

INDIVIDUAL VARIATION IN THE TIMING OF ONTOGENETIC NICHE SHIFTS IN LARGEMOUTH BASS

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Abstract. The transition to piscivory is a crucial ontogenetic niche shift for many primarily piscivorous fishes. An early transition to piscivory may increase growth, decrease mortality, and therefore enhance lifetime fitness. Although much is known about the extent and causes of variation in the timing of the shift to piscivory among species and among cohorts within a species, little is known about the extent and causes of variation in the timing of the switch to piscivory among individuals within a single cohort. Here, I link otolith age and growth analysis to direct diet and stable isotope analyses to examine variation in the timing of the transition to piscivory and its causes among individual members of the 1994 largemouth bass cohort in Paul Lake, Michigan. Stable isotope and direct diet analyses indicate that only a few members of the 1994 cohort were able to shift to and sustain piscivory in their first summer of life (early piscivores), while most cohort members would have to wait until their second summer of life to become piscivorous (late piscivores). Significant differences in growth rate between early and late piscivores emerged shortly after 18 June, the first date of possible piscivory by early piscivores, after which early piscivores began to grow at rates nearly twice that of late piscivores. Otolith and stable isotope analyses combined indicate that an early hatching date was necessary, but not sufficient, to explain variation in the timing of the transition to piscivory. All early piscivores were hatched early in the summer, but many early-hatched members of the 1994 cohort did not shift to piscivory in their first summer of life. A combination of at least 10 days of variation in hatching dates and higher-than-average growth rates was required for early piscivores to switch to and sustain piscivory in their first summer of life. Individuals that were able to make the early transition to piscivory most likely benefited from both increased survival and fecundity over much of their life, the combination of which would confer a substantial fitness advantage upon individuals able to make the early transition to piscivory.

Key words: *cannibalism; growth; intraguild predation; largemouth bass; Micropterus salmoides; niche shifts; ontogeny; otolith; piscivory; size-structured predation; stable isotopes; survival.*

INTRODUCTION

Organisms that undergo large changes in body size typically display pronounced changes in resource use between birth and maturation. These ontogenetic niche shifts (*sensu* Werner and Gilliam 1984) are often manifest as shifts in habitat use or diet with increasing body size (e.g., Werner and Gilliam 1984, Mittelbach 1986, Olson 1996), which can generate complex interactions and dynamics within communities (Werner and Gilliam 1984, Polis et al. 1989, Werner 1992, Olson et al. 1995, Post et al. 1997, Post and Kitchell 1997, Persson 1999). Ontogenetic niche shifts are particularly important for organisms for which resource use, growth rates, and predation risk are strongly related to body size (e.g., Werner and Gilliam 1984, Miller et al. 1988). Ontogenetic niche shifts help maximize fitness by reducing competition with conspecifics through intraspecific resource segregation (Werner and Gilliam 1984), by minimizing predation risk through habitat shifts (Werner

et al. 1983), and by maximizing growth through dietary shifts (Aggus and Elliott 1975, Shelton et al. 1979, Olson 1996).

The dietary shift between feeding on invertebrates and feeding on fish is critically important for fishes that are predominately piscivorous (e.g., primary or specialist piscivores; Keast 1985, Buijse and Houthuijzen 1992, Olson et al. 1995, Mittelbach and Persson 1998). Specialist piscivores are not particularly well adapted to feeding upon zooplankton and benthic invertebrates that are their prey early in life (Werner and Gilliam 1984, Mittelbach and Persson 1998, Hjelm et al. 2000), and delays in the shift to piscivory can lead to slow growth and increased mortality, particularly when in competition with specialist planktivorous fishes (Werner and Gilliam 1984, Persson and Greenberg 1990a, b, Buijse and Houthuijzen 1992, Olson et al. 1995, Stein et al. 1995, Buckel et al. 1998, Mittelbach and Persson 1998). The switch to piscivory often initiates an increase in growth rate that typically translates into larger size and greater survival throughout life for specialized piscivores (Aggus and Elliott 1975, Shelton et al. 1979, Buijse and Houthuijzen 1992, Olson 1996, Buckel et al. 1998, Mittelbach and Persson 1998, Post

Manuscript received 20 May 2002; revised 10 September 2002; accepted 18 September 2002. Corresponding Editor: R. J. Etter.

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et al. 1998). Larger individuals are typically less vulnerable to predation (Miller et al. 1988, Luecke et al. 1990, Post et al. 1998) and have greater energy reserves to survive periods of starvation (Oliver et al. 1979, Toney and Coble 1979, Shuter and Post 1990, Post et al. 1998). Variation in the timing of the switch to piscivory has been documented among species (Mittelbach and Persson 1998) and among cohorts of the same species (Olson 1996, Buckel et al. 1998, Hjelm et al. 2000). Variation in transition dates among species is partially explained by species-specific differences in the allometry of gape size, the timing of hatching, and the size at hatching (Keast 1985, Mittelbach and Persson 1998). Variation among cohorts, where gape size and hatching size are generally invariant (but see Hjelm et al. 2000, Svanback and Eklov 2002), is related to interaction among the relative hatching dates of predator and prey, growth rates in earlier ontogenetic stages, and the availability of appropriately sized fish prey (e.g., Olson 1996). There is, however, almost no direct empirical evidence from natural populations for individual variation in ontogenetic diet shifts (trophic ontogeny) and the effect of these shifts on individual growth and survival (but see Aggus and Elliott [1975], Shelton et al. [1979], Adams and DeAngelis [1987], and van Densen et al. [1996], and for strong indirect evidence, and Brabrand [1995] for evidence from an experimental system).

Here, I document variation in the trophic ontogeny of individual largemouth bass, *Micropterus salmoides*, during their first summer of life in Paul Lake, Michigan. I focus on the transition to piscivory in general because of its impact on community structure and ecosystem function (Carpenter 1988, Kitchell et al. 1994, Mittelbach et al. 1995, Post et al. 1997, 1998, Post and Kitchell 1997), and on the transition to piscivory in the first summer of life specifically because of its importance to largemouth bass growth and survival (Olson 1996). Largemouth bass completely dominate the fish community of Paul Lake (95–99% of the fish biomass in any year; Carpenter and Kitchell 1993) and therefore the transition to piscivory is also a switch to cannibalism (Post et al. 1998), a special case of intraguild predation (Polis et al. 1989) that has important implication for population dynamics and community structure (Fox 1975, Polis 1981, Polis et al. 1989, Post et al. 1997, 1998, Claessen et al. 2000). Young-of-the-year (YOY) largemouth bass are able to prey upon conspecifics that are about half their length (Johnson and Post 1996), which makes it physically possible for YOY largemouth bass to prey upon newly hatched conspecifics (~6 mm in length) at a very small size and early age (~12 mm, ~10–12 d; Johnson and Post 1996). However, adult male largemouth bass protect schools of YOY largemouth bass until they reach ~15 mm in length, obliging YOY largemouth bass to delay cannibalism until they reach a length of 30 mm, the minimum size required to prey upon conspecifics 15

mm in length (Johnson and Post 1996). Some combination of variation in either hatching dates or growth rates is necessary to produce the size difference required to initiate piscivory under these constraints (Adams and DeAngelis 1987, DeAngelis et al. 1991, Wright 1993, Johnson and Post 1996), and once piscivory is initiated, piscivorous individuals must grow fast enough to maintain a 2:1 advantage in length over available prey to sustain piscivory.

