Fish Size and Prey Availability Affect Growth, Survival, Prey Selection, and Foraging Behavior of Larval Yellow Perch

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Abstract.—Zooplankton availability is strongly linked with the growth, survival, and ultimately recruitment of fish during their early life history. We examined how different types of zooplankton affected the growth, survival, and prey selection of larval yellow perch *Perca flavescens* in a series of laboratory experiments. The growth and survival of newly hatched (5–7-mm) to 12-mm yellow perch larvae was greatest when feeding on adult copepods and copepod nauplii. The growth and survival of yellow perch larvae longer than 12 mm was greatest when feeding on adult copepods and small cladocerans. Prey selection patterns closely followed trends in growth and survival; smaller larvae positively selected adult and naucliar copepods, whereas larger larvae selected adult copepods and small cladocerans. Foraging behavior experiments conducted with larvae longer than 12 mm revealed that these fish derived similar energetic gains when feeding solely on adult copepods and small cladocerans. The pathway to this energetic benefit differed substantially between prey types. Adult copepods yielded substantial energy to larval yellow perch because of the minimal handling time involved, despite the lower capture efficiency than with cladocerans. Conversely, yellow perch larvae realized high energetic gain from small cladocerans because of high capture efficiency, despite the higher handling times than with adult copepods. These results illustrate the importance of experimentally quantifying the feeding behavior of fish larvae to gain insight into how larval fish behavior and food type interact to shape larval fish growth patterns.

Understanding the mechanisms influencing recruitment has long been a goal in fisheries ecology. Of interest from a management perspective is the ability to predict year-class strength and set harvest regulations accordingly. Furthermore, identifying recruitment mechanisms will improve our understanding of community structure and species distributions (Bremigan and Stein 1994). Recruitment success in fish is often determined during their early life history (Rice et al. 1987) because most fish experience very high mortality during this life stage (Houde 1994). Although numerous mortality sources act on the early life stages of fish, predation and starvation are generally viewed as the two most ubiquitous ones (Houde 1987; Miller et al. 1988). Both predation and starvation are size dependent (Miller et al. 1988) and strongly interact with growth rate, such that higher growth rates may reduce starvation and predation (Houde 1987; Miller et al. 1990) whereas lower growth rates increase mortality from these sources. Thus, understanding the factors influencing growth during the early life history of fish is important to understanding recruitment and ultimately to achieving better fishery management.

Growth in larval fishes is strongly influenced by the availability of appropriate food items (Welker et al. 1994). Many larval fish rely on small zooplankton as prey due to limited gape width (Bremigan and Stein 1994; DeVries et al. 1998) and reduced visual acuity (Wahl et al. 1993). However, different species of zooplankton differ markedly in morphology and behavior. For example, cladocerans and copepods (two groups commonly ob-

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served in the diets of larval fish) have different swimming patterns and morphology. Copepods are cylindrical with a fairly uniform body width and swim along a smooth path (calanoid copepods) or in a "hop-and-sink" manner (cyclopoid copepods) (Kerfoot et al. 1980). Both of these copepods swim faster and are more evasive than the spherically shaped cladocerans, which move by small jumps through the water column. Furthermore, capture success is generally higher for fish feeding on cladocerans than for fish feeding on copepods (Drenner et al. 1978; Mills et al. 1984). Thus, zooplankton of similar lengths may provide variable energetic benefits to larval fish based on the efficiency with which the fish can capture them.

Despite the importance of larval fish growth and survival in determining eventual recruitment, many studies that have experimentally quantified the relationship between food availability and the growth, survival, prey selection, and feeding ecology of young freshwater fishes have focused on larger juvenile stages (i.e., >20 mm; but see Mayer and Wahl 1997). Although studies of juvenile fish provide important information, they may not be applicable to larvae because of the large morphological and physiological differences between larvae and later life stages (e.g., the former have less gape width, visual acuity, and swimming ability). For example, laboratory experiments and field studies indicated that juvenile yellow perch *Perca flavescens* and bluegills *Lepomis macrochirus* positively selected large cladocerans (Werner and Hall 1974; Mills et al. 1984; Bremigan and Stein 1994). Yellow perch and bluegills also experienced high growth and survival when these prey were abundant, and foraging experiments revealed that cladocerans were energetically more favorable than other prey items. Conversely, most fish larvae have a much smaller gape width and consume smaller zooplankton prey (such as copepods) in the field, suggesting that the role of a particular species of zooplankton is very different for larval fish than for juveniles (Keast 1980; Schael et al. 1991; Fisher and Willis 1997). However, the relationship between zooplankton taxonomic composition and the growth, survival, prey selection, and feeding ecology of most larval fish has not been experimentally quantified. Thus, laboratory experiments that mechanistically examine the role of zooplankton group in influencing the growth, survival, and ultimately recruitment of larval fish are needed to understand recruitment during this critical stage.

