were used at the Saline Fisheries Research Station, Saline, Michigan. Ponds were drained and stocked 9-20 April 1990 with a single density (56 kg/ha) of adult (100–150 mm TL) bluegill. Treatments consisted of 4 densities (23.5, 16.8, 5.6, and 0 kg/ha) of juvenile bluegill, with one, two, two, and four replicates of each density. Juvenile bluegill (25–50 mm TL) were almost all age 1. The age-1 stocking densities were chosen based on the study of Clark and Lockwood (1990) at the Saline Station, which determined that new recruits were never recovered the following spring when the stocking density of 25-50 mm bluegill was 12 kg/ha or greater. Three replicates per treatment were planned; because of a stocking error, age-1 bluegills intended for Pond 9 were put into Pond 8, resulting in one pond having 23.5 kg/ha and four ponds with 0 kg/ha. A tenth reference pond was set up to serve as a control for bluegill predation on zooplankton; this pond was later found to contain a very small population of yearling bluegill, estimated to be approximately 0.4 kg/ha in the spring (44 bluegills weighing 2.69 kg were removed in August, and 52 additional bluegills weighing 4.83 kg and two small green sunfish *Lepomis cyanellus* were present when this pond was drained 7 December 1990).

Zooplankton sampling.–The zooplankton community was sampled from May through mid-August to determine species composition and total density of all zooplankton. Rotifers were excluded from density measurements because they were rarely consumed by bluegills. Samples were collected every week by vertical tows (Welch 1948) with a 30-cm diameter, 20-µm-mesh plankton net. One sample was collected at each of four permanent wooden markers in each pond. Three markers were located equidistantly down the pond center and the fourth marker was within 6 m of the shore. Zooplankton samples from each pond were pooled, stained with Eosin Y, and preserved in 5% formalin with sucrose (Haney and Hall 1973). Zooplankton samples were processed after being rinsed of formalin, diluted to a known volume, and randomly mixed. One or two aliquots of 1.0 mL were then placed under 40´ magnification in a petri dish with grids. Subsample counts were made of approximately 200 individuals and were separated into the following groups: *Bosmina*, *Ceriodaphnia*, *Chydorus*, copepod nauplii, juvenile and adult copepods, *Daphnia*, *Diaphanosoma*, ostracods. For each pond and sampling date through 9 July, the lengths of at least 30 zooplankton were measured from the anterior of the head to the posterior, or the base of the terminal spine, if present, with a computer-aided digitizer or an ocular micrometer. The three zooplankton size groups chosen for analysis were large (0.81 to 2.0 mm), medium (0.41 to 0.80 mm), and total (less than 2.0 mm). The proportion of zooplankton in each size group was multiplied by total zooplankton density to determine the density of each size group.

Regression analysis was used to test the effect of age-1 biomass at stocking on densities of large, medium, and total zooplankton during three time periods (defined below). Because successive zooplankton densities in each pond are not independent observations, a single mean value (Y) for each pond and period was used as

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the dependent variable in the analysis of each size category:

$$Y = \frac{1}{N} \sum_{i=1}^{N} \log_{10}(0.05 + D_i),$$

where D_i is the zooplankton density (number/L) of sample $\underline{i}$ in the period, and $N = 5, 4,$ and 6 samples in periods 1, 2, and 3, respectively. The independent variable was stocking biomass of yearlings (kg/ha). Results from all nine ponds were included in the regression analysis because stocking biomass of yearlings is a continuous variable, not a categorical variable.

Bluegill sampling.–Age-0 bluegill were sampled with a 2.5-m seine (mesh size, 1×3 mm) to determine growth rates and diet. Age-0 fish were sampled every 4-7 d in June and every 14 d thereafter. All age-0 fish were preserved in 95% ethanol. Total lengths (TL) were measured and corrected for shrinkage with an empirically derived relation (Gray 1991) for 5.2- to 36.0-mm bluegills:

$$TL_o = 0.15038 + 1.0480\, TL_p,$$

($N = 52$, $r^2 = 0.998$), where TL_o is total length before preservation (mm), and TL_p is total length (mm) after preservation.

Length-frequency distributions and plots of length versus time were used to identify the first natal cohort in each pond. This cohort was used to determine growth rates in each pond for three reasons. First, individuals from the first natal cohort were captured consistently from early June through mid-August. Second, the effect of age 1s on age-0 bluegills would initially be focused entirely on the first cohort. Third, subsequent natal cohorts were not analyzed because their growth and survival may have been affected not only by age 1s but also by the first natal cohort, which may significantly reduce the zooplankton food supply in these ponds (Latta and Merna 1977).

Gut contents were determined for up to five individual age-0 bluegill from the first natal cohort per pond for each sample period in time periods 2 and 3 (defined below). Analysis of variance was used to evaluate the influence of time period and stocking density of age 1s on mean number of prey per age-0 stomach, for five prey taxa: *Chironomus* midge larvae, ostracods, copepods, large cladocerans (includes *Daphnia* and *Diaphanosoma*), and small cladocerans (includes *Bosmina*, *Ceriodaphnia*, and *Chydorus*).

Population censuses.–The bluegill populations were censused when the experimental ponds were drained in April 1991. Bluegills were separated into three easily distinguishable size groups: adults, large juveniles (stocked as age 1s), and new recruits (young produced in the summer of 1990). The total weight of each size group was measured to the nearest 45.4 g with a spring scale. A length-frequency distribution of new recruits in each pond was obtained by measuring TL (to the nearest 1 mm) on a random subsample of 200-500 new recruits. A weight-length regression for new recruits from each pond was developed with lengths and wet weights (measured to the nearest 0.0001 g) for up to three individuals per 1.0-mm length group. Mean weight was computed from the length-frequency distribution and the weight-length regression. Total numbers of new recruits were estimated by dividing the total weight by the estimated mean weight. Regression analysis was used to test the effect of age-1 biomass at stocking on the density of new recruits at pond draining one year later. The dependent variable was the $\log_{10}(1 +$ number of new recruits per ha); the independent variable was stocking biomass of yearlings (kg/ha). Results from all eight ponds with useable draining data were included in the regression analysis because stocking biomass of yearlings is a continuous variable, not a categorical variable. All statistical tests used a criterion of a $= 0.05$.