I focus on the 1994 cohort in Paul Lake, which had a large range of hatching dates, large size differences among individual bass throughout the summer, and for which there was some preexisting dietary evidence of piscivory by members of the cohort (Post et al. 1998). I use a combination of diet and stable isotope analyses to evaluate trophic ontogeny, and otolith analysis to evaluate individual birth dates and growth rates. I ask the questions: (1) is there evidence for early and sustained shifts in piscivory in this cohort; (2) what was the potential for piscivory among individual in this cohort; and (3) how important was variation in hatching date vs. variation in early growth rates to the initiation and maintenance of piscivory in the first summer of life? Then I discuss the implications of the variation in the transition to piscivory for survival through the first year of life and for future growth and fecundity. I find strong evidence for both early and sustained transitions to piscivory by the oldest and fastest growing individuals in the 1994 cohort, but little potential for a transition to piscivory by average individuals. Individuals able to make this early niche shift benefited from higher growth rates, and this growth advantage likely both increased the probability of surviving the first year of life and may have allowed earlier reproduction and higher fitness.

METHODS

Study site

Paul Lake is a small lake (1.7 ha, maximum depth 15.0 m) located near the northern extent of the largemouth bass range in the University of Notre Dame Environmental Research Center, Gogebic County, Michigan, USA (Carpenter and Kitchell 1993). The Paul Lake largemouth bass population has been unmanipulated and unexploited since it was established in 1976 (Leavitt et al. 1989). Paul Lake and its history are fully described in Leavitt et al. (1989) and Carpenter and Kitchell (1993).

Fish sampling

I sampled YOY largemouth bass through the summer of 1994 using a combination of dip nets (while snorkeling) and a boat-mounted electroshock device. Dip nets can effectively sample YOY largemouth bass <15 mm long in nest schools and were used to sample the 1994 cohort from late May until 22 June when the majority of nest schools dispersed. After 22 June, YOY

largemouth bass were sampled by electroshocking, which can effectively sample YOY largemouth bass $> \sim 25$ mm. Fish between about 15 and 25 mm generally were not vulnerable to the combination of dip netting and electroshocking. This gap in sampling efficiency introduced a noticeable sampling bias against individuals > 15 mm on 22 June, and against individuals < 25 mm in length after 30 June. On each sampling date, all fish caught were measured for length, a subset of fish was measured for mass, and a subset was sacrificed and preserved in ethanol for diet analysis. Fish < 20 mm in length were measured to the nearest 0.5 mm, and fish > 20 mm were measured to the nearest 1 mm. On 20 and 22 August, I conducted a large end-of-the-summer survey of YOY largemouth bass. From the 22 August sample, 97 haphazardly chosen fish were sacrificed for diet, otolith, and stable isotope analyses. The length and mass of each fish was measured before preservation in ethanol.

Stable isotope analysis

I used stable isotope analysis to provide evidence for trophic shifts among individual YOY largemouth bass. The ratio of stable nitrogen isotopes ($\delta^{15}\text{N}$) provides an estimate of trophic position because the $\delta^{15}\text{N}$ of an organism is enriched by $\sim 3.4\text{‰}$ ($\pm 1\text{‰}$) relative to its diet (Post 2002). When organisms feed within the same food chain (i.e., have similar diets that are based on the same ultimate nitrogen source), significant differences in $\delta^{15}\text{N}$ reflect differences in the trophic position of the organisms (Post 2002). In Paul Lake, young-of-the-year largemouth bass that switch to piscivory should have a higher $\delta^{15}\text{N}$ than that of conspecifics that have not switched to piscivory.

I performed stable isotope analyses on 31 of the YOY largemouth bass collected on 22 August 1994. I chose individuals to represent the entire size range of fish collected on that date, but I oversampled the largest fish to better detect early ontogenetic niche shifts. All fish were dried at 40°C for > 48 h, ground into a fine powder using a liquid nitrogen cooled ball mill, and packed into tin capsules for analysis. Stable isotope analysis was performed on a Europa Geo 20/20 continuous flow isotope ratio mass spectrometer at the Cornell University and Boyce Thompson Institute Stable Isotope Laboratory. All stable-isotope values are reported in the δ notation where $\delta^{15}\text{N} = ([^{15}\text{N}/^{14}\text{N}]_{\text{sample}} / [^{15}\text{N}/^{14}\text{N}]_{\text{standard}} - 1) \cdot 1000$. The global standard for $\delta^{15}\text{N}$ is atmospheric nitrogen, and the local working standard was CBT (Cayuga brown trout; $\delta^{13}\text{C} = -25.1$, $\delta^{15}\text{N} = 17.3$).

Otolith analysis

I analyzed otolith microstructures to estimate birth dates for 97 members of the fish caught on 22 August, and to back calculate length and growth for a subset of fish used for stable isotope analysis. Counts of the daily rings of otoliths (sagittal otolith) provide a reli-

able estimate of age in days for largemouth bass in their first summer of life (e.g., Miller and Storck 1984). Otoliths were prepared according to the methods of Miller and Storck (1982) and Isely and Nobel (1987). I counted the number of daily rings in each otolith a minimum of three times. If the three counts were within one day, the mode was taken as the age. If the three counts were not within one day, the otolith was aged an additional two to four times until an age mode became apparent. The age mode was evident after three to five counts for $> 90\%$ of all otoliths.

I used otoliths to back calculate length at age for 12 largemouth bass from which I had obtained both otoliths and stable isotope data. The 12 fish were selected to uniformly represent the distribution of lengths of fish that had or had not made a switch to piscivory in their first summer of life (based on stable isotope analysis). Three of the fish analyzed were early piscivores and nine of the fish were late piscivores. For each fish, otolith length was measured at every fifth daily growth ring and length at age was estimated using the biological intercept (direct proportion) method (Campana 1990, Schramm et al. 1992). Age-specific growth rates were calculated for each 5-d interval between back-calculated length-at-age estimates. I used repeated-measures ANOVA (SAS version 8, PROC GLM; SAS Institute 1999) to evaluate whether the ontogenetic shifts resulted in greater length at age, with ontogenetic status (switched to piscivory or not) as the between-subject effect and age in days as the within-subject effect. A significant main effect of ontogenetic status would indicate that differences in size at age between early and late piscivores were generally maintained across all ages, and a significant interaction between ontogenetic status and age would indicate divergent size at age due to differential growth rates (i.e., the interaction term is testing the slope of the length-at-age trajectory, which is growth rate). I then used the repeated-measures post hoc test PROFILE (SAS version 8; PROC GLM) to evaluate between which ages growth rates differed. Because there were differences in the terminal age among individuals (70–90 d on 22 August), I performed repeated-measures ANOVAs and post hoc tests for all fish up to age 70 d ($n = 12$), and then for the subset of fish that reached an age of 90 d ($n = 7$). Here, I report the main results from the repeated-measures ANOVA for all fish for the period of 0–70 d, which did not differ qualitatively from the repeated measures ANOVA for the subset of fish that realized 90 d. I also present the results from the post hoc test for all fish for ages 0–70 d and for the seven fish subset for ages 75–90 d.