One reason for the paucity of studies that mechanistically examine the role food availability plays in larval fish growth and survival is the difficulty of conducting experiments on such a small life stage. Larval fish experience very high natural mortality (Houde 1994), and maintaining appropriate prey levels requires much time and effort (Chick and Van Den Avyle 1999). Further, observing larval fish during foraging experiments is difficult because of their small size and the small size of their prey items (Mayer and Wahl 1997). Despite these difficulties, we investigated how zooplankton group affects the growth, survival, and prey selection of larval yellow perch among several discreet size-classes of larvae.

We chose to work with larval yellow perch because food availability may be a factor in the reduced recruitment of yellow perch in Lake Michigan since 1989. Changes in the zooplankton assemblage, including reduced zooplankton density and a shift in taxonomic composition, may have acted to decrease the growth and survival of larval yellow perch (Francis et al. 1996). The recruitment of larval yellow perch is thought to be affected by lower survival at low zooplankton densities (Dettmers et al. 2003). Furthermore, yellow perch longer than 20 mm positively select cladocerans, growing best when the latter are abundant (Hansen and Wahl 1981; Mills and Forney 1981; Mills et al. 1989). Little is known, however, about how zooplankton taxonomic composition affects the growth and survival of yellow perch shorter than 20 mm. For this reason, we conducted a series of laboratory experiments that quantified the role of zooplankton availability in structuring larval yellow perch growth and survival.

We began by quantifying the growth and survival of four size-classes of larval yellow perch feeding on different types of zooplankton (i.e., cladocerans, copepods, and rotifers). We then conducted prey selection experiments to determine whether larval yellow perch chose prey items that conferred the best growth. Finally, we quantified the foraging efficiencies of yellow perch larvae to determine the energetic costs of different zooplankton groups and to help explain trends in growth, survival, and prey selection.

Methods

We conducted experiments on four size-classes of larval yellow perch—newly hatched (5–7 mm), small (7–12 mm), medium (12–16 mm), and large (>16 mm)—to account for important ontogenetic changes that occur during early life history, such as first feeding and swim bladder inflation. Because mortality for these sizes can be high, pre-

liminary work suggested that the best approach would be to conduct a series of independent experiments for each size-class of larvae. This design allowed us to characterize the ontogenetic stages in which the preferred zooplankton prey are important to growth and survival.

Yellow perch egg skeins collected from Lake Michigan during late May and early June 2001 were hatched and larvae reared on a diet of brine shrimp *Artemia* spp. and mixed zooplankton in laboratory facilities at the Lake Michigan Biological Station, Zion, Illinois. All experiments were conducted under controlled laboratory conditions, with a photoperiod of 12 h light: 12 h dark and a water temperature of 18.9 ± 0.1°C (mean ± SE). The zooplankton used in our experiments were cultured on site but supplemented with zooplankton from Lake Michigan as needed. Rotifers *Brachionus* spp. were cultured separately. To establish zooplankton treatments, we separated cladocerans and adult copepods from copepod nauplii using 153-µm-mesh sieves.

Growth and survival.—To determine the effect of zooplankton group on larval yellow perch growth and survival, we conducted experiments using the following treatments replicated five times each: cladocerans, adult copepods, copepod nauplii, rotifers, and a foodless control. Common taxa in these groups included rotifers *Brachionus* spp., cladocerans *Ceriodaphnia* and *Bosmina* spp., and cyclopoid and calanoid copepods (both adults and nauplii). Lengths for these groups were as follows: cladocerans, 0.55 ± 0.02 mm (n = 110); copepods, 0.98 ± 0.02 mm (n = 109); copepod nauplii, 0.18 ± 0.004 mm (n = 98); and rotifers, 0.21 ± 0.01 mm (n = 30). Rotifers were included only in experiments with newly hatched larvae because such prey were never observed in the diets of larvae during a pilot study of yellow perch prey selection (Graeb, unpublished data). In contrast, rotifers have been observed in the diets of small larval yellow perch in the field (Whiteside et al. 1985). Thus, 25 aquaria (our experimental unit) were used for the newly hatched yellow perch size-class, and 20 aquaria were used for the small, medium, and large size-classes.

Yellow perch from each size-class (n = 150–200 newly hatched larvae, 75 small larvae, 5 medium larvae, and 1 large larva) were held in 38-L aquaria with randomly assigned zooplankton treatments. The number of larvae used in each replicate changed according to the size-class involved (smaller larvae had higher mortality, requiring more larvae per replicate) and availability (normal

mortality resulted in fewer fish being available at larger size-classes). The treatment densities of the zooplankton were maintained at or above 75 individuals/L; we considered this food level to be ad libitum for larval yellow perch based on the asymptote of a functional response for larval walleyes *Sander vitreus* (formerly *Stizostedion vitreum*) consuming zooplankton (Johnston and Mathias 1994). Treatment densities were estimated every 1–3 d using a polyvinyl chloride tube sampler with an inner diameter of 47 mm. Zooplankton were added every 1–2 d to ensure that zooplankton densities remained at or above 75/L (zooplankton densities were rarely below 75/L).

