

# Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators

Brian D.S. Graeb, Tracy Galarowicz, David H. Wahl, John M. Dettmers, and Mathew J. Simpson

**Abstract:** The ontogeny of piscivory is an important process during the early life history of many fishes, and why ontogenetic patterns of closely related species vary is unclear. We experimentally evaluated the importance of several factors that can determine the switch to piscivory in two predators with different dietary ontogenies: walleye (*Sander vitreus*), a specialist piscivore, and yellow perch (*Perca flavescens*), a dietary generalist. We conducted growth and prey selection experiments across several sizes of both predators using fish, zooplankton, and benthic invertebrates as prey. Walleye exhibited piscivorous feeding behavior throughout all size classes (20–80 mm), whereas yellow perch were generalist predators, showing negative to neutral selection for fish prey and lower growth than walleye when feeding on fish. Walleye foraged more efficiently than yellow perch on all prey types, in part because gape widths of walleye increased more quickly with size. Bioenergetic model simulations showed that walleye grew slower than yellow perch when the proportion of fish was low in diets, but walleye growth was faster than yellow perch on a diet dominated by fish. Feeding behavior, morphology, and life history patterns likely work in combination, allowing walleye to switch to piscivory earlier than yellow perch.

**Résumé :** L'ontogénèse de l'ichtyophagie est une étape importante du cycle biologique de plusieurs jeunes poissons et il n'est pas clair pourquoi les patrons ontogéniques d'espèces apparentées peuvent différer. Nous avons évalué expérimentalement l'importance de plusieurs facteurs qui peuvent favoriser le passage à l'ichtyophagie chez deux prédateurs qui possèdent des ontogénèses alimentaires différentes, le doré jaune (*Sander vitreus*), un piscivore spécialisé, et la perchaude (*Perca flavescens*), un généraliste alimentaire. Nous avons mené des expériences de croissance et de sélection de proies chez diverses tailles des deux prédateurs et utilisé des poissons, du zooplancton et des invertébrés benthiques comme proies. Les dorés ont un comportement alimentaire de piscivores à toutes les tailles (20–80 mm), alors que les perchaudes sont des prédateurs généralistes qui font une sélection négative ou neutre des poissons comme proies; les perchaudes croissent aussi moins rapidement que les dorés lorsqu'ils s'alimentent de poissons. Les dorés sont plus efficaces que les perchaudes pour attraper tous les types de proies, en partie parce que la largeur de l'ouverture de leur bouche croît plus rapidement en fonction de la taille. Des simulations d'un modèle bioénergétique montrent que les dorés croissent plus lentement que les perchaudes lorsque la proportion de poissons dans leur régime alimentaire est faible, mais que les dorés grandissent plus rapidement que les perchaudes lorsque le régime est dominé par les poissons. Le comportement alimentaire, la morphologie et les patterns du cycle biologique concourent tous vraisemblablement à permettre au doré de faire le passage vers l'ichtyophagie plus tôt que la perchaude.

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## Introduction

Many organisms undergo ontogenetic diet shifts during early life-history stages. These shifts often have large implications for individuals, populations, and communities (Werner and Gilliam 1984; Mittelbach and Persson 1998). For many fishes, diet shifts eventually result in piscivory

(e.g., yellow perch, *Perca flavescens*, Fullhart et al. 2002; walleye, *Sander vitreus*, Mathias and Li 1982; largemouth bass, *Micropterus salmoides*, Olson 1996). This switch to piscivory is viewed as favorable to individuals because of the associated increase in growth and survival (Ludsin and DeVries 1997; Persson and Brönmark 2002). Furthermore, the timing and extent of switching to piscivory can influence

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the recruitment of cohorts within a population (Olson 1996). Piscivory can also be important in structuring communities by decreasing the abundance of prey fish available to other predators, or by reducing intraspecific competition and increasing the growth of prey populations (Tonn et al. 1991). Thus, understanding the mechanisms driving the onset of ontogeny of piscivory will improve our understanding of several ecological processes.

Young fish that switch to a piscivorous diet often realize a substantial increase in growth and body condition compared with other fish within a cohort that maintain a diet of invertebrate prey (Keast and McA. Eadie 1985; Buijse and Houthuijzen 1992). Further, these larger (piscivorous) fish experience higher over-winter survival and recruitment compared with smaller (non-piscivorous) cohort members (Ludsin and De Vries 1997). Although the advantages of switching to a piscivorous diet are well documented, little is known either about the mechanisms determining the ontogeny of piscivory in fishes, or why the timing of switching to piscivory among fish species is so variable.

Despite the benefits of switching to a fish diet, the size at which fish switch to piscivory varies widely, with some species switching when they are as small as 30 mm (e.g., walleye), while others can take up to 3 years (e.g., yellow perch). These early and late switching groups have been called “specialists” and “secondary” piscivores (Keast 1985). Optimal foraging theory (e.g., Werner and Hall 1974) suggests that early switching piscivores achieve faster growth because they derive higher energetic returns from fish prey than alternative prey such as invertebrates. Furthermore, some specialist piscivores actively choose fish prey, as opposed to invertebrate prey, because fish prey maximizes net energy intake per time spent foraging, as predicted by optimal foraging theory (Einfalt and Wahl 1997; Turesson et al. 2002). In contrast, secondary piscivores may passively choose prey items based on foraging efficiency and encounter rates (Turesson et al. 2002). These predators may still consume fish prey, but do not actively choose this prey type. Based on optimal foraging considerations, young secondary piscivores are likely to grow best on invertebrate diets, even though they can select fish prey.

To gain insight into the variability in the extent and timing of switching to piscivory, Mittelbach and Persson (1998) related several variables (e.g., spawning date, prey manipulation times, and morphology) among fish species in the northern hemisphere to the ontogeny of piscivory. They concluded that much of the variation in size at switching could be attributed to differences in predator morphology, especially predator gape size, although they did not explicitly explore their results in the context of optimal foraging theory. Larger gape widths may allow early switching piscivores to actively choose fish because they can more efficiently consume fish prey, thus maximizing energy intake. However, Mittelbach and Persson (1998) cautioned that much of the data used in their analysis were focused on age-1 and older fishes. As such, their conclusions may not apply to younger ages, when many fishes switch to piscivory. They recommended comparing age-0 morphology, growth, foraging efficiency, and life history variation of specialist and secondary piscivores to further understand the mechanisms determining the ontogeny of piscivory.