Hatching dates

I estimated the range of hatching dates for the 1994 cohort using both direct observation of nests and otolith age estimates. I conducted nest surveys of the entire lake every 2–3 d from late May until all nests had

hatched in mid-June. On each survey date, all nests were identified and the developmental stage of the eggs was recorded. Hatching dates of nests with eggs that hatched between survey dates were corrected by 1–2 d based on the developmental stage of the eggs prior to hatching and size of fry on the survey date.

Diet analysis

I quantified YOY largemouth bass diets on nine dates in the summer of 1994 (8, 15, 22, and 29 June; 6, 13, and 27 July; 5 and 22 August). Stomach contents of at least 12 individuals were analyzed on each date. All items in the diet were identified to the lowest relevant taxonomic group and enumerated. Diets are presented as percent composition by mass (wet mass) using standardized weights for each prey item (Hodgson et al. 1993). For statistical analysis, prey types were aggregated into eight major groups: small cladocerans (*Bosmina* spp., *Polyphemus pediculus*, *Chydorus* spp.), large cladocerans (*Daphnia* spp.), copepods (including nauplii), *Chaoborus* spp., odonate naiads, larval dipterans, other invertebrates (amphipods, mites, trichopterans), and fish (largemouth bass). For graphical presentation, prey were further aggregated into three groups: zooplankton (cladocerans and copepods), non-zooplankton invertebrates (*Chaoborus*, odonates, dipterans, etc.), and fish.

RESULTS

Nest surveys suggested that all members of the 1994 cohort hatched between 24 May and 12 June, a 20-d range in hatching dates (see Post et al. 1998 for the distribution of hatching dates). Otolith age estimates indicated hatching dates between 23 May and 13 June, a 22-d range. These two independent estimates of hatching dates correspond well given the potential for slight errors in assigning hatching dates to nests and aging fish using otoliths.

By late August, initial size differences produced by the 20-d variation in hatching dates were translated into a strongly skewed length frequency distribution ($n = 349$, skewness = 2.0) with individuals reaching lengths between 39 and 95 mm (Fig. 1). The mean and modal lengths for the 1994 cohort were 53.5 mm and 52 mm respectively, with the majority of fish <65 mm in length. Less than 5% of the cohort reached >70 mm in length, and just 1% reached >90 mm. The largest members of the cohort were 2.4 times longer than the smallest members (39 mm) and nearly two times longer than the mean of members of the 1994 cohort (Fig. 1). The largest members were also over 15 times the mass of the smallest individuals in the cohort (10.4 g vs. 0.67 g). In late August, the largest members of the cohort were all older fish (spawned early in the year); however, older fish ranged in size from the largest to the smallest members of the cohort (Fig. 1b). In contrast, the youngest fish were mostly smaller than average in length (Fig. 1b). Although an early hatching

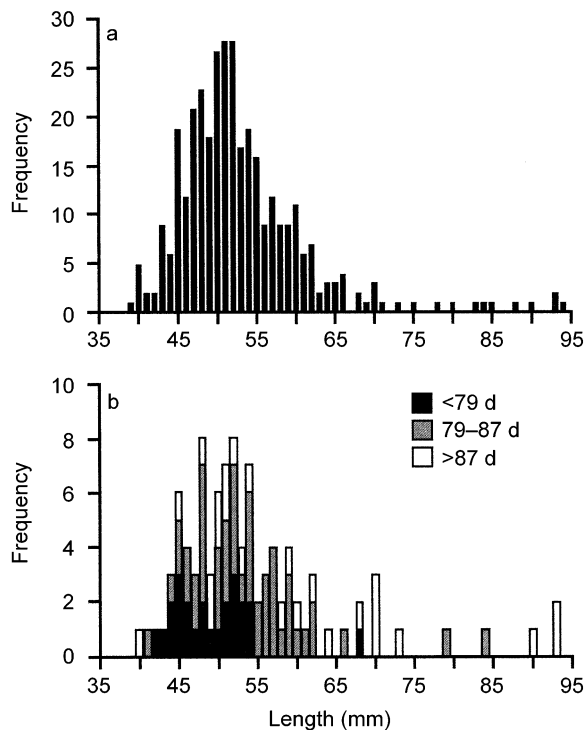


FIG. 1. Length frequency distributions of (a) all young-of-the-year largemouth bass sampled on 20 and 22 August 1994 ($n = 349$), and (b) the length frequency distribution, categorized by age, of the subset of fish ($n = 97$) aged using daily rings from otoliths. Age categories were chosen to represent roughly the youngest 25% of the age distribution (<79 d; $n = 24$), the central 50% of the age distribution (79–87 d; $n = 47$), and the oldest 25% of the age distribution (>87 d; $n = 26$). The top panel is modified from Post et al. (1998).

date was necessary for attaining larger sizes, age was a poor predictor of length ($R^2 = 0.17$; Post et al. 1998).

Direct diet analysis indicated that most members of the 1994 largemouth bass cohort did not become piscivorous in their first summer of life (Fig. 2a), but that the largest individuals in the 1994 cohort were piscivorous through portions of the summer (the largest 10–15th percentile of the length distribution of fish in the diet sample on a given sampling date; Fig. 2b). Summed over the entire summer, the diet (by mass) of the smallest individuals (lower 85–90th percentile of the length distribution of fish in the diet sample on a given sampling date) consisted of 0.08% small cladocerans, 31.61% large cladocerans, 0.24% copepods, 0.02% *Chaoborus*, 3.68% odonates, 53.22% dipterans, 11.14% other invertebrates, and 0.0% fish. The diet of the largest individuals consisted of 0.02% small cladocerans, 18.61% large cladocerans, 0.10% copepods, 0.0% *Chaoborus*, 0.0% odonates, 35.79% dipterans, 6.97% other invertebrates, and 38.50% fish. There were significant differences between the diets of small and large individuals (chi-square test; $df = 7$, $\chi^2 = 16.44$, $P = 0.02$); however, when fish prey were excluded, the diets of the smallest and largest individuals were not