To ensure that newly hatched larvae experienced their first feeding during the experiment, we divided six fertilized egg skeins into approximately equal portions of 175 eggs and allowed them to hatch in randomly assigned aquaria. Aquaria were inoculated with zooplankton treatments after larvae hatched. The experiment started at 2 d posthatch to allow for partial (but not complete) yolk sac absorption. Prior observations showed that newly hatched larvae begin exogenous feeding shortly before the yolk sac is completely absorbed. Initial sizes were determined by either sacrificing larvae at 2 d posthatch (newly hatched larvae) or by sub-sampling 50 individuals at the start of each experiment (larger larvae). Up to five larvae were sacrificed daily to determine growth in experiments with newly hatched and small larvae because these size-classes experienced high mortality. The duration of the experiment was 6 d for the newly hatched size-class, 9 d for the small size-class, and 10 d for both the medium and large size-classes. Analysis of variance (ANOVA) was used to analyze average growth rate (mm/d), and Tukey's honestly significant difference test was used to separate treatment means.

The survival of yellow perch larvae was measured concomitantly with growth. Surviving larvae were counted every morning 2 h after the start of the light period using a small, narrow-beam flashlight. Life tables were generated from these data. Survival functions were then fitted to each size-class and treatment combination (fish that we removed were censored). Cumulative survivorship was analyzed among treatments by means of Wilcoxon chi-square tests. If at least one treatment differed from the others, we separated the survival curves (cumulative survivorship) using the covariance matrix from the Wilcoxon statistics to calculate Z-scores for individual pairwise com-

parison (Fox 1993). Pairwise comparisons were conducted at an overall significance level of 0.05.

Prey selection.—Yellow perch were starved for at least 12 h and then introduced into 38-L glass aquaria that were inoculated with equal densities (50/L each) of cladocerans, adult copepods, copepod nauplii, and rotifers (the latter for newly hatched larvae only). Black plastic was attached to three sides of all aquaria; fluorescent lighting was mounted above the aquaria to increase prey contrast. Larvae were allowed to feed for 1 h and then euthanatized and preserved in a 95% solution of ethanol. Equal prey densities were chosen to give each yellow perch an equal opportunity (by number) to consume a given prey item. Up to five larvae were used per trial for the newly hatched and small size-classes because of the prevalence of empty stomachs among these size-classes; one larva was present during each trial with medium and large larvae. We conducted 10 feeding trials for newly hatched larvae, 72 for small larvae, 8 for medium larvae, and 17 for large larvae. The number of replicate trials varied across size-classes based on the availability of appropriately sized yellow perch. More trials were conducted on smaller larvae to overcome the high occurrence of empty stomachs that we observed in larvae less than 12 mm. Digestive tracts were removed for enumeration and measurement of prey items with a dissecting microscope and digitizing tablet. Prey selectivity was estimated by calculating Chesson's (1983) coefficient of selectivity,

$$\alpha = \frac{r_i/n_i}{\sum_{i=1}^{m}(r_i/n_i)},$$

where r_i is the proportion of food type i in the predator diet, n_i is the proportion of food type i in the environment, and m is the number of prey types available. Selection coefficients were calculated for each fish, but mean values were pooled for each trial. For each size-class, mean selection coefficients and 95% confidence intervals were compared with random feeding ($1/m$) to determine prey selectivity. We concluded that there was positive selectivity if the 95% confidence intervals were above the random-feeding line, neutral selectivity if the 95% confidence intervals overlapped the random-feeding line, and negative selectivity if they were below the random-feeding line.

Feeding behavior.—We quantified capture efficiency and handling time for medium and large larvae feeding on cladocerans and copepods. At-tempts to observe smaller larvae and smaller prey items such as copepod nauplii were unsuccessful because we could not discern successful captures. A single yellow perch was placed in a 4-L rectangular feeding arena blackened on three sides. After an acclimation time of 1.5 h, 10 prey items (copepods or cladocerans) were introduced into the arena. Strikes, captures, and handling times were then observed for 30 min. Five replicate trials were conducted on each zooplankton group and size-class combination, for a total of 20 trials. Capture efficiency (the number of captures per strike) was averaged for each trial. Handling time (the time required to begin active searching after a capture event) was recorded for the first capture event only to avoid interactions between handling times and gut fullness. Capture efficiency was analyzed with a two-factor (larva size and zooplankton group) ANOVA; handling time was analyzed with the Wilcoxon rank sums test because these data were nonnormal.

To quantify more explicitly the energetic benefit of each zooplankton group to perch larvae, we determined the relative benefits (calories) and costs (handling time and capture efficiency) for the medium and large larval yellow perch feeding on cladocerans and copepods. We first determined the average length ($\pm$SE) of the zooplankton group chosen by the two size-classes of larvae from the selection experiments (n = approximately 50 prey items from the diets of randomly chosen fish). For the medium larvae, cladoceran length was 0.73 $\pm$ 0.05 mm and copepod length 0.61 $\pm$ 0.08 mm; for the large larvae, cladoceran length was 0.94 $\pm$ 0.06 mm and copepod length 0.59 $\pm$ 0.03 mm. Then we converted these lengths into biomass based on length–weight regressions from Bottrell et al. (1976). Using our estimated biomass, we determined the number of calories per individual zooplankton based on caloric densities from Cummins and Wuycheck (1970). These caloric values were combined with the average capture efficiency and handling times to estimate the number of calories gained per strike and the number of calories gained per second of handling time by medium and large yellow perch larvae feeding on cladocerans and copepods. Finally, we compared the estimates of net energetic gain using a two-factor (size and prey type) ANOVA. Treatments were separated using least-square means and Bonferroni adjustments when needed.

