

## Growth and Survival of Larval Walleyes in Response to Prey Availability

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**Abstract.**—Although larval fish can be highly susceptible to changes in prey availability, the effects on growth and survival are difficult to examine in the field. In addition, previous studies often have examined these relationships only with zooplankton communities common to northern oligotrophic lakes. We used mesocosm and pond experiments to better understand the relationship between communities of larval walleye *Sander vitreus* (formerly *Stizostedion vitreum*) and zooplankton common to eutrophic midwestern USA reservoirs. Treatments of low, medium, and high crustacean zooplankton density (1–50 individuals/L) were created in mesocosms by filtering pond water. Treatments in ponds were created by adding copper sulfate to create low-density zooplankton ponds and adding liquid fertilizer to create high-density zooplankton ponds. Walleye growth rate (0.7–1.5 mm/d) increased with crustacean zooplankton density in both mesocosms and ponds. Densities necessary to maintain good growth were higher than previously observed at northern latitudes, probably due to lack of large-sized zooplankton. Survival increased with zooplankton density in the mesocosm experiments (11–37%) but not in the ponds. Walleye consumption of zooplankton increased with zooplankton density up to 20–30 individuals/L. At low zooplankton densities, larval walleyes fed more heavily on chironomid larvae. Our results demonstrate the importance of zooplankton abundance and size composition for survival and growth of larval walleyes.

Understanding factors influencing growth and survival of larval fish is important for predicting recruitment. Prey availability, predation, and water temperature have been suggested as factors important for larval fish survival (Miller et al. 1988). Prey availability is thought to be particularly important during the larval stage because it can have a large effect on both growth and survival (Houde 1987; Miller et al. 1988). A decline in abundance

of appropriate-sized prey can cause either slow growth or lead to starvation. Slow growth can affect survival by increasing the time larvae are vulnerable to predation. Starvation can also increase predation by reducing swimming speeds of larval fish, thus making them more vulnerable to capture (Laurence 1972; Rice et al. 1987; Jonas and Wahl 1998). As a result, information on the availability of prey and how it affects growth and survival of larval fish is essential to understanding recruitment.

Almost all larval fish begin feeding on zooplankton; therefore, zooplankton abundance during larval fish development can strongly influence growth and survival. Relationships between zooplankton and larval fish growth and survival have been shown for some fish species in the field (Lemly and Dimmick 1982; Mills et al. 1989; Claramunt and Wahl 2000). However, an almost equal number of studies have failed to show a positive relationship between zooplankton abundance and larval fish growth and survival (Houde 1967; Partridge and DeVries 1999). In addition to suggesting dif-

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ferences in the importance of prey availability across species, these field examinations illustrate the difficulty of separating the importance of prey availability from other factors in large-scale lake studies. Mechanistic experiments are needed to fully understand the importance of prey to larval fish (see Werner and Blaxter 1980; Buckley et al. 1987).

In addition to abundance, zooplankton species composition and size can also affect larval fish growth and survival (Fox 1989; Graham and Sprules 1992; Johnston and Mathias 1994). The maximum size of zooplankton consumed often is regulated by gape size (Graham and Sprules 1992; Bremigan and Stein 1994). Selection for larger zooplankton occurs for some species and can result in higher growth rates (Hokanson and Lien 1986; Fox 1989). Species of zooplankton also can affect larval fish growth and survival, but effects can vary with species of larval fish. For example, walleyes *Sander vitreus* (formerly *Stizostedion vitreum*) feeding on cladocerans survived better than those feeding on copepods (Mayer and Wahl 1997). In contrast, growth of age-0 centrarchids was correlated with the abundance of copepods but not cladocerans (Lemly and Dimmick 1982).

Walleyes are important from both ecological and economic perspectives, and like other fishes, larval walleyes are affected by prey availability. Experimental studies examining growth and survival of larval and juvenile walleyes in northern temperate systems have produced varied results. Survival of larval walleyes increased with density of large *Daphnia* spp. (Li and Mathias 1982) but not with density of a mixed zooplankton assemblage (Johnston et al. 1992). Growth also increased with zooplankton abundance for larval walleyes in rearing ponds at northern latitudes (Canada; Johnston et al. 1992). Growth of older juvenile (7 weeks old) walleyes in experimental ponds was shown to depend largely on chironomid and large zooplankton (>1 mm) densities (Fox 1989). However, in these same ponds, no relationship was observed between survival and prey density. Zooplankton assemblages in these previous experiments were characterized by relatively large cladocerans (>1 mm total length) typical of northern temperate lakes. Zooplankton assemblages found in productive reservoirs in the midwestern USA include more smaller-bodied zooplankton than those found in more northern natural lakes (Bremigan and Stein 1994; DeVries et al. 1998), probably due to a high abundance of plantivorous fish (Brooks and Dodson 1965). Because of the smaller-bodied zoo-