Walleye and yellow perch provide good models to examine the predictions of Mittelbach and Persson (1998) because they are closely related (two genera in the family Percidae), co-occur in many systems, and are piscivorous as adults, yet differ markedly in their timing of switch to piscivory. Diets of age-0 walleye as small as 35 mm are dominated by fish (Mathias and Li 1982); they are considered specialist piscivores. In contrast, yellow perch generally do not consume fish prey until age 1+ at lengths greater than 150 mm; typically they are not primarily piscivorous until age 4+ (Keast 1985; Fullhart et al. 2002). Walleye hatch earlier and at larger sizes (6–8 mm; Marshal 1977) than yellow perch (5–6 mm; Thorpe 1977), presumably leading to a size advantage over their prey (later hatching larval fish); they also possess canine teeth that aid in the grasping of prey (Craig 1987; Mittelbach and Persson 1998), whereas yellow perch lack canine teeth (Craig 1987). Differences among these characteristics may explain differences in the ontogeny of piscivory between walleye and yellow perch. We hypothesized that elements of optimal foraging theory could explain these observed differences in the timing of the switch to piscivory. We predicted the following: (i) walleye actively select fish over alternative prey because fish prey optimize caloric intake and growth, whereas yellow perch passively select prey based on foraging efficiency, with little change in growth among prey types; (ii) walleye gape size at a given length would be larger than that of yellow perch, allowing walleye to consume fish prey more efficiently than yellow perch; and (iii) life history differences favor the tendency of walleye to switch to piscivory at smaller sizes and realize faster growth rates than yellow perch maintaining a mixed diet; however, walleye, as a specialist piscivore, would grow slower than yellow perch if both predators could not switch to piscivory, despite an earlier hatching date.

We tested these predictions by quantifying several factors that may determine the ontogeny of piscivory of walleye and yellow perch. We first quantified prey selection patterns and growth rates of the two predators across several sizes to determine the size at which the switch to piscivory is complete, and if switching to a fish diet resulted in faster growth compared with alternate prey. We then experimentally quantified foraging behavior (capture efficiency and attack rate) to determine if either predator foraged more efficiently on fish prey. We also determined differences in mouth gapes for both predators to assess whether morphology contributed to the timing of diet changes. Finally, we compared the effects of variation in early life history (hatching date) and the ability to switch to piscivory (synchrony with prey fish appearance) or remain on a mixed diet (asynchrony with prey fish appearance) using bioenergetic model simulations. We predicted that growth would be similar for both predators when consuming the same diet despite differences in hatching date, but if either predator was able to shift to piscivory, they would realize faster growth than the other predator maintaining a mixed diet. This modeling approach allowed us to examine growth tradeoffs for both predators with differing hatching dates and a fish-dominated diet compared with a mixed diet. We modeled differing hatching dates, piscivorous and mixed diets, and the combination of hatching date and diet to determine how these two factors influence the growth of walleye and yellow perch. Specifically,

we evaluated whether a specialist piscivore experienced cost in terms of decreased growth when it could not switch to piscivory, as compared with a generalist predator (Mittelbach and Persson 1998).

## Materials and methods

To test our predictions, we designed a series of laboratory experiments to quantify size-specific growth, prey selection, and foraging efficiency of walleye and yellow perch. Each variable was quantified for both predators when offered fish and (or) two alternate invertebrate prey (zooplankton and benthic invertebrates), at two prey densities (high and low). We assessed whether prey selection could predict predator growth, and if so, we then determined whether the patterns could be explained by foraging behavior and morphology. All experiments were conducted during 1998–2001 at the Kaskaskia Biological Station (Illinois Natural History Survey, Sullivan, Illinois) using the same protocols, prey types, and observers. We conducted experiments on 20-, 40-, 60-, and 80-mm size classes of walleye and yellow perch. Predators used in each size class were  $\pm 2$  mm of the target size (i.e., for the 20-mm size class, we used 18- to 22-mm predators). Age-0 bluegill (*Lepomis macrochirus*) were used as fish prey at 20%–25% of the total length of the predator throughout all experiments, except that larval common carp (*Cyprinus carpio*) were used for experiments with walleye in the 20-mm size class. Common carp and bluegill larvae have similar behavior and morphology at these sizes (Galarowicz and Wahl 2005). We used chironomid larvae as our benthic invertebrate prey (mean length = 11 mm, SE = 0.33), and daphnids as zooplankton prey (mean length = 1.7 mm, SE = 0.02). Walleye foraging and growth data were part of another study (see Galarowicz and Wahl (2005) for more details), but were combined with yellow perch data and reanalyzed here.

### Prey selection

We quantified prey selection by observing a single predator foraging on prey items in rectangular (500 L, yellow perch) or circular (300–500 L, walleye) tanks. Although we used different arena sizes for the smaller size classes of walleye, prey densities were similar across all experiments. Fish, chironomids, and zooplankton prey were offered to the predators in two different combinations: (i) low fish ( $10\cdot\text{m}^{-3}$ ), high benthos ( $500\cdot\text{m}^{-2}$ ), and high zooplankton ( $25\cdot\text{L}^{-1}$ ), or (ii) high fish ( $100\cdot\text{m}^{-3}$ ), low benthos ( $25\cdot\text{m}^{-2}$ ), and low zooplankton ( $2.5\cdot\text{L}^{-1}$ ). We selected these combinations to offer the predators fish prey at both high and low densities relative to the other prey items. The prey densities used in our experiment represent high and low relative densities common in Illinois lakes (Welker et al. 1994; Claramunt and Wahl 2000). Prior to the start of each 30-min observation period, a single predator was acclimated in a small holding chamber within the behavioral arena for at least 30 min. During a trial, the number of strikes and captures for all prey items was recorded. Five replicate trials were conducted on both prey combinations offered to all size classes of yellow perch and walleye ( $n = 40$  trials for each species).

To determine prey selectivity, we calculated mean Chesson's (1983) coefficient of selectivity ( $\alpha$ ) for each size class and prey density combination:

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

where  $r_i$  is the number of food type  $i$  in the predator diet,  $n_i$  is the number of food type  $i$  in the environment, and  $m$  is the number of prey types available. Mean alpha values ( $\pm 95\%$  confidence intervals) were compared against random feeding ( $1/m$ ) to determine selectivity.

### Growth

Specific growth rate was quantified for both length (to the nearest 0.5 mm) and mass (to the nearest 0.01 g) over a 7-day period of feeding on a diet of fish, zooplankton, or chironomids. A single juvenile walleye or yellow perch was placed in an aquarium (38 L) in an environmental chamber (20 °C, 12 h light – 12 h dark) and fed one prey type ad libitum. Prey (fish, chironomids, and daphnids) were added daily to each tank. Five to ten replicates were performed for each predator and prey-type combination. Specific growth rate ( $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ , or  $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) was determined as the amount of length or weight gained, given the initial length or weight, over the experimental period. These data were analyzed using a three-factor (predator, prey, and predator size) analysis of variance (ANOVA); data were log-transformed, and means were separated using pair-wise comparisons and stepdown Bonferroni adjustments.