Results

Growth

Zooplankton group influenced the growth of yellow perch larvae across all size-classes. Newly
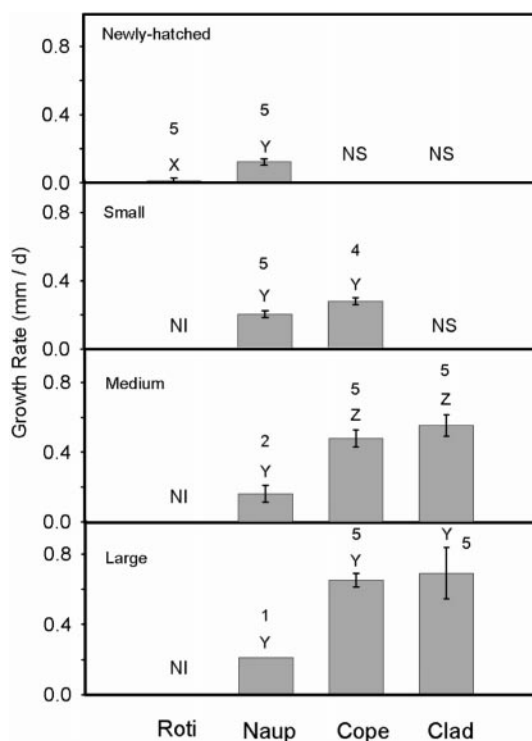
FIGURE 1.—Mean growth rate ($\pm$SE) of newly hatched (5–7-mm), small (7–12-mm), medium (12–16-mm) and large (>16-mm) larval yellow perch feeding on different zooplankton. Abbreviations are as follows: Roti = rotifers, Naup = copepod nauplii, Cope = adult copepods, Clad = cladocerans, NS = no survivors, and NI = not included. The duration of the experiment was 6 d for the newly hatched larvae, 9 d for the small larvae, and 10 d for the medium and large larvae. Sample sizes are noted above the bars; significant differences in growth within each size-class are denoted by different letters.

hatched larvae experienced greater growth ($F_{1,8}$ = 12.94, $P < 0.001$) when feeding on copepod nauplii than on rotifers (Figure 1). Newly hatched larvae in the control, cladoceran, and adult copepod treatments did not survive for the duration of the experiment; these larvae exhibited little or no growth during the time they were alive. For the small yellow perch larvae, growth did not differ when consuming copepod adults or copepod nauplii ($F_{1,7}$ = 4.25, $P = 0.08$; Figure 1). Small larvae in the cladoceran and control treatments did not survive the experiment. The growth of medium larvae also differed across treatments ($F_{2,9}$ = 10.72, $P < 0.001$), cladocerans and adult copepods providing higher growth than copepod nauplii (Figure 1). Large larvae in the copepod nauplii treatment also grew less than larvae in the cla-

doceran and adult copepod treatments even though the differences were not statistically significant ($F_{2,8}$ = 0.54, $P = 0.61$; Figure 1). This result occurred because four out of the five replicates in the copepod nauplii treatment did not survive the experiment. Furthermore, the low growth rate observed in the one surviving replicate was similar to the growth rate of medium larvae in the copepod nauplii treatment (which did have replication and had a statistically lower growth rate than the cladoceran and adult copepod treatments). Thus, the growth rates of medium and large larvae were consistently high when feeding on cladocerans and adult copepods but lower when feeding on copepod nauplii.

Survival

Zooplankton group influenced the survival of newly hatched larvae (Wilcoxon χ^2 = 165.3, df = 4, $P < 0.0001$). However, the patterns of survival were not always consistent with the patterns observed in the growth experiment. Although newly hatched larvae in the cladoceran and copepod treatments did not survive for the duration of the experiment, their cumulative survivorship function did not differ from that of larvae from the copepod nauplii treatment (pairwise comparison of the cladoceran and copepod treatments: Z = 0.91, $P = 0.18$; pairwise comparison of the cladoceran and copepod nauplii treatments: Z = 1.58, $P = 0.06$; Figure 2). Conversely, even though larvae in the rotifer treatment survived for the duration of the experiment, their survival was about as poor as that of larvae in the control treatment (Z = 0.26, $P = 0.40$).