plankton in these reservoirs, we believed that zooplankton densities needed to promote good growth and survival of larval walleyes would be higher than those required in more northern oligotrophic lakes.

Some previous experimental studies have examined the importance of prey availability on growth and survival of larval fish at varied densities (e.g., Welker et al. 1994; Fox and Flowers 1990). However, intraspecific competition based on other factors (e.g., space and associated stress) may cause differences in growth and survival independent of prey availability (Li and Mathias 1982; Gershanovich 1983). For example, walleyes may use more energy to avoid cannibalism at higher densities (Fox and Flowers 1990). These density-dependent effects are difficult to distinguish from growth differences associated with prey availability, so directly varying prey density is required to assess the importance of these effects on growth.

Because few experimental studies have examined the effects of varied zooplankton densities on larval walleyes and because of the potential for zooplankton assemblages to affect larval walleyes, we examined zooplankton availability on larval walleyes at southern latitudes (midwestern USA). We directly varied zooplankton densities at two spatial scales (mesocosms and ponds) to assess the importance of prey availability in determining growth and survival of larval walleye. Mesocosms were used to maintain control over experimental conditions, whereas ponds were used to provide more realistic natural conditions. We then compared our results to those with alternative zooplankton assemblages (i.e., larger bodied) to develop generalizations regarding the importance of prey resources to larval walleye.

## Methods

*Mesocosm experiment.*—Larval walleye were introduced into twelve 1,500-L circular tanks with low, medium, and high zooplankton densities (4 replicates for each group) at the Sam Parr Biological Station located in south-central Illinois. Tanks were located outdoors under ambient light and temperature conditions. Initial zooplankton densities were established by filling tanks with water from a fertilized pond with a high zooplankton density. Treatments were established by using unfiltered water for the high-density tanks, 50% unfiltered water for medium-density tanks, and 10% unfiltered water for low-density tanks. The remainder of the tank was filled by filtering water

through a 64- $\mu$ m-mesh zooplankton net. Initial crustacean zooplankton density (excluding nauplii and rotifers) averaged 2.9/L (SE =  $\pm$  2.2/L) in the low-density tanks, 6.4  $\pm$  2.1/L in the medium-density tanks, and 21.6  $\pm$  5.7/L in the high-density tanks. Zooplankton density varied widely among replicates within treatments. As a result, in addition to treatment effects we also examined correlations between zooplankton densities and walleye growth and survival by using individual tanks as replicates. Each tank was stocked with 200 larval walleyes (9.97  $\pm$  0.06 mm total length [TL]) obtained from the Jake Wolf Memorial Fish Hatchery, Illinois. Larval walleye densities were within the range used in previous experiments with larval fish (Mathias and Li 1982; Welker et al. 1994) and below levels expected to reduce zooplankton densities.

Zooplankton samples were taken from each of the tanks at 3–4-d intervals over a 2-week period. Samples were collected from the entire water column with a 7.6-cm diameter acrylic tube, filtered through a 64- $\mu$ m-mesh screen (DeVries and Stein 1991), and preserved in a 10% formalin and sucrose solution (Haney and Hall 1973). Zooplankters were enumerated by counting three 1-mL subsamples. Copepods were identified as calanoids or cyclopoids; cladocerans were identified to the lowest possible taxon. Lengths (nearest 0.01 mm) were measured from 10 individuals of each taxon.