### Foraging behavior

Behavioral experiments were conducted with all size classes of predators in 72-L aquaria. A single prey type was offered to the predators at both low (either  $13\text{ fish}\cdot\text{m}^{-3}$ ,  $50\text{ benthic invertebrates}\cdot\text{m}^{-2}$ , or  $2.5\text{ zooplankton}\cdot\text{L}^{-1}$ ) and high densities (either  $66\text{ fish}\cdot\text{m}^{-3}$ ,  $200\text{ benthic invertebrates}\cdot\text{m}^{-2}$ , or  $50\text{ zooplankton}\cdot\text{L}^{-1}$ ). We chose these prey densities to have sufficient prey to observe successful captures in a smaller arena while staying within prey range densities observed in Midwestern US lakes. A single predator was acclimated for at least 30 min in a partitioned section of the aquarium, and prey were allowed to acclimate in the remainder of the aquarium for at least 5 min prior to the start of each trial (see Galarowicz and Wahl (2005) for more details). Trials commenced when a predator was released from the enclosure by remotely lifting a partition. During each 15-min trial, we recorded the number of strikes, captures, and prey items consumed. At least five replicate trials were conducted on each size class and prey treatment combination. From these observations, we calculated capture efficiency (the number of strikes per capture), attack rates (the number of strikes per minute), and the total number of prey items consumed. All analyses were conducted using four-factor (predator, predator length, prey type, and prey density) ANOVA (data were log-transformed if non-normal). Means were separated using least-square means comparisons with stepdown Bonferroni adjustments.

## Morphology

Gape widths were estimated across a range of sizes (30–85 mm) for both predators ( $n = 20$  walleye,  $n = 56$  yellow perch). Gape was measured at the narrowest point inside the mouth of each predator using calipers. The relationship between gape width and predator total length was determined with linear regression. To prevent extrapolating beyond the range of our data, we restricted the intercept to the lower bounds of the data by subtracting the smallest length (30 mm) from all lengths. The slopes and intercepts of the regression lines were then compared using analysis of covariance (ANCOVA) to assess differences in gape across length.

## Bioenergetic model simulations

We used the Wisconsin Bioenergetics Model 3.0 (Hanson et al. 1997) to estimate growth and consumption of the two predators under differing diets and hatch date conditions. We used the juvenile walleye and larval yellow perch submodels, as provided by Hanson et al. (1997), for all simulations. Temperature ( $^{\circ}\text{C}$ ) during 2002 at the 1-m depth interval in Lake Mendota, Wisconsin (Kratz 2002) was used to simulate temperature during a typical growing season from a system containing both walleye and yellow perch. Spawning occurred at  $8.5^{\circ}\text{C}$  for walleye and  $10^{\circ}\text{C}$  for yellow perch, the median values from ranges reported by Scott and Crossman (1973). Our simulations started at the commencement of exogenous feeding, 15 days post-spawn for walleye (McElman and Balon 1979), and 27 days post-spawn for yellow perch (Mansueti 1964). Diets in baseline simulations were based on our results from prey selection experiments, with both predators consuming zooplankton until they reached 20 mm. Thereafter, walleye consumed only fish, whereas yellow perch consumed equal proportions of fish, zooplankton, and benthic invertebrates. Caloric densities of prey items were estimated from Cummins and Wuycheck (1971). Predator lengths (mm) were converted to weights, and vice versa, with the length–weight equation developed for walleye and yellow perch in Lake Mendota (Madenjian and Carpenter 1991). We first ran initial simulations for both predators until they reached the average size at age-1, as reported by Mittelbach and Persson (1998; modified from Winemiller and Rose 1992), at the end of one growing season (80 g for walleye, and 5.8 g for yellow perch). Baseline simulations encompassed the entire growing season (April–November) for Lake Mendota, running 228 days for walleye and 213 days for yellow perch. The proportion of maximum consumption ( $p$  value) was standardized at 0.75 for the initial simulation and served as our baseline for comparison in subsequent simulations.

The effect of hatching date was examined by hatching yellow perch on the same day as walleye in the walleye baseline but holding all other model parameters constant. Walleye were similarly hatched on the same day as the yellow perch baseline hatching day while other parameters were held constant. To determine the tradeoffs in growth for a piscivorous diet versus an invertebrate-dominated diet for both predators, we modeled yellow perch growth assuming they switched to a 100% fish diet at 20 mm (the same as walleye baseline). Conversely, walleye growth was modeled assuming a mixed diet containing equal proportions of fish,

zooplankton, and benthic invertebrates (the same as the yellow perch baseline). Finally, the effect of hatching date and diet in combination was examined by hatching yellow perch at the same time and with the same diet as walleye, and vice versa.