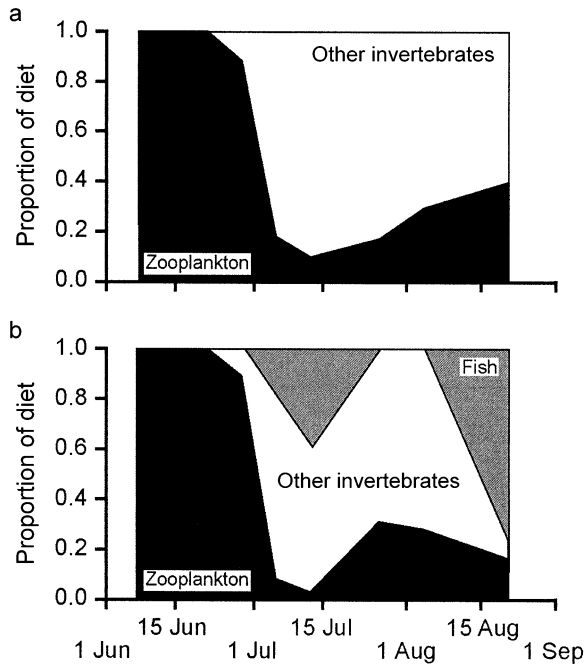


FIG. 2. Diet composition, by proportion of total mass, of young-of-the-year largemouth bass in Paul Lake in the summer of 1994. The top panel (a) shows the diet composition of fish in the lower 85–90th percentile of the length distribution of fish in the diet sample on a given sampling date. The bottom panel (b) shows the diet composition of fish in the upper 10–15th percentile of the length distribution of fish in the diet sample on that date.

significantly different ($df = 7$, $\chi^2 = 4.28$, $P = 0.75$), indicating that the transition to piscivory was the only substantial difference in diet between the largest and smallest members of the 1994 cohort. For the largest

members of the cohort, the first observed incident of piscivory occurred on 6 July (Fig. 2b), and fish were observed in the diets of the largest individuals on all dates for which piscivory was possible (Table 1; piscivory was possible on dates where the mean length of the largest fish in the diet sample was twice the length of the smallest conspecifics in the lake on that date). Summed across the summer, fish accounted for 38.5% of the diet by mass of the largest individuals of the 1994 cohort.

The $\delta^{15}\text{N}$ of young-of-the-year bass in late August varied between 7.1‰ and nearly 9.5‰ (Fig. 3). There was a positive relationship between fish length and $\delta^{15}\text{N}$ for all fish ($n = 31$, $t = 5.37$, $P < 0.01$), but this relationship was driven by the elevated $\delta^{15}\text{N}$ of the four fish >85 mm in length; there was no relationship between length and $\delta^{15}\text{N}$ for fish <85 mm in length ($n = 27$, $t = 1.12$, $P = 0.27$). The mean $\delta^{15}\text{N}$ of fish >85 mm in length (mean = 9.24‰, $SD = 0.19$) was significantly higher than that for fish <85 mm in length (mean = 7.88‰, $SD = 0.35$; one-way ANOVA, $F_{1,29} = 57.7$, $P < 0.01$), strongly suggesting that these individuals were feeding at a higher trophic position than the smaller conspecifics. This interpretation is further supported by the observation that the $\delta^{15}\text{N}$ of fish <85 mm was normally distributed (Fig. 3b; Shapiro-Wilk test for normality, $W = 0.974$, $P = 0.71$) but the $\delta^{15}\text{N}$ of fish >85 mm do not fall along this same distribution (Fig. 3b). The elevated $\delta^{15}\text{N}$ of fish >85 mm in length are not, therefore, simply extreme values drawn from the same distribution as fish <85 mm. The four fish with elevated $\delta^{15}\text{N}$ values were both able to transition to and sustain piscivory in their first summer of life (early piscivores). Fish <85 mm were either unable to transition to piscivory in their first summer of life, or

TABLE 1. The potential for observing cannibalism in diet samples taken in Paul Lake through the summer of 1994.

Date	Mean length of		Length of smallest conspecific	Was piscivory	
	Smallest 85% in sample	Largest 15% in sample		Possible for fish in diet sample?	Observed in diets?
8 Jun	9.5	11.5	7	no	no
15 Jun	12	18	6	no [‡]	no
22 Jun	13	15 [†]	11	no	no
29 Jun	29	37	22	no	no
6 Jul	35	44	22	yes	yes
13 Jul	39	56	29	maybe	yes
27 Jul	41	51	35	no	no
4 Aug	45	56	36	no	no
22 Aug	54	86	39	yes	yes

Notes: All lengths are in millimeters. The mean length of the smallest 85% and largest 15% are for young-of-the-year bass sampled for diet analysis. The largest 15% roughly corresponds to the percentage of bass identified by stable isotopes as switching to piscivory in their first summer of life. Length of the smallest conspecific in Paul Lake is the smallest bass measured on that sampling date. Piscivory was possible when the length of early piscivores was twice that of the smallest conspecific in Paul Lake on that date.

[†] There were many larger conspecifics in Paul Lake on 22 June, but they were not collected for diet analysis.

[‡] Cannibalism was physically possible, but unlikely because of male parental care. See the text and Johnson and Post (1997) for additional details.

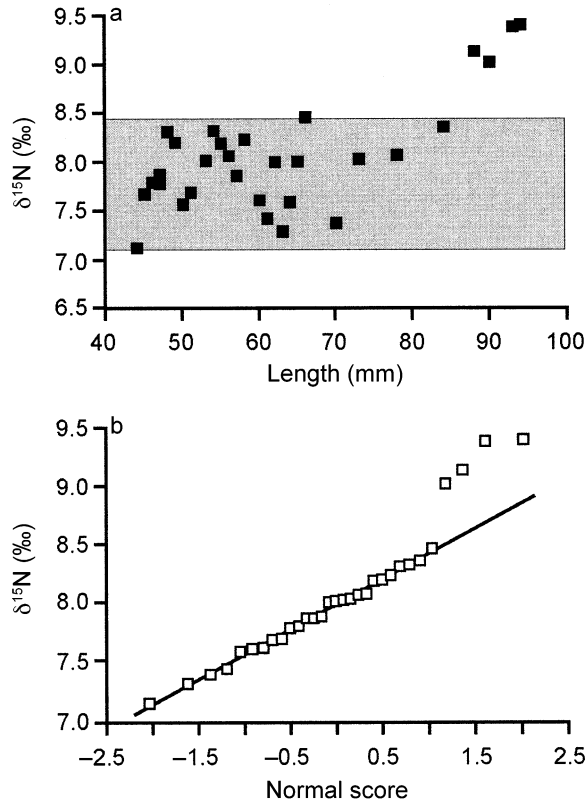


FIG. 3. Stable nitrogen isotope analysis of 31 young-of-the-year largemouth bass sampled on 22 August 1994 showing (a) the relationship between $\delta^{15}\text{N}$ and length and (b) a normal probability plot of the $\delta^{15}\text{N}$ values. The $\delta^{15}\text{N}$ values are normally distributed within the range of 7.1‰ to 8.5‰ for all but the largest individuals (>85 mm), which are outliers.

able to make the transition but unable to sustain piscivory long enough to be recorded in the $\delta^{15}\text{N}$ signature (late piscivores).