Time periods.–The analyses of fish growth and zooplankton abundance were stratified into three time periods. Period 1 was distinguished from period 2 based on the average date that the first natal cohort of age-0 bluegill left the nest and began feeding. These first-feeding dates were estimated in each pond by using the observed growth rate (mm/d) and the mean length on a given date to back–calculate the date

on which mean length of the first natal cohort was 5.5 mm, the size at which larvae become free-swimming (Toetz 1966). Period 2 was distinguished from period 3 because inspection of a plot of length versus time indicated a change occurred in age-0 growth. Age-0 growth was fast and linear in period 2, but was noticeably slower in period 3. The deviation from the fast and linear growth rate in period 2 for each pond was used to determine the transition to period 3.

Results

Presence of Age-0 Bluegills

Age-0 bluegills occurred in 1990 in all four ponds lacking age-1 bluegills and in both ponds stocked with age 1s at 5.6 kg/ha (Table 1). Age-0 bluegill were consistently seined from these ponds from June through August. Although vacated bluegill nests were seen in two of the three ponds containing age 1s at 16.8 or 23.5 kg/ha , age-0 bluegill were neither found in seine hauls nor observed from shore.

Growth of Age-0 Bluegills

Growth was fast through 29 June, but was noticeably slower after 9 July (Figure 1). It was between these sampling dates that period 2 ended and period 3 began. Age-0 growth was 0.49-0.68 mm/d in period 2 but only 0.08-0.19 mm/d in period 3. From period 2 to period 3 there was an increase in the within-sample variation in length among individuals of the first natal cohort; the average standard deviation of length in a pond was 0.67-0.80 mm in period 2 and increased to 1.44-2.60 mm in period 3. Average growth from August 1990 through April 1991 was -0.02 mm/d. Based on extrapolating the growth rate in period 2 back to a size of 5.5 mm, age-0 bluegills began exogenous feeding between 2 June and 9 June.

Even though the density of large zooplankton was rapidly depleted to an average 6 L^{-1} by 18 June, fast growth of age-0 fish continued for an additional 11 to 21 d. Moreover, the growth of age-0 fish was not significantly slower in ponds with age 1s, either in period 2 or in period 3 (1-tailed t-test, P = 0.10; 1-tailed t-test, P = 0.49, respectively). Rather, the transition from fast to slow growth was dependent on the density of all zooplankton. Fast weekly growth occurred until total zooplankton density declined below approximately 50 L^{-1} between the end of period 2 (25 and 29 June) and the beginning of period 3 (9 and 16 July) (Figure 2).

Survival of Age-0 Bluegills

As indicated above, all six ponds stocked with 0 or 5.6 kg/ha of age 1s produced age-0 bluegills. However, all three ponds which contained 16.8 or 23.5 kg/ha of age 1s did not produce any age-0 bluegills (Table 1). Three of four ponds without age 1s produced a mean density of 349,000 new recruits ha^{-1} surviving to the following spring. In the fourth pond (Pond 11), an accurate estimate of density was not obtained due to accidental loss of fish during pond draining. Two ponds stocked with age 1s at 5.6 kg/ha produced a mean spring density of 156,000 age-0 bluegills ha^{-1}, although this value was not significantly different than the mean for ponds without age 1s (1-tailed t-test, P = 0.06). Regression analysis using the full range of stocking levels indicated that stocking density of age 1s had a statistically significant negative effect on the number of new recruits recovered at pond draining.

$$\log_{10}(Y) = 5.817 - 0.288\, X,$$

where Y is 1 + number of new recruits ha^{-1}, and X is stocking biomass of age-1 bluegills (kg/ha); N = 8, r^2 = 0.89. The slope is negative (-0.288) and upper and lower 95% confidence limits do not include zero (-0.195 and -0.381, respectively), indicating that the effect of X is statistically significant.

Year-class failures occurred very early in the summer in ponds with high densities of age-1 bluegill. In the other ponds, including those with 5.6 kg/ha of age 1s, survival of age-0 bluegill after early June was adequate to produce a substantial year class. If age-0 bluegill were present in seine samples in early June in any

pond, then they were found in seine samples throughout the summer, and substantial numbers (at least 140,000 ha^{-1}) were present at pond draining the following spring (Figure 1, Table 1).

Zooplankton

During period 1, total zooplankton density was lower in ponds with higher stocking densities of age-1 bluegills (Figure 3j, k, and l):

$$Y_T = 2.546 - 0.017\,X\,,$$

where Y_T is the mean of the log-transformed total zooplankton densities, and X is stocking biomass of age-1 bluegills (kg/ha); $N = 9$, $r^2 = 0.45$. The slope is negative (-0.017) and this trend is significant: lower and upper 95% confidence limits do not include zero (-0.031 and -0.002, respectively). The same statistically significant pattern was observed for medium zooplankton (Figure 3f, g, and h):

$$Y_M = 2.097 - 0.035\,X\,,$$

where Y_M is the mean of the log-transformed medium zooplankton densities; $N = 9$, $r^2 = 0.39$. Lower and upper 95% confidence limits for the slope do not include zero (-0.068 and -0.001, respectively). A similar pattern was observed for large zooplankton, but the regression was not quite significant (Figure 3b, c, and d):

$$Y_L = 0.708 - 0.074\,X\,,$$

where Y_L is the mean of the log-transformed large zooplankton densities; $N = 9$, $r^2 = 0.35$. Lower and upper 95% confidence limits for the slope just barely include zero (-0.150 and +0.001, respectively).