## Results

### Prey selection

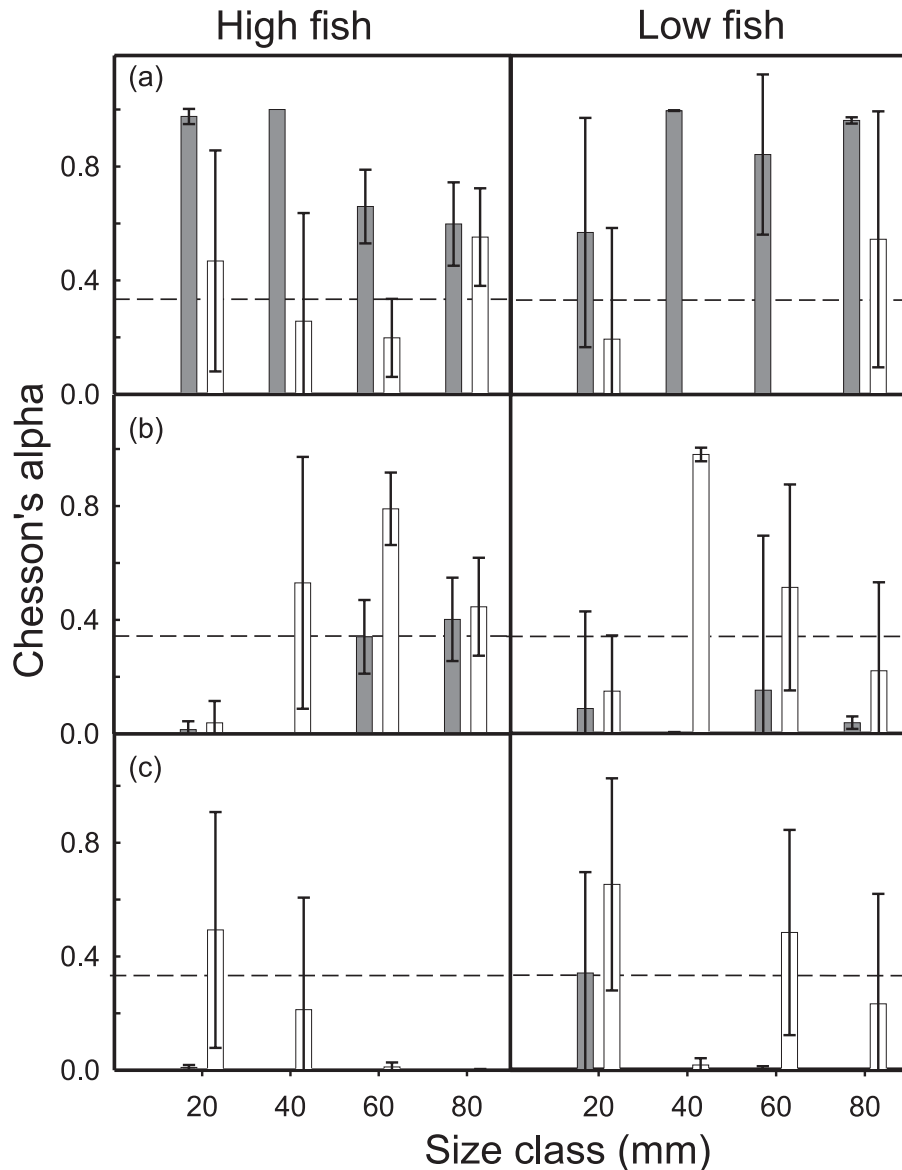
When offered a high proportion of fish prey relative to benthic invertebrates and zooplankton, yellow perch exhibited neutral selection for fish across all sizes, except at 80 mm, where they showed weak positive selection (Fig. 1). Conversely, walleye always exhibited positive selection for fish prey. Walleye avoided benthic invertebrates at 20 and 40 mm, but exhibited neutral selection for them at 60 and 80 mm. Yellow perch positively selected benthic invertebrates at 60 mm, but showed neutral selection at 40 and 80 mm, and avoided them at 20 mm. Yellow perch exhibited neutral selection for zooplankton at 20 and 40 mm, whereas walleye always avoided zooplankton when fish prey were abundant. Overall, yellow perch did not positively select fish prey, despite the high proportion of fish, compared with alternate invertebrate prey. Yellow perch instead selected a mixed diet of fish and zooplankton at smaller sizes and fish and benthic invertebrates at larger sizes. Walleye positively selected fish across all sizes and showed neutral selection for benthic invertebrates at larger sizes.

When offered a prey assemblage of low fish density and high invertebrate densities, walleye positively selected fish at all sizes except 20 mm, and yellow perch did not positively select fish at any size (Fig. 1). Yellow perch positively selected benthic invertebrates at 40 mm, but exhibited neutral selection for chironomids at other sizes. Walleye neutrally selected benthic invertebrates at 20 and 60 mm, but avoided chironomids at 40 and 80 mm. Yellow perch positively selected zooplankton only at 20 mm, whereas walleye avoided zooplankton at all larger sizes (walleye neutrally selected zooplankton at 20 mm). Even when offered fish prey at lower densities relative to alternate prey, walleye maintained positive selection for fish whereas yellow perch exhibited negative to neutral selection for fish prey.

### Growth

Growth rate ( $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ ) was highly variable and interacted significantly across three factors (predator, predator size, and prey type,  $F_{[6,134]} = 3.41$ ,  $P < 0.01$ ). Therefore, we compared the main effect of predator (yellow perch versus walleye) within levels of predator size and prey taxa. Walleye grew faster than yellow perch when feeding on fish prey at 20, 60, and 80 mm ( $t$  test<sub>134</sub> = 2.67–6.04,  $P = 0.05 - < 0.01$ ; Fig. 2). However, yellow perch grew faster than walleye at 40 mm on fish ( $t$  test<sub>134</sub> = 3.14,  $P = 0.02$ ). Walleye and yellow perch gained similar length while feeding on benthic invertebrate prey at all sizes except 80 mm, where walleye grew faster than yellow perch ( $t$  test<sub>134</sub> = 3.21,  $P = 0.01$ ). Yellow perch grew faster on zooplankton prey than did walleye at 40 and 60 mm ( $t$  test<sub>134</sub> = 5.72 and 4.84,  $P < 0.01$ ), but both predators had similar growth rates at 20 mm ( $t$  test<sub>134</sub> = 0.54,  $P = 0.59$ ) and 80 mm ( $t$  test<sub>134</sub> = 0.7,  $P = 0.48$ ) while consuming zooplankton.

**Fig. 1.** Chesson's alpha (mean  $\pm$  95% confidence interval) for walleye (*Sander vitreus*; shaded bars) and yellow perch (*Perca flavescens*; open bars) across different size classes and prey types: (a) fish, (b) benthic invertebrates, and (c) zooplankton. Fish prey were offered at high (left panels) and low (right panels) densities relative to benthic invertebrates and zooplankton. Broken lines indicate random feeding. Values above, below, and near the line indicate positive selection, negative selection, and neutral selection, respectively.



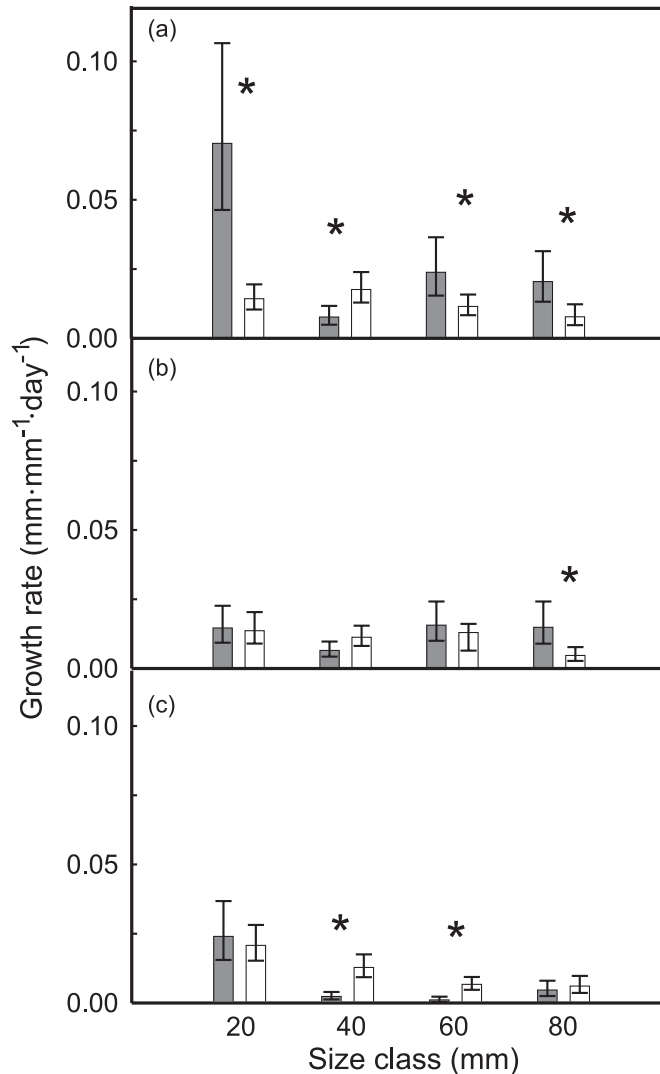
Growth in weight ( $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ) was also significantly affected by a three-factor interaction (predator, predator size, and prey type,  $F_{[6,134]} = 2.36$ ,  $P = 0.03$ ). The smallest size class (20 mm) of walleye gained more mass than the smallest yellow perch size class (20 mm) while feeding on fish prey ( $t$  test<sub>134</sub> = 4.43,  $P < 0.01$ ). Growth was similar for both predators across all larger sizes when feeding on fish prey ( $t$  test<sub>134</sub> = 0.62–2.75,  $P = 0.07$ –1). Walleye and yellow perch gained mass at similar rates across all sizes while feeding on benthic invertebrate prey ( $t$  test<sub>134</sub> = 0.16–2.34,  $P = 0.18$ –1). Yellow perch gained mass faster than walleye when feeding on zooplankton at 60 mm ( $t$  test<sub>134</sub> = 3.31,  $P = 0.01$ ). Overall, growth in weight was relatively similar for both predators across all sizes and prey types. However,