Early piscivores grew at substantially higher rates than did late piscivores (Fig. 4). Back-calculated length-at-age estimates from otoliths indicate that early piscivores were significantly longer at all ages than late piscivores (repeated measures ANOVA on length at age; main effect of ontogenetic status; $F_{1,10} = 7.77$, $P = 0.02$), and early length differences were amplified through time as early piscivores grew significantly faster than late piscivores (repeated measures ANOVA on length at age; time by ontogeny interaction; $F_{13,130} = 11.72$, $P < 0.001$). Although the mean growth rate of early piscivores was higher than that for late piscivores at all ages, growth differences were not significant before an age of 30 d (Fig. 4b; around 23 June for all early piscivores; PROFILE post hoc test). After an age of 30 d, early piscivores realized significantly higher growth rates than late piscivores at most ages (Fig. 4b; PROFILE post hoc test). Early piscivores grew at a mean rate of 1.08 mm/d ($SD = 0.13$) for the first 30 d and 0.89 mm/d ($SD = 0.09$) between the ages of 30–

90 d. Late piscivores grew at a mean rate of 0.84 mm/d ($SD = 0.23$) for the first 30 d, and only 0.52 mm/d ($SD = 0.12$) between the ages of 30–90 d.

DISCUSSION

The transition to piscivory is a crucial ontogenetic niche shift for primarily piscivorous fish such as largemouth bass (Keast 1985, Mittelbach and Persson 1998). Although there is some understanding of the causes of variation in the timing of the transition to piscivory among species and among cohorts within a species (e.g., Olson 1996, Mittelbach and Persson 1998, Hjelm et al. 2000), and both theoretical predictions of and indirect empirical evidence for individual variation in the timing of the transition to piscivory (Aggus and Elliott 1975, Shelton et al. 1979, Adams and DeAngelis 1987, DeAngelis et al. 1991, Wright 1993, Olson 1996,

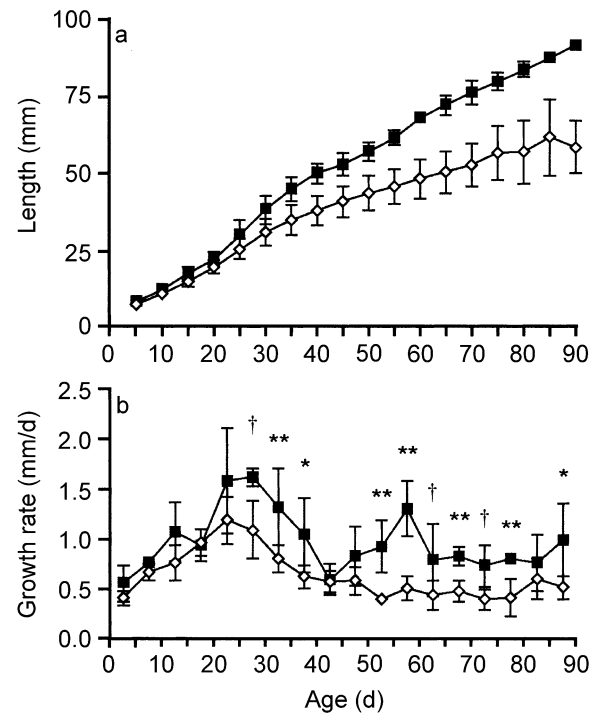


FIG. 4. Mean length at age (a) and growth rates between ages (b) for young-of-the-year largemouth bass identified by stable isotopes as having switched to piscivory (closed squares; $n = 3$) or having not switched to piscivory (open diamonds; $n = 9$ for ages 0–70 d; $n = 4$ for ages 70–90 d). For each panel, the error bars are 95% confidence intervals. All fish were collected on 22 August 1994, and length at age was estimated from otoliths. Growth rates were calculated for each 5-d age period from the length-at-age estimates. Differences in growth rates are indicated as marginally significant (\dagger , $0.08 > P > 0.05$), or significant ($* P < 0.05$; $** P < 0.01$) based on post hoc tests from the repeated-measures ANOVA on size at age (PROFILE post hoc test, PROC GLM, SAS version 8). Mean length of nonpiscivorous fish does not increase monotonically after age 70 because some of the largest nonpiscivorous individuals were younger than 90 d when collected and therefore do not contribute to mean length estimates at older ages.

van Densen et al. 1996), this study provides the first direct empirical evidence in a natural system for the extent and cause of variation in the timing of the transition to piscivory among individuals within a cohort. Stable isotopes and otoliths preserve a record of diet, age, and growth for each individual and, when used in combination, provide a method to link the timing of the transition to piscivory to hatching date and growth rate histories of individuals. Although the sample size is small (a few individuals from one cohort in one lake), the stable isotope data provide clear evidence for variation in the timing of the transition to piscivory among individuals in the 1994 largemouth bass cohort in Paul Lake, and the otolith data provide important clues as to why these differences emerged and how they impact individual growth (and therefore survival and fecundity). Otolith analysis showed that the largest individuals at the end of August were among the oldest members of the 1994 cohort (Fig. 1) and the stable isotope analysis indicates that these largest individuals had both transitioned to and sustained piscivory early in their first summer of life (Fig. 3). Three important questions remain: how robust is the stable isotope evidence for early ontogenetic diet shifts in the largest members of the 1994 cohort, what characteristics allowed the few members of the 1994 cohort to make this important ontogenetic niche shift, and what are the implications for growth and survival of individuals able to make an early transition to piscivory?

Interpreting the stable isotope results

The link between changes in $\delta^{15}\text{N}$ and shifts in trophic position can be obscured by variation in the $\delta^{15}\text{N}$ of prey resulting from spatial and temporal variation in $\delta^{15}\text{N}$ at the base of the food web (a form of baseline variation), differences in the scale of temporal integration by individuals (another form of baseline variation), and slight differences in the trophic fractionation of $\delta^{15}\text{N}$ (Post 2002). YOY largemouth bass in Paul Lake were all born at a similar time of the same year and had the same ultimate diet (i.e., diets were not significantly different when conspecific fish prey were excluded), reducing concerns about baseline variation obscuring comparisons among individuals; however, slight differences in trophic fractionation might be important (Post 2002). The mean trophic fractionation (Δ_N) of $\delta^{15}\text{N}$ is 3.4‰ ($\pm 1\%$, Post 2002); however, any single trophic transfer might realize a Δ_N between 1.4 and 5.4, with most Δ_N s between 2.4 and 4.4‰ (Gannes et al. 1997, Adams and Sterner 2000, Post 2002). This variation around the mean Δ_N of 3.4‰ prompted Post (2002) to advise caution when using $\delta^{15}\text{N}$ to interpret trophic shifts and diet composition from just one or a few trophic interactions, as is the case here. Variation in trophic fractionation of $\delta^{15}\text{N}$, fortunately, is normally distributed around 3.4‰ (Post 2002), which makes a normal probability plot of $\delta^{15}\text{N}$ values (e.g., Fig. 4b) a useful visual tool for detecting shifts

in $\delta^{15}\text{N}$ that derive from changes in trophic position when the isotopic baseline is the same. The $\delta^{15}\text{N}$ of fish <85 mm are normally distributed (Fig. 4b) suggesting that differences in the $\delta^{15}\text{N}$ among these individuals primarily derive from variation in trophic fractionation of $\delta^{15}\text{N}$, not variation in trophic position. In contrast, the same normal probability plot clearly illustrates that the elevated $\delta^{15}\text{N}$ of fish >85 mm in length are not simply extreme values drawn from the same distribution as fish <85 mm (Fig. 4b), but derive from a fundamentally different process; in this case, a shift in trophic position. The stable isotope results, supported by direct diet analysis, indicate that largemouth bass <85 mm in length were able to transition to and sustain piscivory in their first summer of life (early piscivores), a year earlier than other members of the 1994 cohort (late piscivores).