Zooplankton group also influenced the survival of small larvae (Wilcoxon χ^2 = 78.5, df = 3, $P < 0.0001$), but the patterns were as expected based on growth. Larvae in the copepod adult and nauplii treatments had similar high survival (Z = 0.24, $P = 0.41$) as well as the highest growth rate, whereas larvae in the cladoceran and control treatments had similar poor survival (Z = 0.31, $P = 0.39$) and the lowest growth rate (Figure 2). Survival in the medium and large size-classes was also influenced by zooplankton group (Wilcoxon χ^2 = 68.83 and 14.80, $P < 0.0001$ and 0.002, df = 3 for the medium and large size-classes). Survival was high for both of these size-classes when feeding on small cladocerans and adult copepods (Z = 1.19 and 0.00, $P = 0.12$ and 0.50). Larvae in these size-classes that fed on copepod nauplii survived either slightly better than (medium size-class; Z = 3.48, $P = 0.0002$) or similar to (large size-class;
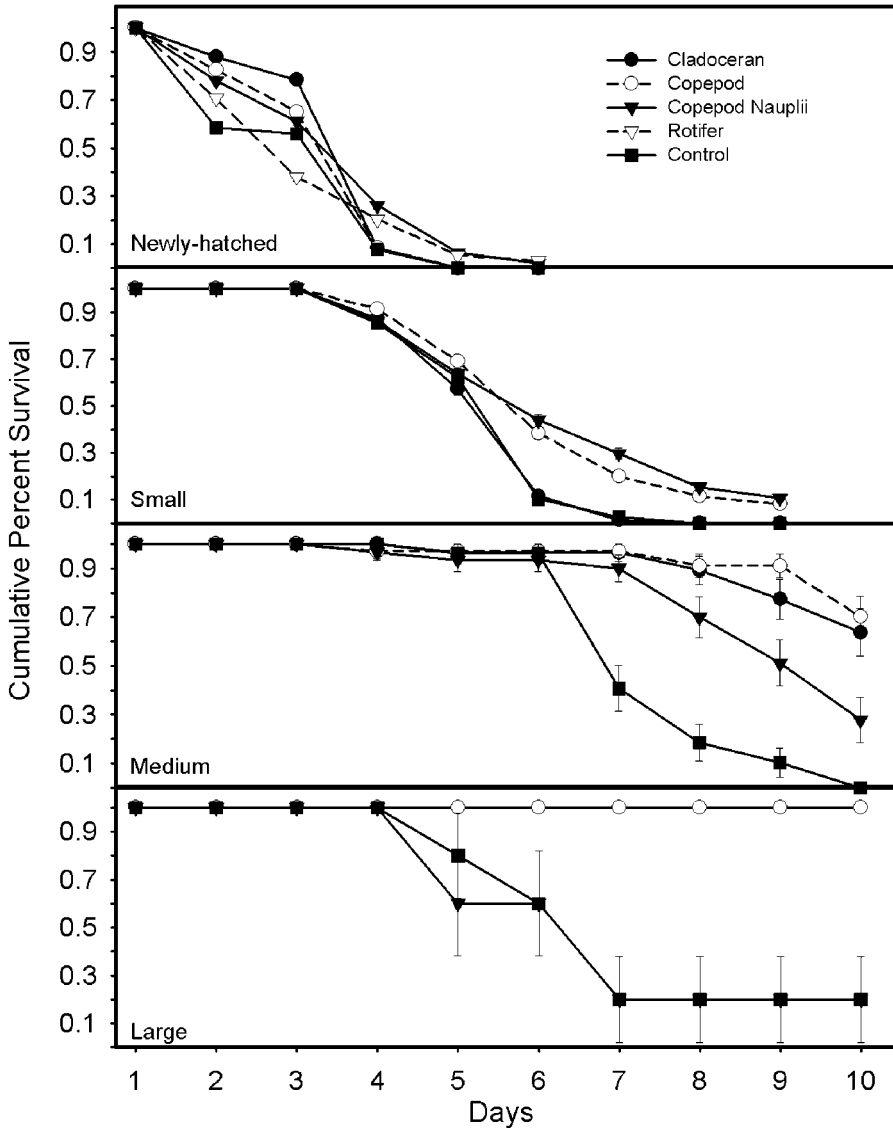
FIGURE 2.—Average cumulative survival (±SE) of newly-hatched, small, medium, and large larval yellow perch feeding on different zooplankton groups and a foodless control. See the caption to Figure 1 for size-class definitions and other details.

$Z = 0.25$, $P = 0.40$) larvae in the control treatment (Figure 2). Overall, the zooplankton group that promoted the highest survival shifted during the early life history of yellow perch; initially, survival was best when feeding on copepods, both adult and naupliar, but then shifted to cladocerans along with adult copepods; survival decreased when feeding on copepod nauplii.