allometric weight differences between the two predators (i.e., yellow perch tended to have greater mass at a given length than walleye) resulted in growth-in-weight comparisons being less robust.

#### Feeding behavior

Attack rates (number of strikes per minute) were higher for yellow perch than for walleye across all sizes and prey types ( $F_{[1,201]} = 5.47$ ,  $P = 0.02$ ). Attack rates were also significantly affected by a two-factor interaction (predator size and prey taxa,  $F_{[6,201]} = 3.47$ ,  $P < 0.01$ ). Within a size class, attack rates were highest for zooplankton, intermediate for benthic invertebrates, and lowest for fish ( $t$  test<sub>201</sub> = 2.36–9.71,  $P = 0.03$ – $<0.01$ ; Fig. 3), except at 80 mm, where at-

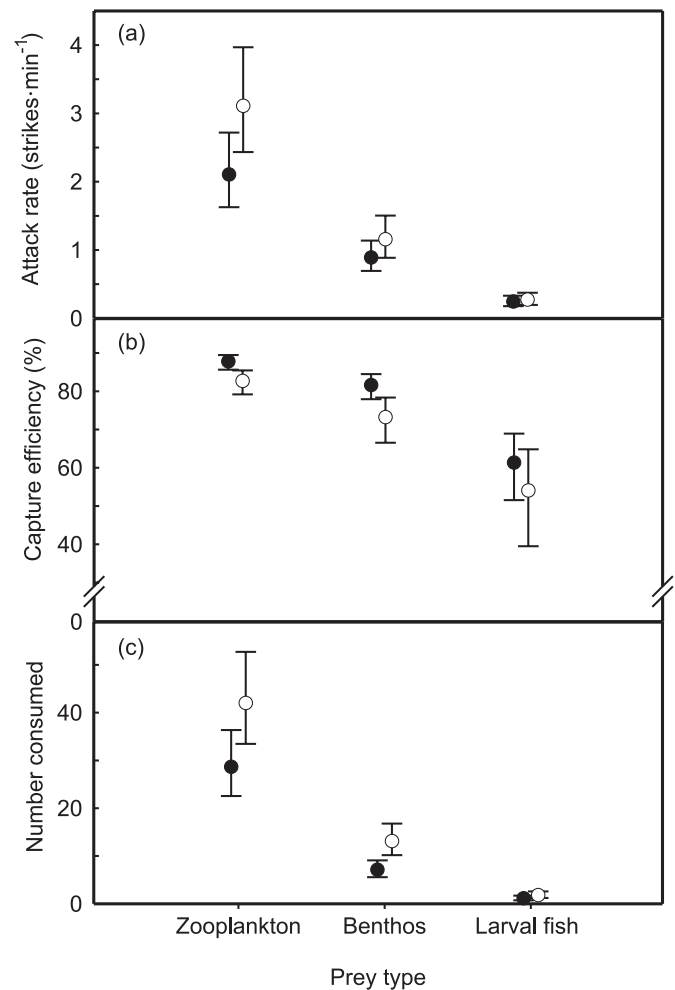
**Fig. 2.** Relative growth rate ( $\text{mm}\cdot\text{mm}^{-1}\cdot\text{day}^{-1}$ ) of juvenile walleye (*Sander vitreus*; shaded bars) and yellow perch (*Perca flavescens*; open bars) across different sizes while feeding on (a) larval fish, (b) benthic invertebrates, and (c) zooplankton. Values are means  $\pm$  95% confidence intervals. Significant differences denoted by asterisks were evaluated for pairwise comparisons of walleye and yellow perch at each size and prey type.



tack rates were similar for benthic invertebrates and zooplankton ( $t$  test<sub>201</sub> = 1.45,  $P$  = 0.15). However, these relationships were similar for walleye and yellow perch, as there was no interaction between predator and either predator length ( $F_{[3,201]} = 1.9$ ,  $P$  = 0.13) or prey type ( $F_{[3,201]} = 0.68$ ,  $P$  = 0.51). Prey density also significantly affected attack rate, with both predators exhibiting higher attack rates at high prey densities (1.25 strikes·min<sup>-1</sup>) compared with low prey densities (0.65 strikes·min<sup>-1</sup>,  $t$  test<sub>201</sub> = 5.92,  $P$  < 0.01).

Capture efficiency (the number of strikes per capture) was significantly affected by predator and prey type. Walleye exhibited higher capture efficiency than yellow perch ( $F_{[1,193]} = 13.67$ ,  $P$  < 0.01). Capture efficiency also differed among prey types for both predators ( $F_{[2,193]} = 50.43$ ,  $P$  < 0.01).

**Fig. 3.** Walleye (*Sander vitreus*; ●) and yellow perch (*Perca flavescens*; ○) foraging behavior on (a) fish, (b) benthic invertebrates, and (c) zooplankton. All behaviors were quantified during 15-min feeding trials. Values are means  $\pm$  95% confidence intervals.



Capture efficiency was highest for zooplankton, intermediate for benthic invertebrates, and lowest for fish prey (Fig. 3). Capture efficiency was not influenced by predator length ( $F_{[3,193]} = 1.66$ ,  $P$  = 0.18) or prey density ( $F_{[1,193]} = 2.48$ ,  $P$  = 0.12). Thus, walleye captured prey more efficiently than yellow perch; capture efficiency was higher for both predators while consuming smaller prey items. These patterns were consistent across all predator sizes and both prey densities.