Because YOY bass all had the same ultimate diet (i.e., diets of late and early piscivores were not significantly different when conspecific fish prey were excluded), the $\delta^{15}\text{N}$ of fish <85 mm in length (late piscivores) provide an end member or baseline from which I can estimate both the percentage of fish in the diet of early piscivores and the magnitude of the trophic shift associated with their transition to piscivory. The proportion of fish in the diet of early piscivores is estimated using the two end-member mixing model

$$\delta^{15}\text{N}_{\text{early piscivores}} = \alpha \cdot \delta^{15}\text{N}_{\text{piscivores}} + (1 - \alpha) \cdot \delta^{15}\text{N}_{\text{late piscivores}}$$

where $\delta^{15}\text{N}_{\text{early piscivores}}$ (hereafter abbreviated as $\delta^{15}\text{N}_{\text{ep}}$) is the measured $\delta^{15}\text{N}$ of early piscivores, $\delta^{15}\text{N}_{\text{late piscivores}}$ (abbreviated $\delta^{15}\text{N}_{\text{lp}}$) is the measured $\delta^{15}\text{N}$ of late piscivores, $\delta^{15}\text{N}_{\text{piscivores}}$ (abbreviated $\delta^{15}\text{N}_{\text{p}}$) is the $\delta^{15}\text{N}$ of a hypothetical individual feeding exclusively on late piscivores, and α is the proportion of fish in the diet of early piscivores. Solving for α gives: $\alpha = (\delta^{15}\text{N}_{\text{ep}} - \delta^{15}\text{N}_{\text{lp}}) / (\delta^{15}\text{N}_{\text{p}} - \delta^{15}\text{N}_{\text{lp}})$. Because $\delta^{15}\text{N}_{\text{p}}$ is not known, but represents a one trophic level shift in $\delta^{15}\text{N}$ from $\delta^{15}\text{N}_{\text{lp}}$, the mixing model can be further simplified by replacing $\delta^{15}\text{N}_{\text{p}} - \delta^{15}\text{N}_{\text{lp}}$ with Δ_N , the trophic fractionation of $\delta^{15}\text{N}$ (Post 2002). The resulting equation, $\alpha = (\delta^{15}\text{N}_{\text{ep}} - \delta^{15}\text{N}_{\text{lp}}) / \Delta_N$, is identical to that used to estimate the trophic position of a consumer relative to an isotopic baseline (Post 2002). Thus, in this case, the proportion of fish in the diet of early piscivores is also the magnitude of the trophic shift associated with the transition to piscivory. Here I used the mean Δ_N of 3.4‰, bounded by a one standard deviation range of 2.4 to 4.4‰ (Post 2002). The mean $\delta^{15}\text{N}_{\text{ep}}$ was 9.24‰. The mean $\delta^{15}\text{N}_{\text{lp}}$ was 7.88‰, but the maximum $\delta^{15}\text{N}_{\text{lp}}$, 8.46‰, offers a more conservative basis for comparison. Compared to the mean $\delta^{15}\text{N}_{\text{lp}}$, early piscivores received around 40% (31–57%) of their nitrogen from piscivory, and early piscivores had a trophic position 0.40 (0.31–0.57) trophic levels higher than that of the

typical late piscivore. Compared to the maximum $\delta^{15}\text{N}_{\text{ip}}$, early piscivores received around 23% (18–33%) of their nitrogen from piscivory and had a trophic shift of 0.23 (0.18–0.33) trophic levels. These stable isotope based estimates of the proportion of fish in the diet of early piscivores correspond closely to the estimate derived directly from diet analysis, which suggests that fish comprised 38.5% of the diet by mass of the largest members of the 1994 cohort.

Isotopic caveats

The $\delta^{15}\text{N}$ signature of an individual integrates temporal variation in the $\delta^{15}\text{N}$ of an individual's diet at the scale of tissue turnover time (Hesslein et al. 1993, Harvey et al. 2002, Post 2002). Because rates of tissue turnover are proportional to body mass (Peters 1983), the stable-isotope signature of small fish integrates a relatively short period of time (e.g., a few to many weeks; Hesslein et al. 1993, Harvey et al. 2002, Post 2002). Accordingly, the stable-isotope evidence presented here cannot exclude the possibility that some individuals <85 mm in length made an early, but temporary, transition to piscivory. A short-lived transition to piscivory early in life would not be clearly recorded in the isotopic signature of individuals at the end of August because much of the biomass produced early in life is diluted or replaced by biomass produced later in life. Likewise, turnover and dilution of tissue produced early in life suggests that the stable isotope approach applied here may slightly overestimate the contribution of fish to the growth of early piscivores.

The potential for piscivory

The transition to piscivory requires both that prey are present and available within the system, and that predators reach a size sufficient to physically consume prey (Olson 1996). Because the transition to piscivory in Paul Lake is a transition to intracohort cannibalism, potential prey are necessarily present in the systems, but parental care by adult male bass prevents potential conspecific prey from becoming available as prey until they reach 15 mm in length. Male parental care delays the availability of potential prey past the point when predation is initially physically possible, and therefore magnifies the absolute size difference between predator and prey required for a transition to piscivory (Johnson and Post 1996). The effect of male parental care on trophic ontogeny of largemouth bass in Paul Lake is analogous to delays in the migrations of young-of-the-year bluegill into the littoral zone on the trophic ontogeny of largemouth bass (Olson 1996), and the effects of delays in the advection of young-of-the-year bluefish into estuaries along eastern North America on the trophic ontogeny of bluefish (Juanes and Conover 1995). A delay in the availability of prey increases the size difference required for piscivory, and makes the transition to piscivory less likely than expected based

on physical constraints alone (Johnson and Post 1996, Olson 1996).

With potential prey present and available, the potential for ontogenetic niche shifts becomes a race in size between potential predators and potential prey in which the outcome depends upon potential piscivores establishing and maintaining a size advantage over their prey (e.g., Shelton et al. 1979, Adams and DeAngelis 1987, Wilbur 1988, Madenjian and Carpenter 1991, Rice et al. 1993, Olson 1996). To transition to and sustain piscivory in their first summer of life, largemouth bass in Paul Lake must first reach and then maintain a 2:1 advantage over the smallest members of the cohort (Johnson and Post 1996). This can only be accomplished by potential piscivores that achieve some combination of faster growth rates or earlier hatching dates than potential prey (Keast 1985, Adams and DeAngelis 1987, Brabrand 1995, Johnson and Post 1996, Olson 1996). It is possible that variation in either hatching date or growth rates alone fully explains the patterns of piscivory observed for the 1994 cohort (i.e., either is sufficient), or that both are required to explain the observed patterns of piscivory (i.e., neither is sufficient, but both are necessary).