Walleye fry were collected on the same dates as zooplankton by light trapping. Five walleyes were retained and measured (nearest 0.01 mm, TL) on each sampling date to determine growth rates. Stomach contents were identified, counted, and measured for each fish. Zooplankton biomass in the diet was calculated from length–weight regressions (Culver et al. 1985). Chironomid biomass was measured as dry weight (nearest 0.1 mg) after being dried in an oven (90°C). Gut fullness was calculated as the dry weight ( $\mu$ g) of the diet divided by the wet weight (mg) of the fish (Fox 1989). Tanks were drained after 16 d and all remaining walleyes were collected. Dissolved oxygen was similar across treatments (repeated-measures analysis of variance [ANOVA];  $F_{2, 71} = 1.15$ ,  $P = 0.35$ ) and stayed within an acceptable range of 7.8–14.6 ppm at 0.5 m below the surface. Water temperatures at this same depth ranged from 10–20°C during the course of the experiment and did not differ among tanks ( $F_{2, 71} = 2.23$ ,  $P = 0.27$ ).

*Pond experiment.*—Pond experiments were conducted at the Sam Parr Biological Station by in-

roducing 4,000 larval walleyes (8.64  $\pm$  0.06 mm TL) into 0.04-ha ponds with low, medium, or high zooplankton density. Because pond experiments were of longer duration, densities of walleyes in the ponds were lower than in the mesocosm experiments to ensure density dependent effects did not occur. Ponds were filled with a natural zooplankton community using water from a nearby reservoir (Forbes Lake). Low-density treatments (initial density excluding nauplii and rotifers = 103  $\pm$  68/L) were established in three ponds by applying copper sulfate (1 ppm) 4 weeks before and 10 d after the introduction of walleye fry. Copper sulfate, a commonly used algacide, produces little residual toxicity and, at the low concentration we used, has minimal effects on fish (Boyd and Lichtkoppler 1979). High-density ponds (433  $\pm$  134/L) were created by adding liquid organic fertilizer (9–18–9 [N:P:K]) to three ponds at a rate of 220 kg/ha beginning 4 weeks before stocking walleye. Fertilizer was added three times per week to maintain Secchi readings below 45 cm. Zooplankton density was intermediate in four untreated ponds (311  $\pm$  53/L). Zooplankton densities within treatments were more variable and higher than those in the mesocosm experiment. The range of zooplankton densities tested encompassed the densities in Illinois reservoirs.

Walleye growth and zooplankton density were monitored every 3–5 d using procedures described for the mesocosm experiments. Initial mortality related to stocking stress was measured by holding 100 fry in each of three containers (0.75 m diameter, 0.6 m deep) and counting the number of dead fry after 24 h (Clapp et al. 1997). Three replicate zooplankton samples were taken from each pond on each sample date. Water temperature, dissolved oxygen, and pH were monitored in each pond throughout the experiment. Water temperatures, which averaged 10.4°C at stocking and increased to 20.0°C at the end of the experiment, did not differ among treatments ( $F_{2, 59} = 0.06$ ,  $P = 0.94$ ). Dissolved oxygen ranged between 8.2 and 11.1 ppm and did not differ among treatments ( $F_{2, 59} = 0.3$ ,  $P = 0.75$ ). Walleyes were collected every 3–5 d by light trapping or seining. Lengths measured on day 13 were used to compare with growth in the mesocosms. The ponds were drained and remaining fish were collected after 35 d.

*Statistical analysis.*—Repeated-measures analysis of variance (ANOVA) was used to test for differences in water quality and zooplankton densities (excluding copepod nauplii and rotifers) among mesocosms and ponds through time. Be-

cause growth and survival can be dependent on species composition, the percentage of total zooplankton composed of cladocerans and adult copepods was tested for differences among treatments using repeated-measures ANOVA. We used ANOVA to test for differences in larval walleye growth and survival among prey density treatments. Multiple comparisons were made with Tukey's test if the overall ANOVA revealed significant differences. Because of the high within-treatment variability in initial zooplankton density, correlational analysis also was used to examine relationships between density of zooplankton and growth and survival of larval walleyes. Density of zooplankton used in correlational analyses was the mean density over the duration of the experiment. Data were tested using the UNIVARIATE procedure in SAS (SAS Institute 1989) and were log-transformed as needed to normalize the distributions before analyses. Differences between the size of cladocerans and copepods consumed by walleyes were compared with a *t*-test. Significance for all statistical tests was set at  $\alpha = 0.05$ .