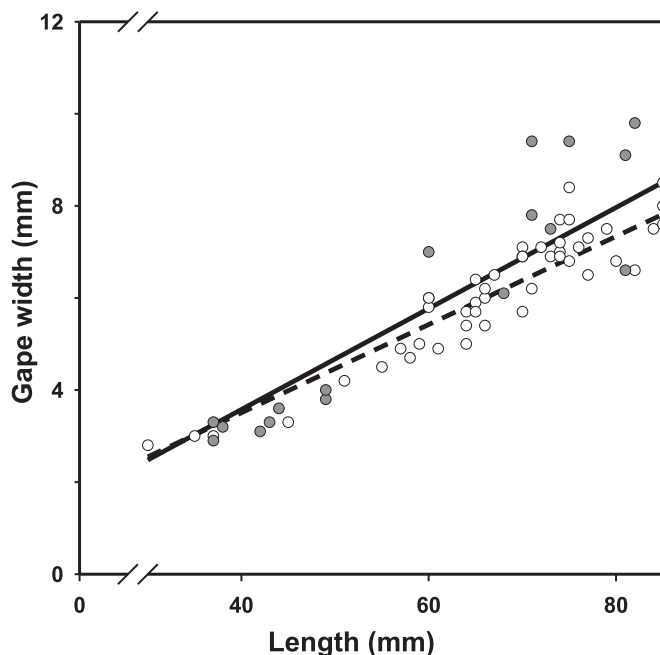
Unlike attack rate and capture efficiency, the number of prey items consumed differed little between yellow perch and walleye (Fig. 3). Because there was a significant three-factor interaction (predator, predator size, and prey type,  $F_{[6,201]} = 2.81$ ,  $P$  = 0.01), we again compared the main effect of predator within levels of predator size and prey type. At 20 mm, yellow perch consumed significantly more zooplankton than did walleye ( $t$  test<sub>201</sub> = 4.06,  $P$  = 0.02). For all other size classes and prey types, yellow perch and walleye consumed similar numbers of prey items ( $t$  test<sub>201</sub> = 0.33–2.66,  $P$  = 0.09–1). Given that the significant three-factor interaction was driven by only one size class and prey type,

**Table 1.** Final weight, consumption, and growth efficiency for yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*) from bioenergetic model simulations.

Predator	Model simulation	Final weight (g)	Total consumption (g)	Growth efficiency (%)
Yellow perch	Initial	6	80	8
	Baseline ( <i>p</i> value = 0.75)	11	126	9
	Early hatch date	11	126	8
	Fish diet	39	245	16
	Early hatch date and fish diet	40	253	16
Walleye	Initial	80	432	19
	Baseline ( <i>p</i> value = 0.75)	53	308	17
	Late hatch date	51	297	17
	Mixed diet	2	34	6
	Late hatch date and mixed diet	2	32	6

**Note:** Baseline *p* value (0.75; proportion of maximum consumption) resulted from initial simulations (average values of growth, diet, and temperature from our study and literature). For both predators, we also simulated switched hatching dates, diets, and both hatching dates and diets in combination.

**Fig. 4.** Gape width-to-length relationships of walleye (*Sander vitreus*; —●—) and yellow perch (*Perca flavescens*; - - ○ - -). Gape width was measured at the narrowest point in the mouth using calipers. Linear regression was used to predict gape width based on total length of predator and provided good fits for both predators ( $r^2 = 0.87$ ,  $P < 0.01$  for both walleye and yellow perch).



we conclude that walleye and yellow perch generally consumed similar numbers of each prey type. However, both yellow perch and walleye did consume more prey in the high-density prey treatments compared with the low-density treatments ( $F_{[1,201]} = 28.78$ ,  $P < 0.01$ ).

### Morphology

Length predicted gape width for both walleye ( $r^2 = 0.87$ ,  $P < 0.01$ ) and yellow perch ( $r^2 = 0.87$ ,  $P < 0.01$ ; Fig. 4). The equations to estimate gape  $G$  based on predator length  $L$  were as follows:  $G = -1 + 0.11L$  for walleye, and  $G = -0.46 + 0.1L$  for yellow perch. Initially, gape widths were

similar for both predators (ANCOVA (intercept) = 1.85,  $P = 0.07$ ), but walleye gape widths increased at a faster rate than those of yellow perch (ANCOVA (slope) = 2.26,  $P = 0.03$ ).