With a long enough period between hatching dates, almost any fish can grow large enough to become piscivorous by preying upon newly hatched prey (e.g., secondary piscivores, sensu Keast 1985). For example, members of the 1994 cohort that were unable to transition to piscivory in their first summer of life were able to become piscivorous in their second summer of life when a new cohort of largemouth bass was hatched (thus the designation late piscivores; see Post et al. 1998 for a discussion of piscivory by the 1994 cohort beyond the summer of 1994). Variation in hatching date, however, can be excluded quickly as the sole explanation for variation in the timing of piscivory because age was a poor predictor of length for the 1994 cohort. Many of the oldest individuals in the lake were among the smallest at the end of the summer (Fig. 2b, Post et al. 1998) and had not made the transition to piscivory. Thus, an early hatching date did not guarantee a transition to piscivory. Yet, early piscivores were all hatched very early in the summer, suggesting that an early hatching date was necessary for individuals to transition to and sustain piscivory. This result is very similar to that obtained from individual-based simulation models (e.g., Adams and DeAngelis 1987, Wright 1993). An early hatching date increases the potential for piscivory in the first summer of life by increasing the size difference between potential predators and their prey, but alone it is not sufficient to explain individual variation in the transition to piscivory.

There was substantial variation in individual growth rates through the summer of 1994 (Figs. 1, 4). If growth rates were constant through the summer (and they are not, which adds a complication that I will address next) and all fish were born on the same date (e.g., 24 May),

then the fastest growing individuals in the 1994 cohort (growth rates of ~ 0.96 mm/d) could reach a length sufficient to prey upon the slowest growing individuals (~ 0.44 mm/d) only around the middle of August, and they would not reach a length sufficient to prey upon those individuals growing just a bit faster (0.46 mm/d) before growth slowed with the arrival of cooler water temperatures in autumn. Although individuals with rapid growth rates could reach a size sufficient to prey upon slower growing individuals by mid-August, the higher growth rates are in part a consequence of becoming piscivorous, making even this outcome very unlikely. Thus, variation in growth rates alone provides little opportunity for a transition to piscivory, much less sustaining piscivory, by members of the 1994 cohort in the first summer of their life.

Growth rates varied through the summer (Fig. 4b), therefore a direct comparison of growth trajectories is a more appropriate way to evaluate the influence of growth rate and hatching date on the potential for piscivory. In general, growth rates for the period before fish reach 30 mm in length are the most important for the transition to piscivory, and growth rates after reaching 30 mm are the most important for sustaining piscivory. Fig. 5a shows the mean gape size through time for early piscivores vs. five versions of the realized growth trajectory of one of the slowest growing individuals in the 1994 cohort (potential prey; hatched on 29 May, reached 55 mm in length on 22 August, growing at a mean rate of 0.44 mm/d). The five potential prey growth trajectories are identical, but staggered by five days to simulate different hatching dates between +0 d (hatched the same day as early piscivores) and +20 d (among the last members of the 1994 cohort to hatch). Transition to and continuation of piscivory requires that potential piscivores have a gape size greater than the potential prey length, once potential prey reach >15 mm in length. Early piscivores were unable to reach a length sufficient to prey upon even the slowest growing member of the 1994 cohort (0.6 mm/d) without at least a 6-d difference in hatching dates (Fig. 5a). With a few days' difference in hatching dates and growth rates nearly twice that of the slowest growing potential prey, early piscivores could have first transitioned to piscivory around 18 June when they reached a length of 30 mm at an age of 25 d. On 18 June, the smallest conspecifics in Paul Lake were around 8 mm in length, but many members of the 1994 cohort would have been around 15 mm in length (Fig. 5a) and therefore available as prey for early piscivores (Johnson and Post 1996). It was shortly after 18 June that fish were first directly observed in the diets of members of the 1994 cohort (Table 1), and it was between an age of 25 and 30 d (just after 18 June for early piscivores) that the first significant differences in growth rate emerged between early and late piscivores (Fig. 4b). With just 6 d difference in hatching dates, late piscivores could transition to but not fully sustain piscivory

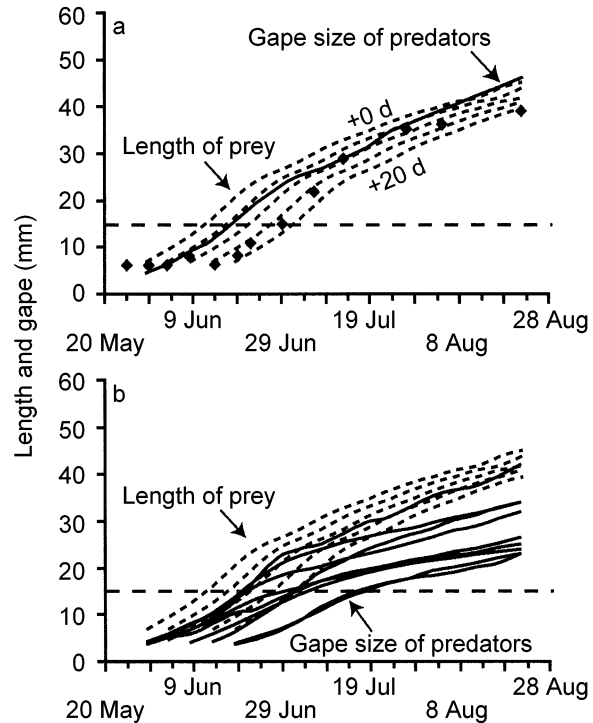


FIG. 5. Relationship between the growth trajectory (length in millimeters) of one of the slowest growing individuals in the 1994 cohort (dashed lines; prey) and gape size for early piscivores (panel a; solid line) and late piscivores (panel b; solid lines). The five prey growth trajectories are identical (dashed lines), but staggered by 5 d to simulate different hatching dates; +0 d is the same hatching date as early piscivores. For comparison, on the top panel are plotted the size of the smallest individual caught on 13 sampling dates (diamonds). Gape size was estimated as 0.5-length (Johnson and Post 1996), where length is from back-calculated length at age estimated from otolith analyses. I present the mean gape size for early piscivores (panel a) because their growth trajectories were similar, and individual gape estimates for late piscivores (panel b) because their growth trajectories were heterogeneous. Piscivory was possible when gape size was greater than prey length, after prey reached 15 mm in length (the horizontal dashed line).

through the entire summer because their growth rates slowed in early July (between 40 and 50 d; Figs. 4b, 5a); however, a 9–10 d difference in hatching dates would have allowed early piscivores to maintain piscivory through the summer of 1994 (Fig. 5a). Clearly, both variation in hatching dates and growth rates are necessary for individuals in Paul Lake to transition to and sustain piscivory in their first summer of life.

In contrast to early piscivores, most of the late piscivores had little or no potential to transition to and sustain piscivory in their first summer of life (Fig. 5b). Seven of the late piscivores were either hatched too late or grew too slowly to make the transition to piscivory. Of the three late piscivores that could have made the transition to piscivory, two did not maintain a high enough growth rate through the summer to sus-

tain piscivory (Fig. 5b). Only one individual classified as a late piscivore by the stable isotope analysis (Fig. 3) could have transitioned to and sustained piscivory in its first summer of life (Fig. 5b). It is not clear why this individual was not piscivorous, or how it maintained such a high growth rate without transitioning to piscivory.

Why these individuals?