## Results

### Mesocosm Experiment

The percent composition of cladocerans and copepods did not differ significantly among the three treatments (repeated-measures ANOVA:  $F_{2, 71} = 1.45$ ,  $P = 0.28$ ). Lengths of the two predominant cladocerans averaged 0.66 mm (SE =  $\pm 0.03$ ) for *Daphnia* spp. and  $0.29 \pm 0.01$  mm for *Bosmina longirostris*. Lengths of copepods were  $0.52 \pm 0.02$  mm for cyclopoids and  $0.70 \pm 0.03$  mm for calanoids. Zooplankton abundance was greatest throughout the experiment in the high-density zooplankton tanks followed by the medium and low treatments (repeated measures ANOVA:  $F_{2, 71} = 9.73$ ,  $P = 0.006$ ; Figure 1). Zooplankton abundance did not decline in any of the treatments through time (Figure 1). Larval walleye total length was greatest in the high-density treatment at the end of the experiment (ANOVA:  $F_{2, 11} = 12.57$ ,  $P = 0.003$ ; Tukey test: df = 9,  $P < 0.05$ ) but was similar in the low and medium treatments (Tukey test: df = 9,  $P > 0.05$ ). Survival of walleye fry in the high-density treatment was significantly greater than in the low-density treatment (ANOVA:  $F_{2, 11} = 8.75$ ,  $P = 0.008$ ; Tukey test: df = 9,  $P < 0.05$ ), whereas the medium density was intermediate and did not differ from the other two (Tukey test: df = 9,  $P > 0.05$ ).

Variability in zooplankton abundance within

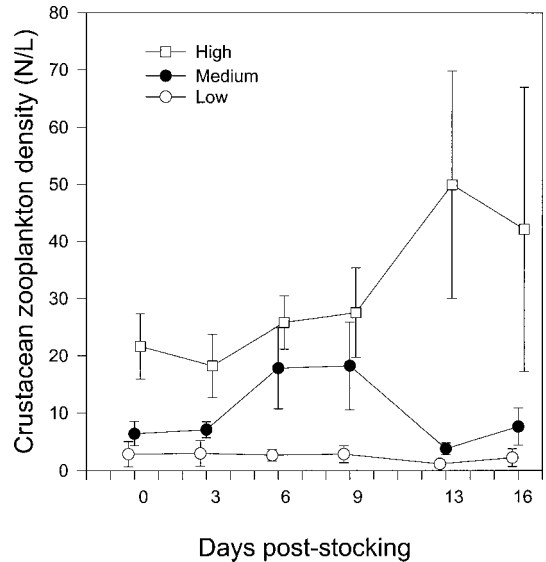


FIGURE 1.—Means and standard errors for crustacean zooplankton densities (excluding nauplii and rotifers) during a 16-d mesocosm experiment with larval walleye. Treatments consisted of four replicate tanks with low, medium, and high zooplankton densities.

treatments was large (Figure 1) and allowed us to further examine the relationship between growth, survival, and prey availability across tanks. Both growth and survival of larval walleyes were related to zooplankton density. Larval walleye growth was positively correlated with crustacean zooplankton density ( $r = 0.85$ ,  $N = 12$ ,  $P < 0.001$ ; Figure 2). Cladoceran density (log-transformed:  $r = 0.83$ ;  $N = 12$ ;  $P < 0.001$ ) accounted for more variation in growth than copepod density (log-transformed:  $r = 0.69$ ,  $P = 0.01$ ), but none of the relationships for individual taxonomic groups were better than for all crustacean zooplankton combined. Survival of larval walleyes (11–37% across all treatments) also was positively related to crustacean zooplankton density ( $r = 0.81$ ,  $P = 0.001$ ; Figure 2).

Zooplankton consumed by walleyes consisted only of large crustacean zooplankton composed entirely of cladocerans and copepods. Smaller zooplankton, such as copepod nauplii and rotifers, never appeared in any walleye stomach (Table 1). Walleyes initially consumed only cladocerans, adding copepods and chironomids to their diets as they grew. Although copepods were available during the entire length of the experiment, chironomids were only present later in the experiment following their colonization of the tanks. The mean size of cladocerans consumed ( $0.86 \pm 0.03$  mm)