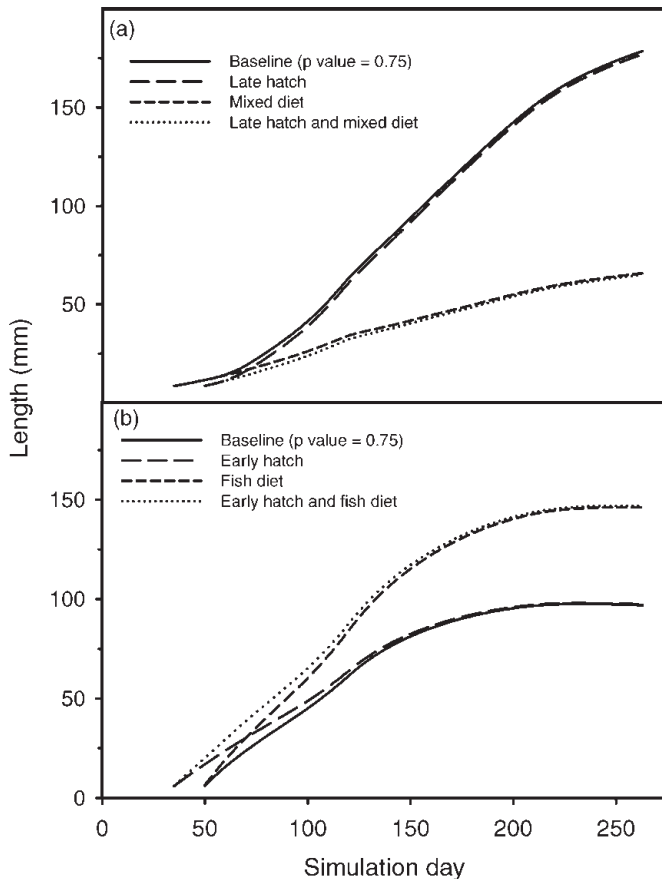
### Bioenergetic model simulations

In initial simulations, the *p* value needed by walleye to reach its final weight was 0.79; for yellow perch, the *p* value was 0.65. With standardized *p* values (*p* value = 0.75), consumption and growth efficiency were slightly higher for yellow perch and reduced for walleye compared with initial simulations (Table 1). Hatching date alone had little effect on growth for both predators. When hatching dates were switched, but diets remained the same, size at the end of the growing season, consumption, and growth efficiency either remained the same (yellow perch) or decreased slightly (walleye) from baseline simulations with standardized *p* values (Fig. 5). In contrast, the proportion of fish in the diet strongly influenced growth for both predators; however, neither predator achieved growth comparable to the baseline of the other. When yellow perch were allowed to switch to a piscivorous diet at 20 mm, their length at the end of the growing season remained 24% lower than for the walleye baseline simulation (Fig. 5). Similarly, when walleye were forced to maintain a mixed diet with equal proportions of fish, benthic invertebrates, and zooplankton, growth was much slower and their size at the end of the growing season was 82% lower than that of yellow perch. When both hatching date and diet were changed, growth and consumption of both predators remained similar to simulations with switched diets only (Table 1; Fig. 5). Overall, walleye realized faster growth rates than yellow perch on a piscivorous diet, but grew much slower than yellow perch on a mixed diet. Conversely, yellow perch did not grow as fast as walleye on a piscivorous diet, but they were able to grow faster than walleye on a mixed diet.

### Discussion

As predicted, walleye, as specialist piscivores, strongly selected fish prey over alternate prey, whereas yellow perch, as generalist predators, displayed negative to neutral selection of fish and favored alternate prey types. These patterns held

**Fig. 5.** Lengths (mm) of age-0 (a) walleye (*Sander vitreus*) and (b) yellow perch (*Perca flavescens*) over one growing season (April–November) from bioenergetic model simulations. Baseline  $p$  value (0.75; proportion of maximum consumption) resulted from initial simulations (average values of growth, diet, and temperature from our study and literature). For both predators, we also simulated switched hatching dates, diets, and both hatching dates and diets in combination.



even when fish prey were offered in lower proportion relative to alternate prey types. Selection patterns were supported by differences in growth of juvenile yellow perch and walleye. Walleye grew faster than yellow perch while feeding on fish prey across most sizes. Interestingly, regardless of walleye size, walleye also grew faster on fish prey compared with other prey types, whereas yellow perch growth varied little across all prey types. We believe that an important reason for this pattern of growth and selection is that walleye actively selected fish prey, likely based on optimal foraging, whereas yellow perch passively selected all prey based on availability and foraging efficiency.

Growth and prey selection from our experiments generally support patterns observed in the field. Within the range of sizes we examined, field data for juvenile walleye showed positive selection for, and strong growth while consuming, fish prey (Mathias and Li 1982). Piscivory is also common during the juvenile period for hybrid saugeye (*Sander canadensis* × *S. vitreus*; Donovan et al. 1997), and in closely related pikeperch (*Sander lucioperca*; Buijse and Houthuijzen 1992). These predators realize a substantial

growth increase after switching to piscivory. Field patterns for growth and prey selection by yellow perch also support our results. Although fish prey has been observed in diets of yellow perch as small as 65 mm, juvenile yellow perch generally consume invertebrates and realize high growth when these prey are abundant (Mills et al. 1989; Fullhart et al. 2002). Thus, in the field, walleye are piscivorous across the range of juvenile sizes that we examined, whereas yellow perch are generalist predators, choosing a diet that may contain fish but is dominated by invertebrates.

Foraging behavior supported, but did not fully explain, the observed differences in prey selection and growth patterns between walleye and yellow perch. Capture efficiency was higher for walleye than yellow perch while feeding on fish prey, suggesting that walleye must expend less energy than yellow perch in capturing fish prey (Einfalt and Wahl 1997). However, it is not clear if the relatively small difference in overall foraging efficiency on fish prey between walleye and yellow perch (e.g., capture efficiency: 61% versus 54%) is large enough to account for the very large differences we observed in prey selection and growth. In a study of selective feeding and growth for esocids, capture efficiencies were greater than threefold more for fusiform prey (>60%) over bluegill (<20%) and these differences conferred higher growth (Wahl and Stein 1988). In contrast with capture efficiency, the overall attack rate of walleye was lower than that of yellow perch. However, because walleye captured prey more efficiently, both predators consumed similar numbers of prey items. Yellow perch attacked prey more frequently to overcome lower capture efficiency. As a consequence, yellow perch likely expended more energy to obtain the same caloric intake as walleye. Given their higher overall foraging efficiency, we expected walleye to outgrow yellow perch for all size classes and prey types (particularly fish prey). However, yellow perch grew faster than walleye while feeding on fish prey at 40 mm, and on zooplankton at 40 and 60 mm. Our results suggest that walleye are fish specialists that actively select their prey. As such, growth suffers accordingly when fish prey are not available, even though walleye forage more efficiently on each prey type compared with perch.

Mouth morphology also differed between yellow perch and walleye, particularly for larger sizes. Predator morphology (particularly gape width) is an important factor regulating piscivory (Olson 1996; Einfalt and Wahl 1997) because larger gapes allow piscivores to capture and handle fish prey more effectively, and small differences could affect foraging success. We held fish prey size constant across size classes of predator (i.e., 20%–25% total length) to provide a constant and optimal predator:prey size ratio. We also ensured that the fish prey used in our experiments were within the limits of gape width for both predators. Because walleye are piscivorous at smaller sizes than yellow perch, we predicted that walleye would have larger gapes across all sizes. In fact, gape widths were similar across smaller sizes of both predators, but walleye gape increased faster than that of yellow perch, resulting in larger gapes for walleye at larger sizes. This may help explain why larger walleye grew better while consuming fish and selected this prey type more strongly than did yellow perch. However, growth and selection differed between predators when gape widths did not differ at smaller sizes.

Although increased gape might explain why larger walleye select for fish prey compared with yellow perch, other factors regulate the differences in selection at smaller sizes. The presence of canine teeth is one morphological attribute that may contribute to the different selection patterns and foraging efficiency observed for walleye compared with yellow perch. Canine teeth may allow walleye to grasp and hold onto prey items more effectively than yellow perch (Craig 1987), allowing them to feed more efficiently on prey that can escape capture. Overall, predator morphology was also an important determinant of prey selection and growth, but did not fully explain the differences in dietary ontogeny between walleye and yellow perch.

The difference in timing of piscivory between walleye and yellow perch is likely a result of an interaction between foraging success and gape width. Although the differences in foraging efficiency and gape width between walleye and yellow perch were relatively small, they always favored walleye to become piscivorous earlier than yellow perch. These conclusions differ slightly from Mittelbach and Persson (1998), who hypothesized that most of the variation in the ontogeny of piscivory was explained by morphological differences among predators. Predators in our study had similar gape widths at smaller sizes (20 and 40 mm), but walleye still foraged more efficiently on fish prey compared with yellow perch. Mittelbach and Persson (1998) speculated that early switching piscivores would also have a higher overall foraging efficiency than fish species switching at larger sizes.