Many individuals hatched early in the summer of 1994 did not become piscivorous in their first summer of life. It is not immediately clear why one early-hatched individual might have an advantage over another, particularly in Paul Lake in 1994 where the first individuals hatched were all likely from a single nest (Post et al. 1998). Individual-based models suggest that genetically identical individuals realizing even slightly above average growth rate can become entrained in a positive feedback that allows earlier trophic transitions and greater prey availability, both of which increase the opportunities for sustained higher-than-average growth rates (Adams and DeAngelis 1987, DeAngelis et al. 1991, Wright 1993). Although variation in the timing of ontogenetic niche shifts of individuals in these models derive from stochastic feeding events (Adams and DeAngelis 1987, DeAngelis et al. 1991, Wright 1993), variation could also arise from intrinsic individual differences in growth rates, morphology (e.g., Hjelm et al. 2000, Holtmeier 2001, Svanback and Eklov 2002), or the propensity for piscivory (Fox 1975, Gould et al. 1980, Polis 1981). Future work should focus on understand how variation among individuals in vital morphological and physiological characteristics might affect the timing of ontogenetic niche shifts under natural ecological condition.

Implications for an early transition to piscivory

The timing of the transition to piscivory by primary piscivores is crucial for growth (e.g., Olson 1996, Buckel et al. 1998, Mittelbach and Persson 1998). Comparisons among species show that the age of first transition to piscivory is strongly and negatively correlated with size at age 1; fishes that transition to piscivory at smaller sizes typically obtain larger size in their first summer of growth (Mittelbach and Persson 1998). Largemouth bass that transition to piscivory in their first summer of life often have growth rates two to three times higher than conspecifics that are still feeding on invertebrates (Shelton et al. 1979, Olson 1996). In Paul Lake, early piscivores grew 1.7 times faster in length after their transition to piscivory than did late piscivores, allowing early piscivores to reach, by the end of the summer, nearly 2.5 times the length (39 mm vs. 94 mm), and over 15 times the mass (0.67 g vs. 10.4 g) of the smallest members of the 1994 cohort. Clearly some, but not all, of the positive skew in the length frequency distribution of the 1994 cohort (Fig. 1) can be explained by an early transition to pis-

civory by a few members of the cohort, as has been suspected for other cohorts of primary piscivores (Shelton et al. 1979, Wright 1993, van Densen et al. 1996).

For many fishes, size at age 1 is typically correlated with size at later ages (Mittelbach and Persson 1998). This is true for largemouth bass in Paul Lake, where there are positive correlations between length at age 1 and length at subsequent ages for fish sampled between 1984 and 1993 (age 2, $n = 595$, $r = 0.615$, $P < 0.01$; age 3, $n = 436$, $r = 0.442$, $P < 0.01$; age 4, $n = 262$, $r = 0.373$, $P < 0.01$; age 5, $n = 138$, $r = 0.328$, $P < 0.01$; based on back calculated length-at-age data from scale samples; D. M. Post, J. F. Kitchell, and J. R. Hodgson, *unpublished data*). Individuals that transition to and sustain piscivory in their first summer of life obtain and typically maintain a substantial size advantage for many years over other members of their cohort.

The size advantage gained by an early transition to piscivores has important implications for survival because most mortality processes for fish are size dependent (e.g., Werner and Gilliam 1984, Miller et al. 1988, Luecke et al. 1990, Post et al. 1998). For example, slower growing fish are vulnerable to predation for longer periods than faster growing fish (Werner and Gilliam 1984, Houde 1989, Luecke et al. 1990) and are often underrepresented in a cohort at the end of the first year of life (Rice et al. 1983, Post et al. 1998). In Paul Lake, predation by adult and juvenile bass is intense during the summer, accounting for nearly all of the estimated summer mortality for the 1993, 1994, and 1995 largemouth bass cohorts (Post et al. 1998). Predation by adult and juvenile bass generally focuses upon the smallest members of the cohort on any given date, and smaller individuals typically suffered higher mortality rates than larger individuals (Post et al. 1998). Furthermore, Paul Lake is near the northern extent of the geographic range of largemouth bass (Lee 1980) and, as such, overwinter mortality, presumably due to starvation (e.g., Oliver et al. 1979, Shuter and Post 1990, Hurst and Conover 1998, Post et al. 1998, Fullerton et al. 2000), is an important constraint on individual survival (Post et al. 1998). Largemouth bass in Paul Lake that reach >55 mm by the end of August have a relatively high probability of surviving the winter, while those individuals <45 mm have a very low probability of surviving the winter (Post et al. 1998). The early growth advantage afforded by the transition to piscivory provides early piscivores with a higher probability of surviving both predation during the summer and starvation over the winter.

Because size differences at the end of the first summer are at least partially maintained at later ages, the differences in growth rate produced by variation in the transition to piscivory have important implications for individual lifetime fecundity. Early piscivores have higher potential lifetime fecundity because (1) at any given reproductive age, early piscivores should be larger than other members of the same cohort, and larger

fish are typically more fecund (Wootton 1990), and (2) they can reach reproductive size a year or two earlier than smaller conspecifics (Baylis et al. 1993). For iteroparous fishes, such as largemouth bass, an earlier age of first reproduction both increases the discounted lifetime fecundity (e.g., early births contribute more to future population growth than later births; Stearns 1976), and could allow an additional year of reproduction (Baylis et al. 1993). Taken together, the growth and survival advantage imparted by the transition to piscivory should substantially increase the lifetime fecundity, and therefore fitness, of individuals able to make an early transition to piscivory in their first summer of life.

Conclusions

The combination of stable isotope and otolith analyses used here provides direct evidence for individual variation in the timing of the transition to piscivory, and provides a link between the timing of this important ontogenetic niche shift and age and growth characteristics among individuals. For the 1994 largemouth bass cohort in Paul Lake, only a few individuals were able to make and sustain the transition to piscivory in their first summer of life. These early piscivores were among the oldest individuals in the cohort and among the fastest growing individuals before the transition to piscivory. All evidence suggests that substantial variation in both hatching date and growth rate were necessary to explain the patterns of ontogenetic niche shifts observed in the 1994 cohort. Individuals able to make the transition to piscivory in their first summer of life realized a substantial size advantage over conspecifics that, if maintained throughout their life, probably increased both their probability of survival and their fecundity.

ACKNOWLEDGMENTS

I thank B. R. Herwig, J. M. Johnson, and D. E. Schindler for assistance in the laboratory and the field. J. J. Isely at Clemson University and members of the otolith analysis lab at North Carolina State provided advice on otolith analysis techniques. Comments by L. M. Puth and two anonymous reviewers, and conversations with and advice from J. F. Kitchell, M. H. Olson, D. E. Schindler, and E. W. Seabloom greatly improved this manuscript. This work was facilitated by the University of Notre Dame Environmental Research Center and the University of Wisconsin–Madison, Trout Lake Station. Funding was provided through research and fellowship support from Electric Power Research Institute and the Graduate Research Training grant for Human Accelerated Environmental Change at Cornell University and the Institute of Ecosystem Studies. Portions of the data analysis and manuscript preparation were performed while a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus.

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