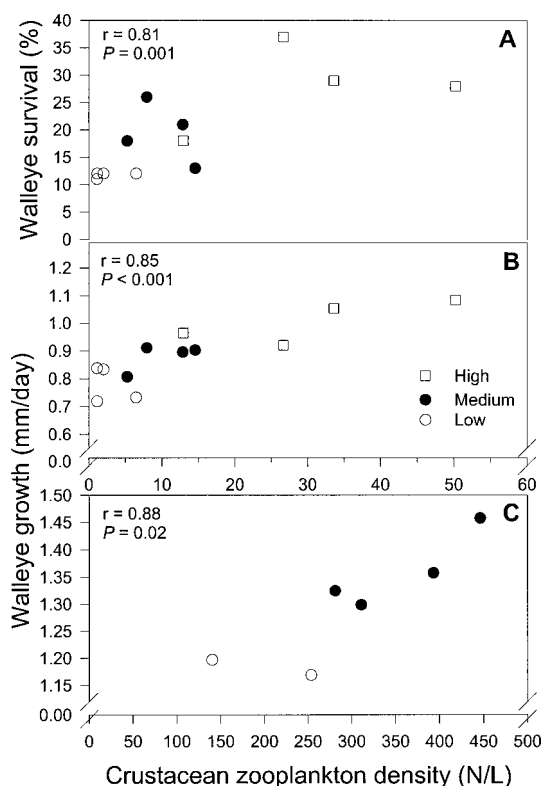


FIGURE 2.—Relationship between crustacean zooplankton density (excluding nauplii and rotifers) and (A) larval walleye survival, (B) larval walleye growth after 16 d in mesocosms, and (C) larval walleye growth after 13 d in ponds. Treatments consisted of low (open circles), medium (solid circles), and high (squares) zooplankton densities.

was significantly larger than for copepods ( $0.66 \pm 0.04$  mm; *t*-test with unequal variances:  $t = 3.86$ ,  $N = 204$ ,  $P < 0.001$ ). Biomass of zooplankton found in the diet was positively correlated to zooplankton density in the mesocosms (log-transformed:  $r = 0.78$ ,  $N = 12$ ,  $P = 0.003$ ). Zooplankton gut fullness followed a type-II functional response, increasing until zooplankton density reached 20–30/L (Figure 3). In contrast, total gut fullness was negatively correlated with zooplankton density ( $r = -0.66$ ,  $P = 0.02$ , Figure 3) due to chironomid consumption. Larval walleyes consumed more chironomids at low zooplankton densities (log-transformed;  $r = -0.73$ ,  $P = 0.007$ ). The numbers and biomass of chironomids eaten increased dramatically when zooplankton densities were fewer than 20/L (Figure 4).

#### Pond Experiment

Pond experiment results were similar to those from the mesocosm experiment with regard to factors influencing growth and prey consumption of larval walleyes. Walleyes fed exclusively on cladocerans and copepods in the ponds. Although chironomid larvae were present in the ponds, they were not observed in the diets. A strong positive relationship between growth and zooplankton density was evident at 35 d, when the ponds were drained ( $r = 0.82$ ,  $N = 10$ ,  $P = 0.046$ ). To allow comparison with the mesocosms, lengths of walleye fry were also examined at day 13 in the ponds and was again dependent on zooplankton density ( $r = 0.88$ ,  $P = 0.02$ ; Figure 2). Combining data from both experimental approaches, we found a

TABLE 1.—Percent composition by dry weight ( $\mu\text{g}$ ) of food items in the stomachs of larval walleyes held in tanks with low, medium, and high densities of zooplankton. Diet samples were taken on five dates during the experiment;  $N$  is the number of stomachs examined on each date.

Days poststocking	Plankton density treatment	<i>N</i>	Percent composition			
			Cladocera	Copepoda	Chironomidae	Culicidae
3	Low	3	100	0	0	0
	Medium	2	100	0	0	0
	High	8	100	0	0	0
6	Low	18	31	12	57	0
	Medium	19	80	20	0	0
	High	19	82	18	0	0
9	Low	17	16	2	82	0
	Medium	18	73	4	24	0
	High	18	98	2	0	0
13	Low	16	0.6	0.4	99	0
	Medium	15	40	1	58	1
	High	17	87	1	12	0
16	Low	11	8	2	90	0.2
	Medium	35	58	1	41	0.1
	High	39	87	0.3	13	0.2