In period 2 the trends with age-1 density were different. Total zooplankton density was now higher in ponds with higher stocking densities of age-1 bluegills:

$$Y_T = 2.217 + 0.022\,X\,;$$

$N = 9$, $r^2 = 0.39$. The slope is positive (0.022) and this trend is significant: lower and upper 95% confidence limits do not include zero (0.001 and 0.043, respectively). In period 2 the influence of age-1 stocking density on large and medium zooplankton was not significant: lower and upper 95% confidence limits of the slope included zero (-0.124 and 0.043 for large, -0.055 and 0.062 for medium zooplankton, respectively).

In period 3, total zooplankton density was significantly higher in ponds with higher stocking densities of age-1 bluegills:

$$Y_T = 1.134 + 0.077\,X\,;$$

$N = 9$, $r^2 = 0.81$. The slope is positive (0.077) and significantly greater than zero: lower and upper 95% confidence limits are 0.047 and 0.108, respectively.

In the reference pond, the abundance of large zooplankton (over 0.8 mm) averaged 27 L^{-1} through period 2 (Fig. 3a). In contrast, in two of three ponds with a high density of age 1s (and no age 0s), the density of large zooplankton averaged less than 5 L^{-1} through period 2 (Figure 3b). A different population flux pattern for large zooplankton was observed in ponds which had age-0 bluegill (Figure 3c, d). In these ponds large zooplankton density averaged 53 L^{-1} on 11 June, which was 2 - 9 d after age-0 bluegill had started exogenous feeding. However, by 18 June in all ponds with age-0 bluegill, density of large zooplankton declined dramatically to an average of 6 L^{-1}. In ponds with age-0 bluegill, the average density of large zooplankton throughout period 2 was not significantly lower in ponds with age 1s (Figure 3c) than in ponds without age 1s (Figure 3d; 1-tailed *t*-test, $P = 0.10$).

In period 2 in ponds with age 1s and no age-0 bluegill, medium zooplankton increased to much higher densities than large zooplankton, averaging over 71 L^{-1} (Figure 3f). In all other treatments, medium zooplankton followed a pattern of population flux similar to large zooplankton (Figure 3g, h). In the reference pond, the abundance of medium zooplankton averaged 28 L^{-1} through period 2 with remarkably little variation (Fig. 3e). Medium zooplankton in the reference pond may not have increased to the higher densities observed in the experimental treatments for two reasons. First,

larvae of the phantom midge *Chaoborus*, which were only common in the reference pond, may have suppressed the abundance of medium zooplankton, because the larvae are predators on medium and small zooplankton (Zaret 1980). Alternatively, the large zooplankton in the reference pond may have suppressed medium zooplankton through competition for food (Brooks and Dodson, 1965).

In ponds with age-0 bluegill, medium zooplankton averaged 188 L^{-1} on 11 June, 2-9 d after age-0 bluegill had started exogenous feeding (Figure 3g, h). As with large zooplankton, densities of medium zooplankton declined dramatically soon after exogenous feeding began. By 29 June, densities of medium zooplankton averaged 10 L^{-1}. In ponds with age-0 bluegill, the average density of medium zooplankton in period 2 was not significantly lower in ponds with age 1s (Figure 3g) than in ponds without age 1s (Figure 3h; 1-tailed *t*-test, $P > 0.10$).

Total zooplankton densities followed a pattern in population flux similar to medium zooplankton for all treatments. In the reference pond, the density of total zooplankton averaged 143 L^{-1} with remarkably little variation from periods 1 through 3 (Figure 3i). In ponds with age 1s and no age-0 bluegill, total zooplankton averaged 252 L^{-1} in period 2 and rarely declined below 250 L^{-1} in period 3 (Figure 3j). This zooplankton level would appear sufficient to maintain age-0 growth and prevent starvation if age-0 fish were present. In ponds with age-0 bluegill, total zooplankton averaged 642 L^{-1} on 11 June, and declined to an average of 31 L^{-1} by 9 July, the start of slow age-0 growth in period 3 (Figure 3k, l).

Diet of Age-0 Bluegills

Following the start of exogenous feeding in period 2, age-0 bluegills primarily consumed small cladocerans, such as *Bosmina*, *Ceriodaphnia* and *Chydorus* (Figure 4). Stomach contents of age-0 bluegill changed significantly from period 2 to period 3 (2×2 ANOVA, effect of period: $P < 0.001$ for small cladocerans, copepods, ostracods, and *Chironomus* midge larvae; $P = 0.007$ for large

cladocereans, such as *Daphnia* and *Diaphanosoma*). Copepods were the most abundant diet item in period 3.

For three of five prey types (*Chironomus* larvae, small and large cladocerans), age-0 diet also varied significantly with age-1 stocking density, and the period × stocking-density interaction was significant (2×2 ANOVA, effect of age-1 density, and period × stocking-density interaction: for *Chironomus* larvae, $P < 0.001$ for age-1 effect, $P = 0.004$ for interaction; for small cladocerans, $P = 0.003$ for age-1 effect, $P < 0.001$ for interaction; for large cladocerans, $P = 0.004$ for age-1 effect, $P = 0.014$ for interaction; for ostracods, $P = 0.086$ for age-1 effect, $P = 0.079$ for interaction; for copepods, $P = 0.999$ for age-1 effect, $P = 0.783$ for interaction). Summarizing the ANOVA results, there were three different patterns to the changes with period and age-1 presence/absence (Figure 4). First, for both small and large cladocerans in period 2, the average numbers per age-0 stomach were greater in ponds containing age 1s than in ponds without age 1s, and the numbers *decreased* significantly from period 2 to period 3; this decrease was greater in ponds with age 1s. Second, for both copepods and ostracods, the average numbers per age-0 stomach *increased* significantly from period 2 to period 3; there were no differences due to age-1 stocking density. Third, for *Chironomus* larvae, a less-preferred prey item, the average number per stomach *increased* significantly from period 2 to period 3, especially in ponds with age-1 bluegills.