Walleye were slightly more efficient foragers across all sizes and prey types, but the magnitude of differences were much smaller than we predicted. Based solely on foraging efficiency, we would have expected walleye to grow faster than yellow perch on all prey types. Because walleye grew faster only with fish prey, we conclude that walleye were actively selecting fish prey based on optimal foraging considerations, which explains why walleye select fish so much earlier than yellow perch, which passively select their prey. Furthermore, fish prey, which have a higher caloric density than invertebrates ( $3698 \text{ J}\cdot\text{g}^{-1}$  for fish prey versus  $2600 \text{ J}\cdot\text{g}^{-1}$  for zooplankton and  $1763 \text{ J}\cdot\text{g}^{-1}$  for benthic invertebrates; Cummins and Wuycheck (1971)), reinforce their active selection by the specialist piscivore. Conversely, yellow perch passively select prey based on foraging efficiency and prey availability alone. Thus, it is likely that both predator morphology and foraging efficiency influence the ontogeny of piscivory, but consideration of selection mode, in the context of optimal foraging, further explains the observed differences between walleye and yellow perch.

The importance of life history variation in determining piscivory was also suggested by Mittelbach and Persson (1998). Although they could not detect a statistical relationship, they speculated that the timing and size at hatching contributed to differences in dietary ontogeny. We explored the role of hatching dates and the ability to consume only fish using bioenergetic simulations. The shift to piscivory is facilitated by the appearance of prey fish availability. Piscivores large enough to consume fish prey as they become available (synchronous) switch early to piscivory and maintain fast growth rates, whereas piscivores poorly matched with the appearance of fish prey are unable to switch to piscivory and maintain slower growth (Persson and

Brönmark 2002). Walleye hatch earlier than yellow perch and at larger sizes; as such, walleye likely gain a size advantage over other age-0 fishes. Conversely, later hatched yellow perch may not achieve a size advantage over fish prey. These differences may enable walleye to grow faster and switch to piscivory earlier than yellow perch simply because they have more fish prey available within gape limits. Our bioenergetic simulations showed that hatching 15 days earlier (yellow perch with walleye hatching date) or later (walleye with yellow perch hatching date) had little effect on growth when diets remained the same. However, if hatching early allowed either predator to switch to piscivory, they realized increased growth compared with maintaining a mixed diet. Thus, hatching time of predators relative to the appearance of fish prey is likely important in facilitating the switch to piscivory, but this mechanism should be further tested in a field setting.

Our bioenergetic simulations were designed to be broadly representative of conditions across the range of both predators. As such, values we used as model parameters were often used or modified from values reported in the literature, but these can be variable. For example, we used 27 days as the duration from hatching to exogenous feeding in our simulations for yellow perch (Mansueti 1964), but values as short as 15 days have also been reported (Scott and Crossman 1973). Both hatching date and duration to exogenous feeding are likely affected by temperature. Even with the incorporation of this variation, our simulations would still indicate that timing of hatching and switching to exogenous feeding had little effect on growth for both predators when diets were held constant. Switching to a piscivorous diet, however, had a very large effect on growth for both predators. We based model diet shifts on results from our prey selection experiments in which walleye positively selected fish across all sizes and yellow perch did not show distinct selection patterns. However, we recognize that field studies have documented variation in diet shifts. For example, walleye have been shown to switch to piscivory at larger sizes than we used for our simulations (i.e., 35 mm in Mathias and Li 1982, compared with 20 mm in this study). Similarly, previous studies of yellow perch food habits show they can have a varied diet, but it is composed mostly of invertebrates for the first several years of life (Fullhart et al. 2002). Despite the potential variation in food habits for these two predators, the importance of fish as prey remained unchanged across a range of prey availabilities in our simulations.

Our growth simulations address the following question: Do specialist piscivores take a higher risk in terms of growth by specializing on fish prey? Specifically, when fish prey are not available to specialist predators, will they experience lower growth than a generalist predator? Because walleye actively seek fish prey based on optimal foraging, when fish prey are unavailable, growth is much slower when walleye maintain and invertebrate diet. Conversely, yellow perch passively select prey based on foraging efficiency and maintain similar growth on invertebrate and (or) piscivorous diets as long as either prey type is efficiently consumed. Mittelbach and Persson (1998) thought that, as specialist piscivores grew, foraging efficiency on non-fish prey would rapidly decline, whereas generalist predators would experience slower

decreases in foraging efficiency on non-fish prey. Our simulations showed that walleye forced to maintain a mixed diet exhibited growth rates much lower than that of yellow perch with a similar diet. We are unsure why growth of walleye was lower than that of yellow perch on a non-fish diet (and conversely, why walleyes grow faster than perch on a piscivorous diet), but other feeding behaviors, such as reactive distance and pursuit, as well as metabolic allometry, would better address optimal foraging and should be considered in future studies. Walleye are specialist piscivores that actively select fish prey; when they switched to piscivory at a small size, they realized very fast growth, but growth was much reduced when walleye could not switch to piscivory. Yellow perch are generalist predators; they did not grow as fast as walleye with a fish diet, but grow faster than walleye with an invertebrate diet.

Walleye, as specialist piscivores, switch to piscivory earlier than yellow perch, and the increase in growth associated with a fish diet may allow them to maintain a size advantage over fish prey throughout the growing season. The early hatching of walleye may help facilitate the switch to piscivory because other fishes hatch later than walleye, but has little direct influence on growth. Conversely, if yellow perch do not switch to piscivory early they realize slower growth, precluding them from switching to piscivory until age 1+. This delayed switch to piscivory may be further exacerbated by the later hatching of yellow perch because other prey fish hatch before or during the same time as yellow perch. As such, differences in feeding ontogeny between walleye and yellow perch may result simply because yellow perch never realize a size advantage over the majority of fish prey available. Life history variation is an important factor affecting the ontogeny of piscivory; however, additional research to understand the mechanisms facilitating the switch to piscivory during early life history, specifically the interactive effects of hatch date and prey fish abundance, is needed.

Our results indicate that the onset of piscivory is driven by a combination of several factors. We investigated three potential factors and found that each supported, but did not fully explain, the patterns of growth and prey selection between walleye and yellow perch. The specialist piscivore (walleye) foraged more efficiently on fish prey, had a mouth gape that increased rapidly, and hatched earlier than the generalist predator (yellow perch). As such, walleye grew faster on fish prey than yellow perch, and strongly selected for fish, whereas yellow perch selected all three prey types. Our results suggest that walleye are actively selecting fish prey based on optimal foraging, whereas yellow perch passively select fish prey based on encounter rates and foraging efficiency. These characteristics in combination help to explain why some fish species switch to piscivory early, whereas others do not.

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