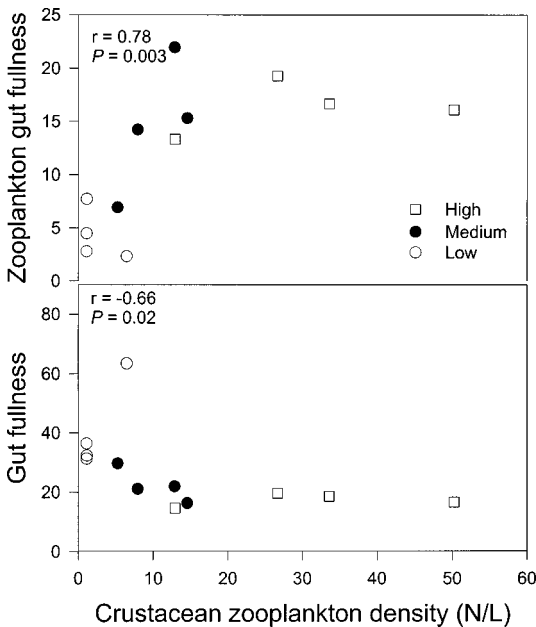


FIGURE 3.—Relationship between crustacean zooplankton density (excluding nauplii and rotifers) and walleye gut fullness of zooplankton only and total gut fullness after 16 d in the mesocosm experiment. Treatments consisted of low (open circles), medium (solid circles), and high (squares) zooplankton densities. Zooplankton gut fullness was calculated by dividing the dry weight ( $\mu\text{g}$ ) of the zooplankton in the diet by the wet weight (mg) of the fish. Gut fullness was calculated by dividing the dry weight ( $\mu\text{g}$ ) of the diet by the wet weight (mg) of the fish. Data were log transformed for analysis.

strong positive relationship between zooplankton density and growth rate (log-transformed:  $r = 0.95$ ,  $N = 22$ ,  $P < 0.001$ ), despite differences in larval walleye density between mesocosms and ponds. Growth increased rapidly with zooplankton densities below 100/L, increasing more slowly above that level (Figure 2).

Initial stocking mortality in the ponds was low (13%). Contrary to the mesocosm experiments, there was no relationship between survival and zooplankton density in the ponds ( $r = -0.58$ ,  $N = 10$ ,  $P = 0.08$ ) at 35 d when the ponds were drained. Walleye mortality was 100% in the high-density ponds; however, after removing these ponds from the analyses, there was still no relationship between zooplankton density and survival ( $r = -0.40$ ,  $N = 7$ ,  $P = 0.38$ ).

### Discussion

Several attributes of zooplankton prey influenced the growth and survival of larval walleyes.

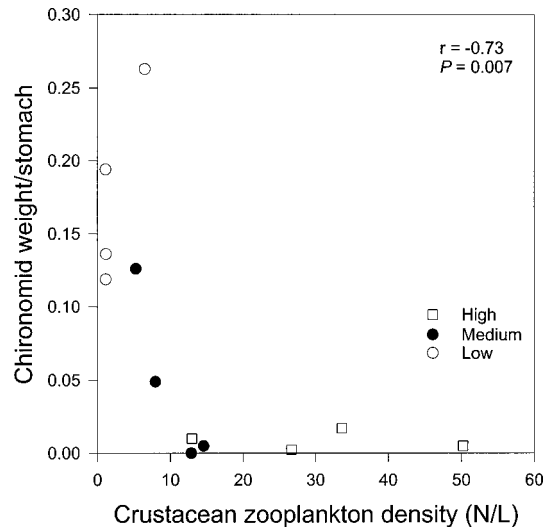


FIGURE 4.—Relationship between crustacean zooplankton density (excluding nauplii and rotifers) and chironomid weight per stomach after 16 d in the mesocosm experiment. Treatments consisted of low (open circles), medium (solid circles), and high (squares) zooplankton densities. Data were log-transformed for analysis.

Prey density had a strong influence on growth of larval walleyes, increasing with zooplankton density in both the mesocosm and pond experiments. Similar results have been found for larval crappie *Pomoxis* spp. and bluegill *Lepomis macrochirus* (Welker et al. 1994; Claramunt and Wahl 2000). In rearing ponds at northern latitudes, zooplankton densities of up to 100/L resulted in greater larval walleye growth; above that density, growth remained constant (Johnston et al. 1992). In our ponds, walleye growth rates increased with zooplankton densities of up to 500/L. Zooplankton densities in our study encompassed those found in natural systems in the midwestern USA. For example, crustacean zooplankton density at the time of year when larval walleye are typically abundant ranged from 3 to 396/L in 10 Illinois reservoirs during a 7-year period (Hoxmeier et al. 1999). Despite different walleye densities between mesocosms and ponds, there was a strong positive relationship between zooplankton density and growth within and across both experimental approaches. Density-dependent effects could complicate these comparisons and comparisons with other studies and would be of most concern in the mesocosm experiment. However, zooplankton densities remained constant throughout the experimental period in both our mesocosms and ponds,

suggesting a lack of both prey depletion and density-dependent effects. The duration of our mesocosm experiments (16 d) was short enough to preclude zooplankton depletion. Our results suggest growth of larval walleye will increase across the range of zooplankton densities found in the Midwest.