Growth of Age-1 Bluegills

The increase in age-1 biomass was similar in ponds with age-0 fish compared to those without age-0 fish (Table 1). In the two ponds stocked with age-1 bluegill at 5.6 kg/ha, the biomass of age 1s increased by a factor of 13. In the two ponds stocked with 16.8 kg/ha and the pond stocked with 23.5 kg/ha, the biomass of age 1s increased by a factor of 12 and 11, respectively. Therefore, age-0 bluegills did not have an appreciable negative effect on age-1 growth.

Fathead minnows

During pond draining, it became evident that fathead minnows *Pimephales promelas* had contaminated each pond. Biomass of fathead minnows was less than 1 kg/ha in seven experimental ponds (and the reference pond); biomass was 28.9 and 63.5 kg/ha in the other two ponds, both stocked with 0 age-1 bluegills (Table 1). In ponds stocked without age-1 bluegills, the combined spring biomass of fathead minnows and new bluegill recruits was remarkably similar in the three ponds with useable data at draining: 112.8, 104.3, and 108.9 kg/ha.

Discussion

Consistent with previous observations, this experiment demonstrated a strong negative effect of a high density ($\geq$16.8 kg/ha) of age 1s on age-0 bluegill recruitment. No age-0 bluegills were produced in the three ponds stocked with at least 16.8 kg/ha of age 1s. All four ponds without age 1s produced age-0 bluegills, with an average of 349,000 ha^{-1} ($N =$ 3) surviving to the following spring.

We examined a potential mechanism for the observed negative effect of age-1 bluegill on age-0 recruitment by testing the hypothesis that age 1s reduce the abundance of large cladocerans, thereby reducing growth of age-0 bluegills and their survival to the following spring. The results of this experiment allowed us to reject this full, compound hypothesis. But we cannot reject some parts of this hypothesis. There was a significant negative relationship between age-1 stocking density and number of new bluegill recruits present the next spring. But the cause does not appear to be a reduced abundance of large zooplankton. Regression analyses of zooplankton densities in period 1, when age-0 fish were not yet feeding, indicated that age-1 bluegill had a significant negative effect on both total zooplankton density and density of medium-sized zooplankton; the effect on large zooplankton was not quite significant. However, during period 2, when age-0 bluegills were present and growing rapidly, there was no

significant effect of age-1 stocking density on the density of large and medium zooplankton.

Age-0 bluegill growth was neither significantly lower in period 2 nor in period 3 in ponds with versus without age 1s (period 2: 1-tailed *t*-test, $P = 0.10$; period 3: 1-tailed *t*-test, $P = 0.49$). In contrast to our hypothesis, growth rates of age-0 bluegill were not dependent on the abundance of large zooplankton. Fast age-0 growth continued to the end of period 2 between 29 June and 9 July. This is 11 to 21 d after large zooplankton were depleted to an average of 6 L^{-1} on 18 June. When densities were at least 50 L^{-1}, the small (<0.40 mm) and medium (0.41-0.80 mm) zooplankton size classes supported a fast age-0 growth rate. This important age-0 bluegill food source, small and medium zooplankton, was not suppressed by age-1 bluegills (Figures 3f and 3j). In fact, in periods 2 and 3, higher levels of age 1s were associated with *higher* total zooplankton densities. Therefore, the observed negative effect of age 1s on age-0 recruitment could not be attributed to our hypothesis that competition for the large zooplankton food source reduced growth of age-0 bluegill and their survival to the following spring.

Miller et al. (1990) and Mills and Forney (1981) suggested that large zooplankton were essential for fast age-0 growth and survival. This is probably correct for many species, but the generalization is not supported by our bluegill data nor the experiments of Confer et al. (1990). Instead, our data show that rapid age-0 growth can be maintained on smaller zooplankton if the density is high enough.

Although we found no significant competition for food between age-1 and age-0 year classes, competition within the age-0 year class appears to reduce their growth. The age-0 growth rate remained fast through period 2 until the total zooplankton density decreased below approximately 50 L^{-1} between time periods 2 and 3 (Figure 2). The decline in all zooplankton is clearly the result of age-0 foraging, because this dramatic population flux only occurred in treatments with age-0 fish (Figures 3k and 3l). The rapid growth in age-0 length (Figure 1) is associated with a rapid increase in total cohort weight and food consumption, which eventually overwhelms production by the prey, producing a

rapid decline in prey abundance and subsequent slow growth of age-0 fish (Breck 1993). We observed that mean length and weight of age-0 bluegills in period 3 was highest in the treatment with age 1s, perhaps because these ponds had lower densities of age-0 bluegills; a difference in density was apparent at pond draining the following spring. Experiments in these ponds conducted by Latta and Merna (1977) also showed that age-0 bluegill growth is strongly related to age-0 density. Because a larger age-0 fish size at the end of the year may be important in reducing overwinter starvation mortality for centrarchids (Shuter et al. 1980; Shuter and Post 1990), reduced age-0 growth may be expected to reduce bluegill year-class strength in the following spring. However, all ponds with age-0 bluegills in summer 1990 had age 1s in April 1991. Moreover, ponds with the smaller-sized age-0 bluegills in August had the highest year-class strength the following spring. Therefore, overwinter survival does not appear to critically affect age-0 bluegill recruitment. Bluegill sunfish may be particularly vulnerable to stunting in part because of their propensity for overwinter survival despite a small size prior to winter.