Prey Selection

Yellow perch larvae generally selected prey that resulted in the best growth and survival. Although there was high variation because of the small sample size (few newly hatched larvae had prey items in their digestive tracts), newly hatched larvae neutrally selected copepod nauplii and adult copepods (Figure 3). Cladocerans and rotifers were never encountered in the diets of newly hatched larvae. Small larvae positively selected adult copepods but negatively selected copepod nauplii even though growth and survival were similar between these two treatments. Cladocerans were also observed in the diets of small larvae, although they
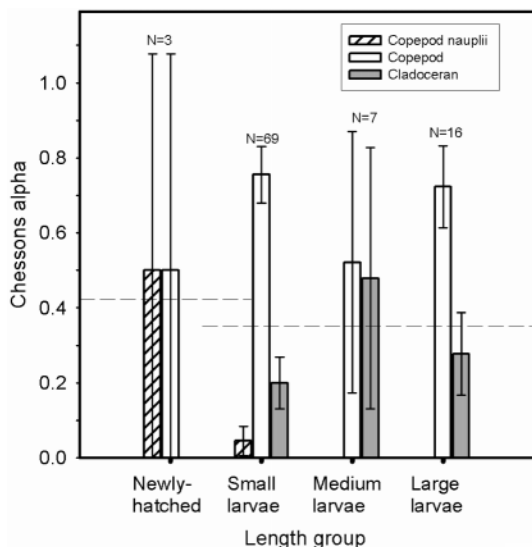
FIGURE 3.—Mean prey selection by larval yellow perch in different size-classes as determined by Chesson's alpha (see text for definition). When the 95% confidence interval (vertical line) lies above the random-feeding (dashed) line, there is positive selection for that prey; when it lies below the line there is negative selection; and when it crosses the line there is neutral selection. The random-feeding line for the newly hatched larvae is different from that for the other larval size-classes because four prey groups were available for newly hatched larvae but only three for the others. Sample sizes (i.e., the number of larvae with diet items in the stomach) are noted above the size-classes.
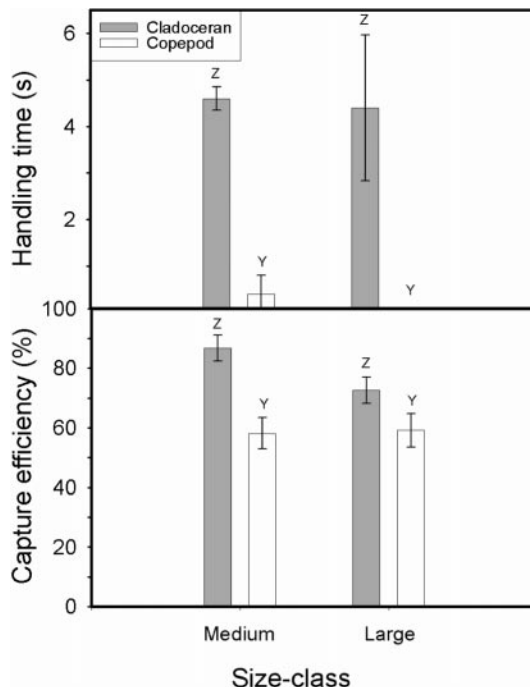

FIGURE 4.—Handling time (i.e., the time from successful capture of the prey to the resumption of searching) and percent capture efficiency (number of captures per strike $\times$ 100) for medium (12-mm) and large (16-mm) yellow perch larvae foraging on cladocerans and copepods. Significant differences are denoted by different letters.

were negatively selected. Medium larvae exhibited neutral selection for both adult copepods and cladocerans but negatively selected copepod nauplii. Large larvae positively selected adult copepods and neutrally selected cladocerans. Overall, adult copepods were neutrally or positively selected across all yellow perch sizes. Selection for copepod nauplii decreased with increased larval fish size, whereas selection for small cladocerans increased.

Feeding Behavior

Capture efficiency by medium and large larvae was higher for cladocerans than for copepods ($F_{1,16}$ = 17.97, $P < 0.01$; Figure 4) but did not differ between the two size-classes ($F_{1,16}$ = 1.76, P = 0.20). Handling time for cladocerans by both the medium (4.7 s) and large size-classes (4.4 s) was consistently higher than for copepods (<1 s for medium larvae and undetectable (recorded as 0 s) for large larvae; $F_{1,16}$ = 30.76, $P < 0.01$; Figure 4). Thus, the higher capture efficiency and higher