Zooplankton size composition is generally smaller in midwestern reservoirs compared with northern temperate lakes (DeVries et al. 1998). Similarly, lengths of crustacean zooplankters in our study averaged 0.62 mm, whereas larger zooplankters were used in a previous study examining walleye growth at more northern latitudes: lengths of 0.7–2.2 mm for *Cyclops bicuspidatus* and 0.8–2.4 mm for *Daphnia pulex* (Mathias and Li 1982). As we hypothesized, densities of zooplankton needed to sustain growth of larval walleye in midwestern reservoirs is higher than predicted, based on studies conducted in more northern areas, probably because of the differences in zooplankter size.

Prey composition also can have a strong influence on larval walleye growth (Hokanson and Lien 1986; Mayer and Wahl 1997). Cladoceran density was more strongly related to growth than was copepod density in the mesocosm experiments but not as strong as both groups combined. Rotifers and copepod nauplii were rarely consumed in our study, similar to that reported in previous studies (Houde 1967; Mathias and Li 1982; Mayer and Wahl 1997). Because caloric values and handling times are similar (Cummins and Wuycheck 1971; Mayer and Wahl 1997), we expected that copepod densities would affect larval walleye growth in a way that was similar to cladocerans. However, in our study cladocerans not only contributed a larger portion of the diet, they also were larger than copepods. Larger zooplankters can translate into better growth and survival for larval fish (Hokanson and Lien 1986). In addition, walleyes orient more frequently towards cladocerans than copepods and have higher survival rates when feeding on cladocerans (Mayer and Wahl 1997). In contrast, larval walleyes in Oneida Lake, New York, ate copepods in proportion to their abundance but selected against cladocerans (Houde 1967; Graham and Sprules 1992). Differences in the size of prey and walleye across studies may account for the differences in observed results (Mayer and Wahl 1997). Our results suggest that the combined density of copepods and cladocerans at the time of exogenous feeding is the best predictor of growth and survival of larval walleyes.

Zooplankton consumption by larval walleye fol-

lowed a type-II functional response, similar to larvae of other fish species (Houde and Schekter 1980; Miller et al. 1992). Walleye consumption, as measured by stomach fullness, increased with zooplankton density to about 20–30/L. In previous aquaria experiments, increased densities of *Daphnia* spp. of up to about 100/L resulted in higher consumption by walleyes (Mathias and Li 1982). Because of the smaller-bodied zooplankton in our study, we expected that consumption rates might be higher than those previously reported. As zooplankton size decreases, the density needed to reach maximum consumption increases for larval walleyes; however, maximum consumption also increases with larval walleye size (Johnston and Mathias 1994). Given that Mathias and Li (1982) used larger walleyes for their feeding studies (19–30 mm TL), the lower estimate of zooplankton density needed to reach maximum consumption in our experiments probably results from differences in walleye size. We predict that future experiments comparing similar-sized walleyes will find that higher densities of zooplankton are needed to reach maximum consumption in midwestern reservoirs compared with more northern lakes because of the presence of smaller-bodied zooplankton communities.

Walleyes undergo a series of ontogenetic diet shifts while switching from feeding on zooplankton to benthic invertebrates (Fox and Flowers 1990) and eventually to fish (Priegel 1969; Mathias and Li 1982). The timing of these diet shifts has generally been attributed to size or age of the fish (Smith and Pycha 1960; Mittelbach and Persson 1998). However, our results suggest that the timing of diet ontogeny may also be influenced by prey availability. When zooplankton is abundant, walleyes may delay their diet shift to benthic invertebrates. Walleyes did not feed on chironomids in the ponds, but they were used heavily when zooplankton density was low in the mesocosm experiments. Larval walleye feeding on chironomids may occur only when zooplankton levels are below a minimum threshold. Similarly, it has been suggested that walleyes delay the switch to piscivory if alternate prey is abundant (Priegel 1969; Li and Ayles 1981). For larval walleye, high consumption of chironomids translated into decreased growth, suggesting that zooplankton are an energetically better prey for larval walleye. Caloric values of cladocerans (21,943 J/g dry weight) and copepods (24,036 J/g dry weight) are similar to chironomids (22,709 J/g dry weight; Cummins and Wuycheck 1971). However, if larval walleye expend more