Fathead minnows may have reduced reduced the recruitment of age-0 bluegills in ponds without age-1 bluegills. Schneider (1972) suggested that fathead minnows may reduce recruitment of age-0 yellow perch through competition for food. He conducted two experiments, both involving treatment of a lake with rotenone to remove all fish, followed by stocking with yellow perch. In the second experiment, a large population of fathead minnows was established before yellow perch were stocked. Fall density of age-0 yellow perch was lower (4,700 ha^{-1}) and length was smaller (53 mm TL) in the presence of the large population of fathead minnows than in the absence of fathead minnows (13,100 ha^{-1}; 69 mm TL). In our ponds at draining, there was a strong negative relationship between fathead minnow biomass and biomass of new bluegill recruits, but only in the ponds stocked without age-1 bluegill (Table 1).

$$Y = 112.81 - 1.134 \, X,$$

where Y is spring biomass of new bluegill recruits (kg/ha), and X is spring biomass of fathead minnows (kg/ha); $N = 3$, $r^2 = 1.000$. Lower and upper 95% confidence limits on the intercept and slope are 112.38 and 113.24, and -1.145 and -1.124, respectively. Though there are only three points, the relationship is strong enough to warrant further investigation of this interaction. In ponds with age-1 bluegills present, we suggest that predation by age-1 bluegills kept the fathead minnow population low. Predation by adult bluegills was not sufficient to keep the fathead minnow population low in all ponds.

Clearly, factors other than competition for food have a more dramatic effect in explaining the negative influence of age 1s on age-0 recruitment. Consider that in ponds with age-1 but no age-0 fish, total zooplankton density averaged 252 L^{-1} in period 2 (Figure 3j), and the minimum density in June was 136 L^{-1}, more than the 50 L^{-1} which would have allowed for fast age-0 growth and high survival (Figure 2) if age-0 fish had been present. Also, in ponds with age 1s, the average density of large zooplankton only increased to 0.4 L^{-1} at the end of period 1 (29 May) whereas they increased to 38 L^{-1} in ponds which also contained the age-0 bluegill (Figure 3b versus Figure 3c). The differences in large zooplankton density may have occurred because 5.6 kg/ha was not sufficient to suppress large zooplankton or because age 1s switched from large zooplankton to more profitable prey (Werner and Hall 1974, 1979), such as bluegill eggs, nest larvae, and exogenously feeding larvae in late May/early June. Such a foraging switch may have released large zooplankton populations from predation.

Predation by age 1s on eggs or free-swimming age-0 bluegill probably contributed to the age-0 recruitment reduction or failure observed in ponds with age 1s. Gray (1991) determined that age-1 bluegill (32-38 mm) can consume bluegill fry in aquaria at rates up to 110±19 prey·predator^{-1}·h^{-1} (mean±2 SE, $N = 11$) for 5.5±0.1-mm bluegill ($N = 6$), the size at which bluegill fry leave the nest and begin feeding (Toetz 1966). Age-0 vulnerability decreases rapidly with increasing fry size (Gray 1991), so that predation by age 1s would be most intense in the first few days of life. For

age-1 bluegill weighing 0.4 g, 16.8 kg of age 1s would number 42,000 individuals, or 10,500 fish if stocked at a rate of 16.8 kg/ha in 0.25-ha ponds. Feeding at this rate, 10,000 age-1 bluegill could consume 1,100,000 fry in 1 h, and many more in a day, easily capable of having a dramatic effect on year-class strength during the first few days after fry leave the nest.

A second mechanism which may reduce age-0 recruitment is that a high density of age 1s prevents adults from spawning. No age-0 bluegills were found in ponds stocked with age 1s at 16.8-23.5 kg/ha, although abandoned nests were observed in two of three ponds. Other studies have shown that reproduction of largemouth bass *Micropterus salmoides* can be partially or completely inhibited by high densities of sunfish, *Lepomis* spp., due to aggressive interspecific interactions (Barwick and Holcomb 1976; Smith 1976; Smith and Crumpton 1977).

When very large bluegill (>230 mm TL, predominantly males) are present in these ponds, spawning can be successful despite a high density of age 1s (Clark and Lockwood 1990). In fact, the density of these very large bluegills is more highly correlated with bluegill recruitment than is the density of the 25-50 mm size class. In our experiment, adult bluegill were only 100-150 mm TL at stocking. They may not have had the size or energy reserves required to spawn successfully despite possible interference from age 1s, or to defend eggs and fry in the nest from predation by age 1s.

The results of this experiment might be different in the presence of piscivores, but the difference would depend on piscivore sizes and numbers and on the response of the age-1 bluegill. Piscivores would be expected to reduce the density of age-1 bluegills, but an appreciable reduction in density might not happen until after bluegill reproduction had occurred. In that case the results might be similar to this experiment. If the presence of piscivores changed the behavior or habitat used by age-1 bluegills, the effect of age 1s on zooplankton and age 0s could be changed as well. The predatory effect of age-1 bluegills on

age 0s might be accentuated if the presence of piscivores caused the local density of age 1s to increase in the vicinity of bluegill nests.

There are several management implications of this study. First, keeping the density of juvenile bluegills low should help prevent missing year classes and favor consistent recruitment. Second, age-0 bluegills can grow well, at least for the first few weeks, on diet of zooplankton if the zooplankton density is greater than 50 L^{-1}. Finally, there is a possibility that fathead minnows may have a negative effect on age-0 bluegills in pond systems.