handling time for cladocerans than for copepods suggest that these two prey items provide similar energetic benefits. The net energetic gain (calories consumed per unit of cost) also supported the idea that cladocerans and copepods provided similar energetic benefits. The net energy gained during a single capture event was similar for cladocerans and copepods when both capture efficiency and handling time were considered. Calories gained per second of handling time was higher for copepods than for cladocerans ($F_{1,16}$ = 14.41, P = 0.02; Figure 5). These differences were similar across size-classes (main effect of larva size: $F_{1,16}$ = 3.17, P = 0.09). Calories gained per strike was significantly affected by the interaction of larva size and prey type ($F_{1,16}$ = 27.69, $P < 0.0001$). Yellow perch larvae in the medium size-class feeding on cladocerans gained more calories per strike than large larvae feeding on cladocerans and both size-classes feeding on copepods (t = 4.63–6.84, df = 16, P = <0.001–0.0017; Figure 5). Large larvae feeding on cladocerans gained similar numbers of calories per strike as medium (t = 1.6,
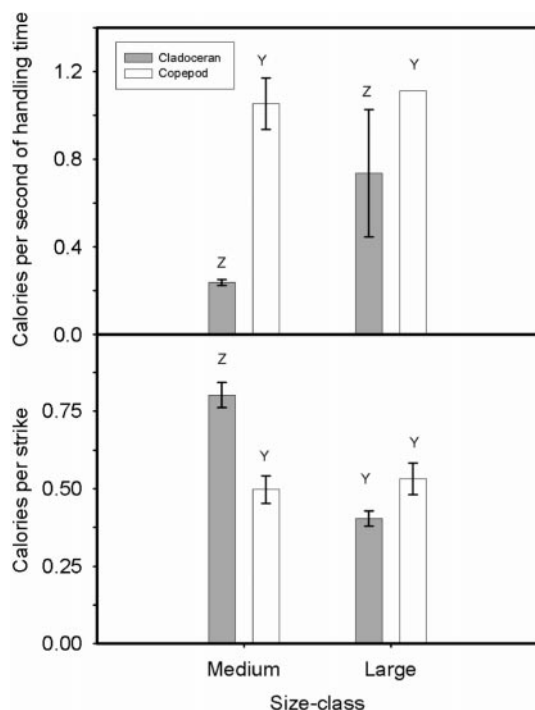
FIGURE 5.—Net energetic gain for medium (12-mm) and large (16-mm) yellow perch larvae feeding on cladocerans and copepods. Mean calories per second of handling time was calculated by estimating the average biomass and caloric density of each zooplankton taxon and dividing by the average handling time. Mean calories per strike was calculated by dividing the average number of calories in cladocerans and copepods by the average number of strikes. Significant differences within each panel are denoted by different letters; $N = 5$ for all replicates.

df = 16, $P = 0.77$) and large ($t = 2.21$, df = 16, $P = 0.25$) larvae feeding on copepods. Taken together, the higher net energetic gain per unit handling time for copepods was generally balanced out by higher net energetic gain per strike while feeding on cladocerans. This tradeoff resulted in similar net energetic gains for both prey types.

Discussion

Our results demonstrate that zooplankton group influences the growth and survival of larval yellow perch. Small larvae (<12 mm) positively selected copepods (both adult and naupliar) and experienced the highest growth when feeding on this group. A diet shift occurred around 12 mm, when larvae began consuming cladocerans along with adult copepods but avoided copepod nauplii. These larger larvae also experienced enhanced growth and survival when feeding on cladocerans and adult copepods than on copepod nauplii. The similarities in the growth and survival of larvae 12 mm or longer when feeding on cladocerans and adult copepods, and their willingness to consume both of these groups, was explained by the similar net energetic gains derived from these prey types. Behaviorally, the high capture efficiency and high handling time for larvae consuming cladocerans contrasted with the low capture efficiency and low handling time when consuming copepods yet resulted in similar net energetic gains between these two prey types.

Growth is one of the most important processes determining recruitment during the early life history of fish (e.g., Crowder et al. 1987; Rice et al. 1987). Furthermore, fish tend to select prey items that optimize their growth and survival (Werner and Hall 1974). Therefore, the patterns we observed during our experiments provide insight into how the availability of zooplankton influences the recruitment of yellow perch during the larval period. The growth of larval yellow perch less than 12 mm long should be high when copepods (both adult and naupliar) are abundant. This finding also agrees with patterns observed in the field, where copepods dominated the diet of small yellow perch (Keast 1980; Whiteside et al. 1985; Fisher and Willis 1997) and were positively selected throughout the larval period (Schael et al. 1991). Yellow perch larvae up to 12 mm did not grow or survive well when feeding on rotifers, nor did they positively select them. Similarly, rotifers were avoided by larval yellow perch from Green Bay, Lake Michigan (Bremigan et al. 2003). However, rotifers are a diverse group of freshwater invertebrates; the poor growth and avoidance that we observed for *Brachionus* spp. may not represent larval yellow perch preference for all rotifer genera. Cladocerans were also less important than copepods for yellow perch larvae smaller than 12 mm, probably because the foraging costs of feeding on cladocerans were high relative to those for copepods. Handling times were always much greater for cladocerans than for copepods in the case of larvae exceeding 12 mm; these costs were offset by the higher capture efficiency for cladocerans. The cost of high handling time may not be offset for larvae smaller than 12 mm because reduced visual acuity decreases capture efficiency (Wahl et al. 1993). In addition to the greater foraging costs associated with cladocerans, their digestibility may be lower than that of copepods (Confer and Lake 1987). Thus, the high foraging costs of cla-

docerans and the total avoidance of rotifers result in poor growth and survival for larval yellow perch less than 12 mm that feed on these groups. Because yellow perch larvae up to 12 mm grew and survived best when consuming adult and naupliar copepods, we predict that the recruitment of small larvae will be best when copepods are abundant.