energy searching, capturing, and assimilating chironomids than zooplankton, that could lead to slower growth. Handling times of bluegills are an order of magnitude higher for chironomids than for zooplankton (Mittelbach 1981). Fox and Flowers (1990) also found that higher chironomid biomass did not lead to an increase in walleye growth. Pond studies have shown a positive relationship between juvenile walleye growth and chironomid density after 7 weeks (Fox 1989), incorporating much larger and older fish than our experiments. Feeding on chironomids may not translate into better growth for the smaller walleye we used given their poor swimming ability. Early feeding on benthic invertebrates could be detrimental to the growth and survival of young walleyes.

Survival was directly related to zooplankton density in the mesocosms but not in the ponds. Survival was determined after 5 weeks in the ponds, whereas it was estimated after 2 weeks in the mesocosms. It is likely that additional mortality occurred in the ponds after the 2-week larval stage, which may have affected these results. In similar pond experiments with juvenile walleyes, Fox (1989) also concluded that prey abundance did not affect survival. In contrast, our mesocosm experiments indicate that prey availability is very important to survival during early life, especially in the first 2 weeks and at low zooplankton densities. Similarly, in a monoculture of large (1.2 mm) *Daphnia*, larval walleye survival increased until zooplankton densities reached 100–200/L (Li and Mathias 1982). We did not find a plateau for survival with the zooplankton assemblages and densities used in the mesocosm experiments. A previous study using mixed species of zooplankton found no relationship between zooplankton density and larval walleye survival in culture ponds with densities above 49/L (Johnston and Mathias 1993). The positive relationship found in our study occurred at zooplankton densities below 50/L. Reduced survival at low zooplankton densities is probably due to either slower growth or starvation. Larval walleye begin to show an increase in mortality after 8 d of starvation (Jonas and Wahl 1998). Although starvation increases cannibalism among larval walleye (Li and Mathias 1982), we observed only two walleye in stomachs in the low-density treatments. In the low-density treatments, prey densities were often below maintenance rations for larval walleyes (5/L; Johnston and Mathias 1996). Smaller, slower growing larvae are more susceptible to starvation because of lower energy reserves, reduced reactive distances, swimming

speeds that limit search ability, and gape restrictions for larger food items (Miller et al. 1988). Our results in combination with previous work emphasizes the importance of zooplankton density to survival of larval walleyes.

Our results have implications to understanding recruitment in natural populations of walleyes and for enhancing stocking programs. Zooplankton density strongly affects growth and survival in larval walleyes. In lakes, low zooplankton density at the time of either natural larval recruitment or fry stocking may result in slow growth and low survival. For example, low zooplankton density (<35/L) corresponded to poor survival of stocked walleye fry in Lake Oahe, South Dakota (Fielder 1992). Matching stocking with periods of high prey abundance may increase chances for survival (Fielder 1992; Stahl et al. 1996). Densities of zooplankton in midwestern reservoirs should be above 100/L during and after walleye fry stocking to assure good growth and up to 500/L for maximum growth. Based on our results, a minimum density of 50/L is required for good larval walleye survival. Monitoring zooplankton densities during the larval stage of walleye development will enable better predictions of walleye recruitment, and matching fry stocking to zooplankton peaks should increase stocking success.

### Acknowledgments

We thank the staff of the Sam Parr Biological Station, Illinois Natural History Survey, for their help in the field and laboratory, especially J. Fossum and P. Hayes. T. Galarowicz, J. Kline, and three anonymous reviewers provided helpful reviews of this manuscript. D. Austen, K. Cottrell, and J. Mick coordinated activities with the Illinois Department of Natural Resources (IDNR). Walleye fry were provided by S. Stuewe and S. Krueger of the Jake Wolf Memorial Fish Hatchery, IDNR. This project was funded in part by the IDNR through Federal Aid in Sport Fish Restoration, Project F-51-R.

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