In conclusion, bluegill are prone to stunting partly because age-0 fish can maintain fast growth even with zooplankton densities as low as 50 L^{-1}. Age-0 bluegill growth is density-dependent, but reduced age-0 growth does not cause massive overwinter mortality even though it may reduce year-class strength. Year-class failure in this experiment was seen only in the ponds receiving the highest densities of age 1s (16.8-23.5 kg/ha), and was most likely due to predation on eggs or larvae. These observations help explain large variations in year-class strength of some stunted bluegill populations. Moreover, they suggest that management strategies which affect age-0 survival have a disproportionate chance of reducing bluegill year-class strength.
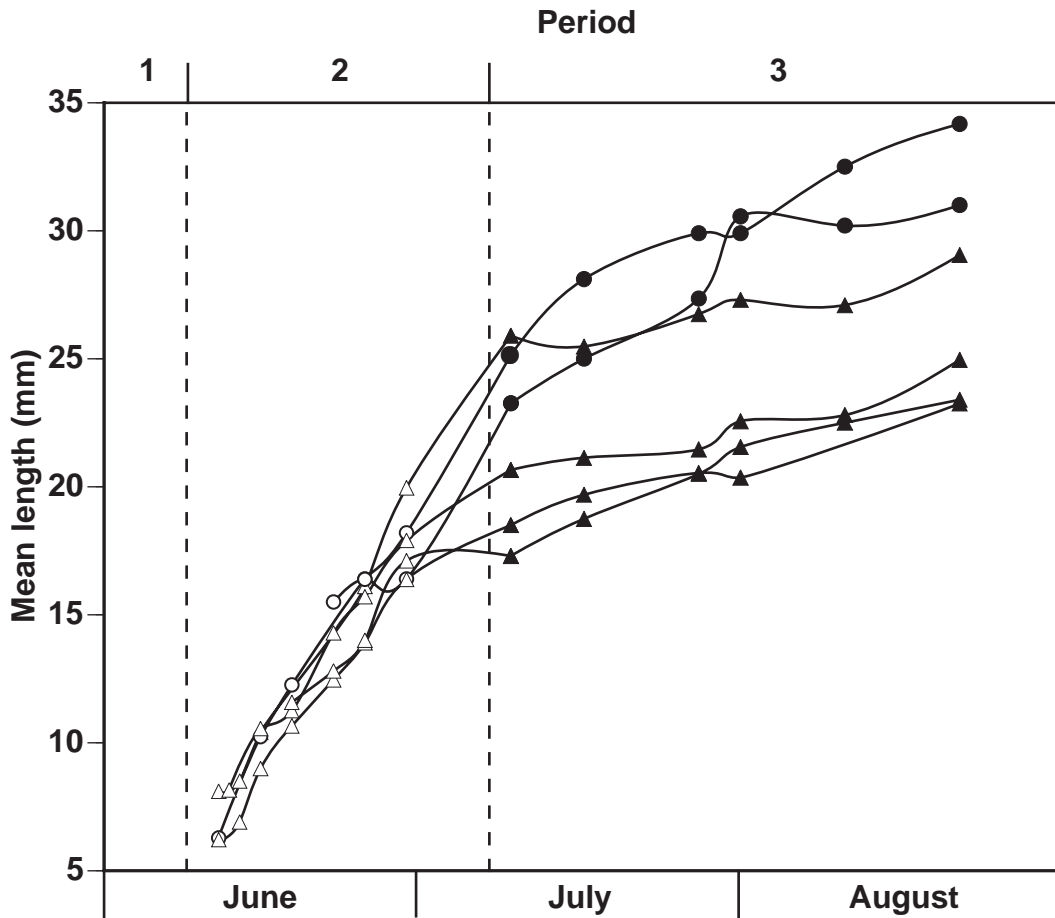
Figure 1.–Mean total lengths of the first natal cohort of age-0 bluegills during period 2 and period 3. Key to symbols: age-1 bluegill stocking densities of 0 kg/ha (triangle); 5.6 kg/ha (circle): open symbols indicate period 2, solid symbols indicate period 3. Average SD of length was 0.67-0.80 mm in period 2 and 1.44-2.60 mm in period 3.