When larval yellow perch were approximately 12 mm long, the zooplankton groups that conferred the highest growth and survival shifted from copepod nauplii to cladocerans and adult copepods. Cladocerans and adult copepods remained important to yellow perch as they grew to 20 mm. This trend probably continues into the early juvenile period, when the growth of yellow perch is best if large cladocerans are abundant (Mills et al. 1989). Although the shift to cladoceran taxa is well documented for yellow perch, our results indicate that cladocerans may become important at smaller fish sizes than previously reported if present at sufficiently high densities. Previous research indicates that larger yellow perch experience an ontogenetic diet shift from copepods to cladocerans around 20–30 mm in systems in which the dominant cladocerans are large-bodied (1.0–2.5-mm) *Daphnia* spp. (Mills et al. 1987; Schael et al. 1991). As a result, growth and recruitment remain high when large cladocerans are present (Mills et al. 1984). We chose to use the smaller *Bosmina* and *Ceriodaphnia* spp. (mean size = 0.55 mm) because they are important in many zooplankton assemblages and were small enough to be available to all sizes of yellow perch larvae (i.e., the larvae were not gape limited). When smaller cladoceran taxa are available, medium and large yellow perch larvae should experience similar growth and survival when feeding on copepods and cladocerans. Although we do not dispute that *Daphnia* are favorable for the recruitment of larger juvenile yellow perch, cladocerans can be as important as copepods for sustained yellow perch growth and survival at smaller sizes (i.e., 12–20 mm) in systems with smaller cladoceran taxa.

The dietary ontogenetic shift from immature copepods to adult copepods and eventually cladocerans during the larval period of yellow perch is similar to that of other larval fishes. For example, black crappie *Pomoxis nigromaculatus*, freshwater drum *Aplodinotus grunniens*, and bluegill all feed on copepod nauplii at small sizes (<8 mm) and then progress to adult copepods and eventually cladocerans with increasing total length and gape width (Keast 1980; Schael et al. 1991). Like yellow perch, these larvae have a transition period at approximately 12–20 mm where both cladocerans and copepods are positively selected. However, larval gizzard shad *Dorosoma cepedianum* continue to select small zooplankton at sizes greater than 13 mm (DeVries and Stein 1992), probably because of the small mouth gape these larvae have (Bremigan and Stein 1994). Although we have not yet quantified it, we would expect most larval fishes to have size-dependent patterns of selectivity and energetic gain that are similar to those we documented for yellow perch feeding on cladocerans and copepods.

Much of the focus has been placed on the role of large-bodied cladocerans (particularly *Daphnia*) when examining the role of zooplankton taxa on the growth and recruitment of young yellow perch (e.g., Mills and Forney 1981; Mills et al. 1989). This focus is based on field and laboratory work with yellow perch exceeding 25 mm; the situation appears to be very different for larval yellow perch. Our results suggest that the availability of copepods and small cladocerans is an important factor in determining the growth and survival of larval yellow perch. These differences in the importance of zooplankton group between larval and juvenile yellow perch are probably driven by morphological differences in both the fish and the zooplankton that affect foraging efficiency. For example, although larvae longer than 16 mm are capable of consuming smaller *Daphnia* (the gape width of 16-mm yellow perch is approximately 1 mm, which is the size of *D. pulicaria*; Schael et al. 1991), the results from our foraging experiments suggest that the cost in terms of handling time would be high. As such, the large-bodied cladocerans preferred by yellow perch longer than 20 mm are probably a poor food source for smaller larvae. Taken together, the availability of the appropriate size and group of zooplankton is critical to recruitment during the entire early life history of yellow perch, from first-feeding larvae through the juvenile stage.

Our findings suggest that the current composition of zooplankton in Lake Michigan (particularly the dominance of adult and naupliar copepods) is favorable for the growth and survival of larval yellow perch. Copepods were important to all sizes of larvae during our experiment, and we believe that the lack of small cladocerans in the current Lake Michigan assemblage (Pientka et al. 2002) will be offset by the presence of adult copepods for larvae longer than 12 mm. The reality in Lake Michigan, however, is a continued pattern of poor yellow perch recruitment (Shroyer and McComish

2000). Because the survival of age-0 yellow perch to fall is related to the density of zooplankton available to first-feeding larvae and recent (1996–1998) densities in Lake Michigan have been 5–30/L (compared with 50–500/L during 1988–1990; Dettmers et al. 2003), the current low density is probably a more important determinant of the growth and survival of larval yellow perch than the taxonomic composition.

Given the importance of the larval stage in fish and the general lack of knowledge about growth, survival, and foraging relationships for larval fish, we encourage more laboratory experiments that mechanistically examine the role of food availability in larval fish recruitment. Our approach of quantifying growth, survival, and prey selection over a range of larval fish sizes was successful in overcoming the difficulties (like high mortality) associated with conducting experiments on larval fish. Further, our foraging behavior experiments identified mechanisms influencing the trends in growth, survival, and prey selection for larval yellow perch. These results were markedly different from those of previous studies conducted on juvenile yellow perch, and we caution about extrapolating the results from experiments on juvenile fish to larval life stages. Further studies that mechanistically examine the role of zooplankton during early life stages will greatly increase our understanding of fish recruitment.

Acknowledgments

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