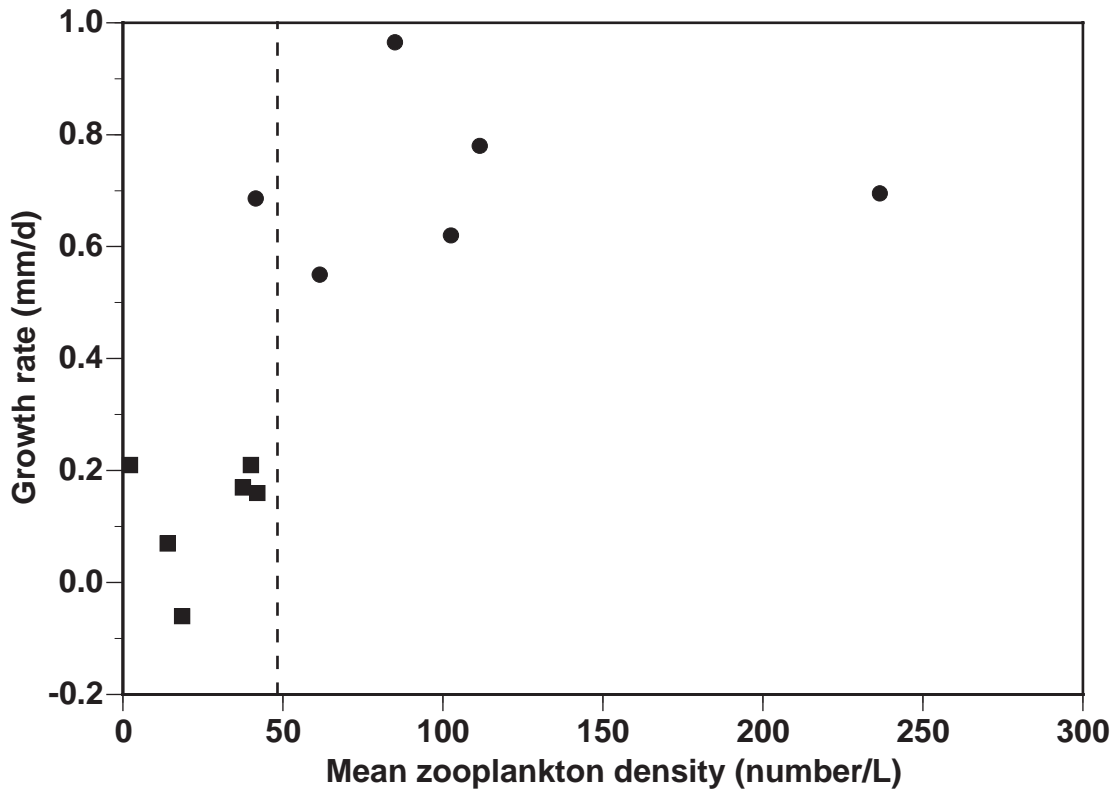
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Figure 2.–Growth rate of the first natal cohort of age-0 bluegills as a function of mean total zooplankton density (excluding rotifers) during the final two sampling dates of period 2 (25 and 29 June, 1990) and the first two sampling dates of period 3 (9 and 16 July, 1990). End of period 2:(circle); start of period 3 (square).
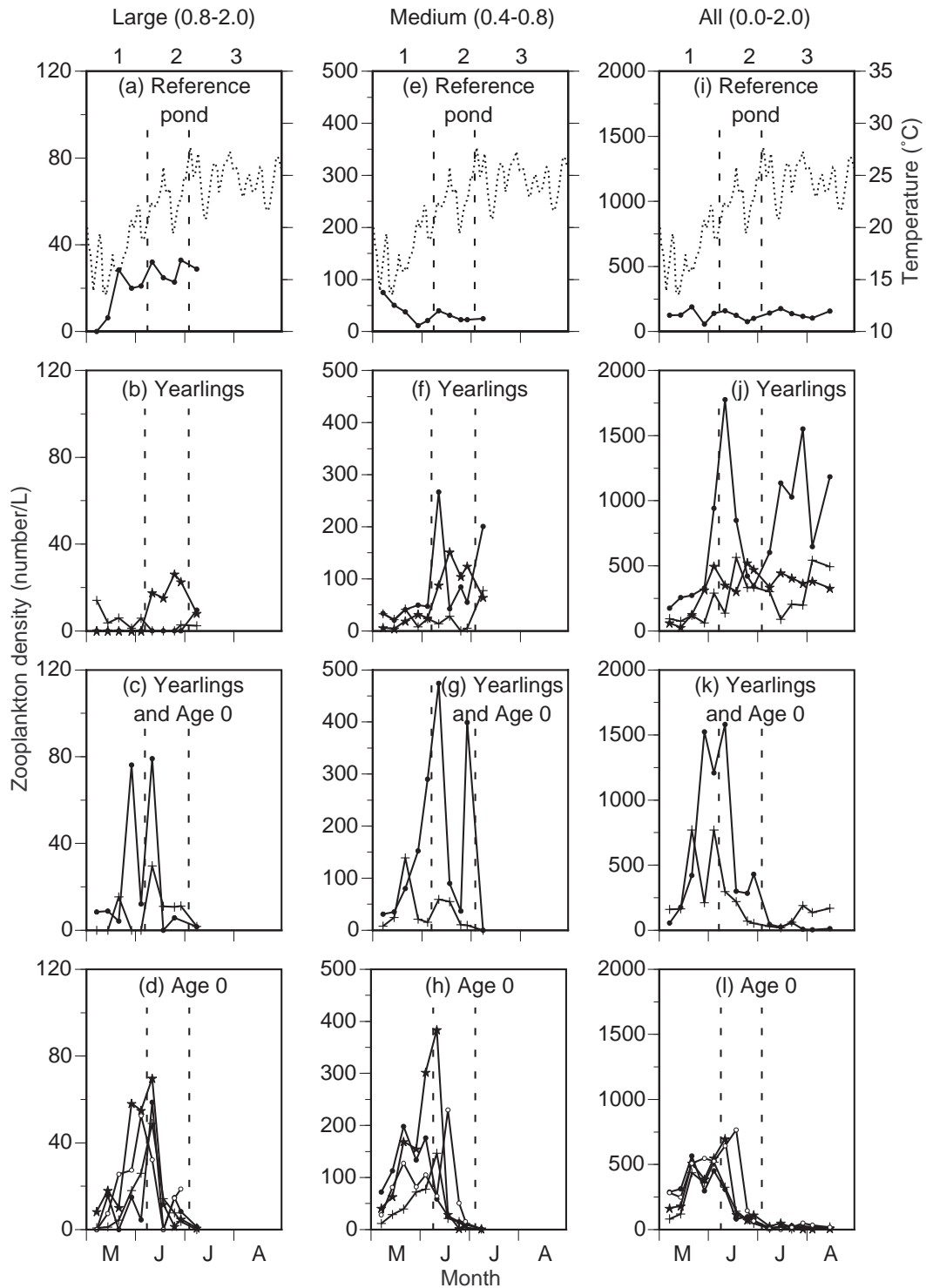
Figure 3.–Changes in density of zooplankton during spring and summer in ponds containing various combinations of adult, age-1 and age-0 bluegill. Vertical lines indicate three time periods during which the zooplankton population flux differed due to the type of fish combination present. The left-hand column shows changes through time for large zooplankton (0.81-2.00 mm); the middle column for medium zooplankton (0.41-0.80 mm); while changes in total zooplankton (excluding rotifers) are shown on the right. The dotted line indicates water temperature and the symbols indicate zooplankton levels for individual ponds. Symbol (star) in panels b, f, and j indicates the pond stocked with age 1s at 23.5 kg/ha.

Period two

Period three

(a) without age-1 bluegill

(b) with age-1 bluegill

Mean number consumed

Chironomus Ostracods Copepods Large cladocerans Small cladocerans

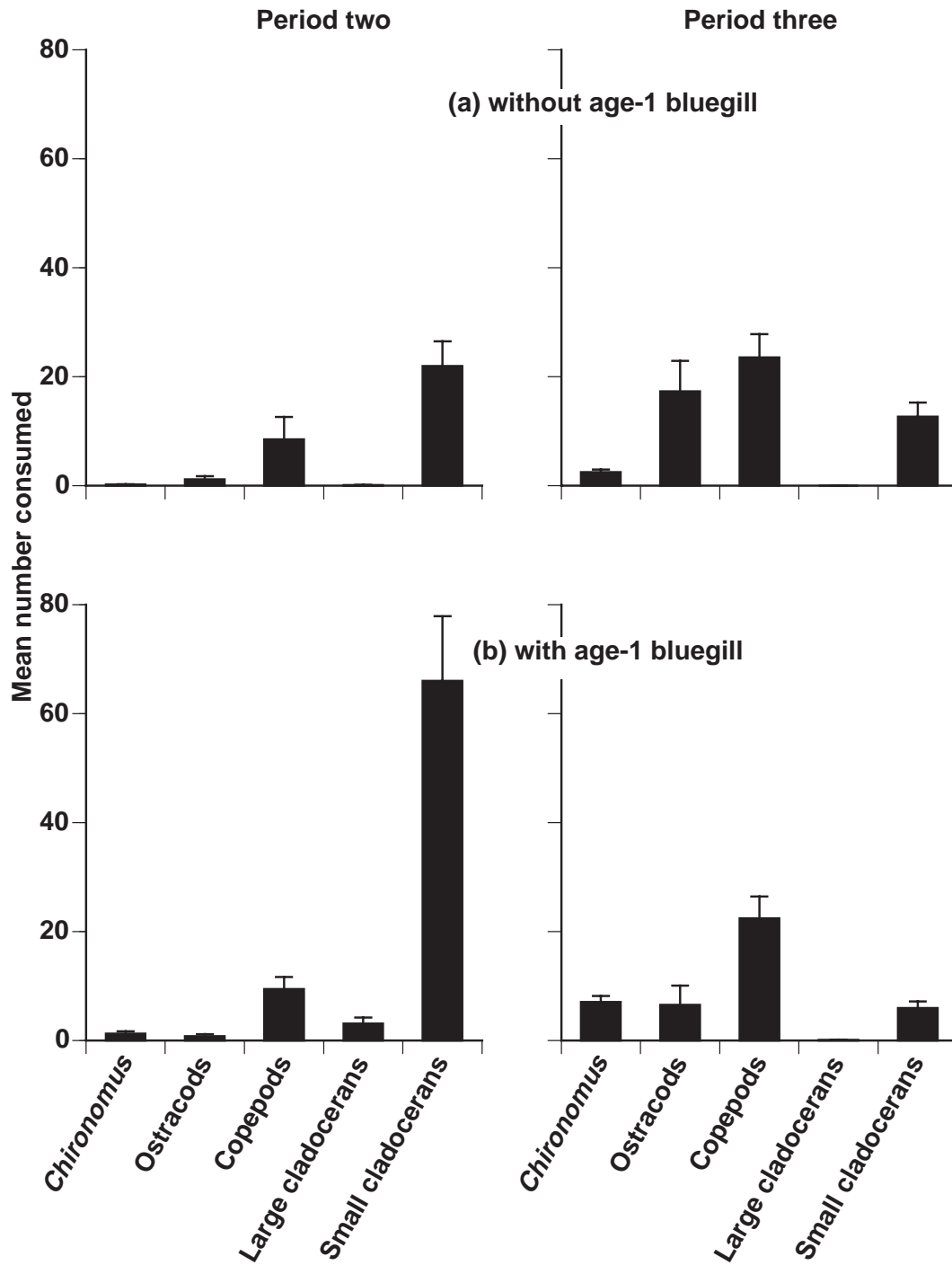*Chironomus* Ostracods Copepods Large cladocerans Small cladocerans

Figure 4.–Mean number (+1 SE) of prey per stomach for age-0 bluegills growing in (a) the absence and (b) the presence of age-1 bluegills during periods 2 and 3, for five prey types. Large cladocerans include *Daphnia* and *Diaphanosoma*. Small cladocerans include *Bosmina*, *Ceriodaphnia*, and *Chydorus*.

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Table 1.–Final size and density of age-1 and age-2 bluegills and fathead minnows at pond draining. Treatment ponds were drained in April 1991; the reference pond was drained December 7, 1990.

Treatment (Age-1 density, kg/ha)	Pond number	Pond area (ha)	Age 1 bluegill					Age 2 bluegill			Fathead minnow density (kg/ha)
			Mean weight (g)	Length Mean±SD (mm)	Mode (mm)	Density (number/ha)	(kg/ha)	Mean weight (g)	Density (number/ha)	(kg/ha)	
0	5	0.30	0.236	26.2±4.2	25	476,000	112.6		0	0	0.2
0	9	0.27	0.236	26.1±3.8	25	173,000	40.8		0	0	63.5
0	11	0.10	0.286	27.4±5.1	25	[a]	[a]		0	0	[a]
0	15	0.29	0.202	25.9±3.1	24	396,000	80.0		0	0	28.9
5.6	10	0.25	0.500	33.0±6.4	27	169,000	84.5	11.18	6,410	71.7	0.9
5.6	17	0.24	0.369	30.6±4.2	27	143,000	52.8	6.93	10,920	75.7	0.2
16.8	2	0.16				0	0.0	6.49	30,140	195.6	0.3
16.8	18	0.20				0	0.0	9.08	22,800	207.1	0.1
23.5[b]	8	0.25				0	0.0	6.34	41,500	263.4	0.5
Reference	7	0.26				0	0.0	92.88[c]	200[c]	18.6[c]	0.0

[a] An unknown number of fish were lost at draining when a failure of the drain gate mechanism forced use of a pump to empty Pond 11; however, 31,000 age-1 bluegill per ha or 8.9 kg/ha and 0.1 kg/ha of fathead minnows were recovered at draining.

[b] Due to a stocking error, Pond 8 received additional 4.5 kg of age 1s intended for Pond 9.

[c] An additional 44 bluegills (169 per ha) weighing 2.69 kg (10.3 kg/ha, mean weight = 61.1 g) had been removed from the reference pond in August 1990.

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